Evaluating the Effect of Temperature on the Planktonic Food-web

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by

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"**Life can only be understood backwards,**
but must be lived forwards"
Søren Kirkegaard

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Contents

Chapter 1. Introduction

The composition and structure of marine pelagic biological communities are of great socioeconomic importance and an integral part of the global carbon cycle (Hays *et al.* 2005). Zooplankton, for instance, plays a pivotal role in mediating the transfer of energy and material (Banse 1995) as they feed on phytoplankton and microzooplankton (Harris *et al.* 2000) and supply numerous higher trophic levels with food (Kiørboe 1998).

The dynamics of marine systems have been studied for many years, whilst physiological and life-history rates of key plankton species have also been extensively investigated (Huntley & Lopez 1992, Müller & Geller 1993, Ikeda *et al.* 2001, Hirst & Bunker 2003, Montagnes *et al.* 2003). Studies have examined how different life-history and physiological rate processes set limits and determine widespread biological structure of pelagic communities, e.g. size spectra (Moloney & Field 1991), predator-prey cycles (Kiørboe 1998) and the abundance and biomass of different trophic levels (Polis *et al.* 1996). But while these investigations typically show profound influence, studies explicitly examining such implications are not common.

Temperature underpins many biological rates, life-history timings and events. As in ectotherms in general (Atkinson 1996), increasing temperature increases growth rates in protists (Montagnes *et al.* 2003), bacteria (White *et al.* 1991), mesozooplankton (Huntley & Lopez 1992, Hirst & Bunker 2003) and phytoplankton (Eppley 1972, Montagnes & Franklin 2001, Bissinger *et al.* 2008), increases mortality and fecundity rates in copepods (Hirst & Kiørboe 2002, Bunker & Hirst 2004) and increases development rates across zooplankton taxa (Gillooly 2000, Hirst & Kiørboe 2002).

The main objective of this thesis is to examine the ways and extent to which temperature affects plankton rate processes and ultimately the structure of the planktonic biomass distribution and food-webs across the global ocean. This is achieved by examining the gross growth efficiency (GGE), which is the percent of

prey biomass consumed that is converted to new organism biomass, of different planktonic taxa and functional (e.g. trophic) groups. GGE is the balance between growth and ingestion, two processes that are often temperature-dependent within taxa, and is an important parameter in assessing the flow and partitioning of material and energy in organisms and biological communities. GGE varies with temperature within individual taxa (Straile, 1997, Rivkin & Legendre, 2001). As both component parts, growth and ingestion, may have inherent errors associated in their calculation from experiments, values of GGE, and subsequently are therefore prone to a greater degree of scatter. This added potential error in GGE values is likely to influence the detection of GGE temperature dependence, with only the most robust trends detected. As a consequence weaker trends, influence by other variables such as nutrient availability, may not be detected.

Following a comprehensive clarification of GGE, detailing the correct method of calculation (Chapter 2, p.5), I compile the largest dataset of GGEs from values reported in the published literature. I then quantify how temperature affects GGE within each taxonomic group, and make comparisons between taxa (Chapter 3, p.17).

To understand how temperature may be fundamentally associated with changes in planktonic food-web structure, I take a macroecological approach. As the examination of the large-scale determinants of species abundance, richness and distribution, macroecological studies have been vital in developing an understanding of the underlying constraints to a wide variety of taxa (Gaston 2000, Gaston & Blackburn 2000, Evans *et al.* 2006). Although the majority of macroecological studies are terrestrial based, the increase in *marine* macroecological studies over the past decade (Foggo *et al.* 2003, Clarke *et al.* 2007 Helaouët & Beaugrand 2007) has helped develop an understanding of the different set of constraints imposed by the marine environment upon life-history, physiology, behaviour and energetics (Wieters 2001, Foggo *et al.* 2003). The use of large geographical scales is particularly useful in developing an understanding of factors promoting species that are prone to high variability in abundance and distribution. Although local fluctuations of nutrients, salinity and temperature can

result in high variability in abundance and distribution of planktonic species "*By subsuming local fluctuations, macroecology reveals meaningful patterns of phytoplankton at large scales*" (Li *et al.* 2002).

Temperature has previously been cited as an important, and often the most influential, variable in shaping phytoplankton biomass and community structure (Fiala *et al.* 1998, Gasiunaite *et al.* 2005), in addition to copepod abundance and distribution (Beaugrand *et al.* 2007, Helaouët & Beaugrand 2007). To investigate whether, over a large geographical scale, planktonic communities vary with temperature I compile a dataset of standing stock biomasses of different taxa using cruise survey abundance data and values reported in the literature. Standing stock biomass is a quantitative measurement of the mass of populations, species, or higher taxonomic groups at the moment of sampling. Here I determine the relationship between standing stock biomass and temperature for different taxonomic groups (Chapter 4, p.58). Subsequently I assess the contribution of different taxa, measured in terms of biomass relative to that of total phytoplankton, to examine whether on a global scale temperature correlates with structural changes in the distribution of biomass within the planktonic food-web.

The impact of diet- and taxon-specific GGEs on the biomass distribution and flux of carbon within food-webs is investigated by developing oligotrophic and eutrophic planktonic food-web models. I use models of relatively low complexity, similar in concept to those previously used to explore the fate of both primary and secondary production (Duarte & Cebrián 1996, Pomeroy 2000, Legendre & Rivkin 2002, Landry & Calbet 2004). Such models are of particular use in the exploration of the fundamental principles and concepts regarding food-web structure, where quantitative rather than qualitative information is desired. Low complexity models also benefit from a lower number of variables and assumptions associated with more complex models, allowing an assessment and conceptual examination of the important factors influencing food-web structure and function.

I assess the importance of GGE values used in planktonic models, and examine the extent to which using a common GGE for all taxa, a feature of many published

studies, produces outcomes that differ from models using taxon- and diet-specific values for GGE (Chapter 6, p.121). The change in biomass structure and carbon flux in response to increasing temperature is determined through the incorporation of temperature-dependent GGE into planktonic models (Chapter 7, p.154). I subsequently compare patterns from my models to those derived using real world data, allowing an assessment of whether, through its effect on GGE, temperature can impact planktonic biomass structure.

Chapter 2. Gross growth efficiency: a clarification and standardisation

Introduction

Gross growth efficiency (GGE) is the percentage of biomass consumed that is converted to new organism biomass over a time interval. GGE, often determined in terms of carbon (Goldman *et al.* 1987, Borsheim & Bratbak 1987, Carlson *et al.*1998), nitrogen (Checkley 1980, Debs 1984, Kiørboe *et al.* 1985), calories (Paffenhöfer 1976) or protein (Ishigaki & Sleigh 2001), and provides information on the partitioning of ingested material into soma and/or reproduction (hereafter referred to as growth), or loss (e.g. respiration, egestion and excretion). GGE is used to describe the flow of organic material through ecosystems (e.g. Landry & Calbet 2004), and has been used to predict material availability to higher trophic levels using simple to complex food web models (e.g. Montagnes *et al.* 1988, Weisse *et al.* 1990, Bockskaler 1993), whilst others have used GGE estimates to predict missing parts of an energy budget (Montagnes *et al.* 1988; Klaas 1997).

Before I detail the methods for obtaining and standardising GGE across the various taxa and studies (Chapter 3, p.17), I begin by demonstrating where GGE expressions are equivalent, how they can be standardised, and where cases of erroneous derivation have occurred (section Errors in GGE, page 13).

Definition and standardisation

GGE can be defined as:

$$GGE = \frac{\Delta B}{\Delta P} \qquad \text{Equation 2.1}$$

where ΔP ($m.t^{-1}$) is the amount of biomass (m) ingested over time (t), and of this ingested biomass the amount converted into new biomass by an organism over the same time period is ΔB ($m.t^{-1}$) which includes biomass lost to mortality, although in most experiments measuring GGE this is assumed to be zero (Table 2.1 details all terms used in equations and their units). Equation 2.1 is equivalent to the equation of Odum (1971) and the more recent uses by Laybourn-Parry (1984) and Sterner & Elser (2002). Although not always, the term ΔB has often been derived from growth rates describing somatic, population, or reproductive growth (Table 1.2).

Growth in some taxa / life-stages is assumed to be represented by a linear increase in body mass with time, while in others growth is assumed to be exponential. In determining GGE it is necessary to determine the change in mass of the predator (ΔB). Because the form of growth differs between individuals, populations, different life-stages, and different taxa (e.g. exponential or linear) then the correct derivation of ΔB (see Table 2.2) and subsequent use in GGE varies (Table 2.3). Below I outline in detail the linear and exponential growth forms, and how these are combined to give GGE.

Linear growth of organism mass with time may be through somatic growth or reproductive output (e.g. copepod egg production, gonozoid production by doliolids). To calculate GGE assuming linear somatic growth, the amount of biomass produced per amount of mass ingested needs to be determined within the same time interval by Equation 2.1, where the amount of prey mass ingested per unit time, ΔP, is calculated by:

$$\Delta P = \frac{P_t}{t} \qquad \text{Equation 2.2}$$

where is the total amount of prey mass ingested between times 0 and t. GGE is thus calculated using Equation 2.1 and ΔB (derivations outlined in Table 2.2, page 7).

Table 2.1 **Notation used in the mathematical expressions, – means dimensionless.**

Symbol	*Description*	*Dimensions*
a	constant	–
b	constant	–
B	predator biomass	m
Bm	mean predator mass	m
Bt	predator mass at time t	m
Bo	predator mass at time 0	m
ΔB	predator biomass assimilated	$m.t^{-1}$
ΔP	prey biomass ingested	$m.t^{-1}$
G	mass specific mass assimilated	t^{-1}
Im	mass specific ingestion rate	t^{-1}
No	predator abundance at time 0	–
Pm	mass specific ingestion rate	t^{-1}
Pt	prey mass ingested between times 0 and t	$m.t^{-1}$
t	time interval	t
μ	predator exponential growth rate constant	t^{-1}
U	predator specific ingestion rate	t^{-1}
x	food concentration	$m.V^{-1}$
yo	non–zero y–axis intercept	–
Y	yield	–

Table 2.2 **Growth types and their correct conversion to ΔB for application in GGE. Examples from different taxonomic groups and growth types from the literature.**

Mass-specific growth rate (d^{-1})	*Growth type*	*ΔB Derivation*	*Examples of use*
$\mu = \frac{\ln B_t - \ln B_0}{t}$	Exponential somatic growth	$\Delta B = \frac{B_0 e^{\mu t} - B_0}{t}$	1–4, 20, 21, 23, 24
$\mu = \frac{\ln N_t - \ln N_0}{t}$	Exponential population growth	$\Delta B = \frac{N_0 e^{\mu t} - N_0}{t} \times B_m$	22, 26, 28–43
	Linear somatic growth	$\Delta B = \frac{B_t - B_0}{t}$	5
	Linear reproductive output		11–19, 25
$G = \frac{\Delta B_t}{B_0}$	Linear somatic growth	$\Delta B = G \times B_0$	6, 23
	Linear reproductive output		7–10
	Linear population growth		27

Table 2.2 Continued

Copepods (Juvenile), 1 (Paffenhöfer 1976), 2 (Copping & Lorenzen 1980) 3 (Berggreen 1988), 4 (Rey-Rassat *et al.* 2002), 5 (Debs 1984), 6 (Jones *et al.* 2002); **Copepods (Adults),** 6 (Jones *et al.* 2002), 7 (Kiørboe *et al.* 1985), 8 (Støttrup & Jensen 1990), 9 (Møller & Nielsen 2002), 10 (Saiz *et al.* 1992), 11 (Peterson & Dam 1996), 12 (Dam & Colin 2005), 13 (Castellani *et al.* 2005), 14 (Calliari & Tiselius 2005), 15 (Kozlowsky-Suzuki *et al.* 2003), 16 (Huskin *et al.* (2000), 17 (Colin & Dam 2002), 18 (Arendt *et al.* 2005), 19 (Dam & Lopes 2003), **Scyphozoans** (ephyra larvae), 20 (Båmstedt *et al.* 1999); **Cladocerans** 21 (Vrede *et al.* 2002), 22 (Nandini & Rao 1998); **Larvaceans**, 23 (Hopcroft & Roff 1995); **Thaliaceans**, 23 (Hopcroft & Roff 1995), 24 (Gibson & Paffenhöfer 2000), 25 (Gibson & Paffenhöfer 2002); **Flagellates**, 26 (Fenchel 1982), 27 (Borsheim & Bratbak (1987); **Ciliates**, 28 (Müller 1991), 29 (Weisse *et al.* 2001), 30 (Weisse 2004), 31 (Jakobsen & Hansen 1997), 32 (Montagnes & Lessard 1999), 33 (Massana *et al.* 1994); **Dinoflagellates**, 34 (Stoecker & Evans 1985), 35 (Feinstein *et al.* 2002), 36 (Buskey *et al* 1994), 37 (Jeong *et al.* 2005); **Microflagellates**, 38 (Landry *et al.* 1984), 39 (Snyder & Hoch 1996); **Nanoflagellates,** 40 (Weisse *et al.*1990); **Bacteria**, 38 (Landry *et al.* 1984), 40 (Weisse *et al.*1990), 41 (Christaki *et al.* 2001), **Rotifers**, 22 (Nandini & Rao 1998), 42 (Lowe *et al.* 2005).

Table 2.3 **Equations used across a variety of studies and planktonic groups to estimate gross growth efficiency (GGE).**

GGE **Correct**	***Equation*** **identifier**	***Taxonomic*** **group**	***Reference***
$\frac{\Delta B}{\Delta P}$	A	Copepods	Rey *et al.* (2001), Kiørboe *et al.* (1985), Castellani *et al.* (2005), Strøttrup & Jensen (1990), Calliari & Tiselius (2005), Huskin *et al.* (2000), Jones *et al.* (2002), Kozlowsky–Suzuki *et al.* (2003), Møller & Nielsen (2001), Arendt *et al.* (2005), Colin & Dam (2002), Saiz *et al.* (1992), Dam & Lopes (2003)
		Ciliates	Stoecker & Evans (1985)
		Dinoflagellates	Buskey *et al.* (1994), Feinstein *et al.* (2002)
		Flagellates	Borsheim & Bratbak (1987)
		Microflagellates	Coffin & Connolly (1997)
		Bacteria	Goldman *et al.* (1987), Amon & Benner (1994), Hansell *et al.* (1995)
		Thaliaceans	Gibson & Paffenhöfer (2002)
		Scyphozoans	Båmstedt *et al.* (1999)

Table 2.3 Continued

$\frac{\mu}{I_m}$	B	Ciliates	Montagnes & Lessard (1999), Massana *et al.* (1994), Weisse *et al.* (2001), Weisse (2004), Müller (1991)
		Flagellates	Fenchel (1982)
Incorrect Category 1 Errors			
$\frac{\mu \times B_0}{P_t}$	C	Copepods	Rey–Rassat *et al.* (2002)
$\frac{\mu \times B_t}{P_t}$	D	Copepods	Berggreen *et al.* (1988)
Category 2 Errors			
$\frac{d\mu}{dIm}$	E	Copepods	Berggreen *et al.* (1988)
		Flagellates	Hansen (1992)
$\frac{d\Delta B}{d\Delta P}$	F	Copepods	Dam & Colin (2005), Dam & Lopes (2003), Peterson & Dam (1996)

When growth is in terms of reproductive output, and growth is assumed to be linear and the organism size itself remains constant, GGE may also be measured using mass-specific growth and ingestion:

$$GGE = \frac{G}{I_m} \qquad \text{Equation 2.3}$$

where the amount of mass ingested per unit time, ΔP, is calculated by Equation 2.2, *G* is derived as in Table 2.2 and *Im* is mass specific ingestion rate of an organism, the amount of mass ingested per predator mass, measured by:

$$I_m = \frac{P_t}{t \times B} = \frac{\Delta P}{B} \qquad \text{Equation 2.4}$$

where *B* is organism mass.

Exponential growth terms have been applied to somatic or population growth where mass increase, ΔB, is dependent on body or population mass. Exponential is the commonly assumed growth form in the population growth of ciliates, dinoflagellates and nano/microflagellates and in the somatic growth of many metazoans (e.g. juvenile copepods, Paffenhöfer 1976, Rey-Rassat *et al.* 2002). Population growth can be measured in terms of increase in numbers or biomass (μ, Table 2.2), which give identical values if organism size is assumed constant. The use of numbers is commonly the currency used to determine the term 'Yield', which is widely used in the protozoan literature. Yield is equivalent to GGE when mass units are used, but is not equivalent if expressed in cell numbers or volume without appropriate conversion to mass (Caron *et al.* 1986, Geider & Leadbeater 1988, Müller 1991, Weisse *et al.* 2001) unless predator and prey have identical cell content concentrations (e.g. carbon per ml). To avoid confusion my discussion of the theoretical basis of GGE will focus on transfer of mass from prey to predator, and not where non-prey derived material is the incorporated into new mass (see Hirst & Lucas 1998, Anderson & Pond 2000).

The GGE of an exponentially growing organism or population can be derived using Equation 2.1. However, an important caveat is that if GGE is calculated using ΔB and ΔP, both must be measured or estimated, over the same time interval, as both vary with time. However, this is not always the case. For instance, ingestion may be measured over a smaller time interval to assume no organism growth (Massana *et al.* 1994, Montagnes & Lessard 1999, and Weisse 2004). To avoid this problem, GGE may be calculated as the ratio of the instantaneous mass-specific growth of the predator over instantaneous mass-specific ingestion rate:

$$GGE = \frac{\mu}{I_m} \qquad \text{Equation 2.5}$$

The amount of mass ingested instantaneously per predator, mass-specific ingestion , is calculated thus:

$$I_m = \frac{P_t}{t \times \langle B \rangle} \qquad \text{Equation 2.6}$$

where $\langle B \rangle$, the average predator biomass during time *t*, as calculated by the equation adapted from Frost (1972) :

$$\langle B \rangle = \frac{B_0 \times \left(e^{\mu t} - 1\right)}{t \times \mu} = \frac{\Delta B}{\mu} \qquad \text{Equation 2.7}$$

Where an exponentially growing population is measured in terms of number of cells for instance, biomass at time 0, *B*o can be derived by:

$$B_0 = N_0 \times B_m \qquad \text{Equation 2.8}$$

where *N*o is the predator abundance at time 0 and *Bm* is the mean predator mass. As organism mass increases over time, it is important that the term $\langle B \rangle$ is used to provide a correct mass-specific ingestion term, as it represents the average predator mass within the time interval *t*.

Errors in GGE

To clarify the more common errors in determination of GGE in the literature, I highlight two categories of error (1 and 2 in Table 2.3). The first category of error is when an incorrect mass-specific ingestion term is used, and subsequently combined with an instantaneous growth rate. Authors have used inappropriate terms such as initial predator/s mass (mass at time 0) or mass at the end of the time interval (mass at time *t*) (Equations D and E, respectively, in Table 2.3), rather than mean mass as specified in Equation 2.6 when calculating mass-specific ingestion. The correct method by which μ and ingested mass should be combined to obtain ΔB, uses mean predator biomass during the time interval (Table 2.3). In practice, errors resulting from Equations D and E are likely to be small as mean biomass is similar to mass at time 0 and at time *t* where mass-specific ingestion is calculated over a small time interval, as is commonly the case. A greater time interval or predator growth rate, will give rise to greater errors. The percentage error as a proportion of the true value of the 200 GGE values reported by Rey-Rassat *et al.* (2002) ranges from 1.3 to 21.9%, with a mean error of 10.8%. The mean of the corrected GGE values is higher (43.4%), but similar to that reported (38.9%).

The second category of error is when GGE is incorrectly derived from the slope of the regression through values for growth plotted against their respective ingestion (Category 2, Table 2.3). Examples have included exponential and instantaneous mass-specific growth terms (μ) plotted against mass-specific ingestion rate (*Im*) (Equation E in Table 2.3) and also ΔB, plotted against ΔP (Equation F) the slope of which is cited as GGE. Equation E gives change in mass specific growth as a function of the change in mass specific ingestion rate, which is not equivalent to GGE. This term could, for example, give a positive value, despite negative growth. Equation G also fails to correctly represent GGE, only approximating it when growth is positive and the slope passes through the origin (i.e. where $\Delta P = 0$, $\Delta B = 0$), which there is no reason to assume should be the case. The extent of errors associated with the use of Category 2 equations is highly variable and can be large for individual data points. The GGE data presented by Peterson & Dam (1996) (n=47) for example, vary

in percentage error from the correct value from 0.8 to 8335% (mean 390.3%) (Table 2.4), that from Dam & Lopes (2003) (n=125) varied between 0.1 to 2955.5% (mean 155.3%), Dam & Colin (2005) (n=15) between 6.8 to 223.3% (mean 72.7%) and from Hansen (1992) (n=7) between 88.1 to 1123.1% (mean 281.5%). The reported GGE values may show a high degree of similarity to the recalculated mean as in the case for data from Peterson & Dam (1996) (77 and 76.5% respectively) and Dam & Colin (2005) (6 and 5.7%). However, larger differences were found in data from Dam & Lopes (2003) (8.8 and 15.5%) and greater still in Hansen (1992) (36 and 12.8%).

In conclusion, I found that although instances of incorrect methods are few, they do exist and can result in highly erroneous results. To prevent the proliferation of incorrect GGE values, the correct methods I have outlined need to be followed.

Table 2.4 **Extent of errors resulting from incorrect GGE calculation. Reported GGE values are those cited by authors, mean GGE is of recalculated values, mean error is the mean difference between reported and actual GGE values, and mean percentage error is calculated as mean error expressed as a fraction of the true value. † The reported GGE value for Rey–Rasset *et al.* (2002) represents the mean value. Data from Peterson & Dam (1996) are reported including all data, and excluding those the authors did not include in deriving their estimate of GGE.**

	Source	Reported GGE (%)	Mean GGE (%)	Mean Error (%)	Mean Percentage Error (%)
Category 1 Error					
	Rey–Rassat *et al.* (2002)	38.9†	43.4	5.2	10.8
Category 2 Error					
	Hansen (1992)	36	12.8	23.2	281.5
	Peterson & Dam (1996) (Reported GGE)	77	78.9	39.6	393.7
	Peterson & Dam (1996) (All data)	77	76.5	39.3	390.3
	Dam & Colin (2005)	6	5.7	2.6	72.7
	Dam & Lopes (2003)	8.8	15.5	10.4	155.3

Chapter 3. Gross growth efficiency in marine plankton: a synthesis with relationships to food and temperature

Introduction

Previous syntheses of plankton gross growth efficiency (GGE; see Chapter 2, p.5 for definition) have often dealt with few taxonomic groups, e.g. bacteria and protozoans (del Giorgio & Cole 1998; Rivkin & Legendre 2001), nano/microflagellates, dinoflagellates, ciliates, rotifers, cladocerans and copepods (Straile 1997). In this study I combine a greater set of plankton data (~2.5 fold greater than available at the time to Straile 1997) from a greater number of taxa, and for the first time explicitly describe the relationships with both food and temperature for understanding material flow within the planktonic food-web.

Effect of temperature within taxa

The relationship between GGE and temperature is a composite of the influence of temperature on the two component parts: ingestion and growth. In addition to growth, ingested mass is allocated to a variety of metabolic processes, i.e. egestion, excretion, and respiration. The sum of these processes would share the same temperature dependence as mass-specific ingestion and growth if GGE does not vary with temperature. Where there are differences in temperature dependencies, the result is GGE will itself vary with temperature. For instance, respiration costs are greater at higher temperatures, which, if ingestion rate and assimilation efficiency remain constant, will result in less efficient growth and decline of GGE with temperature e.g. Angilletta & Dunham (2003).

I use the term taxa to refer to the planktonic groups of bacteria, ciliates, nano/microflagellates, dinoflagellates, rotifers, scyphozoans, ctenophores, doliolids, cladocerans and copepods. Within each planktonic taxon behavioural and physiological processes will differ in their temperature dependence, potentially affecting GGE. Within planktonic taxa, the relationships observed have commonly shown no consistent pattern. My aim is to consolidate studies, to quantify how

temperature affects GGE within each taxonomic group, and to make comparisons between taxa.

Effect of food within taxa

Food concentration influences GGE through its effect on ingestion. At low food concentrations when an organism is not ingesting, growth is negative as its own body mass is used to fuel basal respiration. As food concentration increases, ingestion rate will typically increase, producing a negative GGE until biomass ingested equals that lost from excretion, egestion and respiration (i.e. when growth, and hence GGE, will be zero). Above this threshold concentration, where ingestion is greater than these losses, growth will be positive as will GGE. At low food concentrations we may predict GGE to be negative, and for it to become positive at higher concentrations. At very high food concentrations, however, some species exhibit luxury or superfluous feeding (Conover 1966, Møller 2004) which results in a decline in GGE. Here I quantify how GGE varies with food concentration within each taxonomic group.

Food quality (suitability for efficient production of new biomass) can also affect the GGE of an organism. A diet harder to degrade, low in suitable compounds and/or comprising toxins would either reduce mass assimilated per unit ingested or use mass that could have fuelled growth to improve assimilation: in either case GGE will be reduced. Different organisms under different food conditions, or with different feeding modes may therefore have different temperature dependencies for ingestion and growth, and therefore GGE. For example, the enzymatic degradation of compounds such as glucose has a lower (rate of change associated with an increase in temperature of 10°C) than that of more structurally complex compounds such as tannins (Davidson & Janssens 2006). Higher temperatures may lower the relative costs associated with digestion of more complex compounds, and therefore more ingested mass will be available for growth. Therefore, diet composition may affect how temperature influences GGE between trophic/functional groups with potential differences occurring between for example herbivores, carnivores and detritivores. Such differences may affect the mean and highest GGEs achieved for

different taxonomic groups. Therefore, I investigate if the relationship between GGE and temperature varies between dietary functional groups (herbivores, carnivores, detritivores).

Variation in GGE between taxa

Some of the different taxonomic groups in this study display radical differences in morphology, behaviour and physiology. For example, protozoa and metazoa differ largely in feeding mechanisms (Hansen & Calado 1999, Hansen *et al.* 1994), locomotion, (Sleigh 1989, Alcaraz & Strickler 1988) prey detection and prey type (Hansen *et al.* 1994). Different energy budgets are likely to place different limitations upon the processes responsible for conversion of ingested mass to new biomass. These processes may also have varying degrees of temperature dependence. Therefore, GGEs and their response to temperature may vary between taxa. My aim here is therefore to determine whether different trophic groups show differences in how GGE responds to temperature and food concentration, and to investigate whether the slopes and intercepts of GGE vs. temperature differ.

Material and Methods

Data Compilation

GGE data were taken directly from published values, obtained directly from the authors, or where necessary extracted from figures using GetData Graph Digitizer 2.22. I only accepted data that adhered to the correct definition of this term, with correct calculation, or if I was able to correct an incorrect term (see Errors in GGE section, Chapter 2, p.14). Data from 76 papers were classified into the following taxonomic categories: bacteria, ciliates, nano/microflagellates, dinoflagellates, rotifers, scyphozoans, ctenophores, doliolids, cladocerans and copepods. Life stage information in copepods allowed adult and juvenile phases to be separated. GGE differs with developmental stage in copepods (Paffenhöfer 1976, Rey-Rassat *et al.* 2002), and growth type is typically different between adults and juveniles, with egg

production predominant in the former and somatic growth in the latter. I made no separation of life stage in any of the other taxonomic groups.

Although dry mass (Paffenhöfer 1976, Müller 1991), ash-free dry mass (Båmstedt *et al.* 1999, 2001) and volume (Müller 1991, Hansen 1992, Weisse 2001, 2004) have been used as the currency of GGE, these can be inaccurate and problematic as production of these is not entirely limited simply to consumed prey (see Hirst & Lucas 1998, Anderson & Pond 2000). Although GGE has been derived from measurements in many different units, for consistency and to provide data that were most comparable, I converted all GGE values to carbon (μg C L^{-1}). Different empirical approaches have been used to determine ingestion; here no attempt was made to standardise between these, I assume that reported values of ΔP accurately represent ingested mass. I also assume bacterial growth measurements, often determined via tritiated thymidine or leucine methods, are compatible.

The temperature (°C) under which experiments took place was included in the database. In six of the studies GGE values had not been derived at a single temperature, but rather over a range, however as this range was relatively small ($\leq$ 3°C), I did not consider this a major problem and included this data with the mid-temperature of the range. Food concentrations were converted to carbon (μg C L^{-1}) using appropriate conversion factors or cell carbon concentrations, when these were not supplied in the original paper these were obtained from other published sources. In the bacterial group I did not compile food concentration, as these were almost never available. Other parameters recorded include prey species, growth type (see below), the currency that growth and ingestion were measured in (e.g. carbon, dry mass), method used to calculate GGE and water environment (freshwater, marine, brackish).

If determined without error, GGE cannot exceed 100%, so cases where values were >100% (n=20) were excluded from the main dataset. Whilst GGE values approaching 100% may be unrealistic, GGE values up to 100% were included and assumed to be the product of errors associated with measuring growth and ingestion. However, to examine the influence of excluding GGEs of 100% and above on mean values and

on the significance, nature and extent of significant relationships, datasets that allowed copepod GGEs up to 200% (maximum =185%), 1000% (maximum =680%), 2000% (maximum =1898%) or imposed no limit on copepod (maximum =18107%), scyphozoans (maximum =133%), cladoceran (maximum = 171%), and nano/microflagellate GGEs (maximum values 18107%, 133%, 171% and 100% respectively), were also subjected to statistical tests (p. 21). To allow log10 transformations for statistical treatments, zero and negative GGE values were removed (n=43). In planktonic taxa, mass-specific growth rates are generally assumed to increase in an exponential way over biologically relevant temperatures, i.e. the temperature range excluding extremes (although Montagnes *et al.* 2003 suggest a linear relationship between growth protest growth and temperature). For ingestion, there is also evidence for many species of an exponential response to temperature (Aelion & Chisholm 1985, Toda *et al.* 1987, Massana *et al.* 1994). As GGE is a ratio of these two processes, assuming ingestion and growth are both exponential responses, GGE will also demonstrate an exponential response to temperature. Thus log10 GGE was assumed to approximate a linear relationship with temperature, and my statistical expressions assume this.

Although the nature of the response of GGE to food concentration has not been well documented in the literature, a type II functional response to food concentration is frequently observed for growth (Strom 1991) and ingestion (Deason 1980, Jonsson 1986, Strom 1991, Chigbu & Sibley 1994, Massana *et al.* 1994) of planktonic taxa. At relatively high food concentrations GGE may decrease, as has been observed in ciliates (Verity 1985, Jonsson 1986), microflagellates (Sherr *et al.* 1983, Nakano 1994), dinoflagellates (Strom 1991) and copepods (Paffenhöfer 1976, Harris & Paffenhöfer 1976, Rey-Rassat *et al.* 2002), owing to superfluous or luxury feeding for example. For each taxon I excluded GGE values measured under extremely high food concentrations that were associated with a decline in GGE. Ciliates, nano/microflagellates, rotifers and copepods had limits imposed of 1500, 15000, 8000 and 9000 μg C L^{-1} respectively. This restriction was implemented as extreme concentrations are probably short-lived and relatively unimportant in nature and to give a greater approximation to a linear response after log10

transformation for use in GLMs. Following this removal there is no reason, *a priori*, that the response of GGE to food concentration should differ in form from that of ingestion or growth, i.e a type II functional relationship between GGE and food concentration. Consequently, a log10 transformation was applied to GGE and food concentration to provide a greater approximation to a linear relationship for use in general linear models (GLMs).

Statistical Analyses and Hypotheses Testing

All analyses were conducted using Minitab (MINITAB® Release 14.1). GLMs, which assume a linear relationship between independent and dependent variables, were constructed to test the combined effect of temperature and log10 food concentration on GGE. Temperature and food concentration may co-vary (i.e. there tends to be a relationship between the two variables themselves), especially from experiments where food concentration was not controlled. Therefore the initial model tested was:

$$log10\ GGE = T + log10F + (T + log10F) \qquad \text{Equation 3.1}$$

Subsequently, a backwards elimination selection procedure was employed whereby, if at least one the terms (T, *log10F* or $T + log10F$) was insignificant ($p>0.05$), the interaction term ($T + log10F$) was removed and the model run again, but using adjusted sum of squares. Further models were constructed, removing the term with the highest p value, if above 0.05, until only significant terms were retained, which was considered to be the Minimum Adequate Model (MAM).

All models including an interaction term between independent variables were constructed using sequential sum of squares, which is calculated for each term taking into account all preceding terms in the model, and therefore assuming they are included in the model. Sequential sum of squares is the appropriate method for where interaction terms are present, as the effect of co-variation between independent variables on the response variable is only appropriate after taking into account the effect of the terms comprising the interaction term. Where an interaction term was not present, models were constructed using adjusted sum of

squares, calculated taking into account all other terms, and therefore assuming they are included in the model.

To test whether the slopes of relationships between GGE and independent variables derived using different datasets, models were compared using a GLM as described in Grafen & Hails (2002):

$$log10\ GGE = T + log10F + Dataset + (T \times Dataset) + (log10F \times Dataset) \quad \text{Equation 3.2}$$

where temperature (T, ^{o}C), *log10* food concentration (*log10F*, $\mu g\ C\ L^{-1}$), log10 gross growth efficiency (*log10 GGE*, %) are continuous data, and *Dataset* is a categorical variable representing of one of the two datasets compared. Where a significant (p values <0.05) interaction term ($T \times Dataset$ or $log10F \times Dataset$) is found, this indicates a significant difference in slope (Grafens & Hails 2002).

Effect of Temperature and Food Concentration within Taxa

The effect of temperature, log10 food concentration, and the effect of the interaction between these two variables on GGE were tested using GLMs (Equation 3.1) for each taxonomic group. The combined copepod GGE data revealed that each temperature showed an effect strongly correlated with individual study. Thus to determine any effect of log10 food concentration on log10 GGE I performed additional ANCOVA, which included study as a categorical variable and also for an interaction between temperature and log10 food concentration. The group doliolids were excluded from analyses within taxa, as number of data (n=14) were deemed as too few to gain informative results from. In all taxa where an effect of temperature was detected, I further examined its effect by use of regression analysis within low, medium and high food concentrations. These concentrations were determined by splitting data approximately to give an equal number of data into each food category. However, for rotifers and ctenophores, and for low food concentrations juvenile copepods and scyphozoans, medium food for dinoflagellates scyphozoans and adult copepods, and high food concentration for juvenile copepods, there was a high degree of clustering of GGEs around two temperature values or less. Therefore, to allow biologically and statistically

meaningful relationships, only those food level categories of taxa represented by at least three temperatures were considered.

To examine of the importance of data transformations in providing differences between the relationships obtained this study and previously reported trends, GLMs were constructed to replicate significant models in Straile (1997). These models tested the relationship between GGE (*not* log10 transformed) and log10 food concentration for nanomicroflagellates, temperature-squared for copepods, and both log10 food concentration and temperature-squared for ciliates. For both dinoflagellates and cladocerans,for which GGE did not vary significantly with temperature, temperature-squared or log10 food concentration for all data in Straile (1997), the affect of both temperature and log10 food concentration on GGE were tested using data in this study.

Differences Between Taxa

To test for differences between taxonomic groupings, mean GGEs of each taxa were compared with all others via a simultaneous Tukey test at a 95% confidence level ($p= 0.05$).

Trophic Groups

As heterotrophs and mixotrophs synthesise biomass in fundamentally different ways, all species of ciliates, nano/microflagellates and dinoflagellates were categorised according to whether they were mixotrophic or heterotrophic. All species of nano/microflagellates and dinoflagellates present in this study were heterotrophic. However, the response of GGE to temperature and food concentration was examined for these two groups in the ciliates separately using GLMs described above.

As each taxa varies in the temperature range for which GGEs were measured, an additional test of mean GGEs was made under two different temperature ranges. The range of 13 to 20^{o}C was chosen to compare bacteria, ciliates, nano/microflagellates, dinoflagellates, cladocerans, and copepods, as all had GGEs measured at least over this range. All other taxa (scyphozoans, rotifers,

ctenophores) were excluded as their temperature range did not encompass the entire 13 to 20°C range. An additional test of mean GGEs was employed under the temperature range of 13°C to 25°C which allowed a larger number of data, but excluded copepods.

Diet Type

Ciliate, nano/microflagellate, dinoflagellate and copepod data provided information on the different prey types fed during the studies in which GGE was measured. This allowed values to be categorised into bactivorous, herbivorous, carnivorous, and mixed diet types (n=1366). Subsequently I investigated potential differences in the effect of temperature and food concentration on GGE between diet types within taxa using GLMs as described above. Data were excluded from analyses where diet type was noted as toxic, and therefore likely to influence GGE (n=2, copepods). I also excluded copepods feeding on a mixed diet from statistical analyses owing to its small sample size (n=6). Dinoflagellate data feeding on a mixed diet and copepods feeding carnivorously were derived from one temperature (and food concentration in the case of copepods) precluding analysis of its effect. GGE values were compared between diet types within taxa using one-way ANOVA at a 95% confidence level.

Differences between datasets

To examine whether the exclusion of GGEs of 100% and above affected the significance, and nature (positive or negative) of relationships between log10 GGE and both temperature and log10 food concentration, GLMs were constructed as above for all GGEs of copepods, scyphozoans, cladocerans, and nano/microflagellates. In addition, the copepod datasets with GGE limits of 2000%, 1000%, and 200% were also examined. Where significant variable were determined in datasets allowing GGEs of 100% and above, the models were compared with those considering only GGEs below 100%.

Changes in mean GGE for individual taxa (copepods, scyphozoans, cladocerans, and nano/microflagellates) and all taxa combined, as a result of including GGEs of 100% and above, were examined using a T-Test at a 95% significance level (p values <

0.05) to compare unrestricted datasets to those that include only values below 100%. For copepods, and all taxa combined, additional T-Tests were performed to compare datasets of GGE values constrained to 200%, 1000% and 2000% to the dataset containing only values below 100%.

Results

Effect of temperature within taxa

Log10 transformed GGE was positively correlated with temperature for dinoflagellates, scyphozoans, and ctenophores (Table 3.1, Figures 3.1 & 3.2). Temperature was the only significant variable remaining in the GLMs for dinoflagellates and ctenophores. Ctenophores and scyphozoans had the highest slopes, both at around 0.045 (log10% $^{\circ}C^{-1}$), which correspond to values of approximately 2.8. Dinoflagellates had the lowest slope of 0.038 (=2.4). For cladocerans and bacteria a significant negative relationship was found between log10 GGE and temperature. Cladocera (−0.048) had a slope over twice as steep as bacteria (−0.020) with corresponding values of 0.3 and 0.6 respectively. There was no significant effect of log10 temperature on log10 GGE in ciliates, nano/microflagellates, rotifers, copepods and in adult and juvenile copepods separately.

Non-transformed GGEs of dinoflagellates increased with temperature ($p<0.001$, R-squared=26.3%), whilst cladocerans and copepods did not vary significantly with increasing temperature ($p=0.095$) and temperature-squared ($p=0.621$, R-squared=0.1%) respectively (Table 3.2).

Effect of food within taxa

Log10 transformed GGE was positively related to log10 food concentration for scyphozoans, and juvenile copepods. In the case of the latter group, log10 food concentration was the only significant variable (R-squared=18%). Scyphozoans had a slope of 0.46, more than twice that of juvenile copepods (0.20) and 0.17

Table 3.1 **Relationships between gross growth efficiency (%) and both temperature (°C) and food concentration (μg C L^{-1}) for the different planktonic taxa, tested using General Linear Models (GLMs). Models used sequential sums of squares where the interaction term (between log10 food concentration and temperature) was significant and adjusted sum of squares where it has been excluded. F values and level of significance (*P* value) are also given for each significant variable. The relationship of each variable included in the model is given; positive (+), negative (–), with insignificant terms (p>0.05) indicated by *n.s.***

log10 GGE	Temperature (T) (ºC) *P*	log10 Food Concentration (log10 F) (μg C L–1) *P*	Model Fit (R-squared)	Equation	
Bacteria	<0.001 – F1,112=30.85	*n.s.*	21.7%	log10 GGE = 1.55871 – 0.019655T	0.64
Ciliates	*n.s.*	<0.001 – F1,107=31.71	23.0%	log10 GGE = 1.9934 – 0.26831log10F	
Nano/microflagellates	*n.s.*	*n.s.*			
Dinoflagellates	<0.001 + F1,77=29.96	*n.s.*	28.3%	log10 GGE = 0.7495 + 0.038039T	2.40
Rotifers	*n.s.*	*n.s.*			
Ctenophores	0.011 + F1,68=6.91	*n.s.*	9.3%	log10 GGE = 0.1725 + 0.04455T	2.79
Scyphozoans	<0.001 + F1,121=22.94	<0.001 + F1,121=155.16	57.6%	log10 GGE = –0.8616 + 0.044659T + 0.46475log10F	2.80
Cladocerans	<0.001 – F1,109=15.27	<0.001 – F1,109=47.87	40.0%	log10 GGE = 3.2446 – 0.04753T – 0.35760 log10F	0.33
Copepods	*n.s.*	*n.s.*			
Adult Copepods	*n.s.*	*n.s.*			
Juvenile Copepods	*n.s.*	<0.001 + F1,73=15.76	18.0%	log10 GGE = 0.9011 + 0.20155 log10F	

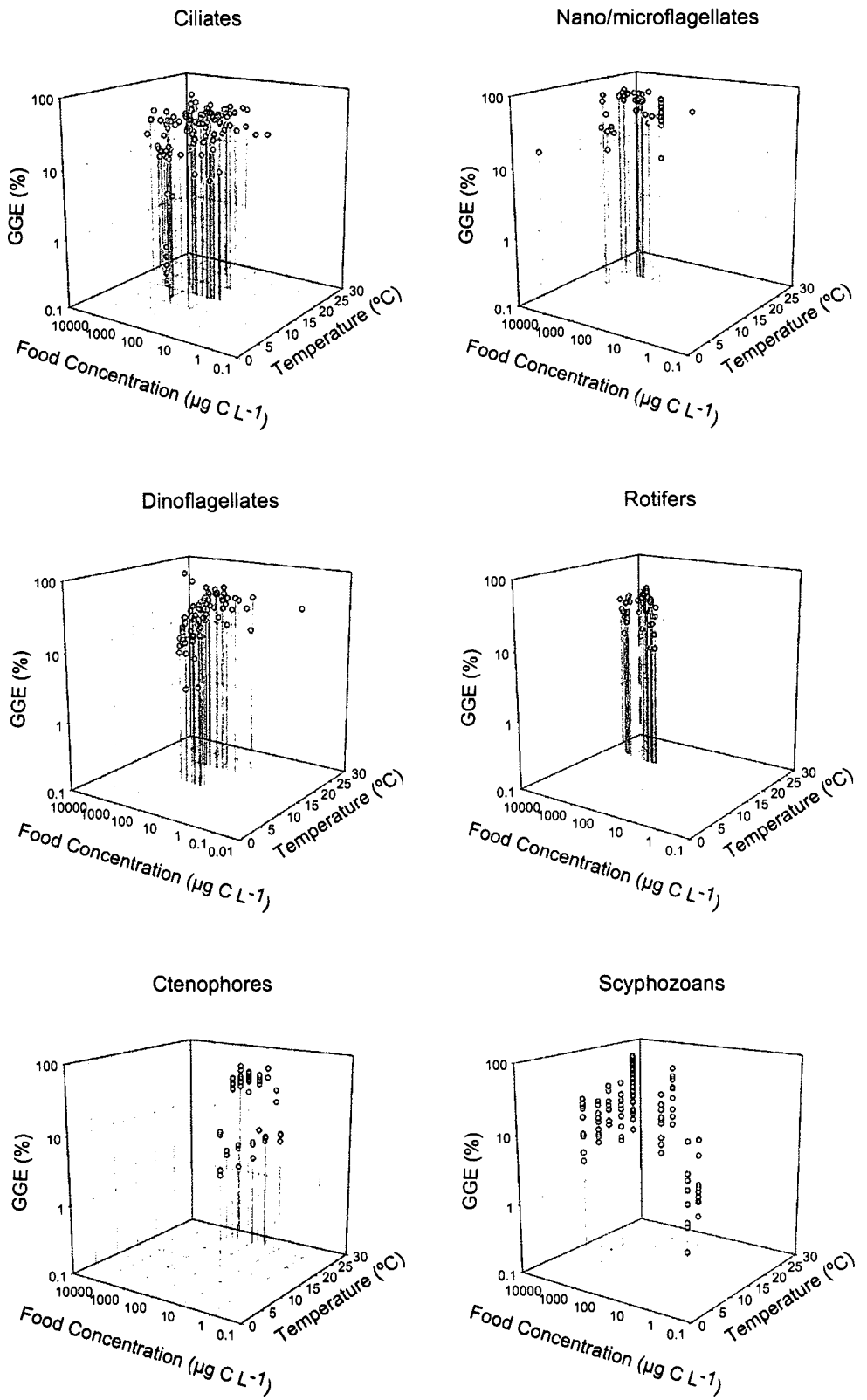
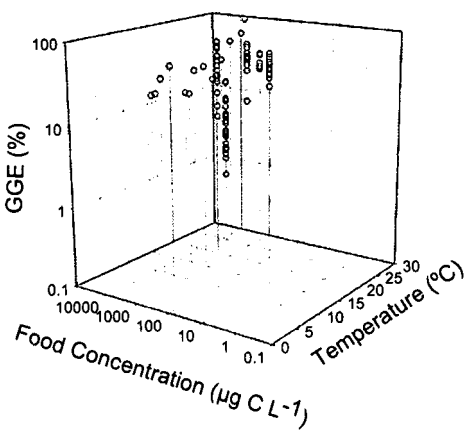
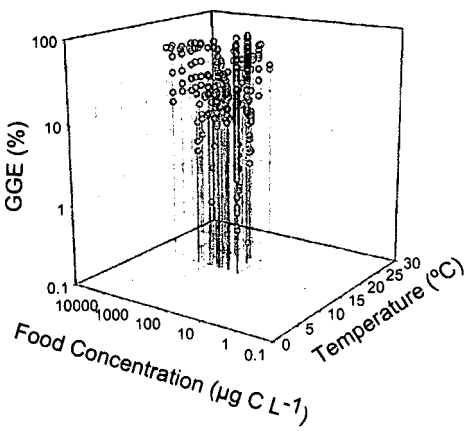


Figure 3.1 Three-dimensional plot of the relationships between log10 gross growth efficiency (GGE, %), temperature (°C) and log10 food concentration (µg C L^{-1}) for different planktonic taxa. Drop lines are included to allow values to be located along each scale.

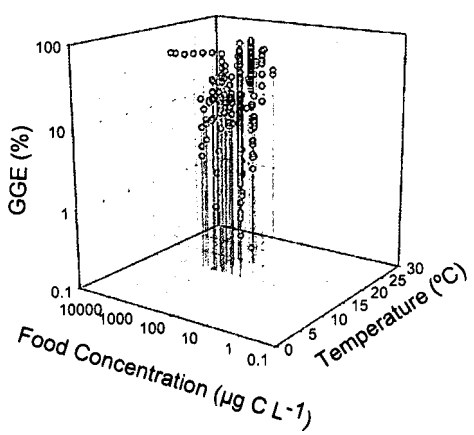
Cladocerans



Copepods



Adult Copepods



Juvenile Copepods

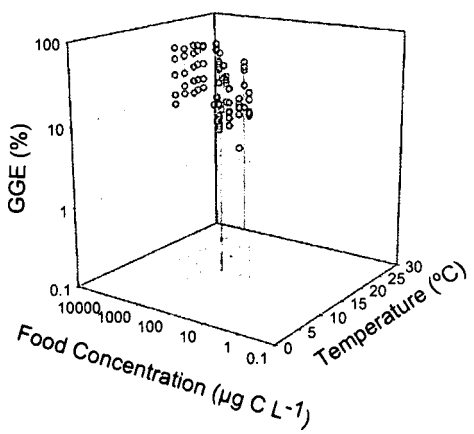


***Figure 3.1** Continued*

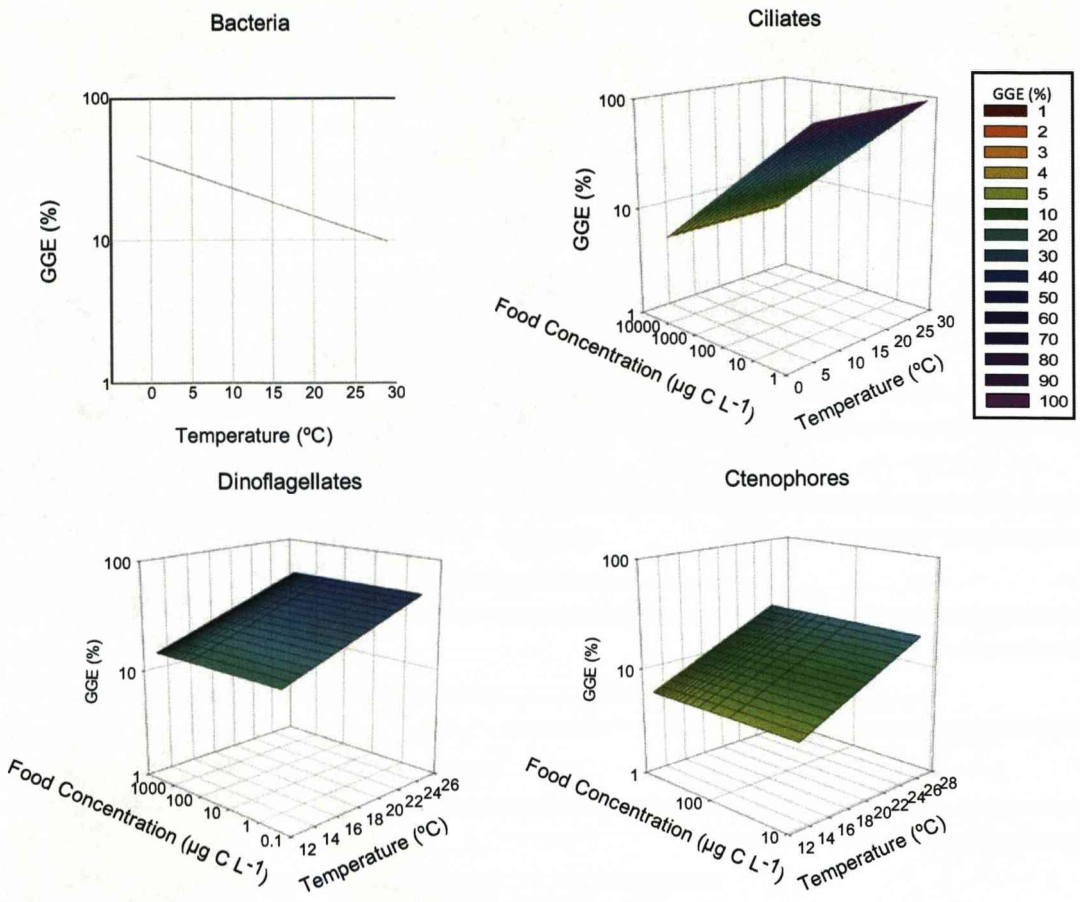


Figure 3.2 Three-dimensional plot of significant relationships between log10 gross growth efficiency (GGE, %), temperature (°C) and log10 food concentration (µg C L^{-1}) for different planktonic taxa. For greater clarity taxa are shown on different scales. As food concentration data were unavailable for bacteria, no scale is shown for this group.

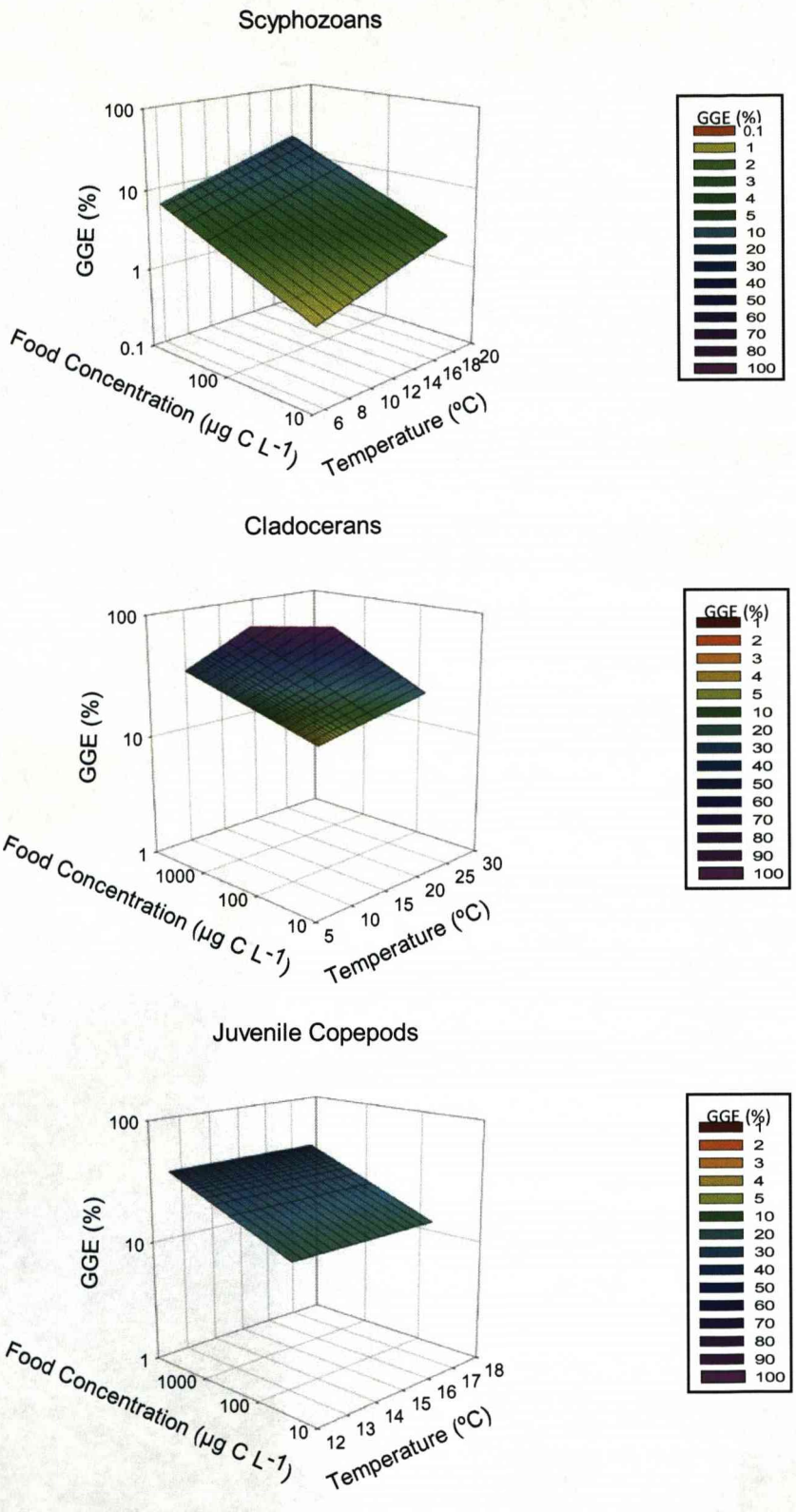


***Figure 3.2** Continued*

Table 3.2 **Comparison of significant variables obtained when comparing models constructed using data in this study, to results reported by Straile (1997). Models from this study were created to replicate the model structure (consisting of the significant variables and transformations) as in Straile (1997). The models constructed test the relationship between gross growth efficiency (not log-transformed, %), and either temperature (°C), temperature-squared (°C), and log10 food concentration (μg C L^{-1}) for nano/microflagellates, ciliates, copepods, dinoflagellates and cladocerans. General Linear Models (GLMs) were employed using adjusted sum of squares. Level of significance (*P* value) are given for each variable tested using data from this study. The relationship of each variable included in the model is given; positive (+), negative (–), with insignificant terms (p>0.05) indicated by *n.s.***

GGE	Study	Temperature (T) (ºC)	Temperature-squared (T) (ºC)	log10 Food Concentration (log10 F) (μg C L^{-1})	Model Fit (R-squared)
Nano/microflagellates	Straile (1997)	n.s.	n.s.	+	
	This Study			n.s. p=0.443	1.2%
Ciliates	Straile (1997)	n.s.	–	+	
	This Study		– p=0.034	+ p<0.001	29.4%
Copepods	Straile (1997)	n.s.	–		
	This Study		n.s. p=0.621		0.1%
Dinoflagellates	Straile (1997)	n.s.	n.s.	n.s.	
	This Study	+ p<0.001		n.s. p=0.478	26.3%
Cladocerans	Straile (1997)	n.s.	n.s.	n.s.	
	This Study	n.s. p=0.095		– p<0.001	27.9%

respectively. In the remaining five taxa I found no relationship with food concentration. A negative relationship was found between log10 GGE and log10 food concentration in ciliates (slope −0.27), and cladocerans, with a greater slope achieved by the latter (−0.36). Using GLMs no significant effect of log10 food concentration on log10 GGE was found in either adult or combined copepod datasets. With increasing log10 food concentration non-transformed GGEs decreased in cladocerans ($p<0.001$, R-squared=27.9%), but did not vary significantly for nano/microflagellates ($p=0.443$, R-squared=1.2%) or dinoflagellates ($p=0.478$, R-squared=26.3%).

Effect of temperature and food within taxa

The log10 GGE of scyphozoans and cladocerans was best described using a GLM that included both temperature and log10 food concentration and temperature (R-squared=58 and 40% respectively). I did not find an interaction between log10 food concentration and temperature in any case studied (i.e. they did not covary for any taxa, diet type, or trophic group).

When examining the effect of temperature within categories of food concentrations, the patterns mirrored the overall positive relationship between log10 GGE and temperature in dinoflagellates and scyphozoans at high concentrations (Figure 3.3). In addition, I detected a negative relationship for copepods at medium food, but did not find relationships at any level of food for ciliates, nano/microflagellates, adult copepods, and juvenile copepods. Non-transformed ciliate GGE was found to decrease with increasing temperature-squared ($p=0.034$) and increase with increasing log10 food concentration ($p<0.001$, R-squared=29.4%; Table 3.2).

Differences between taxa

A comparison of GGEs between taxa revealed that bacteria, dinoflagellates, rotifers, ctenophores, scyphozoans, cladocerans and copepods all had similar mean values, between 23 and 29%, which did not differ significantly from each other (Tukey's Test: $p>0.05$; Figure 3.4). Ciliates had the lowest mean efficiency of 16%, which was

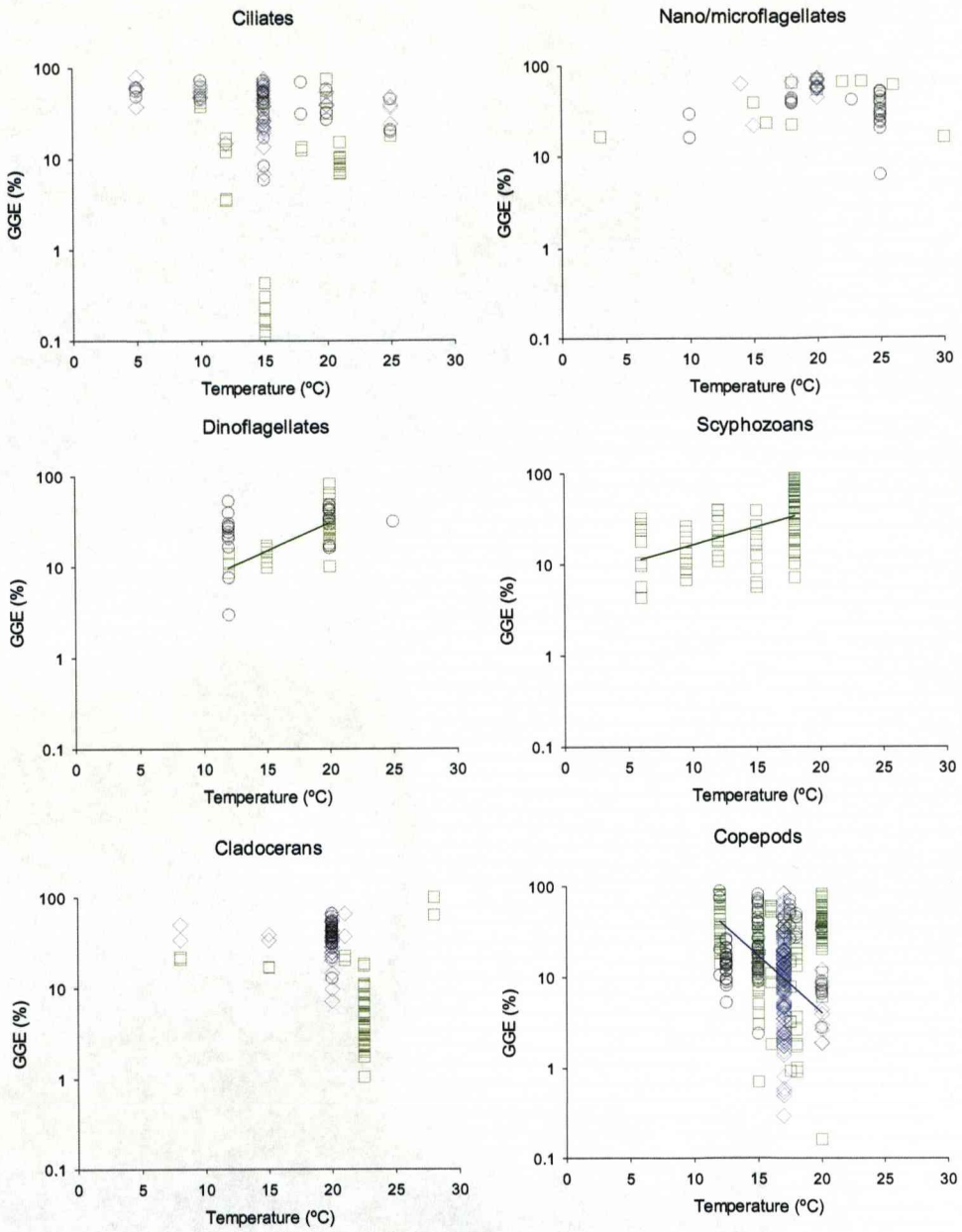


Figure 3.3 Relationship between GGE (%) and temperature (°C) within high (green squares), medium (blue diamonds) and low (black circles) food concentrations (μg C L^{-1}) as outlined in the Methods section for different planktonic taxa (p.23). Significant relationships ($p<0.05$) are indicated by green, blue, or black regressions lines for high, medium, and low food concentrations respectively.

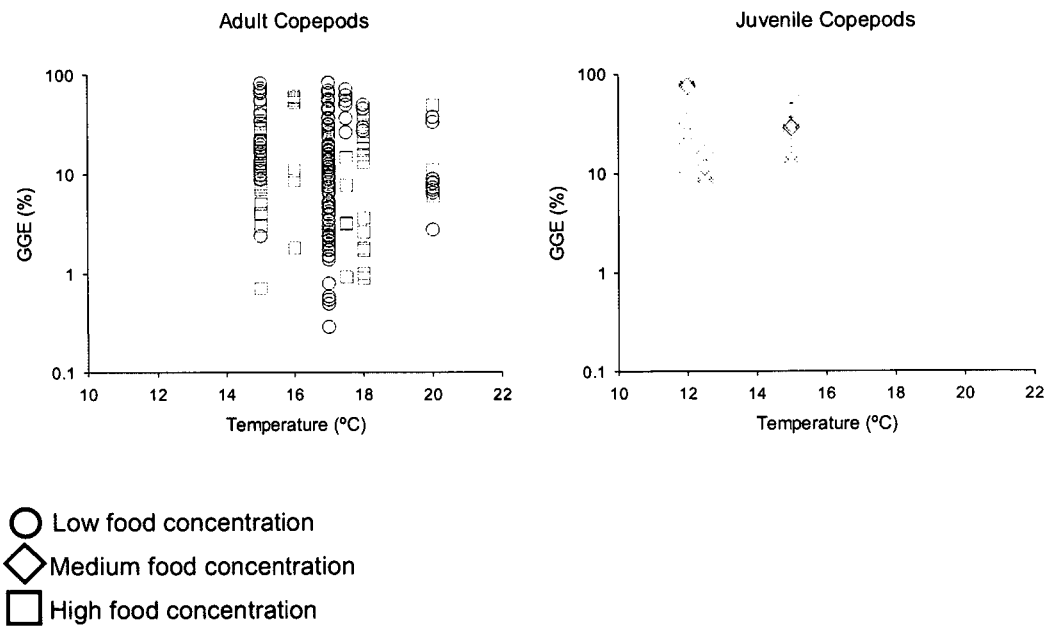


***Figure 3.3** Continued*

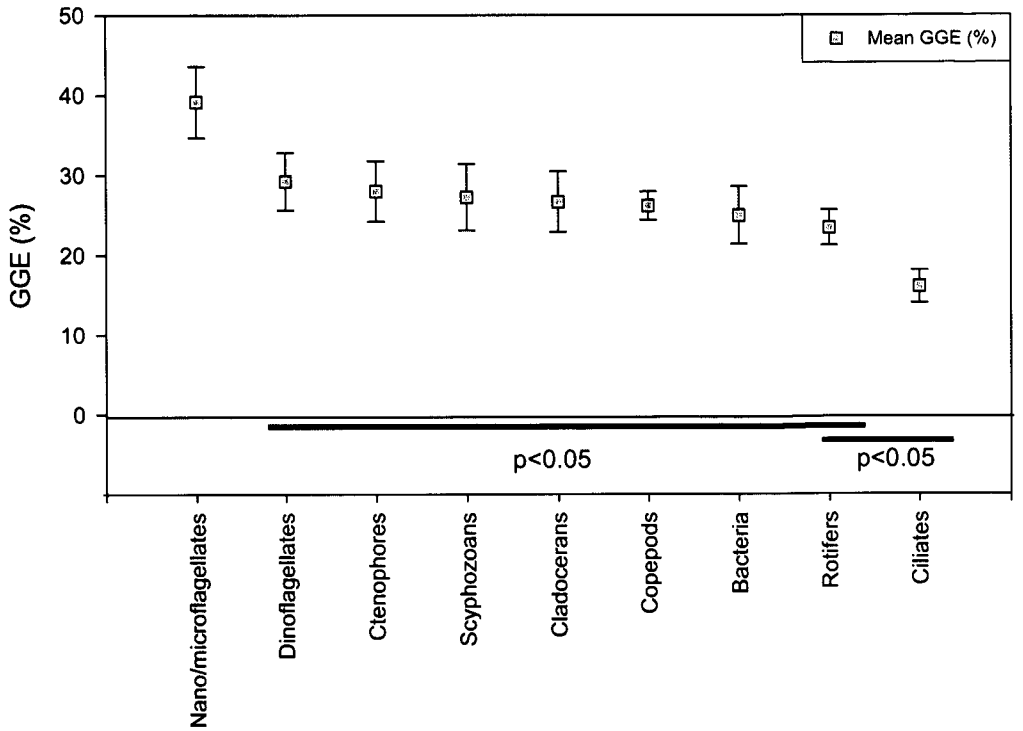


Figure 3.4 Plot for different taxonomic groups of mean GGE with 95% confidence intervals. Taxa are ordered left to right by descending mean GGE. Means that are not significantly different from one another are indicated by the bar connecting them.

significantly lower than all other taxa except rotifers. Conversely, nano/microflagellates achieved the highest mean efficiencies (39%), approximately 1.5 times that of all other taxa, and 2.5 times that of ciliates.

In a comparison of taxa, ciliates had a mean GGE that was significantly lower than all other taxa within both the 13 to 20°C (mean GGE=17.2%) and 13 to 25°C (mean GGE=16.6%) temperature ranges (Figure 3.5). Nano/microflagellates meanwhile, possessed a significantly greater GGE than all other taxa within 13 to 20 °C (mean GGE=51.6%) and all taxa except dinoflagellates within the 13 to 25 °C temperature range (nano/microflagellates=42.3%, dinoflagellates=34.1%). All other taxa possessed intermediate means, although mean copepod GGE (25.4%) was significantly lower than cladocerans (37.5%) and dinoflagellates (34.3%) between 13 to 20°C, and mean cladoceran GGE (25.5%) was significantly lower than dinoflagellates (34.1%) within the 13 to 25 °C range.

Trophic groups

Heterotrophic and mixotrophic ciliates differed in their relationships between GGE and the independent variables. Whilst for heterotroph ciliates log10 GGE showed a significant, negative relationship to log10 food concentration, in mixotroph ciliates log10 GGE was negatively associated with temperature (Table 3.3) with a of 0.3, although both showed similar mean values of 16 and 13% for heterotrophs and mixotrophs respectively (ANOVA: F=1.15, D.F.=1,308, p=0.285).

Diet Type

Using GLMs log10 GGE of ciliates was significantly related to temperature with a positive relationship when feeding bactivorously (=4.1), and negatively to log10 food concentration when feeding herbivorously (Table 3.4). A positive relationship was observed between log10 GGE and temperature for dinoflagellates feeding herbivorously (=4.4). A negative relationship was observed between log10 GGE and log10 food concentration in dinoflagellates. There was no significant relationship between log10 GGE and either temperature or log10 food concentration in nanoflagellates when feeding on a bactivorous or herbivorous diet, nor for when copepods were fed a mixed or herbivorous diet.

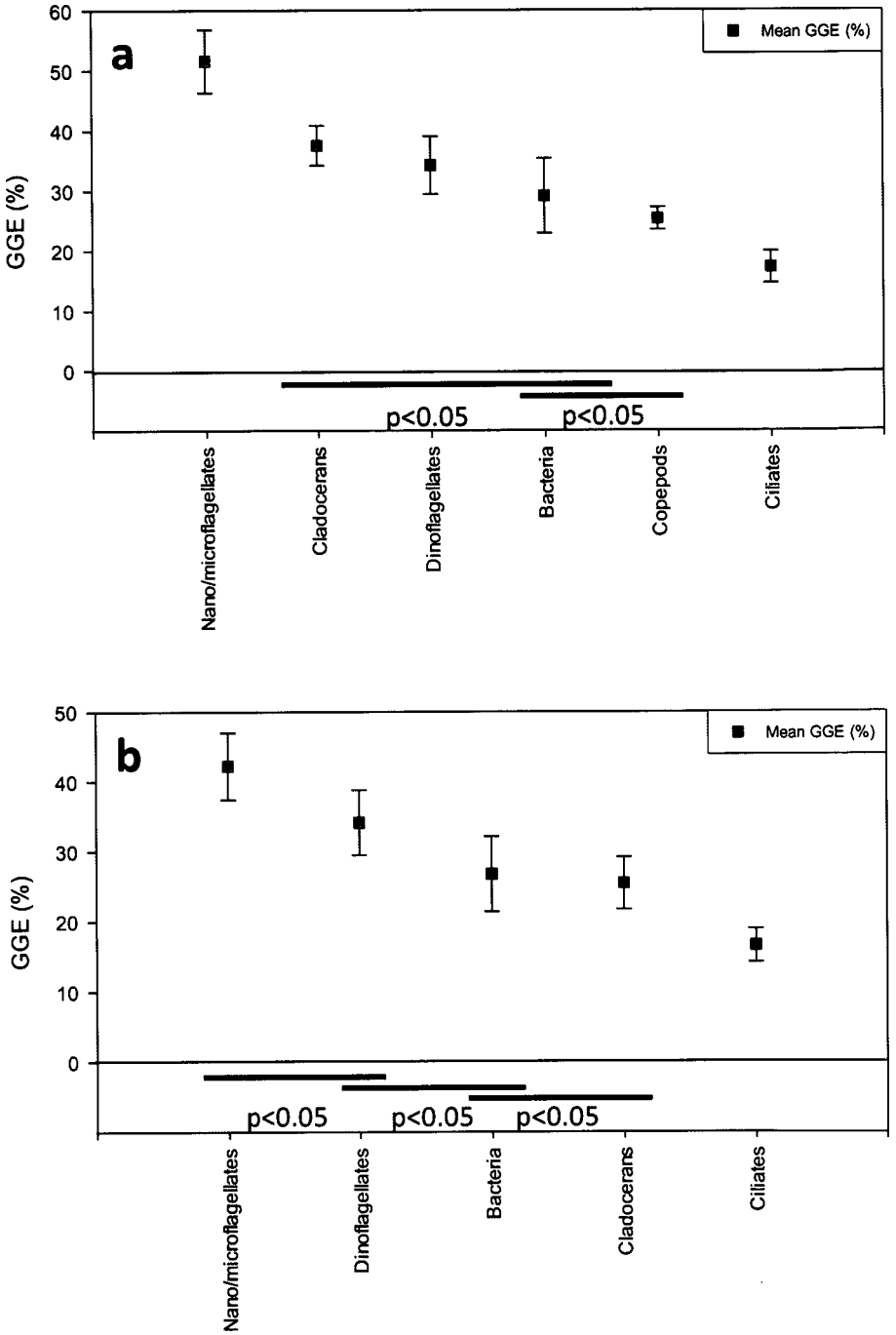


Figure 3.5 Plots for different taxonomic groups of mean GGEs derived from temperature ranges of a) 13 to 20°C and b) 13 to 25°C, with 95% confidence intervals. Taxa are ordered left to right by descending mean GGE. Means that are not significantly different from one another are indicated by the bar connecting them.

Table 3.3 **Relationships between gross growth efficiency (%) and both temperature (°C) and food concentration (μg C L^{-1}) for heterotrophic and mixotrophic ciliates using General Linear Models (GLMs). The relationship of each variable included in the model is given; positive (+), negative (–), with only significant terms included. F values and level of significance (*P* value) are also given for each term.**

Log10 GGE	Trophic Group	Temperature (°C)	log10 Food Concentration (μg C L^{-1})	Model Fit (R-squared)	Equation	Q10
Ciliates	Heterotrophs		p<0.001 – F1,91=26.23	22.6%	log10 GGE = 2.1433 – 0.34075 log10F	
	Mixotrophs	p=0.001 – F1,15=18.14		56.4%	log10 GGE = 2.1571 – 0.05780T	0.26

Table 3.4 **Relationships between gross growth efficiency (%) and both temperature (°C) and food concentration (µg C L^{-1}) for ciliates and dinoflagellates when fed on different diet types, using General Linear Models (GLMs). The relationship of each variable included in the model is given; positive (+), negative (–), with only significant terms included. F values and level of significance (*P* value) are also given for each term.**

Log10 GGE	Diet Type	Temperature (°C)	log10 Food Concentration (µg C L^{-1})	Model Fit (R-squared)	Equation	Q10
Ciliates	Bactivorous	p<0.001 + F1,196=91.91		32.0%	log10 GGE = –0.1957 + 0.061390T	4.11
	Herbivorous		p<0.001 – F1,90=42.46	32.3%	log10 GGE = 2.2721 – 0.38737 log10F	
Nano/	Bactivorous					
Microflagellates	Herbivorous					
Dinoflagellates	Herbivorous	p=0.001 + F1,47=19.53		29.8%	log10 GGE = 0.2190 + 0.06434T	4.40
	Mixed		p=0.038 – F1,27=4.79	15.6%	log10 GGE = 1.9252 – 0.3864log10F	
Copepods	Mixed					
	Herbivorous					

In all taxa fed more than one diet type, significantly higher GGE values were achieved when feeding herbivorously (Figure 3.6). The mean herbivorous GGE was around three times that when fed bactivorously (28 and 9%) for ciliates (ANOVA: $F=103.99$, D.F.=1,308, $p<0.001$) and almost double for nano/microflagellates (62 and 37% respectively) (ANOVA: $F=43.64$, D.F.=1,54, $p<0.001$). Dinoflagellates feeding herbivorously had a mean GGE of 33%, which is over 50% more than when fed a mixed diet when GGE was 20% (ANOVA: $F=14.91$, D.F.=1,75, $p<0.001$). Mean copepod GGEs were significantly lower when feeding carnivorously (15%) than that achieved on a herbivorous diet (27%) (ANOVA: $F=4.95$, D.F.=1,455, $p=0.027$). When feeding herbviorously, nano/microflagellates had a significantly higher mean GGE than all other taxa. However, ciliates, dinoflagellates, rotifers, cladocerans and copepods all showed similar values (24 to 33%) with no significant difference between means (ANOVA: $F=11.71$, D.F.=1,791, $p<0.001$).

Differences between datasets

For all datasets including GGEs greater or equal to 100%, the presence or absence of a significant relationship between log10 GGE, and both temperature and log10 food concentration was identical to that of datasets excluding GGEs of 100% and above (Table 3.5). All copepod and datasets, and the nano/microflagellate dataset with no upper limit of GGE, showed no significant relationship between GGE and both temperature and food concentration ($p>0.05$). With increasing temperature and food concentration, log10GGE of scyphozoans ($p<0.001$, R-squared=58%) increased, and cladoceans ($p<0.05$, R-squared=58%) decreased significantly, which was identical to the nature of relationships determined using datasets that did not include GGEs of 100% and above. However, the slopes describing the change in log10 GGE with increasing temperature, and increasing log10 food concentration, for the unconstrained scyphozoan and cladoceran datasets did not vary significantly from those obtained using datasets that not include GGEs of 100% and above ($p>0.05$; Table 3.6).

Both the datasets for copepods and all taxa combined that excluded GGEs of 1000% and above (copepod mean GGE=28.3%, all taxa=26.7), and the dataset for all taxa

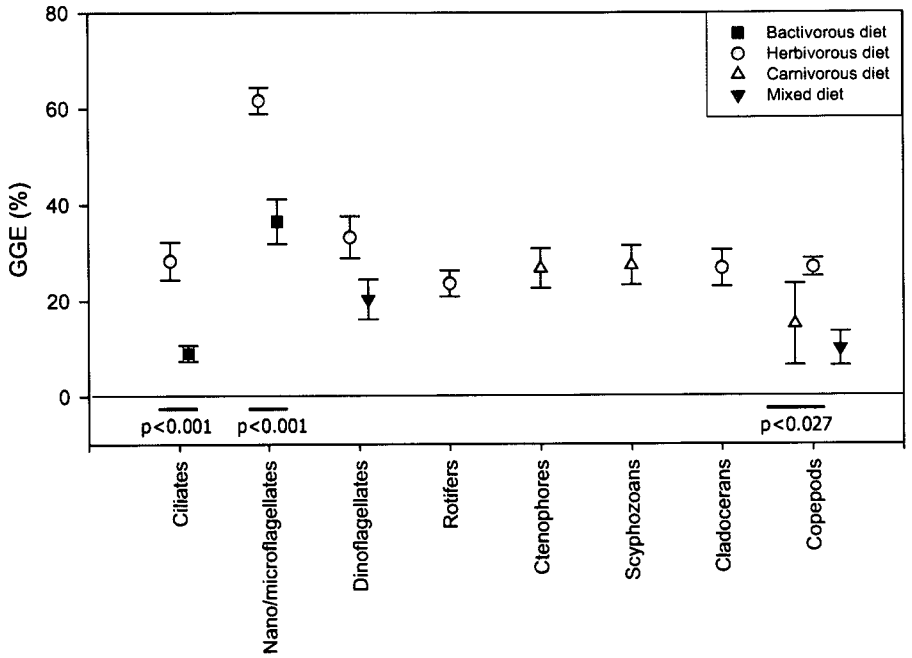


Figure 3.6 Plot of mean GGE for different diet types of taxonomic groups with 95% confidence intervals. Within taxa, significantly different means are indicated, p values, by the bar connecting those compared

Table 3.5 **Relationships between gross growth efficiency (%) and both temperature (°C) and food concentration (μg C L^{-1}) for copepods, scyphozoans, nano/microflagellate and cladocerans. Datasets were comprised of either all available GGE values (All data), or had a limit of 100 imposed for all taxa, in addition to 200, 1000 and 2000 for copepods. General Linear Models (GLMs) were employed using sequential sums of squares where the interaction term (between log10 food concentration and temperature) was significant and adjusted sum of squares where it has been excluded. F values and level of significance (*P* value) are also given for each significant variable. The relationship of each variable included in the model is given; positive (+), negative (–), with insignificant terms (p>0.05) indicated by *n.s.***

log10 GGE	Temperature (T) (ºC) *P*	log10 Food Concentration (log10 F) (μg C L^{-1}) *P*	Model Fit (R-squared)	Equation	Q10
Copepods					
All data	*n.s.*	*n.s.*			
GGE <100	*n.s.*	*n.s*			
GGE <200	*n.s.*	*n.s*			
GGE <1000	*n.s.*	*n.s*			
GGE <2000	*n.s.*	*n.s*			
Scyphozoans					
GGE <100	<0.001 + F1,121=22.94	<0.001 + F1,121=155.16	57.6%	log10 GGE = –0.8616 + 0.044659T + 0.46475log10F	2.80
All data	<0.001 + F1,124=25.75	<0.001 + F1,124=161.30	58.2%	log10 GGE = –0.9196 + 0.047318T + 0.47447log10F	2.97
Nano/microflagellates					
GGE <100	*n.s.*	*n.s.*			
All data	*n.s.*	*n.s.*			
Cladocerans					
GGE <100	<0.001 – F1,109=15.27	<0.001 – F1,109=47.87	40.0%	log10 GGE = 3.2446 – 0.04753T – 0.35760 log10F	0.33
All data	0.022 – F1,111=5.41	<0.001 – F1,111=39.34	31.4%	log10 GGE = 2.8869 – 0.02942T – 0.35421 log10F	0.29

Table 3.6 **Comparison of the regression of the slopes of log10 GGE (%) against temperature (°C) and food concentration (µg C L^{-1}) for datasets including and excluding GGE values of 100 and above for scyphozoans and cladocerans using General Linear Models (GLMs). General Linear Models (GLMs) were employed using dataset (all data or that excluding values 100 and above) as a categorical variable. For interaction terms between Dataset and Temperature, and between Dataset and log10 Food Concentration, P values below 0.05 indicate a significant difference in slopes of the between datasets. The relationship of each variable included in the model is given; positive (+), negative (–), with insignificant terms (p>0.05) indicated by *n.s.***

Temperature (T) (ºC)	**log10 Food Concentration (log10 F) (µg C L^{-1})**	**Dataset**		**Temperature*Dataset**		**log10 Food Concentration*Dataset**		**R-squared**
P	***P***	***P***		***P***		***P***		
Scyphozoans								
<0.001 +	F1,246=48.64	<0.001 +	F1,246=316.38	0.837	F1,246=0.04	0.840	F1,246=0.04	0.854 F1,246=0.03	57.9%
Cladocerans								
<0.001 –	F1,221=31.73	<0.001 –	F1,221=86.32	0.663	F1,221=0.19	0.297	F1,221=1.09	0.965 F1,221=0.00	35.6%

combined excluding GGEs of 2000% and above (mean GGE=28.0%), had mean GGEs significantly greater than their counterparts which excluded GGEs of 100% and above ($p<0.05$; Table 3.7). For all unconstrained datasets (schyphozoans, cladocerans, nanomicroflagellates, copepods, and all taxa combined), copepod GGEs below 200% and 2000%, and all taxa combined below for GGEs below 200% there was no significant difference to datasets that excluded GGEs of 100% and above ($p>0.05$).

Discussion

This study work has found temperature dependence of GGEs in 5 of the 9 planktonic taxa examined (Table 3.1). Across many taxa mean GGE values were not found to differ significantly, except for nano/microflagellates with significantly higher GGE than all other groups (bacteria, dinoflagellates, rotifers, ctenophores, scyphozoans, cladocerans, and copepods), and ciliates with significantly lower GGE than all except rotifers (Figure 3.4). My dataset represents the largest compilation of GGEs, across the greatest number of taxa (nine), with incorrectly determined values corrected or removed. Here I highlight the important issues arising from my results, comparing them with previous findings across species (i.e. Straile 1997).

Differences between datasets

The inclusion of GGE values of 100% and greater did not alter the significance of the independent variables temperature and food concentration in GLMs, in comparison to the datasets for which a GGE limit of 100% was imposed. This indicates that the significant trends between both variables and GGE for scyphzoans and cladocerans were robust enough to resist the influence of GGEs far exceeding that which is theoretically possible. Indeed, the increased mean GGEs as a result of including values of 100% and above, generally did not vary significantly from those imposing a 100% limit. Where differences were observed, for copepod including GGEs up to 1000%, and for all taxa up to 1000 and 2000%, the highest values

Table 3.7 **Comparison of Gross Growth Efficiencies (GGEs) of between datasets comprising all available GGE values (All data), and those excluding GGEs greater or equal to 100 for copepods, scyphozoans, nano/microflagellates, cladocerans, and all taxa combined. Datasets with a GGE limit of 200, 1000 and 2000 were also compared to all available data for copepods, and all taxa combined. Values were compared using a T-test at 95% confidence level, with level of significance (*P* value) given below with degrees of freedom (D.F.)**

	GGE Values	Mean	S.E. Mean	GGE Values	Mean	S.E. Mean	T	P	DF
Copepods	<100	26.6	0.92	<200	28.3	1.1	−1.20	0.231	943
	<100	26.6	0.92	<1000	31.1	2.1	−2.02	0.044	681
	<100	26.6	0.92	<2000	34.9	4.3	−1.89	0.059	537
	<100	26.6	0.92	All data	71.0	37.0	−1.22	0.223	494
Scyphozoans	<100	27.3	2.1	All data	29.5	2.4	−0.69	0.494	241
Nano/microflagellates	<100	39.1	2.3	All data	40.0	2.4	−0.27	0.788	132
Cladocerans	<100	26.7	1.9	All data	28.8	2.4	−0.68	0.495	209
All Taxa	<100	24.7	0.52	All data	40.0	12	−1.25	0.211	1463
	<100	24.7	0.52	<2000	28.0	1.5	−2.01	0.045	1794
	<100	24.7	0.52	<1000	26.7	0.83	−1.99	0.046	2450
	<100	24.7	0.52	<200	25.7	0.59	−1.27	0.204	2858

included (680% and 1898%) are likely to be at least an order of magnitude greater than the maximum possible GGE. As these values are so erroneous, and all datasets including values up to 200% (more than twice that which is possible) do not differ from those imposing a 100% limit, there is evident reason to dispute the comparison of mean GGEs between taxa, and the nature of relationships of GGE with temperature and food concentration for the <100% GGE dataset reported in this study.

Effect of temperature within taxa

I found large differences between taxa both in terms of the significant variables associated with GGE and also the nature of these relationships. My finding of a positive relationship between log10 GGE and temperature for dinoflagellates is consistent with the findings of a previous synthesis by Straile (1997) for this taxon. I found a negative relationship for bacteria, the same pattern found by Rivkin & Legendre (2001), although this is unsurprising as much of my dataset (n=113) was derived from the same studies, and I have only added data (n=18) from three additional studies.

I did not detect a significant relationship between GGE and temperature for nano/microflagellates, which differs from the positive relationship found previously by Straile (1997), but is consistent with some studies within species (Caron *et al.* 1986). I also did not detect a relationship for rotifers, a result mirrored by Straile (1997), which is likely a product of the relatively low number of data available for this taxon. I am the first to report a significant negative relationship for cladocerans, a group for which no relationship was detected previously (Straile 1997). For both ciliates and copepods, for which my data were over 2.5 times that of previous syntheses, the result of no significant relationship contrasts the negative relationship found by Straile (1997). Two groups show a negative relationship between temperature and GGE, bacteria and cladocerans. My synthesis used log10-transformed GGE and food concentration, a combination that has not been previously used. However, the presence/absence of significant variables, and nature of relationships between GGE (not log10-transformed) and both temperature and

food concentration using the transformations as in Straile (1997) were identical to those obtained using log10 transformed GGE and food concentration, and non-transformed temperature for dinoflagellates, copepods and nano/microflagellates, and different to trends reported in Straile (1997). In addition, the negative relationship between food concentration and cladoceran GGE was present in this study was also present when GGE was transformed, but absent in Straile (1997). This suggests that the larger dataset, correction or removal of incorrect GGEs, in my study is likely to explain the disparity with previous studies. Data transformation may be partly responsible for the differences between trends outlines in this study for ciliates however, as non-transformed GGEs and squared-temperature was shown to alter the nature (positive or negative) of relationships.

Increasing temperature is generally associated with an increase in ingestion and growth rate in planktonic taxa (Rassoulzadegan 1982, Peters & Downing 1984, Sharma & Pant 1984, Caron *et al.* 1986), most likely owing to the potential increased rate of biochemical reactions at higher temperatures, although when general thermal tolerances are exceeded values can decline. Instances where GGE temperature dependence is shown must be associated with a disparity in the response of ingestion and growth with temperature. For the three taxa that show a positive response, dinoflagellates, ctenophores and scyphozoans, mass-specific growth rate must have a greater slope against temperature than mass-specific ingestion rate. Growth will have a greater temperature dependence than ingestion if, for example, the amount of energy used per unit mass consumed is lower at higher temperatures. In comparison to other protists, dinoflagellates have lower energetic requirements for locomotion (Crawford 1992), and have lower specific growth rates (Strom 1991, Hansen *et al.* 1997). The lower costs of these processes, in addition to a lower temperature dependence of growth rates (Montanges *et al.* 2003), is likely to provide greater scope for achieving higher GGEs. Conversely, ingestion rate increases at a greater rate than growth rate for taxa that show a negative relationship between GGE and temperature, i.e. bacteria and cladocerans. Ingestion will have greater temperature dependence than growth if, for example, lower water viscosity at higher temperatures allows the predator to capture enough

prey that superfluous or luxury feeding occurs. Alternatively, the biomass of the prey consumed may have been overestimated if sloppy feeding (the partial consumption of prey) occurs, and is not considered. Because I found no temperature dependence of GGE in ciliates, nano/microflagellates, rotifers and copepods, this suggests that the temperature-dependence of growth and ingestion are similar.

Effect of food within taxa

The negative relationship I have reported for ciliates for GGE against food concentration is not consistent with the previous findings of Straile (1997), although a negative relationship has been reported within species (Nakano 1994). My report of a negative relationship for cladocerans, and no relationship for dinoflagellates is supported by previous findings (Straile 1997). A negative relationship indicates that across species a greater level of food results in a lower GGE. This may be an indication that within these taxa, species are saturated with food and a lower GGE results from superfluous feeding, or that ingested mass is processed through the gut at a faster rate at higher food concentrations thereby decrease assimilation and subsequently GGE. If these processes are important in cladocerans assimilation and assimilation efficiency will decreases with increasing food concentration across species. Although these processes can explain the negative relationship in cladocerans, ciliates do not have a gut nor do they feed superfluously. It may be the case that for these taxa both ingestion and growth are greater at higher food concentrations, but that relative increase in ingestion is greater, or that ingestions increases whilst a maximum growth has been achieved, or rate of increase decreasing as it approaches its maximum. A possible reason may be that the method of prey capture has a greater capacity for increase as a result of increased food concentration than growth of the organism. It may be that the biological pathways for creating new mass are reached at lower food concentrations and that the growth of an organism is restricted by other variables or processes at lower food levels than that which limits the mechanism and process of mass ingestion.

In contrast to findings by Straile (1997) and also studies within species (Paffenhöfer 1976, Rey-Rassat *et al.* 2002), I found no relationship between GGE and food for copepods, where my dataset is more than twice that of previous syntheses. Similarly, where a negative relationship has been reported for nano/microflagellates and rotifers (Straile 1997), I have shown there to be no significant relationship. The absence of a significant relationship between GGE and food concentration may be owing to a number of possibilities. Assuming that across species both growth and ingestion are increasing with food concentration, it would appear that they do so at the same rate, and that there is either no limitation to both processes, or that both are impacted equally so that GGE remains constant. Alternatively, if an increase in GGE with increasing food concentration occurs over very low food concentrations and subsequently reaches its maximum, the resulting pattern across species will be heavily influenced by food saturated conditions, thus reducing scope for changes in ingestion and growth, and therefore GGE. In a comparison of taxa that had a negative relationship between log10 GGE and log10 food concentration with those for which no relationship found, the reason for these differences are not immediately apparent. For instance, whilst the protozoan group ciliates and metazoan taxa of cladocerans displayed a negative relationship, protozoan groups of nano/microflagellates and dinoflagellates and metazoan taxa of rotifers and copepods had no significant relationship.

To my knowledge, I am the first to test for a relationship to food for juvenile and adult copepods separately. The positive relationship with food for juveniles, and no relationship for adults therefore represent the only existing reported of the effect of food on GGE. Included as a categorical variable, the effect of study on log10 GGE within adult and juvenile copepods separately, was significant ($p<0.001$), most likely owing to differences in terms of temperature, experimental technique, light conditions, prey quality and size between studies. This emphasises the need to consider effects of 'study' when compiling data across planktonic species.

Differences between taxa

An important result is that taxa differ in their relative efficiencies. Nano/microflagellates were particularly notable for achieving very high GGEs relative to all other taxa (see Figure 3.4). Conversely, ciliates were prominent for their low efficiencies, with a mean of 16%, whilst all other taxa had remarkably similar mean GGEs at 23–29%. The high nano/microflagellate, and low ciliate mean GGEs were also observed within the narrower temperature ranges (13 to 20 °C and 13 to 25°C; Figure 3.5) indicating that differences between taxa are not a product of GGEs being derived from different temperatures. Inclusion of values up to 200% resulted in an increase in GGE of less than 2.5% across taxa. Considering the high degree of error of included values (e.g. over 600%) and the modest increase in mean GGE with their inclusion, I conclude that considering values <100% provides an accurate assessment both within and between taxa. The low ciliate mean GGE in comparsion to other taxa can partly be explained through energetic costs. For instance, ciliate locomotion has higher energetic costs than dinoflagellates (Crawford 1992), which generally achieve higher GGEs. However, whether considering a diet of solely bacteria, or algae, ciliate GGE is also much lower than nano/microflagellates. The possession of greater GGEs indicates that nano/microflagellates are better able to respond to available resources than other planktonic taxa, and helps to explain inherent growth rates two to three times greater than those of ciliates and dinoflagellates (Strom 1991, Hansen *et al.* 1997).

I found no evidence in support of broad differences in GGEs achieved between metazoans and protozoans (Azam *et al.* 1984), nor that metazoans have a higher efficiencies (Calow 1977). Nano/microflagellates and ciliates, both protozoan groups, exhibited the highest and lowest mean values respectively, whilst all metazoan groups had intermediate GGE values. My mean values for all the metazoans are below the range cited as a reasonable estimate of post-embryonic metazoan GGE by Calow (1977). Following the correction of GGEs from five different studies, (see Table 1.3, p. 9), copepods had a similar mean to cladocerans, both much lower than the average of 48% cited for crustaceans (Calow 1977). My results for 3 out of 4 protozoan taxa (ciliates, rotifers and dinoflagellates) are lower

than 30–60% predicted by Caron *et al.* (1990) with the mean GGE of only nano/microflagellates fitting within this range. My mean GGE for ciliates also falls below the range often used or cited of 30–50% (Fenchel 1987, Bernard & Rassoulzadegan 1990, Ohman & Snyder 1991), which is most likely a product of the strict rules concerning the GGE values included in this study (i.e. GGEs derived from volume were not included without appropriate correction), and the increased consideration of low values derived when fed upon bacteria (see *Diet Type* p.53). The mean value of nano/microflagellate GGE is the only protozoan taxon to fall within the range of 30–60% predicted by Caron *et al.* (1990) and is also consistent with the range reported specifically for this taxon (20–63%) (Sherr *et al.* 1983). Although not true of nano/microflagellates and ciliates, my results for seven taxa (i.e. nano/microflagellates, dinoflagellates, ciliates, rotifers, cladocerans and copepods) fit into the 20–30% range found by Straile (1997). A generalised value GGE for all zooplankton is inappropriate as different taxa, particularly ciliates and nano/microflagellates, have different mean values, and also because the majority of taxa have mean values below 30%, which is generally used as an average zooplankton GGE (Landry & Calbet 2004). The differences between mean values and that generally assumed, whereby I obtained a generally lower mean GGE value for most taxa is likely a product of my larger dataset, standardisation and removal or correction of erroneously derived values.

Fundamental differences in morphology, behaviour and physiology of the different taxa are likely to account for some of the differences I observe in GGE. For instance, digestion may be achieved extracellularly (e.g. bacteria), by use of food vacuoles (e.g. ciliates and dinoflagellates), gastrovascular cavity (e.g. scyphozoans) or a complex gut (e.g. copepods and cladocerans). Different taxonomic groups also demonstrate different methods of feeding (raptorial, filter feeding or direct uptake of dissolved organic nutrients), prey detection and capture, types of locomotion, prey composition, growth forms (binary fission, eutely, egg production), size, body–mass scaling and body structure (e.g. single versus multicellular). These differences between organisms affect not only how much and the type of material ingested, but also the proportion of this ingested material allocated to growth. The

energy budget of different taxa will be fundamentally different, and vary with increasing temperature for some groups. Ciliates for instance, will on average allocate approximately 50 and 30% more carbon when feeding on an algal and bacteria diets respectively, towards non-growth processes such as respiration and egestion, in comparison to nano/microflagellates. Both ciliates and nano/microflagellates are consumers of pico-sized phytoplankton (Stockner 1988) and bacteria (Kuuppo-Leinkki 1990). Therefore community structure will impact the amount of material transferred to higher trophic levels, with those dominated by ciliates having higher overall respiration, and likely to reduce overall community efficiency.

The GGEs achieved in the studies I have synthesised are of course from experimental conditions, and therefore not necessarily representative of those found in nature. I suggest one of the primary differences causing disparity may come from food concentration and food type. It is likely that many of the studies included in my synthesis were run at food concentrations exceeding those found in nature, or at least at high levels for a longer period of time. In my dataset the range of food concentrations for all taxa except ctenophores exceeded the maximum food concentrations reported by Huntley & Boyd (1984) of 890 μg C L^{-1} for oceanic environments. For coastal environments the food of ctenophores and dinoflagellates were the only taxa to be appreciably below the maximum *in situ* concentration of 5000μg C L^{-1} reported by one study, although mean dinoflagellate food concentration was above all others (Huntley & Boyd 1984). Dinoflagellates and ctenophores were the only taxa whose mean food concentrations were below 250μg C L^{-1}, the maximum food concentration for oceanic environments reported by López-Urrutia *et al.* (2003) and within the range cited for the oceanic environment above 5°C (Huntley & Boyd 1984).

Assuming food concentration is not high enough to instigate superfluous feeding, one might expect higher efficiencies to be achieved as material is ingested more readily, and growth is not food-limited. Ciliates have been shown to be able to achieve positive growth rates at much lower food concentrations than dinoflagellates (Hansen 1992). This indicates that ciliates are better adapted to

lower food concentrations than other taxa and the efficiencies reported here might be a reflection of experimental food concentrations. The combination of ciliates having ingestion and growth rates approximately three times those of heterotrophic dinoflagellates (Hansen 1992), and the relatively high swimming speeds in ciliates (Hansen *et al.* 1997), suggests high energetic requirements, which if not counteracted by, for instance an increase in ingestion or, as shown in dinoflagellates, a reduction of metabolism in response to low food concentrations (Hansen 1992), will result in the low GGEs observed.

The amount of variation in GGE accounted for by temperature, food or the combination of the two variables differs between 9–58% for individual taxa, with an average of 28%. Therefore, a lot of variation cannot be attributed to these two variables. Additional sources of variation come from many sources, including differences in water volume, food density, food quality, the type of prey and salinity, but may also be intrinsic with the calculation of GGE. Errors may occur if the two components of GGE, growth and ingestion, are measured in fundamentally different ways, for example derived over different durations. The measurements of ingestion and growth may also be inaccurate, compounding errors further when combined to calculate GGE. As with any synthesis across species, there is likely to be increased scatter as a result of the combination of species–specific response to the variables explored. For example, in my synthesis, different species are likely to have different optimum food concentrations for GGE. Compiling these together will therefore result in greater variability in the data. Despite these differences, patterns between GGE and temperature and food were still able to prevail.

Trophic groups

Differences between heterotrophic and mixotrophic ciliates in their response to temperature may be a result of their respective specialisation (Table 3.3). Mixotrophs can synthesise biomass through photosynthesis and the conversion of ingested prey material. Heterotrophic organisms however rely solely upon ingested mass for production. Heterotrophs, therefore, are likely to have a greater degree of specialisation in breaking down prey and synthesising new biomass than

mixotrophs, for instance through greater digestive enzyme production. Enzyme driven processes will be largely temperature dependent, and the positive relationship between GGE and temperature from heterotrophs is a consequence of their specialisation and greater enzyme dependence of production. Perhaps the greater costs associated with the autotrophic component of mixotrophs impact production at higher temperatures, through greater respiration rates for example. Mixotrophs may not be specialised to as greater degree to locomotion, prey detection and capture owing their ability to photosynthesise. Within my dataset, travelling costs are likely to be relatively greater for mixotrophs and as a result, GGEs were lower, especially at higher temperatures.

Diet type

I found in protozoans (ciliates, nano/microflagellates and dinoflagellates) and copepods, higher GGEs were achieved on an herbivorous diet than bactivorous, carnivorous or mixed. Herbivorous feeding represent highers quality prey than bacteria with ingested algae more efficiently converted into body mass, possibly a product of a higher proportion of essential nutrients. Although food concentrations influence GGE, I found mean food concentrations were around twice as high for ciliates and nano/microflagellates when fed on algae, and dinoflagellates when fed a mixed diet, than when fed only bacteria. For copepods, the mixed diet had the highest mean value, over twice that of the carnivorous and herbivorous diets.

Size of prey is likely to be an important factor in determining the relative GGEs on herbivorous and bactivorous diets. Bacteria being a relatively smaller prey item, is likely to incur a greater cost per prey mass in terms of the energy needed for prey capture and handling, than the generally larger algal species. The predator:prey size ration for ciliates and nano/microflagellates when fed bacteria in my dataset were much greater than 8:1 and 3:1, respectively, cited as optimal for growth (Hansen *et al.* 1994). Meanwhile there is evidence that some species of nanoflagellate are unable to sustain their population density when feeding solely on small bacteria (Holen & Boraas 1991), and that the smallest are ingested to a much lower extent by nanoflagellates and ciliates (Gonzalez *et al.* 1990). Dinoflagellates fed on a mixed

diet of algae and bacteria would presumably suffer increased energetic costs than when feeding solely on algae, as the predator:prey ratio is increased far above the optimum of 1:1 size ratio (Hansen *et al.* 1994).

Disparity in GGE emphasises the importance of food type when determining values. For instance, when feeding herbivorously, ciliates obtained a mean GGE that approximates that of four other taxa on the same diet type. Where a taxon feeds on more than one diet type e.g. algae and bacteria, the relative proportion of each food type is of fundamentally important in determining energy flow. For example, I have shown a three-fold increase in GGE can occur between a bactivorous and herbivorous diet in ciliates. The greater proportion of bacteria in their diet in comparison to herbivores is likely to decrease overall GGE in ciliates, nano/microflagellates and dinoflagellates.

Wider implications for ecosystem structure

For GGEs to be appropriately applied to environmental data, there needs to be agreement as far as possible between natural and experimental diets. This can therefore have important implications for the transfer of material through the planktonic food web. It also means that in the natural environment the type of prey standing stock will affect the predator growth efficiency, which can have knock-on consequences for the food web. For instance, ciliates operate with higher GGEs when they are predominantly feeding herbivorously as opposed to bactiverously. Clearly the relative proportion of these prey in there diet will in turn dictate the efficiency of material transfer through parts of the microbial food web.

I have demonstrated that not only does GGE vary between different taxonomic groups, but that prey type is an important determinant. Importantly my data suggests that temperature dependence of GGE differs between taxa. Predicting the effect of temperature on the food-web through its affect on GGE is perhaps not as simple as originally perceived. The flow of primary productivity through the planktonic food web will be complicated by taxon-specific GGE values and temperature dependences of. It is therefore not a matter of temperature causing a uniform increase or decrease of mass flow within the food web and subsequently to

upper trophic levels. The incorporation of relationships determined in this study into existing models that have previously used a singular value across taxa with no temperature dependence (e.g. Stoecker & Evans 1985; Pomeroy 1999; Lewis 2005; Buitenhuis *et al.* 2006) will most likely increase food-web model accuracy.

The impact of temperature dependent GGE of bacteria has been used to predict wider implications of temperature increase on the planktonic food-web (Rivkin & Legendre 2001) and has already been implemented within models (Legendre & Rivkin 2002). Although bacterial respiration can represent a large proportion of community respiration, variation in the response of GGE in different taxa to temperature increase, in order to develop an accurate understanding of energy flow the inclusion of taxon-specific GGEs other than bacteria is vital. For a more comprehensive understanding of the planktonic food-web dynamics I encourage these are built upon by incorporating taxon-specific differences within ecosystem models.

Chapter 4. The Impact of Temperature on Standing Stock Biomass of Planktonic Taxa

Introduction

Standing stock biomass, a volumetric or areal measurement of biomass at the moment of sampling, is fundamental for understanding food–webs. It is a quantitative measurement of the contribution of species, of broader taxa, of trophic levels, and of functional groups to the overall biota. Standing stock biomass has been used to describe plankton community structure (Linley *et al.* 1983, Carrick & Schelske 1997, Booth *et al.* 1993, Lingell *et al.* 1993), and to investigate the relationship between parameters (such as chlorophyll–*a*, temperature, water depth and mixed layer depth) and the distribution of bacteria (Kirchman *et al.* 1993, Kirchman *et al.* 1995), autotrophs (Hewes *et al.* 1990), heterotrophic protozoa (Hewes *et al.* 1990, Dolan & Marrase 1995) and metazoan zooplankton (Borgne 1981). Standing stock biomass values have also facilitated comparison of the biological composition of environments that vary temporally (Booth *et al.* 1993, Buskey 1993, Lingell *et al.* 1993), spatially (Paranjape 1987, Chavez 1989, Peña *et al.*1990, Harrison *et al.* 1993, Zhang *et al.* 1995), and in trophic status (Duarte *et al.* 2000, Bell & Kalff 2001). Standing stock biomasses can also be used to determine carbon budgets and energy flow networks (Linley *et al.* 1983, Baird *et al.* 1991, Boyd *et al.* 1995, Moloney *et al.*1991).

The marine pelagic environment is subject to large variation in primary production, often being seasonal and linked to nutrient availability. Increased nutrient concentration is largely associated with an increase in phytoplankton, the main autotrophic component of the planktonic food-web (Lalli & Parsons 1997). Since phytoplankton is the basis of the marine pelagic food-web, higher levels of nutrients are generally associated with and increase in biomass of not only primary producers which utlise nutrients through direct uptake, but also primary and secondary consumers, as phytoplankton availability is greater, allowing more energy flow through the trophic levels. Equatorial gyres for instance, are areas

notable for low nutrient concentration, and low primary production, as a result of permanently stratified, and relatively stable water column, reducing nutrient flow into the euphotic zone (Jennings *et al.* 2001). However, there area oceanic environments, such as the southern ocean, known as HNLC (high nutrients, low chlorophyll) areas, which possess low levels of phytoplankton despite having relatively high levels of nutrients available. The paradox of HNLC areas is thought to be due to the absence of required minerals, such as iron (Martin 1990, Boyd *et al.* 1996, Boyd *et al.* 2000), but may also be a result of increased grazing by microzooplankton (Frost 1991, Tsuda *et al.* 2007), or a combination of both processes (Price *et al.* 1994).

To some extent variation in primary production is reflected in the standing stock biomass of primary producers and, through trophic cascades, the biomass of higher trophic levels too. The combination of *absolute* biomass values from different study sites and subsequent use within ecosystem models may not be appropriate in all cases because differences in biomass of ecosystem compartments between sites may be obscured by differences in primary production which can affect higher trophic levels. In contrast, by examining biomass values *relative to phytoplankton* we are able to detect which planktonic taxa increase their relative contribution to total biota in response to environmental variables such as temperature. This relative, rather than absolute, measure of standing stock biomass is of great importance in representing changes in the dominance of different taxa, and understanding how the biomass in the planktonic food-web varies with temperature over large geographical scales. Relative biomasses of bacteria (Kirchman *et al.* 1993, Kirchman *et al.* 1995), protozoa (Havens *et al.* 2007) and herbivorous zooplankton (Uye *et al.* 1999) in addition to the pico size component of phytoplankton (Fiala *et al.* 1998, Goericke 1998, Bell & Kalff 2001) have previously been used to highlight planktonic group responses to variables such as nutrient abundance, temperature and latitude. On a large, macroecological scale the influence of local variations are reduced, allowing large-scale trends of the most dominant factors influencing the distribution of organisms to be determined.

There is a scarcity of studies of the thermal effects on relative biomass within the marine literature, but there are indications that relative biomass varies with temperature within freshwater environments. For instance, Protozoa were found to have a far greater relative biomass in warmer subtropical lakes than in cooler temperature lakes within which metazoan zooplankton contributed a greater proportion of plankton biomass (Havens *et al.* 2007). These findings were deemed to be consistent with the hypothesis that subtropical freshwater lakes are subjected to greater top–down control than are temperate lakes.

General trends concerning the relative biomass of different planktonic groups in response to temperature in the marine environment are currently unknown, although several studies of single locations suggest temperature may have a profound effect on the distribution of plankton biomass. In the Baltic Sea, temperature was not only more important in shaping phytoplankton community structure in the marine food–web than level of nutrients, but it was singled out as the most influential variable (Gasiunaite *et al.* 2005). Temperature has been proposed as an important determinant of the abundance and distribution of copepod species in a macroecological context (Beaugrand *et al.* 2007, Helaouët & Beaugrand 2007). Concordantly within the southern ocean, Fiala *et al.* (1998) reported "the distribution of phytoplankton biomass and community structure along the transect appears to be the reflection of the prevailing environmental variations, especially that of temperature".

Temperature may impact the structure of the marine food–web by affecting the rates of production and loss (for example though consumption) of phytoplankton that determine its biomass. The nature of the relationship between phytoplankton biomass and temperature is currently unclear over a global scale, but there is evidence that phytoplankton biomass within the upper 200m of the pelagic open ocean increases with temperature in the Southern Ocean (–0.5 to 5.5°C) in areas where sea–ice was not an issue (Fiala *et al.* 1998). If production and loss rates are affected by temperature to varying degrees between differently sized phytoplankton, then the biomass size–structure may also vary. For instance although the proportion of picoplankton to total phytoplankton does not vary

temporally in the Sargasso Sea over the course of a year (Goericke 1998), the proportion of picophytoplankton to total chlorophyll-*a* increases with decreasing latitudes from around 30 to 50% from 67°S to 49°S respectively, in the Southern Ocean (Fiala *et al.* 1998).

Changes in phytoplankton size-structure in response to temperature are likely to have a large impact on the amount of biomass passing through the food-web to higher trophic levels and the path through to different consumers. Increasing temperature may be associated with a greater influence of bacteria on the fate of planktonic biomass. Within the equatorial Pacific region (12°N to 12°S), bacterial biomass relative to phytoplankton was greatest near the equator, declining with increasing latitudes (Kirchman *et al.* 1995). It is my aim to assess whether similar trends between bacterial biomass, relative to phytoplankton, and temperature exist over a larger scale.

The magnitude of standing stock biomass of a taxonomic group, or trophic level, is a result of many ecological, behavioural, and physiological processes. Standing stock biomass is a balance between production and total mortality, both of which are a composite of many processes. Heterotroph production is a result of processes that include growth rate, respiration rate, feeding rate and prey availability, all of which are heavily influenced by temperature. Standing stock biomass of a taxon can be calculated by:

$$B = \frac{P}{\mu} \qquad \text{Equation 4.1}$$

where P is production and μ is instantaneous growth rate. I would therefore expect a change in standing stock biomass if the ratio between production and growth varies. Both production and growth rate are likely to be influenced by temperature. Within biologically relevant temperatures, growth rates have been shown to be temperature dependent for many planktonic taxa, for instance ciliates (Nielson & Kiørboe, 1994, Montagnes *et al.* 2003, Rose & Caron 2007), dinoflagellates (Montagnes *et al.* 2003), Nano/microflagellates (Caron *et al.* 1986, Rose & Caron

2007), copepods (Huntley & Lopez 1992, Hirst & Bunker 2003, Hirst *et al.* 2003) and bacteria (White *et al.* 1991, Rivkin *et al.* 1996).

One of the limitations of production by a group is its Gross Growth Efficiency (GGE), which is a measurement of the biomass produced per biomass ingested (Chapter 2, p.5), and therefore useful for understanding the proportion of biomass converted from prey to predator. Different taxa not only possess inherently different GGEs, but the degree of GGE temperature-dependence and its direction (positive or negative relationship) also varies between taxa. Consequently, the standing stock biomass of a group may not share the same temperature dependence as phytoplankton, and therefore relative biomass of that group will vary with temperature. Therefore temperature may substantially influence the proportion of phytoplankton biomass flux through the food-web, and level of standing stock biomass of different groups, through its effect on the GGE of an organism, taxon, or trophic level.

In addition, diet type significantly affects the efficiency with which numerically and functionally important taxa convert food into predator biomass. For instance ciliates and dinoflagellates both achieved a greater GGE when feeding on algae than on bacteria, whilst copepods also had a higher GGE feeding on algae in comparison to a carnivorous diet (Chapter 3, p.42). With increasing temperature the contribution of different size categories to total phytoplankton biomass may vary.

Food that is of poor quality for one consumer species may be of high quality for another consumer. Here I use the terms low and high quality food to represent prey that yield, respectively, a low and a high GGE for the relevant consumer. As grazing by zooplankton is largely considered to be size-dependent, the consequences of changes in phytoplankton composition will be to provide a greater source of food to certain herbivorous heterotrophs, thereby impacting the flow of material through the planktonic food-web. Therefore a change in the size-structure within the phytoplankton will impact the flow of material in the planktonic food-web by benefiting those consumers that have an increased proportion of high quality food. Conversely, if prey that can only be processed with a lower GGE

represents a greater proportion of the diet available to a taxon, a greater proportion of biomass will be lost to respiration, excretion and egestion (defecation). Consequently, even though *absolute* amount of biomass of a taxon may increase, greater consumption of low quality prey can potentially decrease *relative* biomass. It is therefore evident that over a macroecological scale temperature, in addition to growth and respiration rates, may substantially influence the distribution of biomass in the planktonic food-web through its effect on the GGE of different taxa, which impacts on phytoplankton community structure.

Although studies have examined the relationship between standing stock biomass and temperature, they have typically focussed on either single species, or on size groups (e.g. Kirchman *et al.* 1995, Fiala *et al.* 1998, Goericke 1998). My objectives are to better describe and understand the relationship between biomass and temperature across a wide range of planktonic groups, providing quantitative relationships that can be utilised in further studies, including those that model the flow of material through the planktonic food-web. Although other environmental parameters, such as nutrient and light availability, influence phytoplankton production, which has knock-on consequences for higher trophic levels, my aim here is to determine whether, as a correlate of some of these variables, temperature is fundamentally linked to changes in the relative biomass of different planktonic taxa over a large macroecological scale and therefore the structure of the food-web.

It has been predicted, for example, that microzooplankton groups become a greater component of the food-web at higher temperatures owing to an increase in the size range of phytoplankton (Conover 1979). As microzooplankton grazing is commonly prey-size dependent, a greater set of resources is available at higher temperatures, thus potentially allowing greater microzooplankton production (Conover 1979). Thus at relatively higher temperatures microzooplankton may become an increasingly important component of the planktonic food-web in terms of carbon flux and providing food for higher trophic levels. Bacterial respiration relative to energy or carbon assimilation has been shown to increase with temperature; thus assimilation of resources from particulate and dissolved organic

matter is less efficient (Rivkin & Legendre 2001). As bacteria play an important role in recycling organic matter in the planktonic food-web, bacterial growth may become the rate-limiting step in carbon flux, with a greater proportion of carbon lost via respiration.

I examine whether the response of biomass to temperature varies across taxa, and the consequence of this on the distribution of biomass in the planktonic community. I use the null hypothesis that there is no change with temperature owing to no significant difference in the scaling of biomass with temperature across taxa. I test the effect of temperature on different levels of taxonomic groups combined from three datasets, termed Gasol, AMT, and MarProd. I combined these datasets to obtain standing stock biomasses of ciliates, dinoflagellates, flagellates, total protozoa, total mesozooplankton and total bacteria. This combined dataset allows an examination of biomasses over a large temperature range, spreading over both hemispheres.

However, the datasets differ in terms of the temperature range they represent. For instance, temperatures within the MarProd dataset (3 to 10°C) are within a smaller range than the Gasol (-1.89 to 17.5°C) and AMT (-1.89 to 27.6°C) datasets, resulting in a cluster of biomass values lower range of temperatures from this study. In order to examine the influence of the data source, for instance as a result of varying methods between AMT and MarProd cruises, I also examine each dataset separately to investigate whether patterns are also reflected over smaller geographical and temperature scales and to better understand the cause of large-scale patterns. The Gasol dataset has broad categories of bacteria, phytoplankton, protozoa and mesozooplankton. The AMT dataset contains more specific categories, with ciliates and dinoflagellates being identified as separate groups. The greatest number of taxonomic groups is examined in the MarProd dataset, which includes a variety of mesozooplankton in addition to protozoan groups. These datasets complement each other well because they are representative of different locations and ranges of temperature, and therefore allow a comprehensive overview of temperature effects on the relative biomass distribution within the planktonic food-web.

Phytoplankton biomass estimates used in this study are derived using chlorophyll-*a* to carbon ratios (Chl*a*:C; see Methods, p.66). However, using a constant carbon to chlorophyll ratio can be a source of great inaccuracy, with the biomass of autotrophs underestimated when chlorophyll concentration is low (Buck *et al.* 1996). I therefore investigate the importance and influence of using Chl*a*:CC, a constant conversion ratio, in comparison to Chl*a*:CT, a ratio specific to the trophic status of the environment, in estimating phytoplankton biomass and its relationship to the relative biomass of different zooplankton groups. I compare the biomass of zooplankton groups relative to phytoplankton by using Chl*a*:CC and Chl*a*:CT: this will show any disparity between zooplankton relative biomass responses to temperature owing to underestimating phytoplankton biomass at low chlorophyll concentrations when using Chl*a*:CC.

The primary objectives of this study are therefore to:

1. Describe the relationships between relative biomass and temperature for a variety of planktonic taxa
2. Examine the impact of temperature on the distribution of standing stock biomass between taxa
3. Examine the importance of using trophic status specific chlorophyll *a*: carbon conversion ratios to estimate relative biomass and its relationship with temperature.

I achieve these by answering the following fundamental questions:

1. How does the biomass and relative standing stock biomass vary within taxonomic groups?
2. Does temperature affect biomass to the same degree among taxonomic groups and therefore impact planktonic food-web structure?
3. Are there significant changes in the relative biomass, and relationship with temperature of zooplankton taxa as a result of using trophic status specific chlorophyll-*a* : carbon ratios rather than a constant ratio?

Methods

I first describe the different datasets used within this chapter, outlining the variables used and their calculation, before detailing the way in which they were analysed. The three separate datasets, referred to as the Gasol, MarProd and AMT datasets are now discussed separately.

Datasets

Gasol

The data, obtained from the author, comprised autotrophic, bacterial, protozoan and mesozooplankton biomass (μg C L^{-1}) in addition to primary production (μg C L^{-1} d^{-1}) and chlorophyll-*a* (μg L^{-1}), from over 80 literature studies between 1967 and 1993 (see Gasol 1997 for more details). Where possible, studies were included that reported all four groups simultaneously, but those for which one or more groups are missing are also included. Latitudinally, the sample sites range from 75°N to 77°S (Figure 4.1). I revisited the primary literature for measurements of temperature (°C), in addition to further spatial data (latitude and longitude, °) which were added to the dataset where possible. Temperature values were either from *in situ* measurements or those reported during bottle experiments.

MarProd

These data were from the Marine Productivity RRS Discovery cruise 262, in the North Atlantic in the spring of 2002 (for the full report of this cruise see Richards *et al.* 2002). I obtained abundances of phytoplankton and protozoan taxa (ciliates, flagellates and dinoflagellates, from CTD (conductivity, temperature, depth) measurements, and metazoan zooplankton (bryozoans, chaetognaths, cnidarians, copepods, non-copepod crustaceans, ctenophores, echinoderms, molluscs, platyhelminths/nemerteans and polychaetes and tunicates) sampled from Autosampling Recording Instrumented Environmental Sampler (ARIES) tows, Ocean sampler (OS) tows and Dual Methot (DM) net tows. Abundances were converted into number of individuals per litre (no. l^{-1}). Phytoplankton and zooplankton

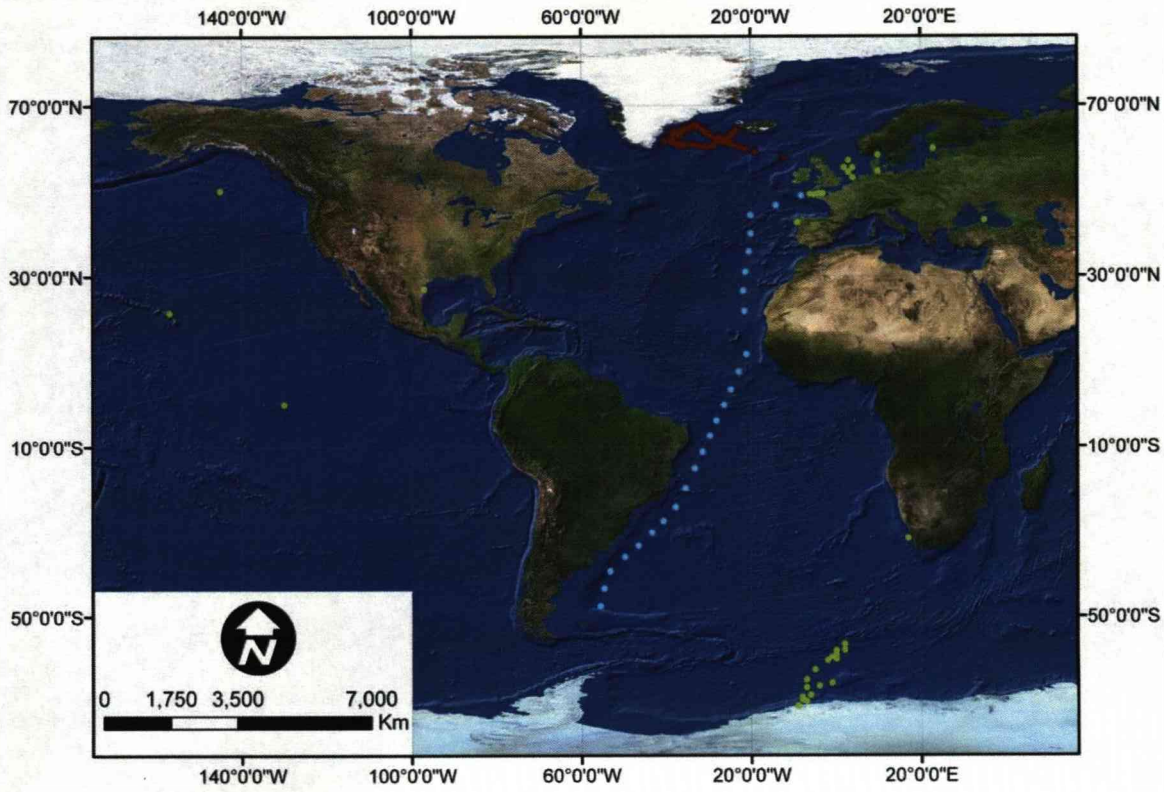


Figure 4.1 The location of sample sites from the Gasol (•),MarProd (•), and AMT(•) datasets, and used in this study.

abundances were converted into biomass by multiplying by a carbon content value (μg C ind^{-1}). Where possible carbon content for each individual species was calculated from estimates from the published literature (Appendix 1), and life-stage specific for mesozooplankton (i.e. nauplii, copepodite and adult for copepods) (Appendix 2), or in the case of ciliates calculated from available estimates of cell volume and the commonly used carbon density of 190 fg C μm^{-3} which allows for shrinkage for cells preserved with Lugol's solution (Putt & Stoecker 1989) (Appendix 3). Where species-specific values were unavailable, average carbon content values derived from other members of the same genus or higher taxonomic grouping were used (Appendix 1). Owing to potentially large differences in carbon content between autotrophic, heterotrophic and mixotrophic dinoflagellates, species were categorised into one of these trophic groups using evidence from the literature (Appendix 4), and their carbon contents were then calculated from values reported in Menden-Deuer & Lessard (2000). Algal species carbon contents were converted into biomass using for non-diatom species an average calculated from values reported in Mullin *et al.* (1966), and for diatoms using an average diatom carbon content derived from values digitised from Menden-Deuer & Lessard (2000) using computer software program GetData Graph Digitizer 2.24 (Appendix 1). Where species-specific carbon content values were unavailable for metazoan species, the appendices of Hirst *et al.* (2003) were used to calculate average values (Appendix 2).

Each sample site was determined using spatial (latitude and longitude) and temporal (date and time) data. Biomass from each site was averaged from samples taken in the upper 200m of the water column in order to encompass the metazoan component of the pelagic food-web, which often sink below the photosynthetic biota to avoid predation. Biomass values were complemented with average temperature within the top 100m (°C), which I assume to be the temperature of the mixed layer only. Average temperature was calculated using measurements from CTD profiles, which were from the same, or nearest sample site as determined by spatial (latitude and longitude) and temporal (time and date) measurements. Chlorophyll-*a* (μg L^{-1}) measured with an *in situ* chlorophyll fluorometer is considered here a suitable proxy for phytoplankton biomass.

AMT

I obtained data from the Atlantic Meridional Transect cruise 2, located in the Atlantic Ocean, from Port Stanley (Falkland Islands) to Plymouth (UK) from April to May 1996. For a full report of this cruise see Robins (1996). Abundance data were from CTD casts for bacteria, and phytoplankton and microzooplankton using Niskin bottles, and standing stock biomass measurements for bacteria and phytoplankton. I also use production values measured by -thymidine and -leucine uptake methods for bacteria and incubated bottle samples for phytoplankton. Species were classified into groups of either bacteria, pico- (0.2-2μm), nano- (2-20μm) and micro- (>20μm) phytoplankton, coccolithophores, flagellates, diatoms, ciliates, dinoflagellates or picoplankton (including heterotrophs <2μm), and converted to biomass using appropriate carbon content estimates (Appendices 1 & 3). Temperature (°C) data were assigned to each abundance, biomass and production value using CTD measurements matched according to temporal (date and time) and spatial (latitude and longitude) information, at the nearest depth. Average values of biomass and temperature of the water column were derived for each site using spatial (latitude and longitude) and temporal (date and time) data.

All data

In order to make comparisons across all three data sets, protozoan taxa were combined into a single category of Total Protozoa, and to compare the Gasol and MarProd dataset all mesozooplankton were combined together, as used by Gasol (1997). I combined all three datasets to allow analysis of log10 biomass and log10 relative biomass for protozoa and mesozooplankton, whilst the AMT and MarProd datasets were combined for dinoflagellates, and Gasol and AMT datasets combined for ciliates and flagellates. For all groups within the Gasol, MarProd and AMT datasets relative biomass (RelBio) of each taxonomic group was calculated as the proportion of biomass (μg C L^{-1}) per phytoplankton biomass (μg C L^{-1}). I derived phytoplankton biomass in carbon from chlorophyll-*a* measurements (μg l^{-1}), which were available in all datasets, and using a conversion factor. I employ two conversion methods to estimate phytoplankton from chlorophyll a concentration, using what is herein referred to as the constant (Chl*a*:CC) and trophic-specific

(Chl*a*:CT) conversation ratios. To convert chlorophyll-*a* (μg C L^{-1}) to carbon (μg C L^{-1}) I used a constant conversion ratio, Chl*a*:CC, of 50 as used by Cho & Azam (1990) and Christian & Karl (1994). For trophic specific carbon conversion values, Chl*a*:CT, I used a ratio of 90 for oligotrophic conditions, and for meso/eutrophic waters a ratio of 30 was used, as found by Eppley (1968) and consistent with Geider (1987) and that reported in Buck *et al.* (1996). I classified oligotrophic conditions as those that had a chlorophyll-*a* concentration below 30 μg l^{-1}, after Agawin *et al.* (2000), which is similar to that of Cho & Azam (1990) (<50 μg l^{-1}), whilst those greater were deemed meso/eutrophic.

Comparison of polar regions

To investigate the influence of geographical region of the ocean on planktonic biomass, rather than temperature, I compare the biomass and relative biomass of protozoa for latitudes exceeding 50°N using MarProd data, and greater (i.e. closer to the southern pole) than 50°S (Southern Ocean) using the Gasol dataset. Regressions between both log10 biomass and log10 relative biomass and temperature are derived for both regions, whislt a T-test at a 95% confidence interval is used to compare mean biomass and relative biomass values. Protozoa were the only group for which it was possible to compare in this way, as mesozooplankton were not available for the Southern Ocean, and bacteria biomasses were not representedin the MarProd dataset.

Statistical Analyses and Hypotheses Testing

All analyses were conducted using Minitab (MINITAB® Release 14.1). Using ordinary least squares linear regression I tested the effect of temperature on the log10 biomass and also on log10 relative biomass derived using Chl*a*:CT and Chl*a*:CC for each taxonomic group within the AMT, Gasol and MarProd datasets, at a 95% significance level (*p* values <0.05). I subsequently performed similar regressions on log10 biomass of total bacteria, total protozoa and total mesozooplankton using data combined from the three datasets.

For each taxonomic group within the AMT, Gasol, and MarProd datasets I performed t-tests to compare the difference in log10 relative biomass derived using

trophic-specific chlorophyll-*a* to carbon ratios (Chl*a*:CT) and a constant ratio (Chl*a*:CC). Further t-tests compared the log10 relative biomass derived from the two ratios, for total bacteria, total protozoa and total mesozooplankton using data combined from all three datasets. To compare the slopes of regressions between relative log10 biomass and temperature, for biomass values derived using Chl*a*:CC and Chl*a*:CT, I created a general linear model (GLM) as described in Grafen & Hails (2002):

$$\log10RelBio = T + Ratio + (T \times Ratio) \qquad \text{Equation 4.2}$$

where temperature (T, °C) and relative biomass (*log10RelBio*, µg C L^{-1} / µg C L^{-1}) are continuous data, and the conversion ratio (*Ratio*) is a categorical variable of either Chl*a*:CT or Chl*a*:CC. Where a significant ($p<0.05$) interaction term was found (T x *Ratio*), the slopes were significantly different (Grafen & Hails 2002). In addition, as temperature may be associated with changes in chlorophyll-*a* concentration, and biomass of autotrophs has been shown to be underestimated at low chlorophyll-*a* concentrations (Buck *et al.* 1996), I examine the difference between relative biomass values derived using Chl*a*:CT and Chl*a*:CC standardised to different temperatures (Equation 4.3).

$$\log10RelBio = (S \times T) + Int - R \qquad \text{Equation 4.3}$$

where the slope, or gradient, (S), and intercept (*Int*), are from regressions between relative biomass and temperature described above. Residuals, (R), were derived from the output of regressions and represent deviation from the mean for each datum. Using taxa of the Gasol dataset I standardised relative biomass values to six different temperatures that encompassed the range between maximum and minimum found in the dataset (-1.85, 0, 5, 10, 15 and 17.5°C), for all groups using equations derived from ordinary least squares regressions. For each group, I compared using a t-test, log10 relative biomass values derived using Chl*a*:CT and Chl*a*:CC (standardised to each temperature).

Results

log10 Biomass and Temperature

Combined dataset

Biomass decreased significantly with increasing temperature (3.0 to 27.6°C) for ciliates ($p<0.001$, R-squared=42.0%) and flagellates ($p<0.001$, R-squared=81.9%) (Figure 4.2; Table 4.1). I observed a positive relationship between log10 biomass and temperature for dinoflagellates ($p<0.001$, R-squared=53.4%), total protozoa (−1.9 to 27.6°C, $p<0.001$, R-squared=14.7%) and total mesozooplankton ($p<0.001$, R-squared=25.0%). The biomass of the remaining group, bacteria, although not significant at the 95% confidence level testes, showed a tendency to increase temperature (slope= 1.098, $p=0.086$, R-squared=2.7%).

Gasol

There were positive relationships between log10 biomass and temperature (5.2 to 17.5°C) for autotrophs ($p<0.001$, R-squared= 53.8%), heterotrophs ($p<0.001$, R-squared= 42.3%), bacteria ($p<0.001$, R-squared= 19.5%), protozoa ($p<0.001$, R-squared= 45.4%) and mesozooplankton ($p<0.001$, R-squared= 56.4%) (Figure 4.3; Table 4.2).

MarProd

For each of the thirteen taxa (ciliates, dinoflagellates, flagellates, bryozoans, chateognaths, tunicates, cnidarians, copepods, non−copepod crustaceans, ctenophores, echinoderms, platyhelminths/nemerteans, and polychaetes) (Table 4.3), total protozoa and total mesozooplankton I found log10 biomass did not vary significantly with temperature (2.8 to 9.8°C; $p>0.05$). The remaining two taxa, molluscs ($p=0.017$, R-squared= 16.0) and polychaetes ($p=0.017$, R-squared= 15.3) showed a positive relationship.

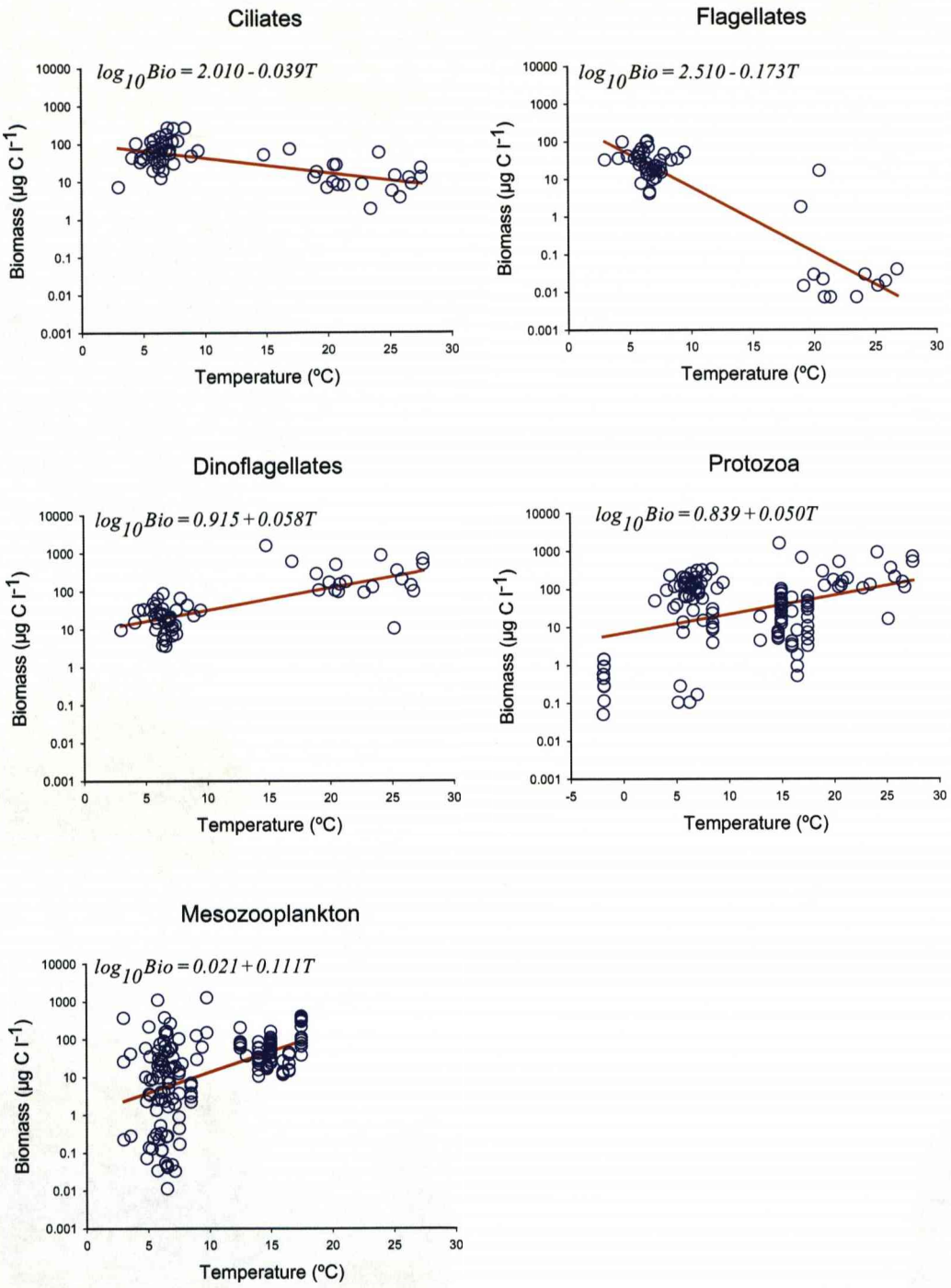


Figure 4.2 Relationships between biomass (µg C L^{-1}) and temperature (°C) for various planktonic taxa. Both biomass and temperature data are mean values derived per study site from the combined dataset dataset

Table 4.1 **Regressions of log10 biomass (μg C L^{-1}, log10Bio) of ciliates, dinoflagellates, flagellates, bacteria, total protozoa and total mesozooplankton against temperature. Biomass values were derived from mean values for each sampling site in the combined dataset (see methods p.66). Equations of significant relationships are shown only (p<0.05). Model fit is measured by R-squared.**

	F	P	Model Fit	Equation	Mean Biomass (μg C L^{-1})	S.E. Mean
Ciliates	41.35	<0.001	42.0	log10Bio= 2.01 – 0.039T	34.96	1.15
Dinoflagellates	62.95	<0.001	53.4	log10Bio= 0.915 + 0.058T	41.68	1.21
Flagellates	217.56	<0.001	81.9	log10Bio= 2.51 – 0.173T	5.38	1.54
Bacteria	2.99	0.086	2.7		36.62	1.11
Total Protozoa	22.48	<0.001	14.7	log10Bio= 0.839 + 0.050T	21.01	1.15
Total Mesozooplankton	55.40	<0.001	25.0	log10Bio= 0.021 + 0.111T	12.75	1.15

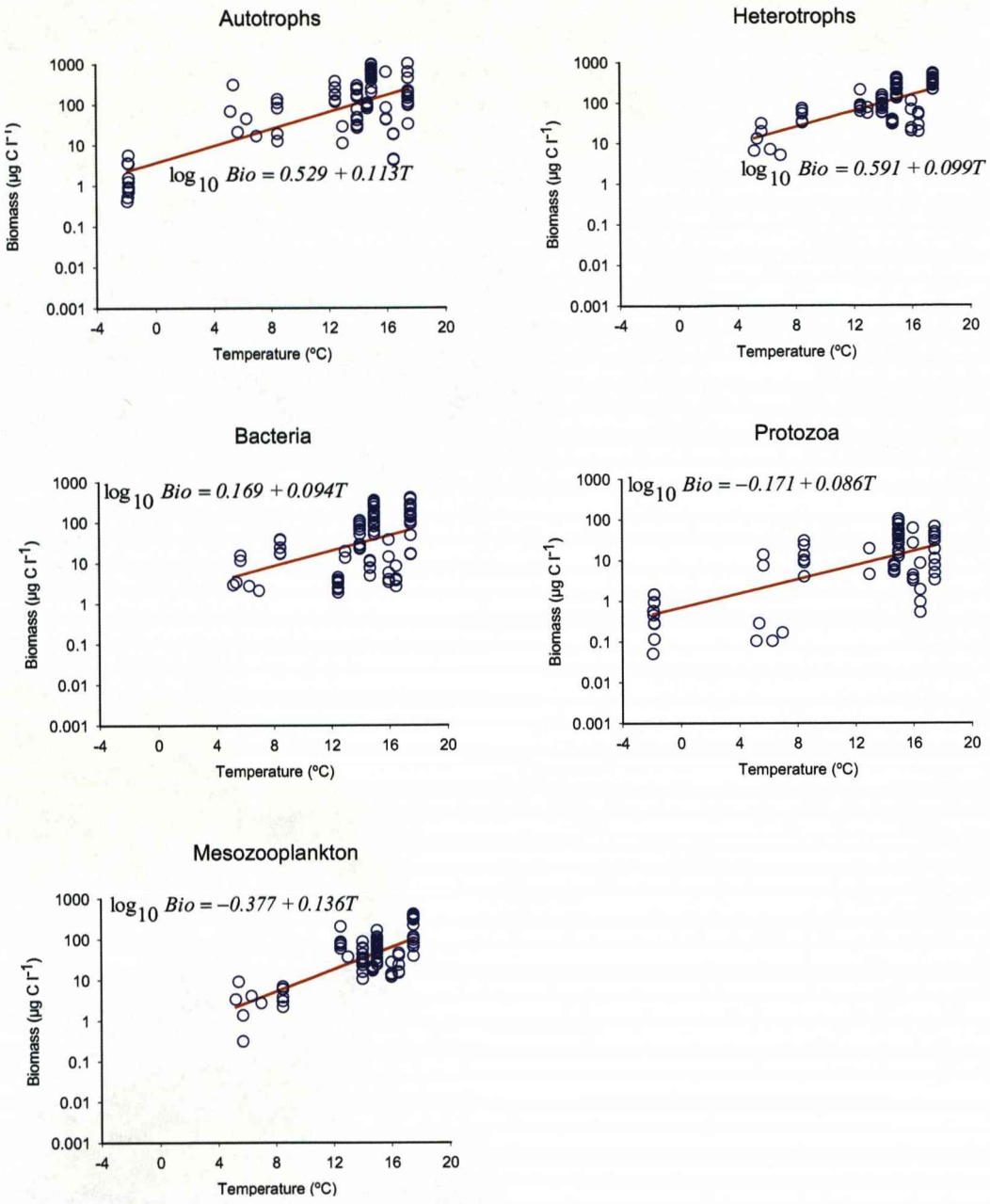


Figure 4.3 Relationships between biomass (µg C L^{-1}) and temperature (°C) for various planktonic taxa. Both biomass and temperature data are mean values derived per study site from the Gasol dataset.

Table 4.2. **Regressions of log10 biomass (µg C L^{-1}, log10Bio) of autotrophs, heterotrophs, bacteria, protozoa and mesozooplankton against temperature. Biomass values were derived from mean values for each sampling site in the Gasol dataset. Equations of significant relationships are shown only (p<0.05). Model fit s measured by R-squared.**

	F	P	Model Fit	Equation	Mean Relative Biomass (µg C L^{-1}/µg C L^{-1})	S.E. Mean
Autotrophs	111.68	<0.001	53.8	log10Bio= 0.529 + 0.113T	84.20	1.15
Heterotrophs	62.30	<0.001	42.3	log10Bio= 0.591 + 0.099T	107.45	1.11
Bacteria	20.61	<0.001	19.5	log10Bio= 0.169 + 0.094T	39.38	1.12
Protozoa	58.19	<0.001	45.4	log10Bio= −0.171 + 0.086T	10.61	1.17
Mesozooplankton	109.88	<0.001	56.4	log10Bio= −0.377 + 0.136T	17.99	1.15

AMT

I found no significant relationship between log10 biomass and temperature (14.8 to 28.0°C for ciliates (p=0.083, R-squared= 15.8%), diatoms (p=0.051, R-squared= 19.8%), coccolithophores (p=0.670, R-squared= 1.0%), and flagellates (p= 0.308, R-squared= 10.4%) (Table 4.4). In addition, I also detected no significant relationship for dinoflagellates(p=0.340, R-squared= 5.1%). The log10 biomass of picoplankton increased positively and significantly with increasing temperature (p=0.033, R-squared= 22.9%), whilst all three size categories of phytoplankton, 0.2–2μm, (p=0.001, R-squared= 40.2%), 2–20μm (p<0.001, R-squared= 70.1%) and >20μm (p=0.001, R-squared= 66.6%) all decreased (6.8 to 25.4°C; Figure 4.4). Bacteria log10 biomass, derived by leucine uptake, also decreased with increasing temperature (p=0.001, R-squared= 39.4%), whilst the decreasing trend derived by thymidine was marginally non-significant (p=0.054, R-squared= 15.2%).

Comparison of chlorophyll-a to carbon ratios

Using either a constant (Chl*a*:CC) or trophic specific (Chl*a*:CC) chlorophyll-*a* to carbon conversion ratios for phytoplankton provided identical results for many groups in terms of the nature of the relationship (positive, negative or no significance) between log10 relative biomass and temperature, and mean values and slope of regressions. I first outline differences in results obtained using either Chl*a*:CC or Chl*a*:CT. Where results are identical I report only regressions involving relative biomasses using Chl*a*:CT, with results using a constant chlorophyll-*a* to carbon ratio (Chl*a*:CC) and table of results for individual datasets found in the appendices.

Combined

In the combined dataset the nature of relationships were identical for all groups, whilst slopes did not vary significantly (p>0.05) between relative biomasses derived using Chl*a*:CC and Chl*a*:CT (Figure 4.5; Table 4.5). Mean bacterial relative biomass was significantly lower using Chl*a*:CT in comparison to Chl*a*:CC (p=0.017, T=-2.40, n=148) whilst all other groups did not vary significantly (p>0.05) (Table 4.6).

Table 4.3 **Regressions of log10 biomass (μg C L^{-1}, log10Bio) of different planktonic taxa in the MarProd dataset, against temperature. Biomass values were derived from mean values for each sampling site. Only taxa of n>10 are shown and equations are of significant relationships (p>0.05). Model fit measured by R-squared.**

	F	P	Model Fit	Equation	Mean Relative Biomass (μg C L^{-1}/μg C L^{-1})	S.E. Mean
Ciliates	1.79	0.188	4.5		15.52	1.11
Dinoflagellates	0.92	0.344	2.5		3.53	1.14
Flagellates	1.13	0.295	3.0		25.11	1.13
Bryozoans					0.07	3.24
Chaetognaths	0.56	0.457	0.8		0.02	1.28
Tunicates	0.04	0.840	0.1		0.01	1.82
Cnidarians	0.78	0.382	2.1		737.39	1.13
Copepods	0.64	0.425	0.9		0.54	1.25
Non- Copepod Crustaceans	0.05	0.825	0.1		2.87	1.30
Echinoderms	0.52	0.485	4.2		0.98	1.60
Molluscs	6.28	0.017	16.0	log10Bio= −3.51 + 0.471T	0.35	1.84
Platyhelminths/ Nemerteans	5.43	0.102	64.4		0.28	2.97
Polychaetes	6.30	0.017	15.3	log10Bio= −5.52 + 0.250T	0.0002	1.34
Total Protozoa	4.12	0.050	10.0	log10Bio= 1.62 + 0.068T	109.29	1.10
Total Mesozooplankton	2.07	0.154	2.6		0.77	0.14

Table 4.4. **Regressions of log10 biomass (µg C L^{-1}, log10Bio) of different planktonic taxa in the AMT dataset, against temperature (°C, T). Biomass values were derived from mean values for each sampling site. Only taxa of n>10 are shown and equations are of significant relationships (p<0.05). Model fit measured by R-squared.**

	F	P	Model Fit	Equation	Mean Relative Biomass (µg C L^{-1}/µg C L^{-1})	S.E. Mean
Ciliates	3.37	0.083	15.8		12.68	1.23
Diatoms	4.38	0.051	19.6		0.18	1.76
Dinoflagellates	0.96	0.340	5.1		199.53	1.28
Coccolithophores	0.19	0.670	1.0		1.02	1.29
Flagellates	1.16	0.308	10.4		0.0004	1.99
Picoplankton	5.33	0.033	22.9	log10Bio= 1.46 + 0.022T	91.79	1.09
Phytoplankton						
0.2–2µm	14.78	0.001	40.2	log10Bio= 0.697 – 0.051T	0.53	1.21
2–20µm	51.68	<0.001	70.1	log10Bio= 1.29 – 0.094T	0.31	1.31
>20µm	43.80	<0.001	66.6	log10Bio= 1.43 – 0.113T	0.19	1.39
Bacteria						
Leucine	14.30	0.001	39.4	log10Bio= 2.01 – 0.036T	21.88	1.15
thymidine	4.13	0.054	15.2		963.61	1.10
Total Protozoa	1.09	0.311	5.7		220.50	1.26

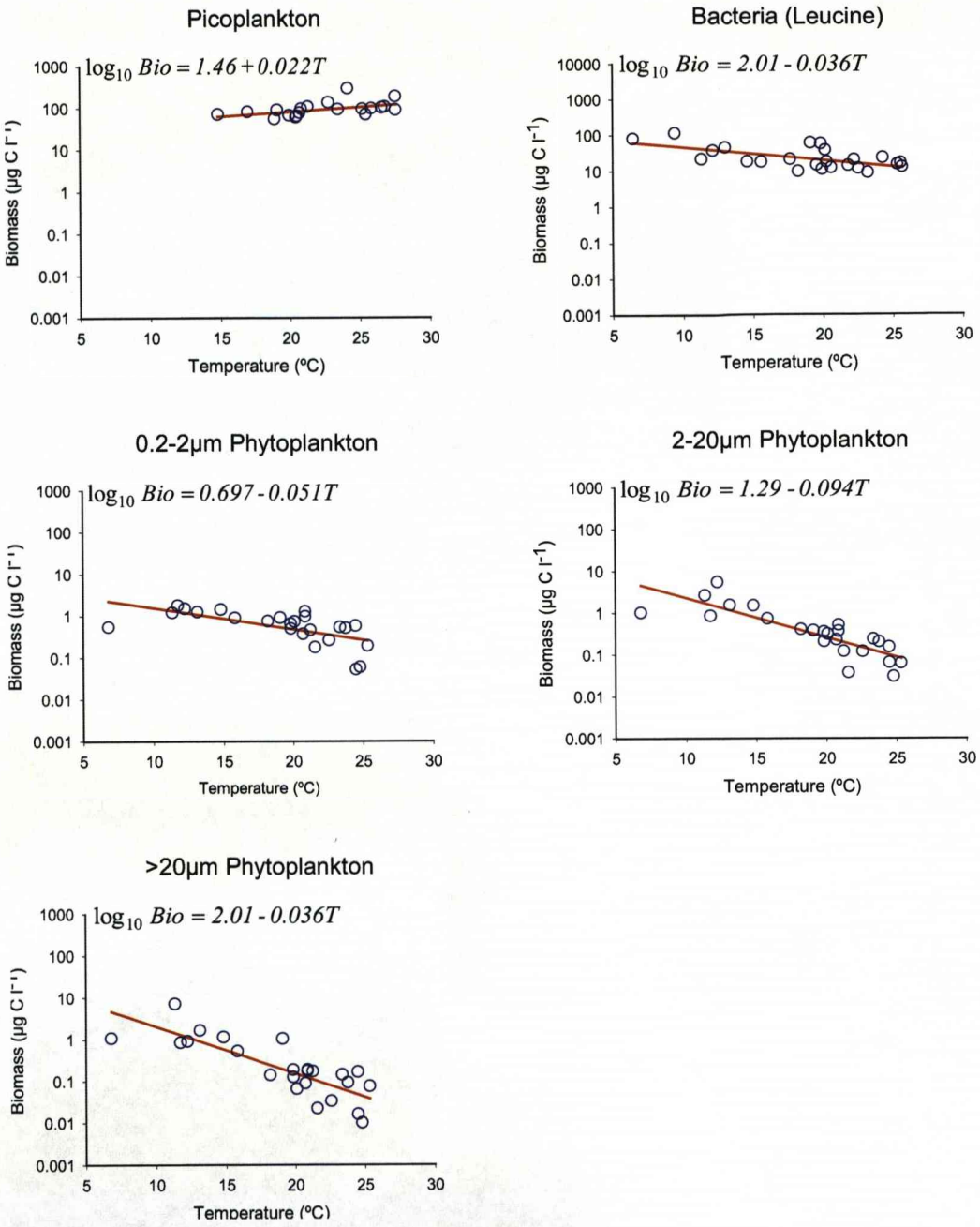


Figure 4.4 Relationships between biomass (µg C L^{-1}) and temperature (°C) for various planktonic taxa. Both biomass and temperature data are mean values derived per study site from the AMT dataset.

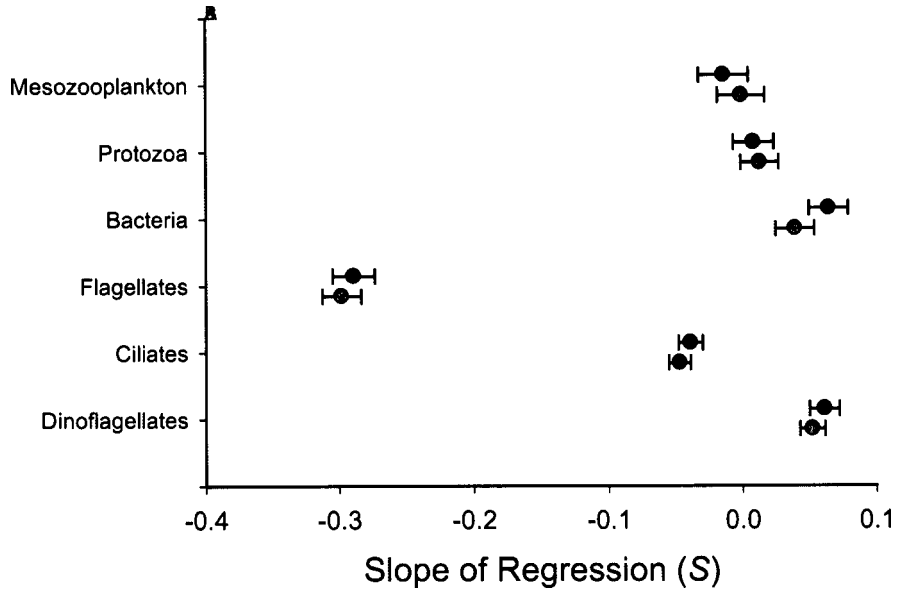


Figure 4.5 Slope of the regression of log10 biomass relative to total phytoplankton (μg C L^{-1}/μg C L^{-1}) against temperature for different planktonic groups derived from using either a constant (Chl*a*:CC, •) or trophic specific (Chl*a*:CT,•) chlorophyll-*a* to carbon ratios. Biomass values were derived from the combined dataset. Error bars representing standard error of the slopes derived from general linear models as described in the Methods section (p.66).

Table 4.5. **Comparison of the regression slopes of log10 biomass relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) against temperature (°C, T). Phytoplankton biomass was derived from chlorophyll-*a* concentration using a constant (Chl*a*:CC) and trophic specific ratios (Chl*a*:CT), for each group in the combined dataset. Biomass values were derived from mean values for each sampling site in the combined dataset. Slopes and their standard error (Slope S.E.) are given for regressions of Chl*a*:CC and Chl*a*:CT biomasses, with details of the statistical test described in the Methods section (p.66). Model fit is represented by R-squared values, with significant differences present where p<0.05.**

	Chl*a*:CC		Chl*a*:CT			
	Slope	**Slope S.E.**	**Slope**	**Slope S.E.**	**P**	**Model Fit**
Ciliates	−0.0385	0.0090	−0.0472	0.0081	p=0.477	33.68%
Dinoflagellates	0.0607	0.0111	0.0521	0.0093	p=0.551	38.07%
Flagellates	−0.2891	0.0157	−0.2977	0.0145	p=0.691	89.34%
Bacteria	0.0644	0.0146	0.0392	0.0145	p=0.224	13.72%
Protozoa	0.0080	0.0151	0.0127	0.0142	p=0.820	0.55%
Mesozooplankton	−0.0143	0.0186	−0.0011	0.0176	p=0.608	0.80%

Table 4.6. **Comparison of log10 biomass of different planktonic taxa in the combined dataset, relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) using different chlorophyll-*a* to carbon ratios, constant (Chl*a*:CC) and trophic specific (Chl*a*:CT) using a T-test at 95% confidence level. Biomass values were derived from mean values for each sampling site, with taxa of n>10 are shown only.**

	Chl*a*:CC		Chl*a*:CT		P	N	DF
	log10 Relative Biomass		log10 Relative Biomass				
	Mean	S.E. Mean	Mean	S.E. Mean			
Ciliates	0.325	0.085	0.354	0.084	0.808	52	101
Dinoflagellates	0.357	0.110	0.387	0.095	0.844	52	99
Flagellates	−0.940	0.310	−0.890	0.320	0.912	47	91
Bacteria	−0.698	0.052	−0.528	0.048	0.017	148	292
Protozoa	−0.570	0.082	−0.460	0.077	0.348	185	366
Mesozooplankton	−0.850	0.076	−0.689	0.072	0.128	184	365

Gasol

In the combined and Gasol datasets the nature of log10 relative biomass–temperature relationships was identical when using either a constant (Chl*a*:CC) or trophic specific (Chl*a*:CT) chlorophyll-*a* to carbon conversion ratios for phytoplankton. The slope of regressions did not vary significantly for all groups except autotrophs, for which a greater positive slope, and therefore temperature dependence was found using Chl*a*:CT ($p<0.001$, $F=24.77$, R-squared=61.86%). Relative biomasses were significantly greater when derived using trophic-specific values (Chl*a*:CT) than constant chlorophyll-*a* (Chl*a*:CC) to carbon ratios for autotrophs ($p<0.001$, $T=-4.17$, $n=164$), heterotrophs ($p=0.005$, $T=-2.84$, $n=127$), bacteria ($p=0.004$, $T=-2.89$, $n=128$) and mesozooplankton ($p=0.044$, $T=-2.03$, $n=136$) (Figure 4.6; Table 4.7), which corresponds to an increase in relative biomass of 39, 56, 60 and 58% respectively. For protozoa, I did not detect a significant difference between values ($p=0.063$, $T=-1.87$, $n=132$).

MarProd & AMT

For all groups in the MarProd and AMT datasets I found no significant difference ($p>0.05$) between log10 relative biomasses, and the slopes of regressions ($p>0.05$) between log10 relative biomass and temperature, using Chl*a*:CC and Chl*a*:CT (Figure 4.7). There were differences in the nature of relationships between log10 relative biomass and temperature for some groups in both the MarProd and AMT datasets which are discussed below.

Temperature-adjusted Relative Biomass

Using temperature-adjusted values of the Gasol dataset, mean log10 relative biomass derived using Chl*a*:CT remained significantly greater than Chl*a*:CC when adjusted to all temperatures (-1.89, 0, 5, 10, 15, 17.5°C) (Figure 4.8). For both heterotrophs and bacteria, the increase in relative biomass declined from 95% at -1.89°C to approximately 52% at 17.5°C. Values derived using Chl*a*:CT were also greater when adjusted to five of these temperatures (-1.89, 0, 5, 10, 15°C) in mesozooplankton, the percentage increase representing an increase in relative biomass of 95% at the lowest temperatures down to 57% at 15°C. At the highest

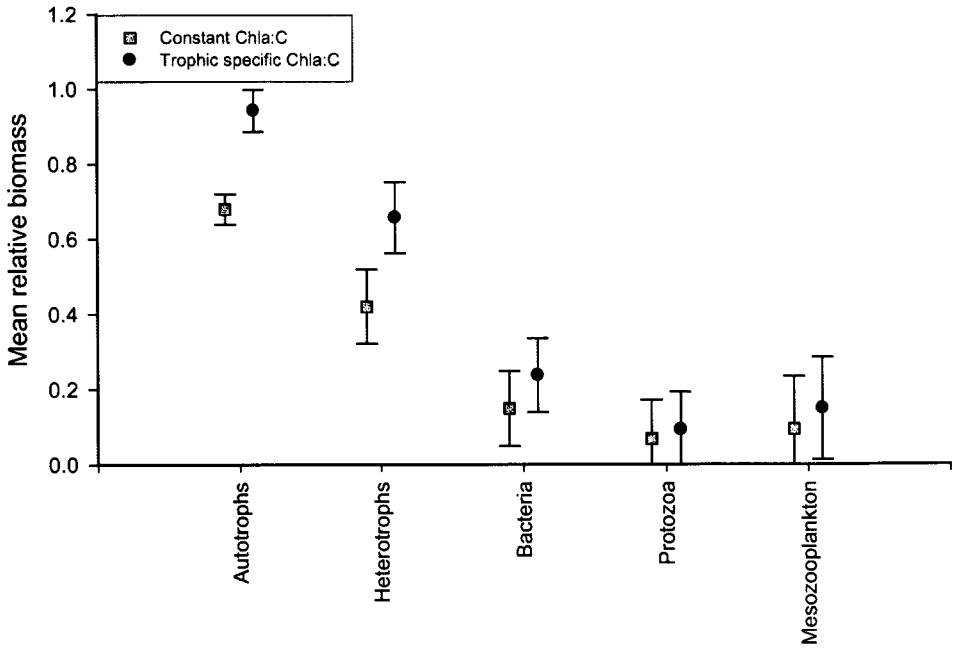


Figure 4.6 Mean biomass of autotrophs, heterotrophs, bacteria, protozoa and mesozooplankton, relative to total phytoplankton (μg C L^{-1}/μg C L^{-1}) derived from chlorophyll-*a* concentration using a constant (Chl*a*:CC) and trophic specific (Chl*a*:CT) ratios. Autotrophs are considered as phytoplankton (including zoochlorellae-bearing protists) by Gasol (1997). All biomass values were derived from the Gasol dataset. Error bars represent 95% confidence intervals.

Table 4.7 **Comparison of log10 biomass of autotrophs, heterotrophs, bacteria, protozoa and mesozooplankton, relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio), using different chlorophyll-*a* to carbon ratios, constant (Chl*a*:CC) and trophic specific (Chl*a*:CT). Biomass values were derived from the Gasol dataset and compared using a T-test at 95% confidence level. Biomass values were derived from mean values for each sampling site, D.F.= degrees of freedom, N= number of data.**

	Chl*a*:CC		Chl*a*:CT		N	P	DF
	log10 Relative Biomass		log10 Relative Biomass				
	Mean	S.E. Mean	Mean	S.E. Mean			
Autotrophs	-0.168	0.020	-0.026	0.028	164	<0.001	290
Heterotrophs	-0.375	0.049	-0.183	0.047	127	0.005	249
Bacteria	-0.827	0.050	-0.624	0.049	128	0.004	253
Protozoa	-1.167	0.052	-1.032	0.050	132	0.063	261
Mesozooplankton	-1.022	0.070	-0.824	0.068	136	0.044	269

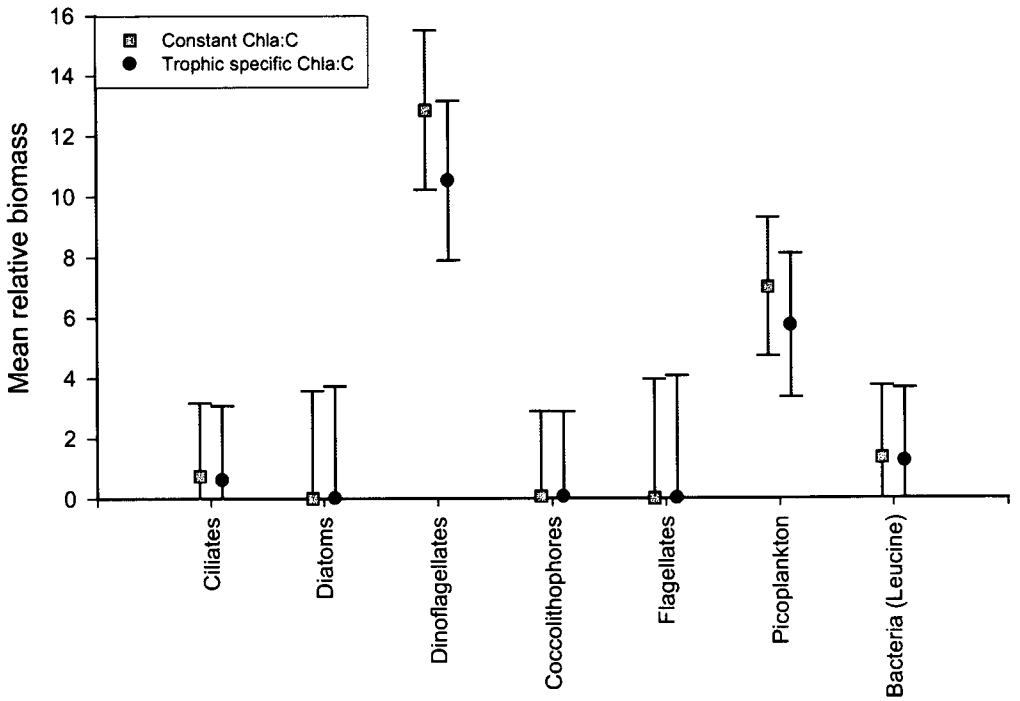


Figure 4.7 Mean biomass of various taxa, relative to total phytoplankton (μg C L^{-1}/μg C L^{-1}) derived from chlorophyll-*a* concentration using a constant (Chl*a*:CC) and trophic specific (Chl*a*:CT) ratios. Biomass values were derived from the AMT dataset. Error bars represent 95% confidence intervals.

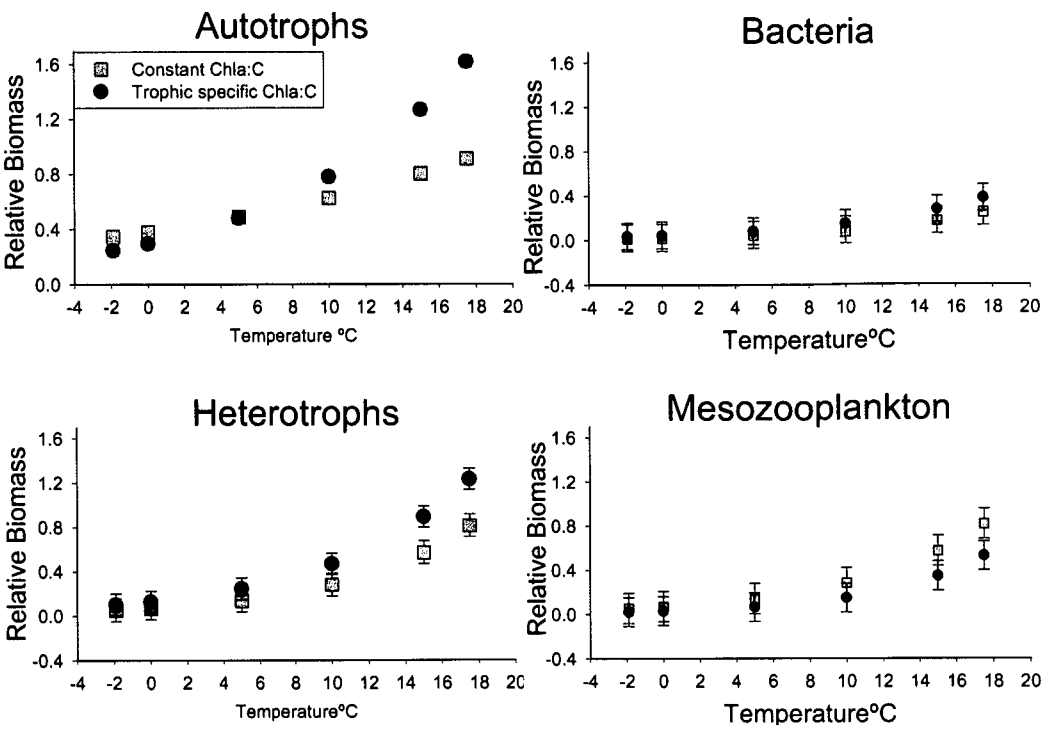


Figure 4.8 Mean autotroph, heterotroph, bacterial and mesozooplankton biomass, adjusted to five different temperatures, relative to total phytoplankton (μg C L^{-1}/μg C L^{-1}) derived from chlorophyll-*a* concentration using a constant (Chl*a*:CC) and trophic specific (Chl*a*:CT) ratios. Biomass values were derived from the Gasol dataset.Error bars represent 95% confidence intervals.

temperature of 17.5°C I detected no significant difference between Chl*a*:CC and Chl*a*:CT derived log10 relative biomass values (p=0.055, T=1.93, n=83). For autotrophs, I found significant differences between log10 relative biomass values adjusted to five temperatures , with those derived from Chl*a*:CT being lower at −1.89 and 0°C (a 41 and 29% decrease in relative biomass respectively), and higher at 10, 15, and 17.5°C (24, 58, 78% increase in relative biomass) than when using Chl*a*:CC. At 5°C however, I found no significant difference in log10 relative biomass calculated using Chl*a*:CC and Chl*a*:CT (p=0.742,T= −0.33 n=94).

Log10 Relative Biomass and Temperature

Combined dataset

Relative biomass of both ciliates (p<0.001, R-squared=40.7%) and flagellates (p<0.001, R-squared=90.4%) biomass decreased significantly with increasing temperature (Figure 4.9; Table 4.8.). As with absolute biomass, relative biomass of dinoflagellates increased significantly (p<0.001, R-squared=38.8%). Relative biomass of bacteria also increased with temperature (p=0.008, R-squared=8.1%), whilst total protozoa (p=0.374, R-squared=0.7%) and total mesozooplankton (p=0.951, R-squared=0.0%) showed no significant relationship.

Gasol

Within the Gasol dataset log10 relative biomass increased for heterotrophs (p= 0.001, R-squared= 12.5%), bacteria (p= 0.009, R-squared= 8.2%) and mesozooplankton (p= 0.001, R-squared= 12.3%) (Figure 4.10). However, log10 relative biomass of protozoa did not vary significantly with temperature (p= 0.180, R-squared= 2.7%). Although results were identical using Chl*a*:CC and Chl*a*:CT, mean biomasses were significantly greater using the latter for autotrophs, heterotrophs, bacteria and mesozooplankton (p<0.05) (Table 4.9).

MarProd

Within the MarProd dataset the relative biomass of flagellates was found to decrease with increasing temperature (p= 0.006, R-squared= 20.7%) (Figure 4.11).

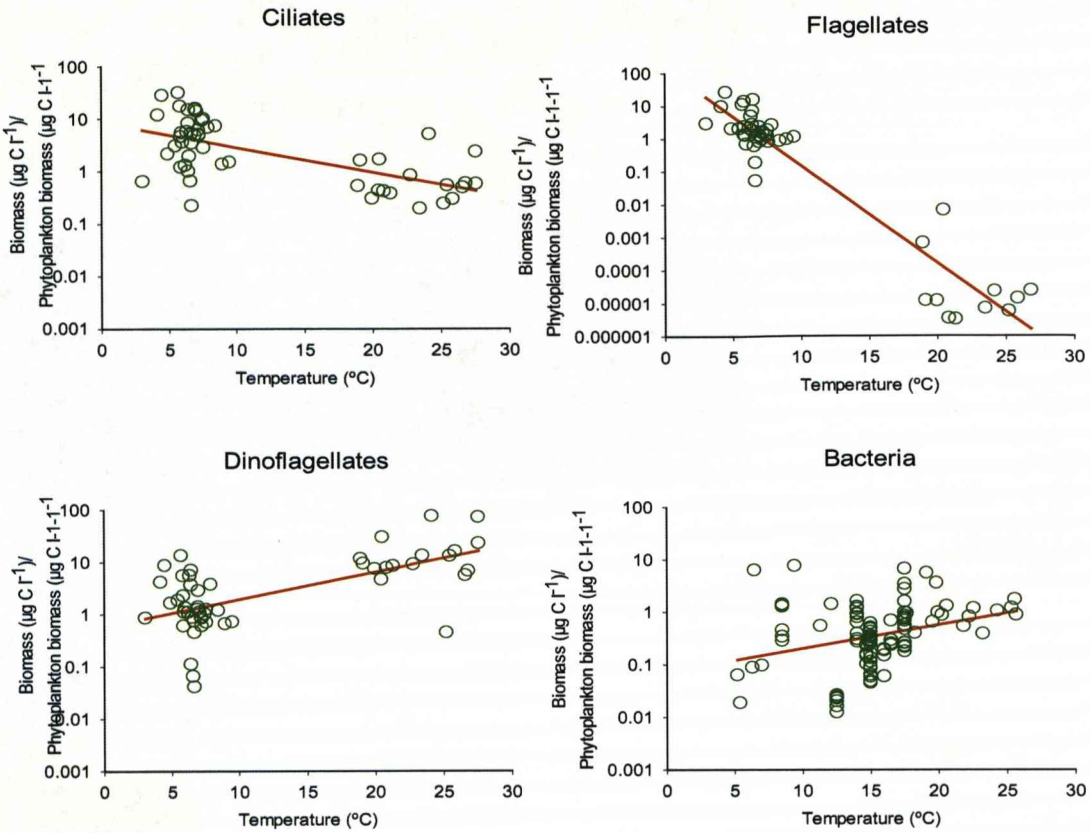


Figure 4.9 Relationships between biomass (µg C L^{-1}) relative to phytoplankton (µg C L^{-1}) and temperature (°C) for various planktonic taxa. Total phytoplankton was derived from chlorophyll-*a* to carbon concentration ratios specific to environmental trophic state, Chl*a*:CT. Both biomass and temperature data are mean values derived per study site from the combined dataset. Note the y-axis plot of flagellates is on a different scale to other taxa for illustration purposes.

Table 4.8. **Regressions of log10 biomass of ciliates, dinoflagellates, flagellates, bacteria, total protozoa and total mesozooplankton, relative to total phytoplankton biomass (μg C L^{-1} / μg C L^{-1}, log10RelBio) derived from chlorophyll-*a* concentration using trophic specific ratios (Chl*a*:CT) against temperature (°C, T). Biomass values were derived from mean values for each sampling site in the combined dataset. Equations of significant relationships are shown only (p<0.05). Model fit measured by R-squared.**

	P	Model Fit	Equation	Mean Relative Biomass (μg C L^{-1}/μg C L^{-1})	S.E. Mean
Ciliates	<0.001	40.7	log10RelBio= 0.922 – 0.047T	2.26	1.21
Dinoflagellates	<0.001	38.8	log10RelBio= –0.240 + 0.052T	2.44	1.24
Flagellates	<0.001	90.4	log10RelBio= 2.17 – 0.298T	0.13	2.08
Bacteria	0.008	8.1	log10RelBio= –1.09 + 0.039T	0.30	1.12
Protozoa	0.374	0.7		0.34	1.19
Mesozooplankton	0.951	0.0		0.20	1.18

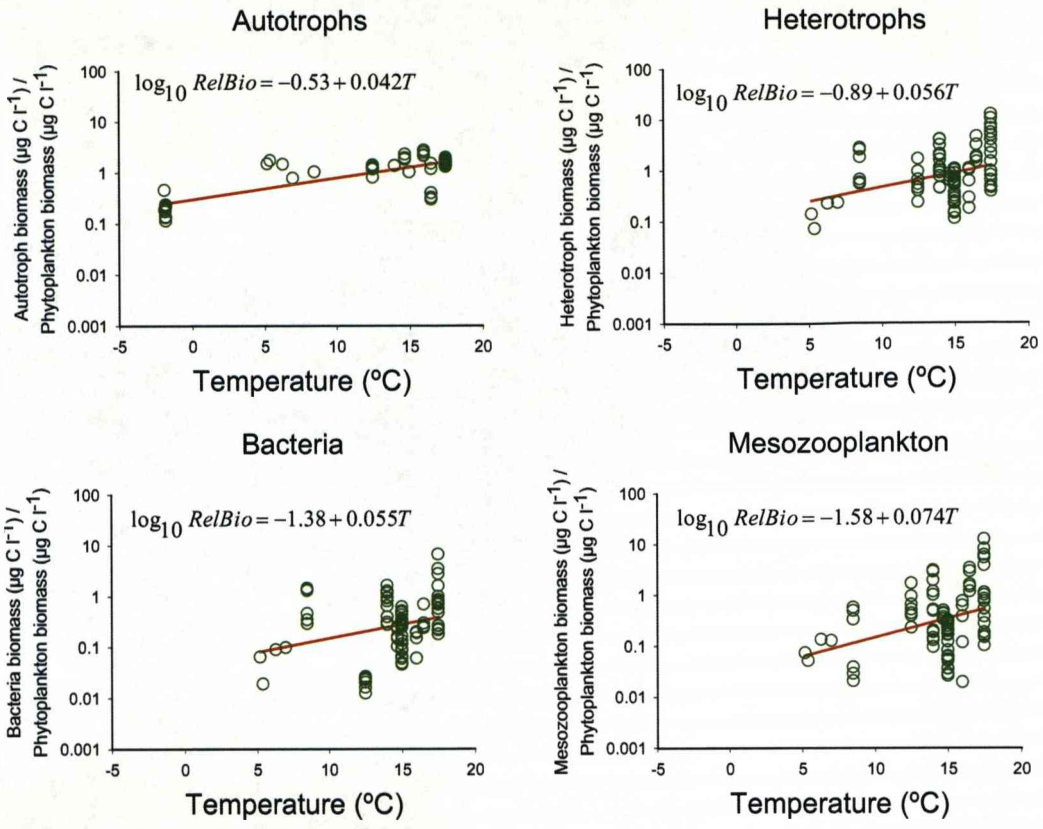


Figure 4.10 Relationships between biomass (µg C L^{-1}) relative to phytoplankton (µg C L^{-1}) and temperature (°C) for various planktonic taxa. Total phytoplankton was derived from chlorophyll-*a* concentration using trophic specific ratios, Chl*a*:CT. Both biomass and temperature data are mean values derived per study site from the Gasol dataset.

Table 4.9. **Regressions of log10 biomass of autotrophs, heterotrophs, bacteria, protozoa and mesozooplankton, relative to total phytoplankton biomass (μg C L^{-1} / μg C L^{-1}, log10RelBio) derived from chlorophyll-*a* concentration using trophic specific ratios (Chl*a*:CT) against temperature (°C, T). Biomass values were derived from mean values for each sampling site in the Gasol dataset. Equations of significant relationships are shown only (p<0.05). Model fit measured by R-squared.**

	P	Model Fit	Equation	Mean Relative Biomass (μg C L^{-1}/μg C L^{-1})	S.E. Mean
Heterotrophs	0.001	12.5	log10RelBio = −0.891 + 0.056T	0.66	0.047
Bacteria	0.009	8.2	log10RelBio = −1.38 + 0.055T	0.24	0.049
Protozoa	0.180	2.7		0.09	0.05
Mesozooplankton	0.001	12.3	log10RelBio = −1.58 + 0.074T	0.15	0.068

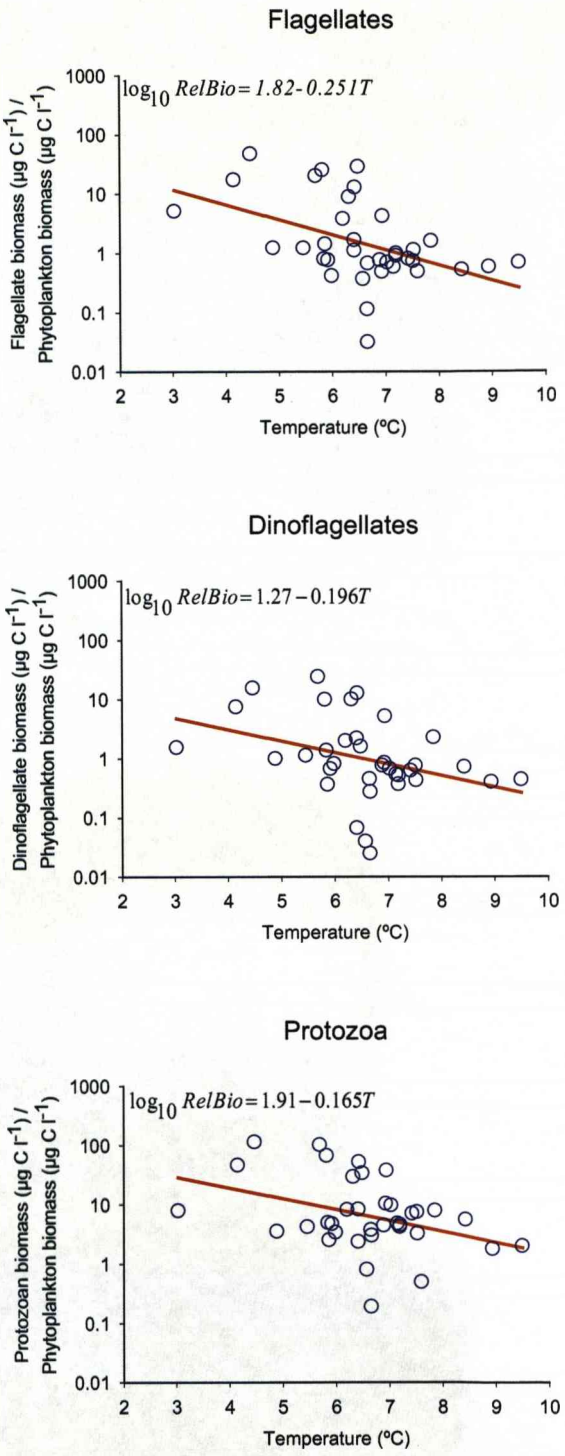


Figure 4.11 Relationships between biomass (µg C L^{-1}) relative to phytoplankton (µg C L^{-1}) and temperature (°C) for various planktonic taxa. Total phytoplankton was derived from chlorophyll-*a* concentration using a constant ratio, Chl*a*:CC. Both biomass and temperature data are mean values derived per study site from the MarProd dataset.

Meanwhile ciliates, total mesozooplankton and all mesozooplankton groups (chaetognaths, tunicates, copepods, non–copepod crustaceans, ctenophores, echinoderms, molluscs, polychaetes, and cnidarians), all showed no significant relationship ($p>0.05$, R-squared= 0.1 to 17.0%). Whilst log10 relative biomass dinoflagellates ($p= 0.033$, R-squared= 13.1%) and total protozoa ($p= 0.039$, R-squared= 12.3%) both decreased with increasing temperature using Chl*a*:CC, both did not vary significantly using Chl*a*:CT ($p>0.05$, R-squared=5.0 to 10.7%).

AMT dataset

I found that log10 relative biomass decreased significantly with increasing temperature for the two largest phytoplankton size categories, 2–20μm ($p<0.001$, R-squared=55.9%) and >20μm ($p<0.001$, R-squared=49.0%) (Figure 4.12). The relative biomass of dinoflagellates, ciliates, diatoms, coccolithophores, flagellates, total protozoa, bacteria-thy and the smallest phytoplankton size category, 0.2–2μm, did not vary significantly with temperature ($p>0.05$, R-squared=0.1 to 9.5%). Relative biomass of picoplankton (which contained heterotrophs) increased with temperature using a constant chlorophyll-*a* to carbon ratio, Chl*a*:CC, ($p=0.031$, R-squared=27.5%), but did not vary significantly using Chl*a*:CT. Conversely, relative biomass of bacteria-leu decreased with temperature using Chl*a*:CT ($p=0.045$, R-squared=20.5).

Comparison of Polar Regions

Although the log10 biomass of total protozoa within both the>50 °N, (MarProd dataset; $p=0.05$, R-sqaured=10%) and>50°S regions (Gasol dataset; $p=0.06$, R-squared=34%) did not vary with temperature under a 95% confidence level, both showed a positive, albeit insignificant trend (Table 4.10). There was also no significant relationship between log10 relative biomass and temperature of total protozoa in both >50°N ($p=0.199$, R-squared=5%) and >50°S ($p=0.895$, R-squared=0.2%) regions using the constant chlorophyll-*a* to carbon ratio. When using trophic specific chlorophyll-*a* to carbon ratios, protozoan log10 relative biomass within the >50°N region had a significant and negative relationship with temperature ($p=0.039$, R-squared=12%), whist within the >50°S region no

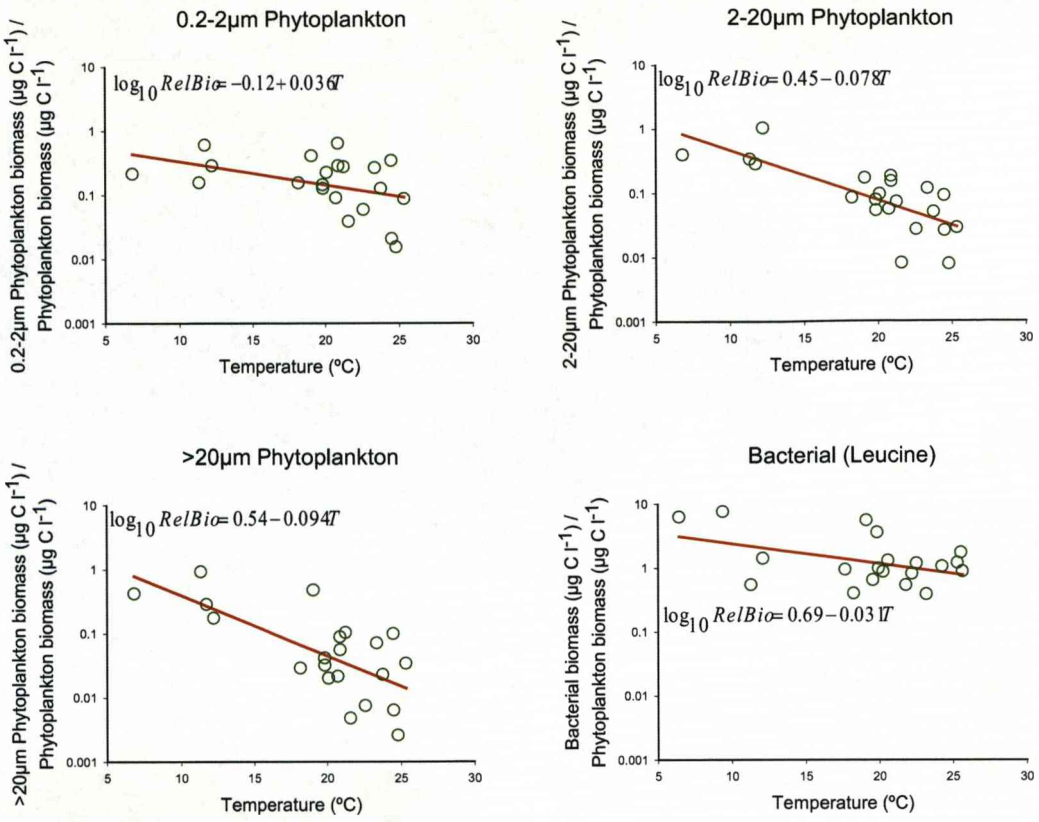


Figure 4.12 Relationships between phytoplankton biomass (µg C L^{-1}) relative to total phytoplankton (µg C L^{-1}), and temperature (°C) for three size categories, 0.2–2µm, 2–20µm and >20µm and bacteria (leucine uptake). Total phytoplankton was derived from chlorophyll-*a* concentration using trophic specific ratios, Chl*a*:CT. Both biomass and temperature data are mean values derived per study site from the AMT dataset.

Table 4.10. **Regressions of both log10 biomass (µg C L^{-1}, log10 Bio) and log10 biomass relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) using different chlorophyll-*a* to carbon ratios, constant (Chl*a*:CC) and trophic specific (Chl*a*:CT), of total protozoa against against temperature (°C, T) for regions exceeding 50°N (MarProd dataset) and 50°S (Gasol dataset). Biomass values were derived from mean values for each sampling site. Equations of significant relationships are shown only (p<0.05). Model fit measured by R-squared.**

	P	Model Fit	Equation	Mean Relative Biomass (µg C L^{-1}/µg C L^{-1})	S.E. Mean
Log10 Biomass					
Gasol (>50°S)	0.060	33.9%	log10 Bio = 16.3+ 9.18T	2.57	1.45
MarProd (>50°N)	0.050	10.0%	log10 Bio = 1.62 + 0.0675T	130.3	12.0
Log10 Relative Biomass					
Gasol (>50°S) Chl*a*:CT	0.895	0.2%		0.226	0.131
Gasol (>50°S) Chl*a*:CC	0.895	0.2%		0.245	0.075
MarProd (>50°N) Chl*a*:CT	0.039	12.3%	log10 RelBio = 1.91 – 0.165T	13.06	2.34
MarProd (>50°N) Chl*a*:CC	0.199	5.0%		17.09	4.57

significant relationship could be determined (p=0.895, R-squared=0.2%). Mean protozoan biomass, and biomass relative to total phytoplankton biomass, calculated using either a constant or trophic specific chlorophyll-*a* to carbon ratios, was significantly greater, by approximately and order of magnitude, in the >50 ^{o}N region in comparison to biomasses more southerly than 50^{o}S (p<0.01, Table 4.11).

Discussion

Protozoa

Although total absolute biomass of protozoa increased with temperature, its relative biomass showed no temperature dependence. My results for total protozoa are therefore in contrast to predictions by Conover (1979) and for findings of greater relative biomass in warmer freshwater lakes which was argued to be consistent with greater top-down control (Havens *et al.* 2007). However, I found that over a large temperature range, two ecologically important protozoan taxa responded differently to increasing temperature. Whilst higher temperatures were associated with a decrease in the contribution of biomass to the planktonic food-web by ciliates, dinoflagellates increased in relative biomass (Figure 4.13).

The results of this study differ from those over smaller geographical ranges such as the Inland Sea where the proportion of ciliate biomass to total microzooplankton increased with chlorophyll-*a* concentration (Uye *et al.* 1996) cited as the result of advantages that protozoans possess over micrometazoans at higher food concentrations (Uye *et al.*1996). Despite the higher mass-specific metabolic rates of ciliates compared with metazoans (Heinbokel, 1978, Verity, 1985, 1986) and an ability to consume smaller prey (Stoecker & Egloff 1987, Stoecker & Capuzzo, 1990), results in this study suggest that higher temperatures are not consistent with ciliates out-competing metazoan zooplankton for shared food resources. The contribution of ciliates to the marine planktonic food-web may be largely dependent on the availability of bacteria, which they are known to consume within

Table 4.11 **Comparison of biomass (µg C L^{-1}, log10 Bio) and biomass relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) using different chlorophyll-*a* to carbon ratios, constant (Chl*a*:CC) and trophic specific (Chl*a*:CT), of total protozoa for regions exceeding 50°N (MarProd dataset) and 50°S (Gasol dataset). Biomass values compared using a T-test at 95% confidence level. Biomass values were derived from mean values for each sampling site, D.F.= degrees of freedom, T-value= T.**

	MarProd (>50°N)		Gasol (>50°S)		T	P	DF
	Mean	S.E. Mean	Mean	S.E. Mean			
Biomass	130.3	12.0	2.57	1.5	-10.54	<0.001	40
Relative Biomass Chl*a*:CT	13.1	2.3	0.226	0.585	-5.48	<0.001	34
Relative Biomass Chl*a*:CC	17.1	4.6	0.245	0.075	-3.68	0.001	34

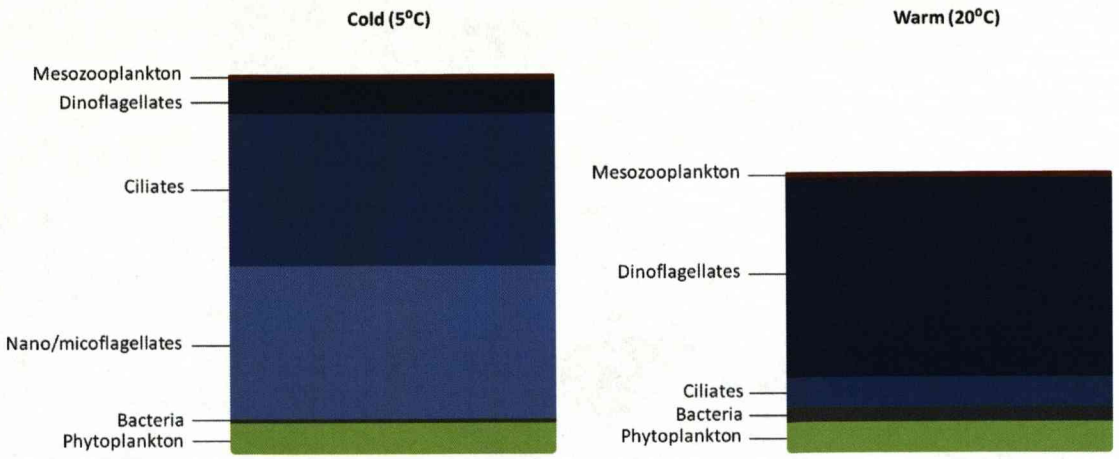


Figure 4.13 The contribution of planktonic components (bacteria, nano/microflagellates, ciliates, dinoflagellates and mesozooplankton) to community biomass, relative to total phytoplankton biomass for a typical cold (5°C) and warm (20°C) environment. Relative biomass values for bacteria, nano/microflagellates, ciliates and dinoflagellates were calculated using equations derived from significant regressions between log10 relative biomass and temperature in the combined dataset. For mesozooplankton mean relative biomass from the combined dataset was used for both environments, as relative biomass did not vary significantly with temperature for this group.

the natural marine environment (Sherr & Sherr, 1987; Sherr *et al.*, 1989, Uye *et al.* 1996), with strong links between the two groups found in freshwater lakes (Gates & Lewg 1984). The greater proportion of bacterial biomass within the planktonic food-web with increasing temperature indicates a greater prey resource for ciliates, and is indicative of increased domination of the microbial food-web, (Uye *et al.* 1999). However, results here suggest ciliates do not respond to increased bacterial availability by increasing their relative standing stock biomass. Ciliates and dinoflagellates play an important role in the transfer of primary production to higher trophic levels (Mironova 2009) including copepods. However, the absence of a detectable change in relative ciliate biomass in response to temperature may be a result of several, non-mutually exclusive, processes including increased predation by metazoan zooplankton, greater competition for shared resources, or a decline in efficiency of processing prey. Although copepods have been shown to be able to control ciliate populations in Long Island Bay, (Lonsdale et al. 1996) the increase in relative biomass of dinoflagellates, and the absence of change in mesozooplankton relative biomass suggests that greater competition for shared resources from fellow protists may be more important in limiting the contribution of ciliate biomass to the planktonic food-web rather than predation from higher trophic levels.

The absence of a coupling between the relative biomass of ciliates and bacteria may arise from significantly lower gross growth efficiency (GGE) of ciliates with respect to all other zooplankton taxa examined in Chapter 3 (p.36) . Not only did ciliates have a lower average GGE, but their efficiency was significantly lower when feeding on bacteria than on algae (p.42). If the increase in the proportion of bacteria in the food-web observed is reflected in a greater contribution of bacteria within the diet of ciliates, the average GGE of ciliates will be lower as a greater proportion of biomass consumed by ciliates will be lost, for example to respiration, inhibiting the ability of ciliates to maintain a higher relative biomass in the food-web. A decline in average efficiency may be lessened owing to the observed temperature dependence of ciliate GGE when feeding on bacteria. I reported in Chapter 3 that increased temperatures are associated with an increase in ciliate GGE with a of 4.11 (p27). However, using the equation that describes the relationship between

log10GGE and temperature, I find that even at the highest temperature (25°C) for which it was determined, the GGE when feeding on bacteria remains below that of the average achieved feeding on algae.

Alongside ciliates, the protozoan group of dinoflagellates are numerically (Hansen 1992) and functionally an important part of the microzooplankton, with their grazing of diatoms and flagellates at times exceeding that of mesozooplankton (Johnson & Allen 2005). My study shows that total contribution of dinoflagellates in terms of relative biomass to the planktonic food-web increases with temperature. In spite of higher respiration rates generally observed at increased temperatures, dinoflagellates may be able to take advantage of increased prey availability as a result of several competitive advantages over ciliates, thereby increasing dinoflagellate relative biomass. For instance, whilst autotrophic dinoflagellates are able to cope well in oligotrophic tropical and subtropical waters by migrating vertically in the water column to take advantage of higher nutrients, heterotrophic dinoflagellates may benefit from greater growth efficiency, prey size breath, and lower locomotion costs compared with ciliates (Crawford 1992, Hansen *et al.* 1994). In comparison with fellow protozoan taxa of nanoflagellates and ciliates, the metabolic costs associated with locomotion are much lower in both growing and starved dinoflagellates (Crawford 1992).

In addition, there is evidence to suggest that dinoflagellates are better able to survive low prey abundances than ciliates (Jakobsen & Hansen 1997), which provides greater resistance to local extinction in the natural environment. As shown in Chapter 3, at higher temperatures mean dinoflagellate GGE increases, therefore increasing the amount of production from a given amount of prey (p.27). Dinoflagellates are able to feed on a wide variety of prey with smaller dinoflagellates directly competing with ciliates for nanophytoplankton, whilst larger dinoflagellates can consume prey such as diatoms and some dinoflagellates that are generally considered too large for ciliates (Hansen 1992, Hansen *et al.* 1994). The ability of dinoflagellates to consume a wider breadth of prey sizes may allow them to cope with changes in the size-structure of available prey that gives them the competitive advantage over ciliates, whilst the presence of higher growth rates may

enable them to respond more quickly to increases in prey availability in comparison to mesozooplankton such as copepods (Hansen 1992). As phytoplankton biomass increases with temperature, dinoflagellates may also benefit from increased production if phytoplankton represents a greater proportion of their diet. When feeding omnivorously dinoflagellates were not only found to have lower GGEs in comparison to a diet of solely algae by approximately 10%, but GGEs decreased with increasing food concentration. These competitive advantages may enable dinoflagellates to better resist local extinction and maintain a greater relative biomass in the planktonic food-web at higher temperatures because of the negative geographical correlation between temperature and nutrients (Lalli & Parsons 1997). At lower temperatures meanwhile, the lower specific growth rates of dinoflagellates in comparison to ciliates (Montagnes *et al.* 2003) may restriction production to a greater extent than other processes by reduced the ability of dinoflagellates to respond to local fluctuations in prey availability.

As higher dinoflagellate relative biomass in the planktonic food-web increases with temperature, there is an increased likelihood harmful species being able to maintain a viable population in areas in which are likely to produce conditions facilaiting a bloom (coastal nutrient upwelling). I therefore argue that with increasing global sea surface temperatures due to increased concentration of greenhouse gases in the atmosphere, may be associated with an increase in the frequency of harmful dinoflagellate blooms, which is likely to have serious elogical and economic consequences. The upwelling of nutrients into the euphotic zone as a result warmer summer waters in temperate regions is associated with large blooms, or "red tides", of dinoflagellates (for example, *Alexandrium acatenella*, *Gymnodinium mikimotoi*, *Dinophysis acuta*). Such blooms can have serious consequences on the pelagic environment, by depleting oxygen (Altamirano & Sierra-Beltrán 2008), damaging breathing or feeding structures of fish and bivalves (Hallegraeff 1992, Matsuyama *et al.* 1999) and through the production of toxins which build up and transfer through the food chain to species including seafood consumed by humans, causing conditions including paralytic shellfish poisoning (PSP) and neurotoxic shellfish poisoning (NSP). Dinoflagellate blooms impacts not

only the marine food-web, but also cause economic loss. For example, a Gymnodinium bloom in 1998 has been estimated to kill fish stocks valued at US$40 000 000 in Hong Kong alone.

Differences between ciliates and dinoflagellates in biomass and relative biomass with increasing temperature may also be reflected in change in species richness. Over broad scales evidence suggests that species richness of marine pelagic taxa tends to increase with decreasing latitude (Clarke & Crame 1997), whilst temperature is said to be the best correlate of available energy (Gaston 2000). As smaller populations are associated with greater extinction risk (Lande 1993), ciliates may be less speciose in warmer environments if a greater number of species succumb to local extinction as a result of lower biomass. Although other processes may determine species richness (Evans *et al.* 2005), there may be a disparity between the relationships of ciliate and dinoflagellate species richness with temperature.

Bacteria

I found strong evidence to suggest that bacteria relative biomass increases with temperature over a large scale. Within both the combined and Gasol datasets, I demonstrated a positive relationship using either a constant or trophic specific chlorophyll-*a* to carbon ratios. Within the AMT dataset however, relative biomass decreased with increasing temperature using a trophic status specific chlorophyll-a to carbon ratio and for bacteria derived via leucine uptake method. Bacteria relative biomass derived from thymidine uptake showed no significant change with temperature when considered solely within the AMT dataset, whilst neither was significant using a constant chlorophyll-*a* to carbon conversion. Uye *et al.* (1999) reported that relative biomass of bacteria was greater in oligotrophic areas than those of higher nutrient concentration. Therefore the observed increase in bacterial relative biomass with temperature within the Gasol dataset may be partly due to the lower trophic status of warmer waters, and supports the theory that a microbial food chain becomes increasingly predominant at higher temperatures.

Ciliates also play an important role in controlling bacteria abundance and size structure (Turley *et al.* 1986), whilst the regeneration of bacteria depends on the availability of dissolved organic matter in the water column. Ciliates convert food into biomass with an efficiency far below other consumers of bacteria (dinoflagellates and nano/microflagellates), thereby releasing a greater proportion of carbon, up to 90% of that consumed if feeding solely on bacteria. Therefore the co-dependence of bacteria and ciliates is likely to be stronger than with other protozoa. As a consequence, the decreased relative biomass of ciliates at higher temperatures, if not compensated for by an increased turnover rate, will result in a lower rate of bacteria regeneration from that which would be otherwise be expected. Although the planktonic food-web plays a vital role in the sequestration of atmospheric , (Hays *et al.* 2005) its impact is unlikely to be equal on a large geographical scale. Colder regions of ocean, where bacteria production is more efficient (Rivkin & Legendre 2001), are likely to have a stronger link between bacteria and ciliates, greater recycling of carbon, allowing a greater overall planktonic biomass. As a consequence greater carbon recycling and greater biomass, colder oceanic regions are likely export a greater amount of carbon, through the sinking of organic matter out of the euphotic zone, than warmer environments, i.e. lower latitudes.

Mesozooplankton

On a global scale I found that although *absolute* biomass of mesozooplankton increased with temperature, its *relative* biomass did not vary significantly. As with ciliates (protozoa), my results differ from examples of studies of freshwater lakes, where the contribution of metazoan zooplankton was found be greater in cooler temperate lakes than in subtropical lakes (Havens *et al.* 2007).

The absence of a change in mesozooplankton across a large range of temperatures and latitudes is an important result to note. As copepods constitute the majority of mesozooplantkon, (up to 80% in terms of biomass, Kiørboe 1997) they play a pivotal role the in transfer of primary consumers to higher trophic levels such as fish, with up to 88% of their ciliate and dinoflagellate production consumed by copepods

(Lignell *et al.* 1993). The ubiquitous presence of copepods suggests they are able to perform important functions across a wide range of latitudes and temperature regimes such as regulating biogeochemical fluxes in the pelagic environment through the production and subsequent vertical flux out of the euphotic zone of faecal pellets (Lampitt *et al.* 1990,) which represents approximately 10% of all particulate flux (Riser *et al.* 2006), and the remineralisation of material through the consumption or damage of faecal pellets (Kiørboe 1997).

As previously discussed, the increase in relative biomass of dinoflagellates suggests an increased competition for shared resources, which may be exploited more readily by dinoflagellates which possess higher growth rates (Hansen *et al.* 1997), thereby impose restrictions on the production achieved by mesozooplankton. In addition, with change in the biomass structure of the planktoinc food-web, copepods are likely to vary the proportion of each prey consumed. For instance, the diet of copepods consists of ciliates to a lesser degree with increasing phytoplankton concentrations (39% and 22% at <50 and >500 μg phytoplankton carbon l^{-1} respectively; Calbet & Saiz 2005).

Since copepods and mesozooplankton in general are unlikely to consume a substantial fraction of total phytoplankton production (Lignell et al 1993, Verity 1993, Hansen 1997), the fraction copepod biomass in the planktonic food-web is driven mainly by microzooplankton abundance. The relative decrease in available food to copepods as a result of decreased ciliate relative biomass at higher temperature is likely to be compensated, at least in part, by the higher abundance of dinoflagellates. Switching to the most abundant microzooplankton prey has been shown to be an active mechanism in copepods (Kiorboe et al 1996, Gismervik & Anderson 1997), whilst microzooplankton may be the preferred prey due to their optimal size in comparison to the smallest, pico-sized phytoplankton Bergreen *et al.* 1988, Hansen *et al.* 1994).

The absence of a variation in mesozooplankton relative biomass in the combined dataset may be a result of changes in the structure within this taxon, with some metazoan groups or species favoured over others. Although mesozooplankton

groups other than copepods demonstrated temperature dependence of GGE, trends varied between taxa. Perhaps because of low mass-specific metabolic rate, GGE increased with temperature for ctenophores and scyphozoans, and due high metabolic costs cladoceran GGE decreased. Mean while the GGE of cladocerans decreased with increasing temperature, suggesting due to high maintenance costs this taxon is disfavoured in warmer, especially low productivity waters. However, in the absence of evidence of global changes of dominant species (or higher taxon) within mesozooplankton, I find no direct evidence to suggest mesozooplankton relative biomass to be a direct result of metazoan GGE temperature-dependence.

Relative biomass may also be constrained if, within mesozooplankton, there is competition between species. With increasing temperature I would expect an increase in biomass of species adapted to warmer environments, which are able to better grow and exploit food resources, and hence increase their biomass.

Phytoplankton

In contrast to all other size categories of phytoplankton, there was evidence for the contribution of the smallest fraction, picophytoplankton (0.2-2μm) to total phytoplankton to increase with temperature in the AMT dataset. In conjunction with increased relative *production* in warmer environments (Marañón *et al.* 2001) these findings lend support to the growing consensus of an increased dominance of picophytoplankton with increasing temperature (Agawin *et al.* 2000, Caroppo 2000, Senga & Horiuchi 2004). I suggest that the reason the relative biomass of picophytoplankton increases whilst larger size categories of phytoplankton do not, may be owing to the inherent competitive advantages of picoplankton in oligotrophic conditions, and to a relatively reduced predation pressure. At higher temperatures picophytoplankton are likely to be at a competitive advantage because of their increased ability to obtain and utilise nutrients in areas of low nutrient content in comparisons to larger autotrophs (Agawin *et al.* 2000, Donald *et al.* 1997) due to the increased nutrient affinity of smaller phytoplankton which have higher surface area to volume ratios (Fogg 1986, Raven 1998). They also have higher growth and photosynthetic rates under nutrient-poor conditions in comparison to

larger phytoplankton (Cole *et al.* 1986). My results are also consistent with predation by higher trophic levels playing a role in structuring phytoplankton biomass. As metazoan relative biomass increased with temperature it is also likely that their grazing of large phytoplankton, in addition to protists, also increases. As a result, grazing pressure by protists on picoplankton, and competition for nutrients by larger phytoplankton are both reduced, allowing picoplankton to establish a greater standing stock biomass at higher temperatures.

The structure of the planktonic food-web may be largely determined by the structure of the autotrophic component under varying temperature regimes. Increase in the proportion of picophytoplankton biomass at the expensive of larger autotrophs will fundamentally affect the resources available to different heterotrophic zooplankton. An increase in contribution of picoplankton to the autotrophic component will favour smaller heterotrophic herbivores which are able to exploit the smaller prey, resulting in a lower flux of biomass directly to higher trophic levels such as metazoans. As copepods achieve their daily carbon intake at lower carbon concentrations when feeding on larger phytoplankton (Frost 1972), phytoplankton structure may also have a direct impact on metazoan zooplankton.

Dataset Differences

Variation in the relative biomass-temperature relationships observed within individual datasets (Gasol, AMT, and MarProd) in comparison to the combined dataset outlines the importance of scale in determining global patterns of marine biota. For example, whilst dinoflagellate relative biomass displayed a negative relationship with temperature in the MarProd dataset, which comprises a relatively narrow geographical and temperature range (3 to 10°C), the inclusion of biomasses sampled at higher temperature and lower latitudes reveals a general increase in the proportion of dinoflagellates to total planktonic biomass. As local disturbances and fluctuations of environmental variables are diluted over a macroecological scale, study of a reduced latitudinal range is likely to be more susceptible to local variations that inhibit the detection of broad trends. Consequently, the absence of a detectable change in the proportion of metazoan biomass in the MarProd dataset

may suggests its latitudinal range was not adequate to determine large scale patterns within the marine environment.

Although protozoa of both polar regions (>50°N and >50°S) showed a weak increase in biomass with temperature, both biomass and relative biomass were greater in the north. The order of magnitude difference in biomasses between regions cannot be sufficient explained by differences in temperatures (>50°S below 5°C, >50°N up to 10°C). It is likely that the low biomass values of the >50°S region are a product of the high nutrient, low chlorophyll paradox which is a feature of the Southern Ocean (Jennings *et al.* 2001), with the relatively low phytoplankton production constraining the protozoan biomass.

Comparison of Chlorophyll-a to Carbon Ratios

For the most part, using either a constant chlorophyll-*a* to carbon ratio, or values specific to the trophic state of the environment did not alter the nature of the relationship (positive, negative or no significance), mean values, or the slope of regressions for the majority of groups in the combined, and individual datasets. The main exception was within the Gasol dataset, where if using a constant conversion ratio for all levels of chlorophyll-*a* underestimating heterotroph, mesozooplankton and bacterial biomass relative, if we assume Chl*a*:CT to be the more appropriate ratios. Although the trends obtained showed little variation between chlorophyll-*a* to carbon ratios used, there was generally a greater model fit, measured by R-squared, using Chl*a*:CT than Chl*a*:CC. Whilst the slope and nature of the regression between bacterial relative biomass and temperature did not significantly vary using Chl*a*:CC or Chl*a*:CT, mean relative biomass was greater using the latter in the combined dataset. The disparity between phytoplankton biomass derived using :CC or :CT may be greatest in individual studies at single temperatures. When adjusted for temperature, I found the difference in relative biomass between values derived using Chl*a*:CC and Chl*a*:CT to decrease with increasing temperature for heterotrophs, bacteria and mesozooplankton. This is consistent with an underestimation of autotrophic biomass at lower chlorophyll-*a* levels (Buck *et al.* 1996), which are associated with higher temperatures. With increasing latitude the

relative abundance of light available to phytoplankton and sea surface temperature decrease. However, higher latitudes are also associated with a greater amount of water mixing caused by wind action which increases supply of nutrients to the surface levels (Lalli & Parsons 1997). Therefore, over a large geographical scale as temperature increase is associated with decreasing nutrient availability.

Summary

Across a global scale, changes in temperature are associated with fundamental changes in the contribution of functionally and numerically important planktonic taxa. Whilst I found no evidence to suggest broad changes in the proportion of protozoan and mesozooplankton biomass, there were important changes within protozoa with increasing temperature. The impact of temperature on the biomass of different planktonic groups is likely to be through its effect on the many temperature-dependent physiological, ecological and behavioural processes, which influence the efficiency with which prey is converted into predator biomass (GGE). The disparity between the response of ciliate and dinoflagellate biomass with temperature may be partly due to inherent differences in GGE and its temperature dependence. My study is therefore compatible with the notion that through its influence on individual species, temperature can help determine the structure of the planktonic food-web. As such, my results emphasise the importance of considering taxon-specific rates and processes, such as growth rates, mortality rates and gross growth efficiencies, to develop a more accurate understanding of the structure of the planktonic food-web. Changes in the relative biomass on taxa considered in this study will have consequences for other pelagic groups. Rotifers for instance, are known predators of bacteria, flagellates and ciliates, and help recycle carbon, making it available to the microbial community (Arndt 2004).

Chapter 5. Mass-Balanced Models of Planktonic Food-webs

Introduction

The purpose of this chapter is to outline mass-balanced approaches used to model food webs, give an indication of their use, assumptions and limitations, and to provide a justification for the model approach taken in Chapters 6 (p.121) and 7 (p.154). It is clear that models using ecosystem compartments based on size and on trophic groups or taxa both have their place in ecological modelling so long as they are applied appropriately and assumptions taken into account. Concepts from these models are an important influence in the low complexity models of Chapters 6 and 7, which allow the incorporation of taxon-specific GGEs, although there are distinct differences. The most important distinction is that the approach in the following chapters is concerned with understanding how production and biomass relative to phytoplankton are affected through the influence of temperature on taxon-specific GGEs, whereas other studies are often concerned with the *absolute* values.

Flow-based Approach

A common method of modelling the planktonic food-web, refered to here as flow-based approach, involves using estimates of the flow of energy, or nutrients such as carbon or nitrogen, through different compartments. Models are often structured so that compartments may represent a population, species or whole trophic levels. Flow-based models, for example those using the modelling program Ecopath (see http://www.ecopath.org) and its variations, have been widely used to model ecosystems, and continually to be developed to improve realism and accuracy in describe ecological processes. Its product, when equations are solved, is a holistic view of the food web, and a snapshot of the energy flux through the system. The strength and direction of energy flow of all compartments influencing the ecosystem are estimated and allow a path/network analysis of the marine ecosystem food web (Ulanowicz 1998). Flow-based models allow trophic

interactions and energy fluxes to be evaluated and comparisons to be made between different systems, which can help describe the functioning of model ecosystems. Researchers have used this approach to model ecosystems in the open ocean, reefs (Arias-González 1997), mangroves (Vega-Cendejas & Arreguín-Sánchez 2001), reservoirs (Harvey & Kareiva 2005), agricultural land (Dalsgaard & Oficial 1997), and gyres (Pauly & Christensen 1996). This approach allows the construction of a representation of a food web, which can be used to represent present systems, make predictions of potential impacts such as the effect of actual and potential impact of invasive species upon individual species/compartments and the ecosystem as a whole (Harvey & Kareiva 2005), or recreate historical ecosystems (Buchary 2001). Flow-based models have been used to predict environmental impacts such as fishery loss owing to power plant placement (Lin *et al.* 2004) and human exposure to toxic pollutants within the diet, and the impact climate change will have on this through its affect on the marine food web (Booth & Zeller 2005).

This approach may be used to predict the effect of changes to the ecosystem, and the impacts on specific species/compartments. To obtain a model of the ecosystem than contains resources, trophic interactions and pathways is a useful tool, and the flow-based method gives mass-balanced approach to looking at energy flux. With the addition of dynamic and spatial components to flow-based models a greater specificity and accuracy is achieved, which may be of great benefit, for example, to fisheries management and in making decisions for marine protected areas (Watson *et al.* 2000, Salomon *et al.* 2002, Zucchetta *et al.* 2003) .

As flow-based methods are a holistic view of the ecosystem studied, it can be used in order to determine areas in which data are absent or deficient, and to predict values that are unavailable or unreliable with the literature, for instance respiration of a specific compartment. Although outlined in great detail elsewhere (Vega-Cendejas & Arreguín-Sánchez 2001, Christensen & Walters 2004) variables determined include total system ascendance, system throughput, development capacity, ecosystem maturity, Finn's cycling index and path length, transfer efficiencies, omnivory index, average trophic levels, mixed trophic impacts and

dependency on primary productivity of each compartment. The latter two measurements are included within the modelling package itself. The development of steady state, mass balanced ecosystem models can enhance our understanding of not only the flow and direction of material, and importance of individual pathways, but keystone species (Libralato *et al.* 2006). Keystone species are those that despite having a relatively low biomass, have a great importance in influencing the ecosystem structure and subsequently the flow of energy and material within it. Flow-based models often uses a mass balanced approach, whereby the ecosystem is constructed using compartments that represent species, tropic or functional groups, and the flow of energy, or other currency such as nitrogen or carbon, to other compartments using know links estimated. The parameters used should be those that are appropriate for achieving mass–balance over the time interval modelled, often a year, or sometimes a season. For each compartment input of energy is equal to output, and this forms the basis of the central equation:

$$P_i - B_i M2_i - P_i(1 - EE_i) - EX_i = 0 \qquad \text{Equation 5.1}$$

where *Pi*, *Bi*, and *M2i* are production, biomass and predation mortality of compartment i respectively, EE*i* is the ecotrophic efficiency (the fraction of the production that is either passed up the food web or exported) and *EXi* is the export of *i*. This basic equation is often elaborated in order to take into account differential predation rates between prey for different compartments is represented by:

$$B_i\left(\frac{P}{B}\right)_i EE_i - \sum_{j=0}^{n} B_j\left(\frac{Q}{B}\right)_j DC_{ji} - EX_i = 0 \qquad \text{Equation 5.2}$$

where P/B is the production biomass ratio, and Q/B is the consumption/biomass ratio of i. *DCji* is the fraction of prey (i) in the average diet of predator (j). In order to

achieve mass balance certain terms are required, namely export and diet composition, and at least 3 out of biomass, production, consumption and ecotrophic efficiency. If only three are known, then the fourth parameter is estimated by achieving by balancing all other terms. Where all parameters are known, EE is the portion estimated in order to achieve mass balance. Respiration rates can either be inserted if known, or can be derived using the program itself through balancing the equation central to its function. It is unlikely that perfect mass balance is achieved via the input of parameters. Parameters may have to be adjusted in order to give a system that is a greater approximation of a realistic ecosystem. There are adjustments that can be employed in order to determine whether the model produced is one that is with the realms of possibility. If all parameters are entered into the model then the EE obtained can give an indication of the balance of the model. If EE is greater than one for instance then the model should be considered not balanced, as is the case if flow to detritus is negative, or if unrealistic gross growth efficiencies are obtained. The realism of the model may be further explored by comparing output values to real ecosystems, for instance the best fitting model can be deteremined statistically through comparison of residuals. Sensitivity analysis allows an investigation into possible outcomes upon the model by varying parameters upon which less certainty has been placed. With differing degrees of confidence in different parameters, there is likely to be many potential solutions. These can be tested using Monte-Carlo simulations or by trial and error. Therefore this procedure can be an important tool in calculating an unknown parameter, where all others have been determined.

The use of flow-based models offer advantages but also some limitations, which are intrinsically linked to the assumptions of the model itself. However, these limitations can largely be overcome using input values that are appropriate to the assumptions made (Pauly & Christensen 1996). For instance assuming a constant proportion of each prey that contribute to the diet of the predator remains constant, may be an incorrect assumption if a long-term model is the desired product. Therefore if a long term, for instance annual model is required, then values used to represent the proportion of each prey should reflect this and an annual

average should be used in this case. In its most basic form flow-based models may not take into account biomass production and diet change between seasons, or size/age based trophic interactions. Again, the input values used need to reflect the average values over the time period over which the model is a representation.

A greater degree of accuracy will be obtained if input values have been determined simultaneously and under the same conditions. Heterogenous data sources are likely to represent a fundamental constraint on model accuracy. For logistical reasons, this is unlikely to be the case in the vast majority of instances and so must be supplemented often with appropriate values from the literature. Although previous software incarnations assumed steady state conditions, this is no longer a requirement and therefore instances where the primary assumption was that conditions under the time frame considered were approximately steady state are no longer necessary.

Inverse Approach

Another approach to creating mass balanced ecosystems models is the inverse approach. Whilst it shares similar assumptions with flow-based approaches, in that an approximately steady state system is assumed, its use is to provide the most optimal solution that is as close to mass balance as possible, i.e. inputs equalling outputs. As its name suggests, this method differs to the flow-based approach, by inserting standing stock biomass estimates of each compartment into the model and subsequently determining the rate of flow between each compartment.

As there may be many possible solutions that give approximately an equal good fit, parameters can be constrained to give greater realism e.g. limits may be imposed on assimilation and production efficiencies. The aim of giving an optimal balanced solution can be a useful tool in identifying possible weaknesses in current data, identifying differences between the empirical derived estimates and model predictions of parameters, and comparing different types of flow networks (Vézina & Platt 1988). Again, the availability of data can heavily influence the outcome of the results obtained in terms of variability and accuracy. Where parameters for the

ecosystem modelled are well established, with independent verification then this provides a greater confidence in the derived flow rates of the ecosystem. It should also be noted that this approach does not necessarily produce an accurate representation of the flow rates within an ecosystem, but provides the simplest solution from the input values provided. The simplest solution and the true system may not be mutually exclusive, and so care must be taken when interpreting results.

Size–spectra

In contrast to the treatment of organisms in terms of species, functional groups, or compartments, this method uses size as the major discriminatory factor. As such, it relies heavily on size-based processes across taxa, such as growth, production, respiration, and predation, and takes advantage of the high similarity displayed by different species. It has been observed that patterns across species are related to size structure, with a power-law dependence often cited (Armstrong 1999). This approach also relies on the size-dependent feeding of planktonic ecosystems, in that organisms are generally consumed by larger predators. Size–spectra models, which are described in detail elsewhere (Sheldon *et al.* 1972, Benoît & Rochet 2004) commonly represent continuous flow of energy through the ecosystem, assuming a generalised growth function and loss term (respiration), both of which are size-dependent (Silvert & Platt 1978). Some models do incorporate different trophic levels in the model, e.g. phytoplankton, zooplankton and fish, whilst maintaining a strong size-dependent structure (Stock *et al.* 2008).

Thus energy is assumed to flow from small to large organisms, allowing inferences to be made about ecosystem structure and energy transfer efficiencies from observing the biomass spectrum. These assumptions have been further extended into comparisons of ecosystems, and more specifically comparing the slope of normalised biomass-size spectrum to infer transfer efficiencies and production of different trophic levels (Martin *et al.* 2006, Stock *et al.* 2008), whilst the intercepts can also be compared, for instance between seasons. Although similarities in the slopes of normalised biomass-spectra have been noted, differences have also been

observed and attributed to trophic status (Sprules & Munawar 1986) seasonal factors (Gaedke 1993) and ecosystem composition (Raimbault *et al.* 1988). This method can be useful for determining the flux of energy through a system where the effect on component parts is not the main focus. This has important applications, for example, for understanding the amount of energy reaching fish, which may have important social and financial implications.

This approach does not however take into consideration potential differences between taxa, which may be disadvantageous, undesirable or simply not feasible if a taxon-specific property is likely to have a significant affect on the ecosystem studied (Armstrong 1999). The attraction of this approach is partly owing to its simplicity. If indeed the biomass spectrum, although just a snapshot of the ecosystem, can reveal important information on its structure, energy flow and function, then this approach would be a vital tool, especially from a practical and logistical perspective. One of the advantages of this method is that species do not have to be forced into compartments or trophic levels in order to satisfy the representation of the ecosystem used. These groupings may be made out of convenience and not reflect shared characteristics, such as response of respiration, growth and mortality for instance. Where there is no reason to assume that there are differences between species this is to the benefit of the size-spectra method.

Overview

It has been noted that in order to achieve a model representation as accurate as possible to that observed in nature, then species-specific attributes may be required in addition to shared, size-based patterns between species. In some respects, the two model types, the flow-based models and size-spectra, are converging, with Armstrong (1999) outlining models that attempt this. In essence, the type of model chosen is likely to have advantages and disadvantages. Mass balanced models may have reduced simplicity, but the information they provide is limited. In their simplest form they do not take seasonality into account, and therefore cannot be easily compared to real world data of specific regions and time

periods. The biomass of each compartment should be an estimation of the time period modelled. Size-spectra meanwhile offer a simpler comparison to *in situ* conditions, as plankton size spectra is often an easier measurement to make. Again, in its simplest form, seasonality may be an issue, but more complex models have been developed for both to take these into account. Without seasonality and other dynamic constructs, care needs to be taken when interpreting and comparing results. However, they do allow identification of important pathways within an ecosystem and exploration of potentially important factors, and exposure of their potential effect.

Model Implemented

I use mass-balanced models to examine the impact of gross growth efficiencies on the flow of carbon production and biomass structure in the planktonic food-web. My aim is not to quantify biomass or production of different taxa or compartments, but to examine the influence of taxon- and diet specific, in addition to temperature dependent GGEs on the production and biomass structure of the planktonic food-web. Therefore, the highly complex flow-based, and size-spectra models is not needed for my approach, although there are similarities and shared concepts. The two models used in Chapters 6 and 7 represent the first attempts to examine the influence of taxon-, diet- and temperature specific GGEs of zooplankton on predicted carbon flow in the marine environment, and are briefly outlined below.

In Chapter 6 the impact of using taxon- and diet-specific GGEs, as derived in Chapter 3, on predicted production and biomass structure is examined. Simple mass-balanced models, akin to those employed using flow-based models, are constructed using Microsoft Excel. The food web constructed consists of zooplankton taxa of nano/microflagellates, ciliates, dinoflagellates and copepods, feeding on an autotrophic input of phytoplankton (partitioned between pico-, nano- and micro- size categories), and, as per the planktonic model of differing ocean environements by Landry & Calbet (2004) which assumed the ratio of

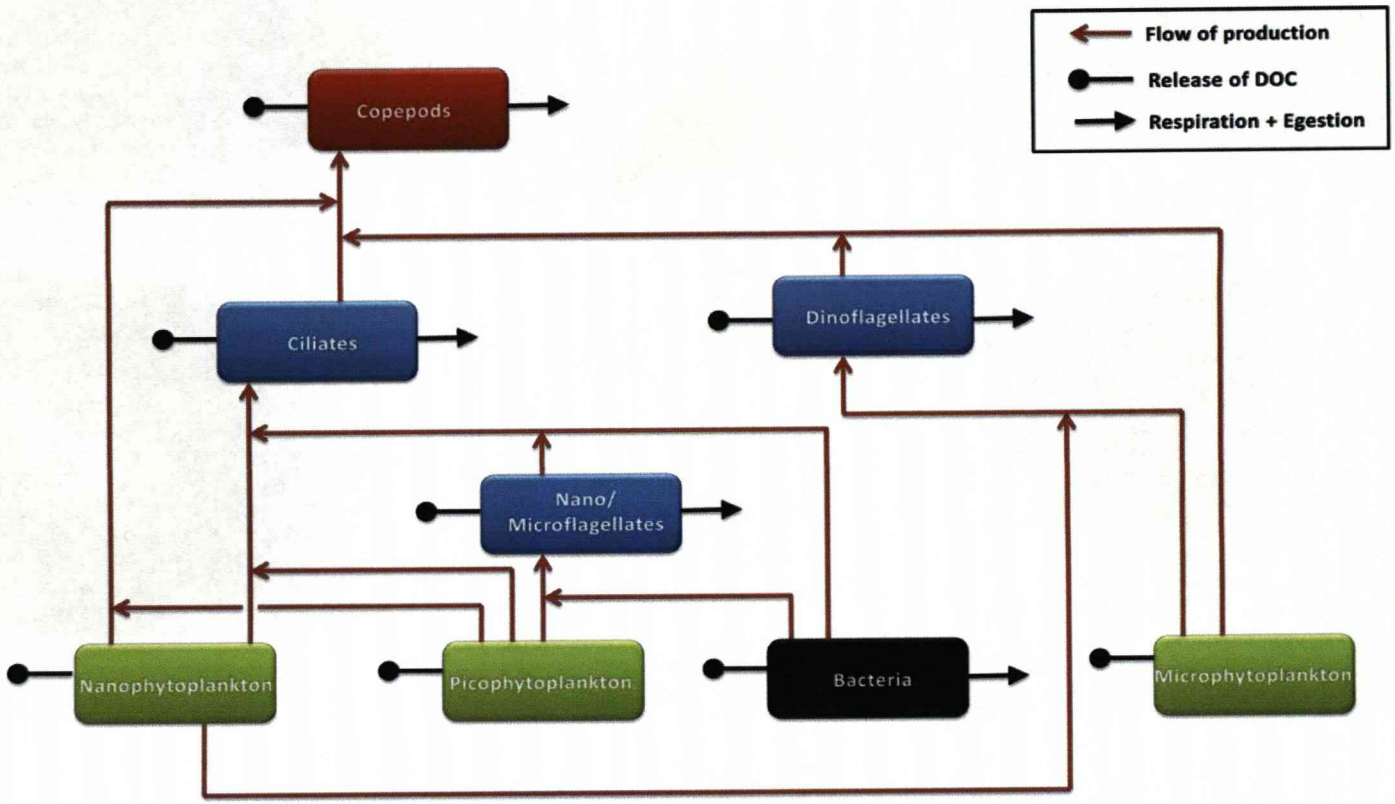


Figure 5.1 Structure of the mass–balanced planktonic food–web assumed in the models. Red lines indicate flow of production from prey to predators, whilst outputs of each component (excretion, egestion and export) are shown by black markers. Phytoplankton production (100 units split between pico-, nano-, and microphytoplankton as described in section *Autotrophic input* p. 109-111) is used to initialise the model, in addition to bacterial production (15 units).

bacterial production to phytoplankton production to remain constant, an input value that represents net bacterial production. Production is transferred to heterotrophic planktonic groups using estimates of clearance efficiency (percentage of available prey consumed) and GGEs, which is similar to way in which production is transferred between compartments of the planktonic models exploring the link between biomass size-spectra and ecosystem dynamics by Stock *et al.* (2008). The main difference is that compartments in the model of Stock *et al.* (2008) were categorised according to size and not taxonomic groups. As highlighted by the flow-based approaches, growth rates used to convert production to standing stock biomass are average values appropriate to the time period examined. Subsequently the model is developed further in Chapter 7 to incorporate temperature-dependence of GGEs (as in Chapter 3), specific growth rates and level of bacterial production, enabling the extent to which temperature, through its influence on GGEs, effects on the flux of carbon and biomass structure of the planktonic food-web.

Chapter 6. Potential Impact of Diet and Taxon-Specific Gross Growth Efficiencies on Planktonic Food-web Structure: An Investigation Using Simple, Mass-balanced Models

Introduction

Models of relatively low complexity have been effectively used to explore the fate of primary and secondary production (Duarte & Cebrián 1996, Pomeroy 1999, Legendre & Rivkin 2002, Landry & Calbet 2004, Berglund *et al.* 2007). Such models are of particular use in providing qualitative, rather than quantitative, output and predictions, which aid the conceptual development of food web structure. In particular production and biomass pyramids have aided our understanding of food web constraints through the comparison of localities varying spatially (Gasol *et al.* 1997), with temperature, and in response to increased nutritional state (Duarte *et al.* 2000). Such studies allow broad generalisations about the impact of environmental variables such as nutrient availability and temperature, providing evidence of the prominent patterns and most important physiological and ecological processes that impact ecosystem structure and dynamics. The use of mass-balanced models can not only help determine parameters that are prone to error, or difficult to measure in the natural environment, but also provide "*the opportunity to control the internal consistency of the underlying measurements and assumptions, and to define reasonable bounds for individual process rates which have not been measured*" (Gaedke & Straile 1994).

As a measure of the proportion of ingested food converted into body mass, gross growth efficiency (GGE) is a useful concept used in comparative and theoretical discussions concerning the structure and flux of material through food webs (see Chapters 1 & 2). Ecosystem models using GGE often include a variety of planktonic taxa which vary in behaviour, physiology and morphology. It is common, however, for models to assume a common GGE value for all planktonic taxa (Stoecker & Evans

1985, Pomeroy 2000, Anderson & Turley 2003, Landry & Calbet 2004, Lewis 2005, Buitenhuis *et al.* 2006). A value commonly used is the mean GGE value derived by Straile (1997) of approximately 0.33, although values in the range of 30 to 40% have also been used (Montagnes *et al.* 1988, Landry & Calbet 2004). However, as discussed in Chapter 3, these taxonomic groups can have fundamentally different GGE values, with ciliates and nano/microflagellates notable for having particularly low and high average values respectively. Another common assumption of ecosystem models is that predators convert different prey types with the same efficiency (Montagnes *et al.* 1988, Landry & Calbet 2004), despite food quality or suitability being a fundamental constraint on GGE. Differences in GGE were found for several planktonic taxa when feeding on different diet types or were either herbivorous, carnivorous, bactivorous or consuming a mixture of prey types.

Food-web models are a simplification of the actual complex food web structure and of energy flow displayed in natural ecosystems and are often a compromise between "*the modeller's desire to reduce the problem to its simplest terms and the empiricist's desire to reproduce detailed behaviors of recognizable organisms and ecosystems.*" (Marine Zooplankton Colloquium 2001). Assumptions such as a common GGE value for all zooplankton taxa have undoubtedly helped in the formation of simple to complex models. However, as differences in physiological and behavioural rates and processes are observed between biological components of the planktonic food web, the effect of assuming similar GGEs across diverse taxa and diets should be explored to determine to potential impact upon ecosystem model accuracy.

Owing to the complex nature of the food-web, with multiple food sources contributing with varying degrees to predator diet, the impact of using taxon-specific values on flow of primary production through the planktonic food-web to higher trophic levels such as copepods, is in need of investigation. Here I investigate whether major changes to the structure of the planktonic food-web in terms of production and biomass result from the use of taxon-specific and diet-specific GGE values, or whether using a common mean GGE value for all taxa is of little consequence in terms of energy flow through the planktonic

food-web. Therefore by investigating the effect that GGE variation can have on planktonic food-web structure, this study, although of relatively simple complexity, represents one of the first steps in understanding how physiological rates can limit the flow of energy through the planktonic food-web.

The aim here is to explore the potential effect of GGE on the structure of the planktonic food-web in terms of flow of primary production through different taxonomic components (ciliates, nano/microflagellates, dinoflagellates and copepods). This is achieved through the development of simple, mass-balanced models of planktonic food-webs oh high and low nutrient concentrations, which are used to predict the flow of production through the food-web using different GGEs. Subsequently these models are used to predict the production of each heterotrophic component, and standing stock biomass, relative to total phytoplankton. The question asked in this work is how is food-web structure impacted by assuming a) a common value for GGE for all taxa, b) taxon-specific GGEs and c) diet and taxon-specific GGEs?

Methods

The extent to which models are simplified should be appropriate to the aims of the investigation. With this in mind, the model used here is considered appropriate for investigating the principle aims of this study. The model used is a simplification of the food-web using compartments that represent the following taxonomic groups: pico, nano, and microphytoplankton, bacteria, ciliates, nano/microflagellates, dinoflagellates and copepods (Figure 5.1 p. 118). Nano- and microflagellates are grouped as one compartment and, in addition to bacteria and dinoflagellates, are considered to be heterotrophic. The models developed represent the annual planktonic food-web of low nutrient areas, LNA (oligotrophic, low nutrient input and maximum phytoplankton growth rates < 0.2 generations day^{-1}) and high nutrients areas, HNA (relatively high energy input and maximum phytoplankton growth rates >0.2 generations day^{-1}) planktonic food-web, and therefore all associated flow rates and relative production values are also considered to be annual averages, incorporating potential bloom and non-bloom conditions. The

flow of carbon through the food-web is investigated using a mass-balanced approach, akin to many Ecopath (Pauly & Christensen 1996, Christensen & Walters 2004) and size-spectra methods (Stock *et al.* 2008), whereby all flows of energy are accounted for, with the flow into the food-web equalling energy output.

The model was developed using Microsoft Excel and based on ecological and physiological parameters. The food-web is initialised using a given amount of primary productivity (100 units of carbon), split between phytoplankton size categories in accordance with reported values. As phytoplankton represent the majority of total primary production in the ocean (95%, de Vooys 1979), for the purposes of simplicity I assume this component represents the total fraction (100%). The flow of primary production through the food-web was determined using simple rules regarding levels of primary production, compartments predated, amount of prey consumed (clearance efficiency, *CE*) (Table 6.1) and the efficiency with which ingested prey mass is converted into predator mass (gross growth efficiency, *GGE*) (Table 6.2). This approach is akin to that of Landry & Calbet (2004) in that prey production and GGE values are used to derive predator production, but differs in that a greater number of smaller taxonomic groups are used and grazing efficiencies are estimated using values reported from the literature. The approach employed here allows the full use of mean GGE values for different diet types and taxonomic groups from Chapter 3. Mass-balance for each compartment was achieved by assuming ingested mass is either respired, excreted, egested or contributes to production (Figure 6.1). Therefore for each heterotrophic component:

$$Ingestion = Production + Respiration + Egestion + Excretion \qquad \text{Equation 6.1}$$

The production of each compartment was assumed to be consumed by predators or exported from the system. Standing stock biomasses, derived using specific growth rates, are assumed to remain constant, with no accumulation, and therefore the food-web is in an assumed steady-state. Therefore for all compartments:

$$Production = Mortality + Export + Additional\ Mortality \qquad \text{Equation 6.2}$$

Table 6.1 **Clearance efficiencies, in terms of percentage of prey production consumed, for each predator, applied in models of low (LNA) and high (HNA) nutrient areas.**

Taxon	Prey	Symbol	Prey Production Consumed (%)
Ciliates	Nanophytoplankton	CE*CilNP*	60
	Nano/microflagellates	CE*CilNMF*	100
	Bacteria	CE*CilB*	15
Nano/microflagellates	Picophytoplankton	CE*NMFPiP*	33
	Bacteria	CE*NMFB*	75
Dinoflagellates	Nanophytoplanklon	CE*DNP*	5
	Microphytoplankton	CE*DMP*	40
Copepods	Picophytoplankton	CE*CopPiP*	14
	Nanophytoplankton	CE*CopNP*	15
	Microphytoplankton	CE*CopMP*	30
	Ciliates	CE*CopCil*	15
	Dinoflagellates	CE*CopD*	15

Table 6.2 **Gross growth efficiencies (GGE, %) used for models of low (LNA) and high (HNA) nutrient areas. Suite A values are derived from Straile (1997), whilst suite B, which represent taxa–specific values, and suite C, taxa and diet–type specific GGEs, are derived from Chapter 3. For suite C, values marked with an asterix (*) are non–diet type specific, but average mean values.**

			GGE (%)			
Taxon	**Prey**	**Symbol**	**Suite As**	**Suite Aj**	**Suite B**	**Suite C**
Ciliates	Picophytoplankton	*GGECilPiP*	33	24.7	16	28
	Nanophytoplankton	*GGECilNP*	33	24.7	16	28
	Nano/microflagellates	*GGECilNMF*	33	24.7	16	16*
	Bacteria	*GGECilB*	33	24.7	16	9
Nano/microflagellates	Picophytoplankton	*GGENMFPiP*	33	24.7	39	62
	Bacteria	*GGENMFB*	33	24.7	39	37
Dinoflagellates	Nanophytoplankton	*GGEDNP*	33	24.7	29	33
	Microphytoplankton	*GGEDMP*	33	24.7	29	33
Copepods	Picophytoplankton	*GGECopPiP*	33	24.7	26	33
	Nanophytoplankton	*GGECopNP*	33	24.7	26	33
	Microphytoplankton	*GGECopMP*	33	24.7	26	27
	Ciliates	*GGECopCil*	33	24.7	26	15
	Dinoflagellates	*GGECopD*	33	24.7	26	15

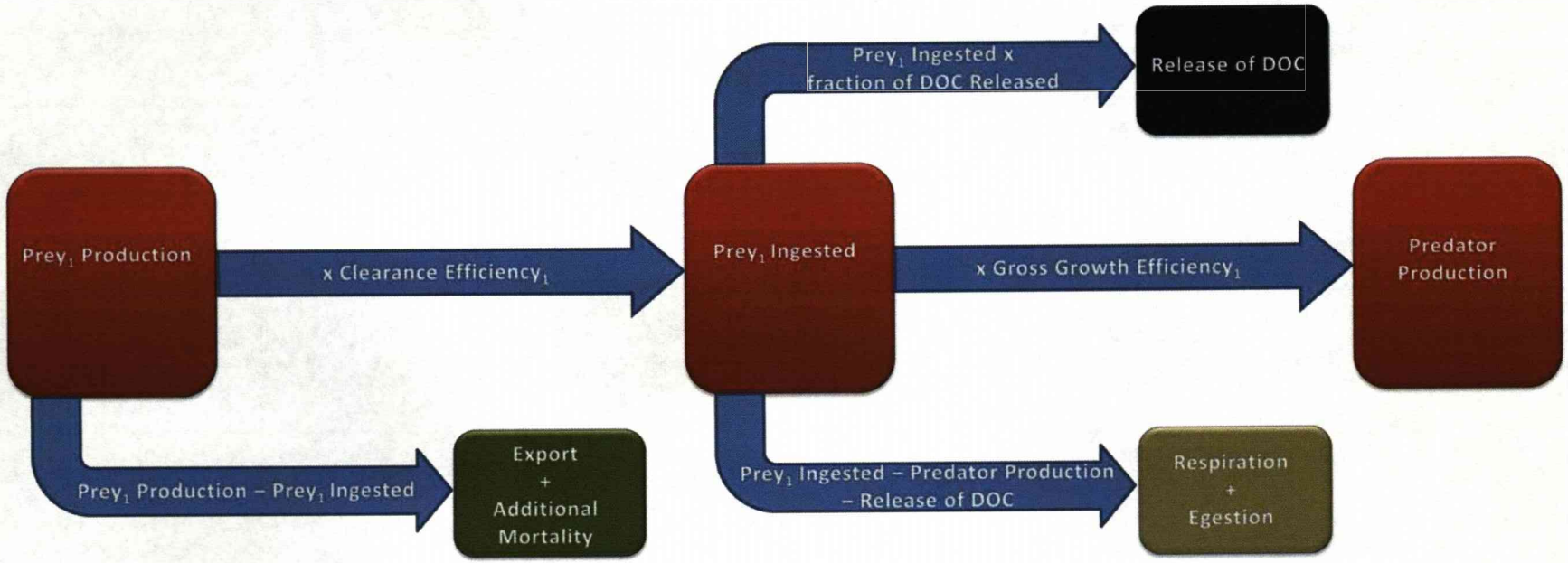


Figure 6.1 Simplified diagram of the flow production for each heterotrophic component of the planktonic the mass balanced food web model used in this study. For illustration purposes the consumption of only one prey type is shown, indicated by the subscript, 1.

As the nutritional state of the marine environment may have fundamental implications for the structure and functioning of its biota, separate models of low (LNA) and high (HNA) nutrient areas were developed using appropriate grazing efficiencies and autotrophic input values where possible. Where appropriate the parameter values used are specific to either LNA or HNAs. I used values reported within the literature to provided informed values of autotrophic and bacterial input, grazing efficiencies, respiration, excretion and gross growth efficiencies. The rationale behind the choice of these parameter values is outlined below.

Autotrophic Input

Production values for all autotrophic components (and also heterotrophic bacteria) were assumed to gain carbon from the DOC pool alone, are needed to initialise the models used. An important requirement is that relative to each other these input values are in the ratio that approximates that which represents relative annual production values. Pico-, nano- and microphytoplankton production values were chosen to approximate relative to each other based upon values found within the literature. The relative production values of the autotrophic components of the food-web modelled here are likely to vary with the nutritional state of the environment. Values were chosen to represent LNAs and HNAs following a literature search (Appendix 21), with greater justification of the values chosen given in the following sections.

Picophytoplankton

Although the contribution of picophytoplankton to total primary production shows considerable variation in the open ocean, it is generally much greater than in coastal estuarine environments (Tremblay & Legendre 1994, Marañón *et al.* 2001). This is in contrast to an increase in the contribution of picophytoplankton biomass to total phytoplankton, which has been shown to increase with trophic state over a global scale (Uitz *et al.* 2006). Whilst increased nutritional state is associated with an increase in picophytoplankton productivity, its relative contribution decreases significantly (Agawin *et al.* 2000, Bell & Kalff 2001), with environments of high nutrient concentrations generally having a much lower proportion (Stockner 1988).

Although at high nutrient levels picophytoplankton can represent 61% of total primary production (Marañón *et al.* 2001), their proportion is commonly less than one third, with reported ranges of 0–32% of total productivity (Weber & El–Sayed 1987, Stockner 1988) and mean values below 10% (Agawin *et al.* 2000). On the whole, studies undertaken in oligotrophic conditions report picophytoplankton to be the dominant fraction of phytoplankton, and contributing a greater proportion of total primary production than in areas of high nutrients, with values greater than 50% (Agawin *et al.* 2000, Marañón *et al.* 2001) and up to 90% (Stockner 1988) and even 100% reported (Teixeira & Gaeta 1991). The dominance of picophytoplankton production in oligotrophic waters (low nutrients concentrations) has been argued to be a result of greater affinity for nutrients (Donald *et al.* 1997, Raven 1998) and light absorbtion efficiency (Augustí *et al.* 1994) in comparison to larger autotrophs, owing to increased surface area to volume ratio, therefore maintaining a high nutrient uptake. Thus I have considered 55% and 30% of total primary productivity to be reasonable estimates of picophytoplankton contribution for use within the modles of LNA and HNA respectively.

Nanophytoplankton

The proportion of primary productivity derived from nanophytoplankton can be very high in nutrient–rich, polar regions (16 to 92%; mean 53%, Weber & El–Sayed 1987) and temperate regions (81%, O'Reilly and Bush 1984), although the range reported is large. In oligotrophic conditions, however, nanophytoplankton contribution is likely to be much lower, with the global analysis by Marañón *et al.* (2001) reporting a value of 30% of total primary productivity. Therefore in the models presented here it is assumed that nanophytoplankton production is 30% of total primary productivity for the LNA model and 55% for the HNA.

Microphytoplankton

In addition to contributing a relatively small proportion of biomass in oligotrophic waters (10% Uitz *et al.* 2006), microphytoplankton production is also a small fraction of total productivity (13%, Marañón *et al.* 2001). A similar fraction of

production by microzooplankton is generally observed in upwelling and temperate regions (15 and 21% respectively, Marañón *et al.* 2001). As there was no detectable significant difference in global microphytoplankton contribution to total primary production with increasing nutritional state (Marañón *et al.* 2001), I assume a value of 15% for both trophic models.

Bacterial Input

Bacterial production in the food-web can be very high, for instance it can be equal to 45% of production by phytoplankton in the open ocean (Hanson & Lowery 1983), 98% in coastal upwelling zones (Lucas *et al.* 1986) and 3000% in Antarctic waters (Rivkin 1991). The range of values reported can vary to a great extent (see Ducklow & Carlson 1992). In the euphotic zone of the open ocean, bacterial production varies considerably (5-92%), whilst global bacterial production has been estimated to be between 54 and 110% of global primary production. However, globally these values are cited as being probably too high (Ducklow & Carlson 1992), and therefore lower values are considered more appropriate when applied to global models, for instance 10-15% (Anderson & Ducklow 2001, Landry & Calbet 2004) and 20% (Cole *et al.* 1988), which are comparable with values of around 20% from frontal regimes in the open ocean (Ducklow & Carlson 1992). As no clear evidence was found within the literature regarding a disparity between areas of high and low nutrients in terms of bacterial production relative to primary productivity, the value of 15% seems a reasonable compromise for use within both models.

Clearance Efficiencies

The second parameter used within the models concerns the proportion of prey consumed by the predator. This term, referred to here as clearance efficiency, represents the average percentage of annual production of prey consumed by each of its predators. The values used within these models were chosen based on literature values of clearance efficiency and the proportion that each prey contributes to predator diet (Appendix 22).

Predation of Phytoplankton

Nano/microflagellates are an important grazer of the smallest fraction of primary production (Kuhn 1997), and combined with ciliates (Sherr *et al.* 1986, Stockner 1988, Šimek *et al.* 1995) and copepods (Stockner 1988) play a key role in controlling marine picophytoplankton production. For both the LNA and HNA models I assume that consumption of picophytoplankton production by nano/microflagellates (39%), ciliates (17%) and copepods (14%) was in accordance with that compiled from the literature by Stockner (1988), assuming that all available picophytoplankton is consumed.

The proportion of nanophytoplankton removed by ciliates varies with trophic status, with a greater proportion removed in areas of higher nutrients. In keeping with values reported for environments of low (Rassoulzadegan *et al.* 1988) and high nutrients (Verity 1987) I assume 22 and 52% of nanophytoplankton production is removed by ciliates respectively. These assumed values equate to 28% removal of total phytoplankton in the HNA model. This value closely matches the annual means reported by both Verity (1987) and Capriulo & Carpenter (1983), and falls within the range of 10–60% of primary production grazed by ciliates (Capriulo and Carpenter 1980; Verity 1987; Leakey *et al.* 1992) and annual means of 8% (Rysgaard *et al.* 1999) to 49% (Nielsen & Kiørboe 1994).

The impact of heterotrophic dinoflagellates on the removal of primary production can be equally important as ciliates in oceanic waters (Lessard & Swift 1985). Here it was assumed that heterotrophic dinoflagellates grazed 5% of nanophytoplankton and 40% of microzooplankton production for both model types, which corresponds to a removal of around 8% of total phytoplankton production, which is comparable to the annual mean values reported by Rysgaard *et al.* (1999). In total, ciliates and dinoflagellates remove nearly 60% of nanophytoplankton production in the HNA models, which is similar to values reported by Verity (1986).

Microphytoplankton is considered to represent a large proportion of copepod diet, for example up to 72% (Ortner *et al.*1980), varying seasonally from 22 to 81% (Roman & Gauzens 1997). Average copepod grazing has been reported as around

20% of primary production (Calbet 2001, Huskin *et al.* 2006), although annual primary production consumed by copepods may be as low as 13% (Kiørboe & Nielsen 1994). The proportion of microphytoplankton grazed by copepods seems to vary according to trophic conditions however, with studies reporting a greater clearance efficiency under oligotrophic conditions. In environments of high nutritional state copepod removal of primary productivity was found to vary between 10 and 15% (Calbet 2001, Calbet & Prairie 2003), whilst mean loss of microphytoplankton production to copepods in oligotrophic waters varied between 40.4 and 74% (Calbet 2001, Calbet & Prairie 2003). I therefore assume copepods to consume 60% of microphytoplankton within the LNA model, and 15% in the HNA. Nanophytoplankton appears to be a relatively small part of the copepods diet, measured as approximately one sixth of that of microphytoplankton (12%, Ortner *et al.* 1980) and therefore I assume 10% of nanophytoplankton to be grazed by copepods in the LNA model. With an increased proportion of nanophytoplankton, I may expect grazing to be greater than one sixth of that of microphytoplankton in the HNA model. To compensate for this, I also assume 10% of nanophytoplankton production is consumed by copepods in the HNA model.

Predation of ciliates and dinoflagellates

Although protozoa may constitute up to 80% of mesozooplankton diet (Vézina *et al.* 2000), they are likely to generally be a smaller portion, closer to the 16% that ciliates and dinoflagellates contributed to copepod diet (Ortner *et al.* 1980). Indeed, ciliates commonly contribute a relatively low proportion of copepod diet of 20% to less than 10% (Montagnes *et al.* 1985, Kiørboe & Nielsen 1994). For both LNA and HNA models 20% of both ciliate and dinoflagellates production was assumed to be grazed, which approximated 15% of the copepod diet (10 & 20% respectively).

Predation of nano/microflagellates

The amount of heterotrophic nanoflagellate production consumed by ciliates can be extremely high, with the entire production commonly reported as being grazed (Weisse *et al.* 1990, Šolić & Krstulović 1994). It was therefore assumed that the entire proportion (100%) of available nano/microflagellate production was consumed by ciliates in both models.

Predation of bacteria

Ciliates and nano/microflagellates are primarily responsible for the removal of bacteria in the aquatic environment (Sanders *et al.* 1992), commonly grazing a high proportion of its production (for example up to 154%, Šolić & Krstulović 1994). Studies consistently report heterotrophic nanoflagellates removing over 80% of bacteria production or more (Šolić & Krstulović 1994, Callieri *et al.* 2002). Of the fraction of bacteria production not consumed by nano/microflagellates, ciliates tend to graze a large proportion, meaning that the majority of bacterial production is generally consumed (90%, Kuuppo-Leinikki). Ciliates have been shown to consume less than 15% (Dolan 1991) and up to 38% (Rassoulzadegan *et al.* 1988) of bacteria production. As there appears to be no significant difference in proportion of bacteria grazed by ciliates between environments of high and low nutrient levels (Rassoulzadegan *et al.* 1988), for both models I assume 15 and 80% of bacterial production was consumed by ciliates and nano/microflagellates respectively.

Respiration

The source of bacterial carbon in the models is solely from DOC uptake. The amount of carbon respired and excreted by bacteria ranges between 50 to 75% (Vézina & Platt 1988, Vézina *et al.* 2000). The portion of carbon directed to respiration by bacteria, protozoa, micro and mesozooplankton has been reported as at least 20% of that which is ingested (Vézina & Platt 1988, Vézina *et al.* 2000). Of the total amount of carbon ingested by protozoa, the proportion that is respired, excreted or egested was considered as 50–75%. For copepods, the portion of ingested material portioned to respiration has been shown to range between 10–56%, although an average of 25% of the carbon ingested from primary production was reported by Calbet (2001). The percentage of copepod respiration was found to decrease with increasing food availability, with the percentage of ingested food respired (or excreted) 32, 14 and 12% for low, moderate and high food conditions (Kiørboe *et al.* 1985).

Respiration of phytoplankton (0.7–200μm in size) has been determined as ranging between 5 and 30% gross primary production (Vézina *et al.* 2000, Vézina & Platt

1988). For all phytoplankton groups it was assumed that respiration represented 15% of gross primary production. For bacteria, ciliates, nano/microflagellate, dinoflagellates and copepods, respiration and excretion were assumed to be 20 and 10% of ingested carbon respectively.

Excretion

For copepods, excretion may be equal to respiration (range 33–100% of respiration, Vézina & Platt 1988), although it may be a significantly lower proportion, such as 28% of the sum of excretion and respiration (Steinberg *et al.* 2000). As 10% of carbon ingested has been assumed to be excreted previously for all protozoa and mesozooplankton (Vézina *et al.* 2000, Vézina & Platt 1988), this value is also assumed to be an appropriate figure for ciliates, nano/microflagellates, dinoflagellates and copepods in the LNA and HNA models presented here.

Gross Growth Efficiencies

The proportion of ingested material converted to production is referred to as gross growth efficiency (GGE). In the absence of evidence suggesting a difference in the GGE of different taxa between areas of high and low nutrient concentrations, I assume identical values for both model types. Both the LNA and HNA models were run using one of four different suites of GGE values. For suite As, the GGE of all compartments (bacteria, ciliates, nano/microflagellates, dinoflagellates and copepods), was assumed to be 0.33, the mean value found by Straile (1997), for all planktonic taxa, and commonly used to represent the GGE of all planktonic taxa in planktonic models. Suite Aj also uses a common GGE for all taxa, but with a reduced efficiency of 0.247 as derived in Chapter 3 as a result of a vastly greater dataset and removal of incorrect values, and is included to examine whether it is the value of GGE that is important in determining an accurate distribution of planktonic biomass. Suite B uses mean, taxa-specific values for bacteria, ciliates, nano/microflagellates, dinoflagellates and copepods as derived in Chapter 3, p.36. GGEs applied in suite C are specific to each taxon and to the diet type (bactivorous, herbivorous, carnivorous or mixed diet) of the predator. GGE values used in all three suites are outlined in Table 6.2. A diet–specific average GGE value was not

available for ciliates feeding on heterotrophic flagellates, and so the average taxa–specific GGE values, as in suite B, was applied in this instance.

Specific Growth Rates

To give a standing stock biomass distribution to enable comparisons with real world data, additional parameters are needed. Values of instantaneous mass specific growth rate, μ (d^{-1}) were sought from the literature for all groups in order to provide a reasonable estimate of average *in situ* growth rates (Table 6.3). Compartments were converted to standing stock estimates by: production/growth rate = standing stock biomass, and expressed as a proportion of total phytoplankton biomass. For all heterotrophic groups I assumed the same specific growth rate for both the HNA and LNA models for two reasons. Following a literature search I was unable to confidently distinguish between trophic condition and growth rates, for instance mean ciliate growth rate in upwelling areas (Hendrikson *et al.* 1982) fell within the range of offshore values (Rassoulzadegan *et al.* 1988). In addition, any differences in specific growth rate that may occur between environments of high and low nutrients are likely to be the product of food availability, as the functional response of specific growth rate to food availability has been described in numerous planktonic taxa. As I derive production values of each heterotrophic group relative to total phytoplankton, and account differences in autotrophic structure by varying input values, I consider it appropriate to use identical specific growth values for the LNA and HNA models.

Additional factors may also influence specific growth rates of planktonic taxa. For instance, the degree of seasonality may affect growth rates by providing a lower degree of variation in light and temperature at lower latitudes than high latitudes. In this I therefore consider all specific growth rates used to represent annual mean values. As nutrient availability is likely to have an impact on phytoplankton specific growth rates I used values specific to the LNA and HNA models. To account for disparity between trophic environments I used mean open ocean specific growth rates for the LNA modeland mean coastal rates for the HNA model.

Table 6.3 **Mean specific growth rates (μ, d^{-1}) of ciliates, dinoflagellates, nano/microflagellates, copepods and phytoplankton reported in the literature. Mean growth rates marked with an asterisk (*) were converted from rates reported per hour (h^{-1}).**

Taxon	Mean Growth Rate	Source	Notes
Ciliates	1.32*	Hansen *et al.* (1997)	Maximum growth
	1.225	Strom (1991)	Maximum growth, herbivorous diet
	0.62	Hendrikson *et al.* (1982)	Upwelling
	0.35 to 1.0	Rassoulzadegan (1982)	Mediterranean
	1.273	Derived from Rose & Caron (2007)	
Dinoflagellates	0.936*	Hansen *et al.* (1997)	Maximum growth
	0.624*	Hansen (1992)	Maximum growth
	0.813	Strom (1991)	Maximum growth
	0.445	Derived from Rose & Caron (2007)	
Nano/microflagellates	3.19*	Hansen *et al.* (1997)	Maximum growth
	2.414	Strom (1991)	Maximum growth
	1.917	Derived from Rose & Caron (2007)	
Copepods	0.158*	Hansen *et al.* (1997)	Maximum growth
	0.159	Hirst & Bunker (2003)	Sac spawners
	0.147	Hirst *et al.* (2003)	Broadcasters
Phytoplankton	0.83	Hendrikson *et al.* (1982)	Upwelling
	0.1 to 0.8	Welschmeyer *et al.* (1991)	Subarctic pacific
	0.53 to 0.79	Murray *et al* (1994)	Range, equatorial pacific– upwelling
	0.64	Murray *et al* (1994)	Equatorial pacific– upwelling

Table 6.3 continued

	0.69	Thomas (1970)	Pacific- oligotrophic
	1.66	Rassoulzadegan *et al.* (1988)	Meditteranean
	0.42	Derived from values in Goldman *et al.* (1979)	Coastal Value
	0.95	Derived from values in Goldman *et al.* (1979)	Open ocean
	4.57	Koblentz-Mishke & Vedernikov (1976)	Oligotrophic
	1.59	Koblentz-Mishke & Vedernikov (1976)	Mesotrophic
	0.10	Koblentz-Mishke & Vedernikov (1976)	Eutrophic
	0.59	Calbet & Landry (2004)	Oceanic
	0.67	Calbet & Landry (2004)	Coastal
	0.72	Calbet & Landry (2004)	Tropical
	0.69	Calbet & Landry (2004)	Temperate
	0.44	Calbet & Landry (2004)	Polar
	0.31	Derived from Calbet & Landry (2004)	Coastal,Polar
	0.58	Derived from Calbet & Landry (2004)	Coastal, Temperate
	1.19	Derived from Calbet & Landry (2004)	Coastal, Tropical
	0.46	Derived from Calbet & Landry (2004)	Oceani, -Polar
	0.56	Derived from Calbet & Landry (2004)	Oceanic, Temperate
	0.66	Derived from Calbet & Landry (2004)	Oceanic, Tropical
	1.00	Derived from Calbet & Landry (2004)	Estuary, Temperate
	0.77	Derived from Calbet & Landry (2004)	Estuary, Tropical
Bacteria	0.06	Kirchman *et al.* (1993)	Subarctic pacific
	0.0003 to 10.17	White *et al.* (1991)	Marine, range
	0.44	White *et al.* (1991)	Marine
	0.007 to 30.81	White *et al.* (1991)	Estuarine & Coastal, range
	1.75	White *et al.* (1991)	Estuarine & Coastal
	0.40	Rivkin *et al.* (1996)	All temperatures
	0.39	Rivkin *et al.* (1996)	Temperatures ≤4ºC
	0.41	Rivkin *et al.* (1996)	Temperatures >4°C

Whilst I acknowledge that the open ocean is not uniformly oligotrophic, I believe that difference between coastal and open ocean specific growth rates to give a reasonable proxy between phytoplankton growth rates of areas of low and high nutrient availability. I derived average specific growth rates (d^{-1}) derived for ciliates, dinoflagellates, and flagellates (which were assumed to be representative of nano/microflagellates) using data from the appendix of Rose & Caron (2007). I found the mean average specific growth rate of dinoflagellates to be approximately one third of that of ciliates, which closely matches the findings of Montagnes *et al.* (2003). I use a copepod growth rate of 0.15 $d-^{1}$ which is highly comparable to the average rates reported by Hirst & Bunker (2003) for adults and juveniles. I assume bacterial growth rate to be identical to the mean value reported by White *et al.* (1991) for marine environments (0.44 d^{-1}), which is highly similar to that reported by Rivkin *et al.* (1996) (d^{-1}).

Standing Stock Biomass

Compartments were converted to standing stock estimates by: production/growth rate = standing stock biomass, assuming primary production approximates 50 and 350 g C m^{-2} for nutrient poor and rich waters respectively. These values were derived assuming global marine phytoplankton production is 45 gigatons (Gt) of carbon $year^{-1}$ (Falkowski *et al.* 1998), nutrient poor and rich waters represent 30 and 70% of total primary productivity respectively (Marañón *et al.* 2003) and 75 and 25% of total ocean coverage (Lewis *et al.* 1986).

Sensitivity Analysis

Due to the variation in nature of the associated with many of the variables used to in my models, a sensitivity analysis was performed in order to determine upper and lower confidence limits of production and biomass values in all LNA and HNA models. In addition to the clearance efficiencies (Table 6.1), gross growth efficiencies (GGEs; Table 6.2), bacterial input (p. 129) and specific growth rates (p. 133) employed in the LNA and HNA models, values that were 10% above and below each of these variables were derived to derive upper and higher terms. Subsequently, each of these terms at a time were inserted into the model, to determine whether an increased or reduction in biomass and production of each

compartment (copepods, dinoflagellates, ciliates, nano/microflagellates, bacteria) resulted in their inclusion. Through the combination in the model of upper and lower terms that increased biomass and production, the upper confidence limit was obtained. Similarly, by using a combination of terms that produced the lowest possible biomass and production, I derived the lower confidence limit.

The concept of introducing parameter values above and below that used in the main model to determine the impact on model output is identical in concept to that employed by Fasham *et al.* (1990) in a dynamic, nitrogen based model of the planktonic food-web, although they examined the influence on annual net primary productivity using upper and lower limits for each term separately. However, in the natural environment parameter values such as growth rate and gross growth efficiency are not independent from one another, and therefore with the possibility of co-variation of parameters, I consider the examination of the combined impact of upper and lower limits to be a stricter, more robust and appropriate method of exampling biomass structure.

In the subsequent interpretation of results, I consider there to be noteworthy differences in between biomass, and production where there is no overlap in the range of upper and lower confidence values. Where the range of biomass and production values of a food-web compartment overlaps with another, this cannot be considered a significant difference due to the variability of parameter values.

Results

Production

In terms relative to primary productivity, although copepods production was greater in both the LNA and HNA models (7.8 and 5.4% of phytoplankton productive respectively) models using suite As, it did not exceed the confidence limits of production using suites B and C (Figure 6.2).

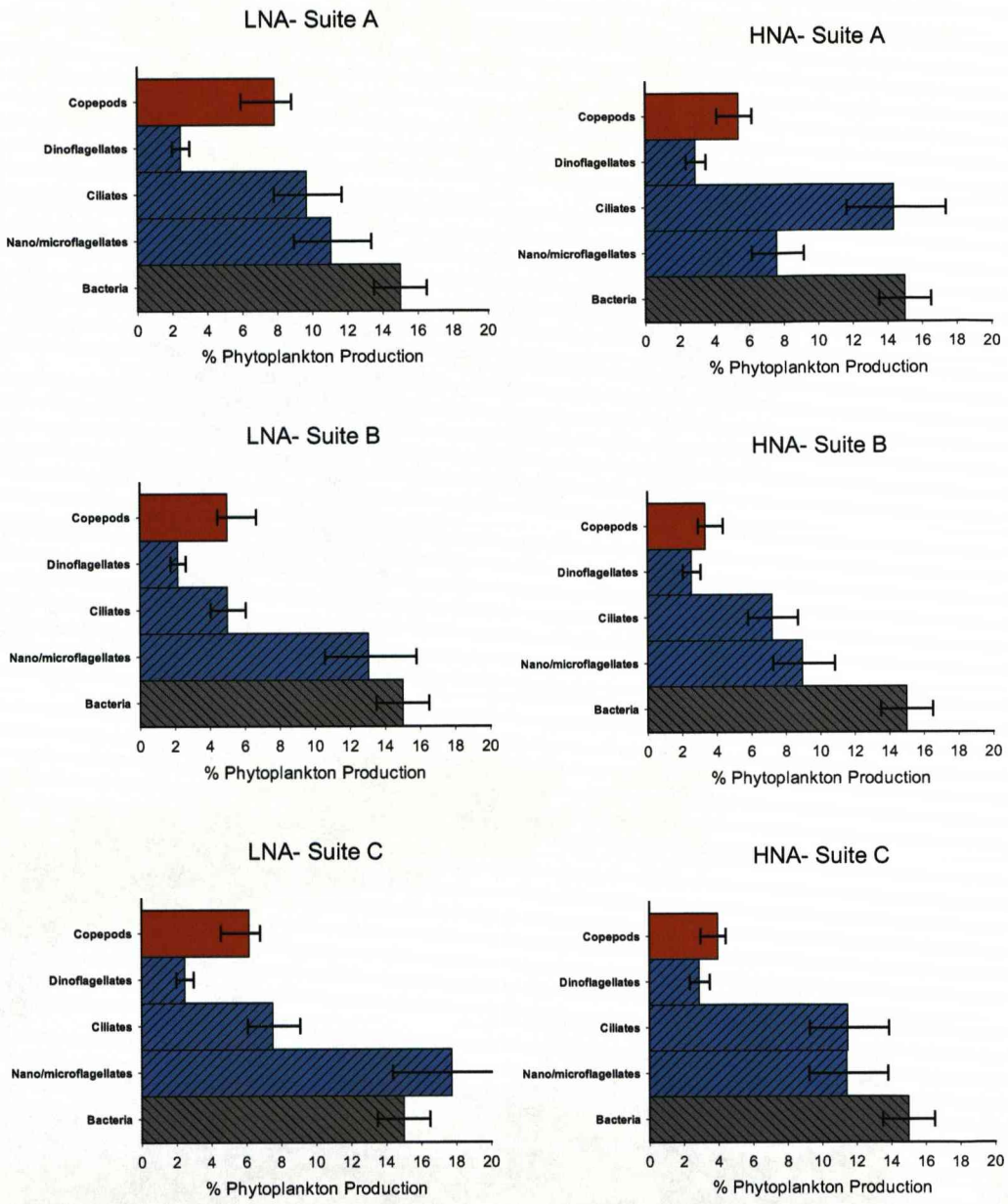


Figure 6.2 Production relative to primary production (%) using a common GGE value of 33% for all taxa (suite A), taxa–specific mean GGE values (suite B) and diet type and taxa–specific values (suite C) from a model of the planktonic food–web in areas of low (LNA) and high nutrients (HNA).

For ciliates, production was far greater using suite As (LNA=9.6%, HNA=14.4% of phytoplankton production) and approximately twice that derived from suite B did not vary beyond the confidence limits produced using suite C in models of nutrient poor and rich environments (upper limits: LNA=6.0%, HNA=8.7%). However, whilst ciliate production did not vary between suites B and C for the LNA model, a greater production (11.5%) was observed using suite C (taxa-, and diet-specific GGEs) in comparison to suite B (7.2%, upper limit=5.8%).

Dinofllagellate production remained constant between GGE suites used in both the LNA (2.2 to 2.5%) and HNA (2.5 to 2.9%) models. In contrast, nano/microflagellates were the only group for which suite C produced the highest production value, (LNA=17.7%, HNA=11.4%) which exceeded the upper limit produced using suite As (LNA=11.0, HNA=7.6% of primary productivity). The use of suite B provide estimates of nano/microflagllete production (13.05 and 8.9% of primary productivity for LNA and HNA models) intermediate of those derived using suite As and C, but did not vary significantly from either.

Although the use of a lower value GGE for all planktonic taxa, suite Aj resulted in a decrease in nano/microflagellate, dinoflagellate and copepod production production, only ciliate production decreased below the lower limit determined using suite As in the LNA model (Table 6.4, Figure 6.3) Ciliate production using suite Aj was approximate a third lower than with suite As, representing a decrease of 1.7% in terms of primary production. However, no discernable difference in production could be detected for any of the groups between HNA models using suites As and Aj.

Standing Stock Biomass

Although estimates of standing stock biomass were greatest for copepods using the common mean GGE for all taxa as in suite As, with values of 16.2 and 77.7 g C m^{-2} under the LNA and HNA models respectively, they did not exceed the upper limits of values derived using suites B and C (Figure 6.4).

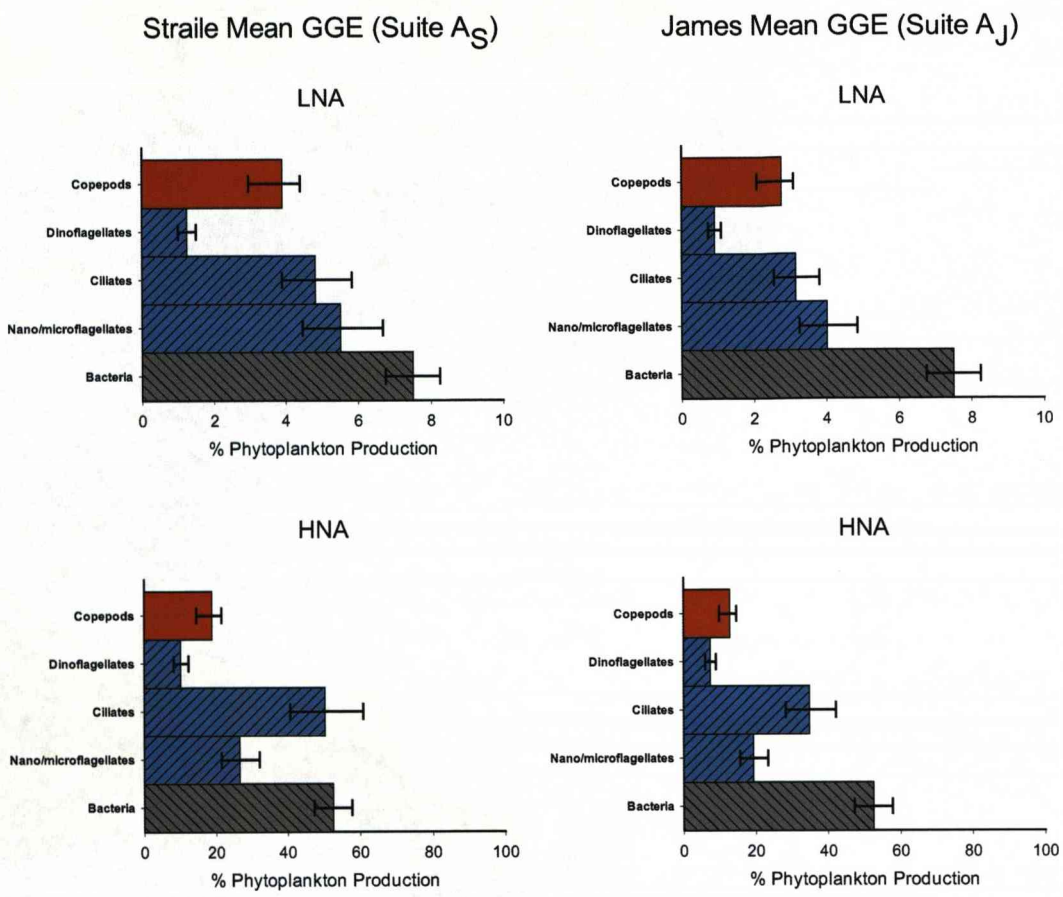


Figure 6.3 Production relative to primary production (%) using a common GGE value for all taxa of 33% (from Straile 1997, suite As), and 27.4% (derived in Chapter 3, suite Aj) from a model of the planktonic food-web in areas of low (LNA) and high nutrients (HNA).

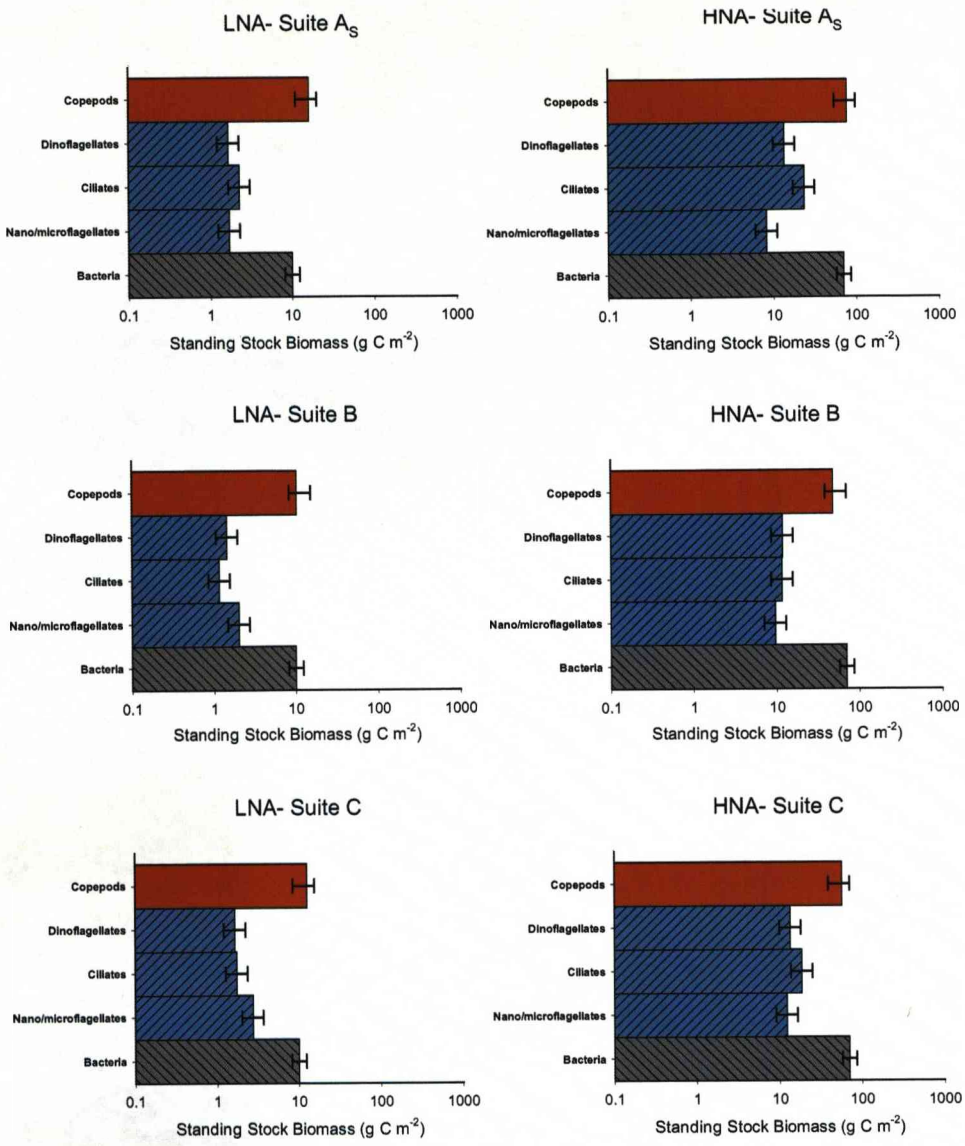


Figure 6.4 Average standing stock biomass (g C m^{-2}) of different zooplankton groups in areas of low (LNA) and high (HNA) nutrients, estimated using a model of the planktonic food-web assuming either a common GGE value of 33% for all taxa (suite A), taxa-specific mean GGE values (suite B) and diet type and taxa-specific values (suite C).

Standing stock biomass of ciliates was also greatest using suite , with values of 2.2 and 23.3 g C m^{-2} for the LNA and HNA models (Figure 6.4) approximately twice that estimated using suite B (LNA=1.2%, HNA=11.7%), and exceeding its upper confidence limit. Using suite C, however, provided intermediate estimates of biomass in the LNA and HNA models (1.7 and 18.6 g C m^{-2}), which did not differ from suites As or C using the confidence limits.

For nano/microflagellates, although biomass estimates were higher using suite C (LNA=2.7, HNA=12.3 g C m^{-2}) in comparsion to suites B (LNA=2.0, HNA=9.6 g C m^{-2}) and As (LNA=1.7, HNA=8.2 g C m^{-2}) they cannot be considered to be significant greater, as there was an overlap in confidence limits across all suites.

Although lower using suite B, dinoflagellate standing stock biomass was relatively constant across GGE suites, and did not differ within LNA (As=1.6, B= 1.4, C= 1.6 g C m^{-2}) and HNA (As=13.4, B= 11.8, C= 13.4 g C m^{-2}) models.

Although both LNA and HNA models using the mean derived in Chapter 3 (suite Aj) resulted in a decrease estimated standing stock biomass values remained within the confidence limits of values derived using the common mean GGE from Straile (1997) (suite As), for all heterotrophic compartments (Table 6.4, Figure 6.5). The use of suite Aj instead of suite As resulted in a reduction of biomass by approximately 30% for copepods (16.2 to 11.4 Gt) and ciliates (2.2 and 1.5 g C m^{-2}), and just over 25% for nano/microflagellates (1.7 and 1.24 g C m^{-2}) and dinoflagellates (1.6 and 1.2 g C m^{-2}) in the LNA models. Within the HNA models, the reduction in biomass as a result of using suite Aj, in comparison to suite As, was approximately 30% for ciliates (23.3 and 16.14 g C m^{-2}), 25 % for copepods (77.7 and 52.9 g C m^{-2}) and 27% for both dinoflagellates (13.4 and 9.8 g C m^{-2}) and nano/microflagellates (8.2 and 5.9 g C m^{-2}).

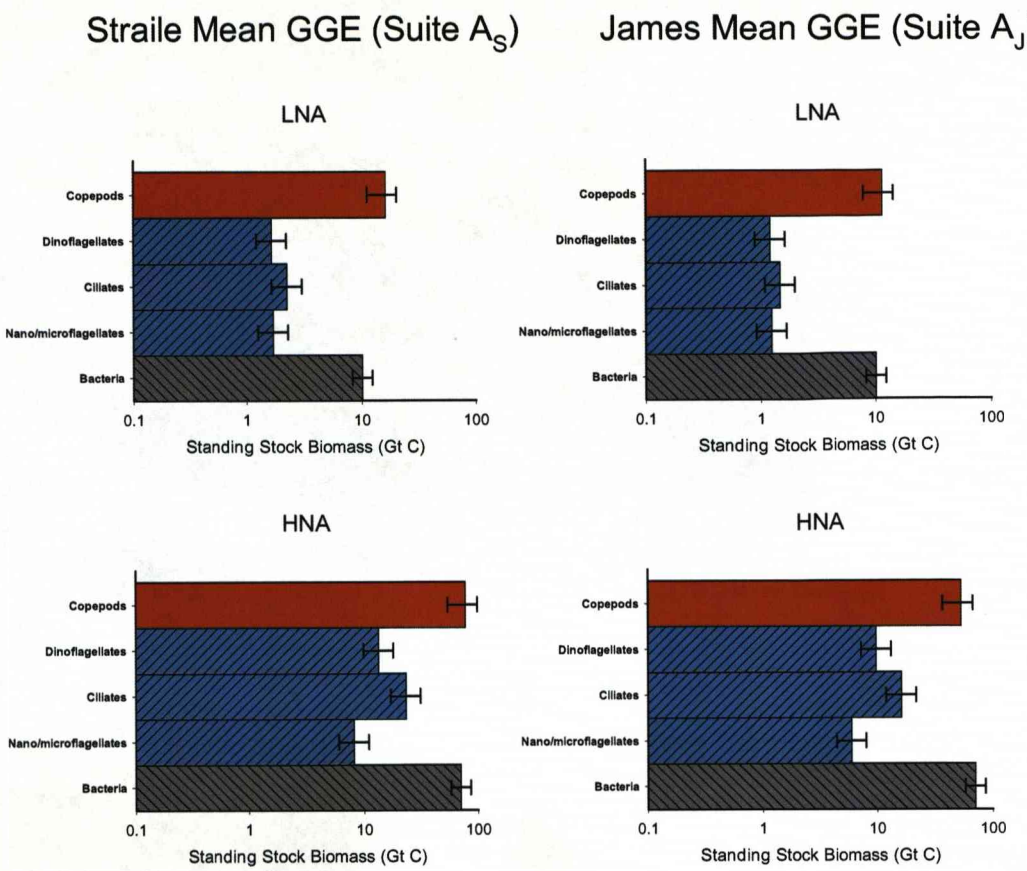


Figure 6.5 Standing stock biomass (g C m^{-2}) of different zooplankton groups in areas of low (LNA) and high (HNA) nutrients, estimated using a model of the planktonic food-web assuming a common GGE for all taxa of either 33% (from Straile 1997, suite As), and 27.4% (derived in Chapter 3, suite Aj).

Table 6.4 **Production (as a proportion of total phytoplankton production , % PP) and standing stock biomass (g C m^{-2}) estimates of nano/microflagellates, ciliates, dinoflagellates, copepods and bacteria using a common GGE value for all taxa derived from Straile (suite As), and Chapter 3 (Suite Aj). Upper and lower production limits are indicated by – and + respectively, the derivation of which is described in the method section.**

Production

GGE Suite	Model	Bacteria			Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
		% PP	–	+	% PP	–	+	% PP	–	+	% PP	–	+	% PP	–	+
Straile Mean (suite As)	LNA	7.5	6.8	8.25	5.5	4.5	6.7	4.8	3.9	5.8	1.2	1.0	1.5	3.9	3.0	4.4
Straile Mean (suite As)	HNA	52.5	47.3	57.8	26.5	21.5	32.1	50.3	40.7	60.8	10.1	8.2	12.2	18.8	14.4	21.5
James Mean (suite Aj)	LNA	7.5	6.8	8.25	4.0	3.3	4.9	3.1	2.5	3.8	0.9	0.7	1.1	2.8	2.1	3.1
James Mean (suite Aj)	HNA	52.5	47.3	57.8	19.3	15.6	23.3	34.8	28.2	42.1	7.35	6.0	8.9	12.8	9.8	14.6

Biomass

GGE Suite	Model	Bacteria			Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
		g C m^{-2}	–	+	g C m^{-2}	–	+	g C m^{-2}	–	+	g C m^{-2}	–	+	g C m^{-2}	–	+
Straile Mean (suite As)	LNA	10.06	8.23	12.29	1.70	1.25	2.28	2.24	1.64	3.01	1.64	1.21	2.21	16.2	11.09	20.25
Straile Mean (suite As)	HNA	70.40	57.60	86.04	8.16	6.01	10.96	23.30	17.15	31.32	13.41	9.87	18.03	77.68	54.04	98.67
James Mean (suite Aj)	LNA	10.06	8.23	12.29	1.24	0.91	1.66	1.45	1.07	1.96	1.20	0.88	1.61	11.37	7.77	14.19
James Mean (suite Aj)	HNA	70.40	57.60	86.04	5.93	4.37	7.98	16.14	11.88	21.70	9.75	7.18	13.11	52.89	36.65	66.91

Discussion

This study shows that potentially important differences in the amount and path of energy flow through the planktonic food-web in terms of primary productivity can arise through the use of different GGE values within ecosystem models. Changes in the relative production of the components (ciliates, nano/microflagellates, dinoflagellates and copepods) of the food-web model are a result of changes in the proportion of primary productivity distributed through different paths. There seems to be no consistent pattern in terms of a universal change in relative production of all components of the food-web as a result of the suite of GGE values applied, which in itself is an important factor to note. This is likely owing to the complex nature of the food-web, even at the relatively low complexity modelled here. There are a number of broad patterns resulting from this study, however.

Production

Although there was a general increase in copepod production using a common GGE value for all taxa (suite As), the largest increase was for ciliates, where production, as a percentage of total phytoplankton production, was estimated to be up to twice that of when considering taxa- and diet-specific GGEs. If it is assumed that using taxon- and diet-specific mean GGEs of suite C gives a greater approximation and increased accuracy to planktonic food-web models then several important conclusions may be made. Overestimation of ciliate production as a result of assuming a common mean GGE for all taxa is likely to have important consequences on our understanding the pelagic food-web as a whole since ciliates perform many important ecological functions. At times ciliates can consume up to 100% of daily primary production, and up to 49% of total annual phytoplankton production (Nielsen & Kiørboe 1994) and provide a link between the microbial food-chain to higher trophic levels (Calbet 2008) including copepods (Levison *et al.* 2000).

The determination of accurate estimates of mean production for ciliates, which are frequently a dominant part of microzooplankton as a whole (Nielsen & Kiørboe 1994), is particularly important in areas of relatively low nutrient concentrations.

Oligotrophic waters are associated with an increased prevalence of smaller phytoplankton (Calbet & Landry 1999), which able to extract nutrients from the water (Donald et al. 1997, Raven 1998), and absorb light with a greater efficiency (Augustí *et al.* 1994) than larger species. Although mesozooplankton groups such as copepods are generally unable to consume the smallest components of phytoplankton and microzooplankon (e.g. nano/microflagellates) (Calbet & Saiz 2005), ciliates are important grazers of the nano- and picophytoplankton (Capriulo & Carpenter 1983, Verity 1987, Šimek *et al.* 1995), Therefore in nutrient poor areas, which constitute three quarters of total ocean, ciliates, which can contribute a sizeable portion of copepod diet (Lignell *et al.* 1993), have an increased responsibility in controlling the availability of material to secondary consumers, and are therefore high susceptible to ecosystem models using GGEs of reduced accuracy.

Without considering taxa- and diet-specific GGEs, it is likely that aspects other than ciliate production will also be overestimated, such as nitrogen excretion, cited as a significant contribution to allowing primary productivity to be sustained through the summer in the East China Sea (Ota & Taniguchi 2002). Ciliates also play a key role in the regeneration of dissolved organic phosphate, making it available to bacteria at a faster rate than mesozooplankton (Johannes 1965). However, the rate of regeneration, and therefore the strength of a ciliate-bacteria link, is likely to be overestimated if planktonic food-web is derived using a common GGE value.

In contrast to production values derived considering only taxa-specific GGEs (suite B), ciliate values were greater when diet type–specific GGEs are also considered. This demonstrates that considering only taxa-specific values may in fact underestimate ciliate production. Since bacteria are more abundant in nutrient poor regions (Cho & Azam 1990), and ciliate GGE was far lower when feeding on bacteria, than on algae, the consideration of diet type, in addition to the proportion of each prey type to total diet, is vital if we are to improve accuracy of ecosystem models.

Dinoflagellate relative production showed little variation in response to the different GGEs used in the models. Estimated values of relative production between

2.5 and 2.9%, however seem reasonable approximations considering dinoflagellate can consume 6% of annual phytoplankton production in nutrient rich areas (Rysgaard *et al.* 1999).

In terms of the relative distribution of production between groups, there is an increased domination by nano/microflagellates as a result of considering taxon- and diet-specific GGEs. This indicates there significant potential for the underestimation of this group in ecosystem models, and is consistent with evidence that within nutrient poor regions flagellates are the primary grazers of phytoplankton, exceeding the grazing pressure of ciliate and dinoflagellates (Not *et al.* 2007, Calbet 2008). Although increase in relative nano/microflagellates production was predicted with the use of taxa-specific means, owing to its relatively greater efficiency than all other taxa, the fact that relative production was increased further with additional consideration of diet type-specific GGES (suite C) was not predicted and again outlines the complexity of understanding potential impacts on the flow of energy through an ecosystem.

As copepods are the dominant component of mesozooplankton, understanding their production has important implications for predicting food-availability to higher trophic levels including commercially important species such as fish (Pauly & Chistensen 1995). Copepod production, which ranged between 5% and 7.8% in nutrient poor, and 3.3 and 5.9% in nutrient rich conditions, seems a reasonable estimates considering copepods have been reported as consuming 0.02 to 44% of phytoplankton production (Lignell *et al.* 1993, Capriulo & Carpenter 1983).

Using suite C estimated nano/microflagellate production was twice that of ciliates in nutrient poor, and equal to ciliates in nutrient rich conditions. Using common GGE values across taxa however, predicts nano/microflagellate production to be slightly higher (by approximately 13%) than ciliate production in the LNA model, and only half of ciliate production in the HNA model.

The use of taxon-specific GGEs consistently provided estimates of ciliate, nano/microflagellate, dinoflagellates and copepod relative production lower than when diet type was taken into consideration. My results suggest that owing to the

impact that different prey types can have on GGE, the proportion that each prey type contributes to the diet of a predator is an important consideration. It would seem inappropriate to use a mean GGE value that has been derived using different prey type to describe the efficiency of a predator in converting all prey types into its own biomass. For instance, it would be inappropriate to apply a mean GGE value that had been derived from 90% of values on a poor diet type and therefore low efficiency, and 10% of values on highly suitable, common prey type. The proportion of different prey types to predator diet is an important factor when each type is converted with different efficiency. Therefore using diet type and taxa-specific GGEs is likely to provide a more accurate prediction in ecosystems models, unless a mean GGE value which is weighted with respect to the average proportion of diet types is used, which to my knowledge has not been calculated.

Total microzooplankton production (nano/microflagellate, ciliates and dinoflagellates) using GGE suite As, provided a higher estimate in the nutrient rich (HNA) model (87% of phytoplankton production) than using suite Aj (61%), which are reasonably similar to values derived for costal ocean in Calbet & Landry (2004), derived using a constant GGE for all taxa, and in measurements from the coastal Gulf of Alaska (Strom *et al.* 2007).

Standing Stock Biomass

Using a different suite of GGE had a similar impact on standing stock estimates as it did on relative production, with the lowest estimates derived using taxon-specific values for ciliates, dinoflagellates and copepods, and using suite A for nano/microflagellates in nutrient poor and rich waters. Interestingly, despite large differences in their mean GGEs, when using suite C, ciliate and nano/microflagellate standing stocks were fairly similar in the HNA model.However, only the standing stock biomass of ciliates varied significantly between models using different suites of GGEs, with taxa-specific values producing estimates half that when using a common GGE across taxa. As consequence, it may be considered that ciliate production, and subsequent availability of material to higher trophic levels, may be grossly overestimated. Assuming global marine production to be 45 gigatons of

carbon year^{-1}, and that nutrient poor and rich regions contribute 30 and 70% of total primary production respectively (Maraňón *et al.* 2003) using a common GGE mean instead of taxa-, and diet specific means would overestimate global ciliate production by approximately 0.28 Gt C year^{-1} in nutrient poor, and 0.91 Gt C year^{-1} in nutrient rich environments.

Estimated average standing stock biomass of copepods was in the range of 10 to 16.1 g C m^{-2} between GGE suites in the low nutrient model, which are comparable to the estimated production of secondary consumers in the Inland Sea (Uye et al. 1997). The contribution of ciliates to total microzooplankton biomass ranged between 25 to 40% in nutrient poor model, and 35 to 52% in the nutrient rich model is reasonably comparable to values reported in marine systems (Uye *et al.* 1996: 40 to 69%, James & Hall 1995: 30%) but greater than that achieved in nutrient poor lakes (5 to 10% of total plankton biomass; Gates 1984).

In terms of the distribution of biomass and production in the planktonic food-web between models using either the mean GGE for all taxa from Straile (1997), or in Chapter 3, there was no significant change in terms of increased domination by one compartment single compartment (Figure 6.5, Table 6.4). These results indicate that although overall efficiency of the food-web changes with the value of GGE used for all taxa, influence the level of total micro- and mesozooplankton production (and also biomass), there is little scope for change in the distribution of production, and biomass, between planktonic compartments, at least in low complexity models.

Nutrient poor v nutrient rich models

In comparing model types, using GGE values of suites A, B and C it was found that production relative to primary productivity and standing stock biomass were both greater for ciliates, nano/microflagellate, dinoflagellates and copepods in the HNA model. Within taxonomic groups the impact of using different suites of GGE values was consistent between models of low and high nutrients. The similarities between model types may imply a relatively consistent impact of using more specific GGEs, but may also be a product and reflection of the simple model approach used.

Since protozoa contribute heavily to total community respiration, (Calbet & Landry 2004) a key observation note to make is that all three protozoan groups, nano/microflagellates, dinoflagellates and ciliates, had a greater biomass, relative to total plankton biomass in nutrient rich model, than in the nutrient poor. Although bacterial biomass is greater in the HNA model, its contribution to total biomass decreases, which is consistent with the increased role of bacteria in oligotrophic environments (Cho & Azam 1990).

Further refinements may not only enhance the specialisation of the LNA and HNA, but also aid in our understanding and quantifying the impact of specific GGEs on the structure and flow of energy through the planktonic food-web. A major parameter, for example is temperature which has particular importance as GGE within taxonomic groups have been shown to vary with temperature (Chapter 3, p.27) and oligotrophic regimes are commonly in warmer waters which impacts numerous aspects such as species growth and respiration rates. For instance, in the models presented here bacterial production was a constant proportion of primary productivity. However, GGE of bacteria has been shown to be negatively associated with temperature (Rivkin & Legendre 2001), impacting the relative amount of primary productivity portioned to bacteria. As a fundamental environmental variable which has been shown to impact organism physiological, life-history and ecological rates, its inclusion into further models exploring the potential impact of GGE on the food-web is essential.

Summary

Through the use of a mass-balanced model of relatively low complexity the GGE values used within food-web models were shown to have important consequences on predicting the distribution and flow of primary productivity through the planktonic food-web. This analysis has shown that using a common GGE value for all taxa can be inappropriate, and can, for instance, result in gross overestimation of ciliate production and biomass. Using only taxa-specific means, may also introduce unnecessary inaccuracy owing to the proportion of different diet types synthesised into predator biomass with different efficiencies. Using diet and taxa-specific GGEs

takes into account not only differences between taxa in their inherent ability to convert prey into their own biomass, but also the different efficiencies of prey types and their contribution to the total diet. The variation in predicted production and standing stock biomass of different taxa between suites of GGEs not only highlights the complexity of understanding even relatively simple marine food-webs structure, but also emphasises the need for the use of the most appropriate terms.

In recommendations by the Marine Zooplankton Colloquium 2 (2001) for future research the topic of zooplankton and biogeochemical cycles was highlighted as an important issue, with the question posed: "*What are the roles of zooplankton in supporting the microbial loop, and are they fundamentally different for protistan versus metazoan consumers?*" Although there are examples of where taxon-specific growth efficiencies have been applied to some extent (Vézina & Platt 1988, Pomeroy 2000), such cases are in the minority. Now that mean GGEs have been derived for a range of planktonic taxa feeding on different prey types, it would seem appropriate and prudent to incorporate these values into future ecosystem and food-web models.

Chapter 7. Impact of temperature on planktonic food-web structure: An investigation using simple, mass-balanced models.

Introduction

Temperature has a profound influence on all planktonic taxa, affecting behaviour, growth rates (Huntely & Lopez 1992, Nielson & Kiørboe 1994, Montagnes *et al.* 2003, Hirst & Bunker 2003) mortality (Hirst & Kiørboe 2002), respiration (Verity 1985, Caron *et al.* 1986, Del Giorgio & Williams 2005) and metabolic rates (Ikeda *et al.* 2001) to name a few. These physiological and ecological rates often vary between taxa and, through their impact on production and prey consumption, influence the efficiency with which prey is converted into predator biomass (gross growth efficiency, GGE). Temperature has been associated with changes in GGE, with a negative relationship observed for bacteria (Rivkin & Legendre 2001), for ciliates feeding on bacteria (Chapter 3, p.41), and positive for dinoflagellates. Temperature, posited as best correlate of species richness in the marine environment (Gaston 2000), is also associated in large scale changes in relative production of bacteria (Hoppe *et al.* 2001), community structure (Gasiunaite *et al.* 2005), and distribution of autotrophic (Fiala *et al.* 1998) and heterotrophic (Beaugrand *et al.* 2007, Helaouët & Beaugrand 2007) components of the planktonic food web.

Although GGEs are commonly used in ecosystem models, a single value is commonly used across all taxa (Stoecker & Evans 1985; Pomeroy 2000; Lewis 2005; Buitenhuis *et al.* 2006). Where taxon-specific GGEs have been used, they tend to be across broad taxa, for instance a common GGE used for all protozoa and for all metazoan zooplankton (Nielsen & Kiørboe 1991, Nielsen *et al.* 1993). Even fewer studies implement GGEs specific to individual protozoan taxa, as demonstrated by Lignell *et al.* (1993). The identification of a relationship between bacterial GGE and temperature has allowed its subsequent use in predicting carbon flux (Rivkin &

Legendre 2001). On the topic of the temperature-dependence of bacterial GGE Rivkin & Legendre (2001) stated "Incorporation of these new relationships into biogeochemical models could profoundly influence our estimates of global carbon cycling and remineralization by marine food webs." It is my aim to incorporate temperature-dependent GGEs into a simplified food web to determine the potential impact that temperature may have on carbon flow and the distribution of biomass between planktonic taxa. As GGEs of ciliates and dinoflagellates, two numerically and functionally important protists (Lessard & Swift 1985, Verity 1986, Weisse *et al.* 1990, Šolić & Krstulović 1994), responded differently to increasing temperature, and since ciliates are known bacterial grazers, and dinoflagellates gernally do not consume bacteria, I therefore suggest that with increasing temperature there is a large scope for change in production and biomass between taxa.

The value of GGE used can have important consequences on the predicted path and quantity of carbon flow to higher trophic levels. In a simplified model by Landry & Calbet (2004), the impact of using different GGE values for microzooplankton on the carbon availability to mesozooplankton was great enough for them to state *"differences in computed results for GGEs of 30% and 40% and the possibility of systematic variability related to trophic richness are substantial enough to merit attention."* The simplified, mass-balanced models used in this study represent the first attempt to address the issue of taxon-, diet-specific, and temperature-dependent GGEs on the planktonic food web and indicate that important structural changes, particularly within protozoa. Determining how production and biomass structure of protozoa varies with temperature is likely to enhance our understanding of how carbon flux through the planktonic food web varies globally. Using diet- and taxon-specific GGEs takes into account not only differences between taxa in their inherent ability to convert prey into their own biomass, but also the different efficiencies of prey types and their contribution to the total diet. I aim to investigate how, through its influence on GGE, temperature may impact the biomass structure and the flow of primary production through nutrient poor and rich planktonic food-webs. In addition, I examine whether

changes in production and biomass structure of the planktonic food-web resulting from the inclusion of taxon- and diet specific GGEs, are consistent with increasing temperature.

Methods

The model I use is a simplified, mass-balanced, representation of the planktonic food webs, and is identical in structure to the model in Chapter 6 (p.123), but with added temperature-dependent parameters. Autotrophic input values of phytoplankton, predator clearance efficiencies, respiration and excretion were identical to those used in the non-temperature dependent model, and therefore direct the reader to Chapter 6 (p.128) for the values and justification. Temperature-dependence of bacterial input, GGEs, and specific growth rates were incorporated for both LNA and HNA models, with polar, temperate and tropical temperature regimes represented by 3, 15 and 25°C respectively. Here I outline the temperature-dependent parameters included in my model, and their justification.

Bacterial input

On a global scale bacterial production, as a proportion of phytoplankton production (BP:PP), has been shown to scale with temperature by Hoppe *et al.* (2001). I digitised the reported relationship between the published ratios of bacterial production, determined via leucine uptake, to phytoplankton production, against temperature for the southern hemisphere using GetData Graph Digitiser version 2.24:

$$log_{10}(BP{:}PP) = 0.476 + 0.0409T \qquad \text{Equation 7.1}$$

where T is temperature (°C). As no clear evidence was found within the literature regarding a disparity between nutrient poor and rich conditions in terms of bacterial production relative to primary productivity, I use equation 7.1 for both models.

Gross Growth Efficiencies

The proportion of ingested material converted to production is referred to as gross growth efficiency (GGE). In the absence of evidence suggesting a difference in the GGE of different taxa between nutrient poor and rich waters, I assume identical values for both model types. Both the LNA and HNA models were run using one of three different suites of GGE values. For suite D, the GGE of all compartments (bacteria, ciliates, nano/microflagellates, dinoflagellates and copepods), was assumed to be 0.33, the mean value for all planktonic taxa derived in a synthesis by Straile (1997) and commonly used in ecosystem models (Pomeroy 2000, Lewis 2005, Buitenhuis *et al.* 2006) (Table 7.1). For Suite E GGE values are temperature dependent for dinoflagellates and bacteria according to the regressions derived in Chapter 3 (p.27), and taxon-specific means for ciliates, nano/microflagellates and copepods. The GGE values applied in suite F are specific to taxon and diet type (bactivorous, herbivorous, carnivorous or a mixed diet). Values were derived from taxon- and diet-specific regressions where GGE was found to be temperature dependent (ciliates feeding on bacteria, dinoflagellates feeding on algae). Where no temperature dependence was derived for diet-specific values, taxa-specific regressions were used, and where these where absent taxon- and diet-specific means were used as outlined Table 7.1. In order to examine the influence of temperature dependent GGEs, and allow a comparison between the temperature dependent model presented here with that of chapter 6, GGE suite G, which uses non-temperature dependent taxa specific means, and GGE suite H, non-temperature dependent taxa- and diet specific means, were also used.

Specific Growth Rates

To convert production into biomass, temperature- dependent instantaneous mass specific growth rate, μ (d^{-1}) were sought from the literature for all groups in order to estimate *in situ* growth rates. The relationship between specific growth rate and temperature for planktonic taxa is often described by exponential equations or values (Tables 7.2). For all groups of phytoplankton (pico, nano and micro) I derived mean specific growth values from the appendix of Calbet & Landry (2004) for three geographical regions, polar, temperate and tropical. For temperatures below 5°C

Table 7.1 **Gross growth efficiencies (GGE, %) used for the low (LNA) and high (HNA) nutrient models. Suite D values are derived from Straile (1997), whilst suites E and F, include temperature-dependent taxa–specific, and both taxa and diet–type specific GGEs respectively. Suites G and H represent taxa–specific, and both taxa and diet–type specific GGEs respectively, without temperature dependence. All GGEs are derived from Chapter 3. For suite F, values marked with an asterisk (*) are non–diet type specific, but average mean values.**

		Model	Gross Growth Efficiency (GGE, %)				
Taxon	**Prey**	**Notation**	**Suite D**	**Suite E**	**Suite F**	**Suite G**	**Suite H**
Ciliates	Picophytoplankton	*CilGGEPP*	33	16	28	16	28
	Nanophytoplankton	*CilGGEPN*	33	16	28	16	28
	Nano/microflagellates	*CilGGEF*	33	16	16*	16	16*
	Bacteria	*CilGGEB*	33	16	log10 GGE = –0.196 + 0.0610T	16	9
Nano/ microflagellates	Picophytoplankton	*FGGEPP*	33	39	62	39	62
	Bacteria	*FGGEB*	33	39	37	39	37
Dinoflagellates	Nanophytoplankton	*DGGEPN*	33	log10 GGE = 0.750 + 0.038T	log10 GGE = 0.219 + 0.064T	29	33
	Microphytoplankton	*DGGEPM*	33	log10 GGE = 0.750 + 0.038T	log10 GGE = 0.219 + 0.064T	29	33
Copepods	Picophytoplankton	*CopGGEPP*	33	26	27	26	33
	Nanophytoplankton	*CopGGEPN*	33	26	27	26	33
	Microphytoplankton	*CopGGEPM*	33	26	27	26	27
	Ciliates	*CopGGECil*	33	26	15	26	15
	Dinoflagellates	*CopGGED*	33	26	15	26	15

Table 7.2 **Temperature dependence of specific growth rates (μ, d^{-1}) ciliates, dinoflagellates, nano/microflagellates, copepods and bacteria reported in the literature. Where the upper limit of growth with increasing temperature was determined, this is indicated by stating Max growth. The range of temperatures for which dependences were determined indicated by minimum (Min.) and maximum (Max.) values. Q10 values marked with an asterisk (*) were derived from equations.**

	Growth Rate			Temperature (°C)		Notes
Taxon	**Q10**	**Equation**	**Source**	**Min.**	**Max.**	
Ciliates	2.6		Nielsen & Kiørboe (1994)	4	19	Mean (Temperate Coastal)
	2.2 to 3.0		Nielsen & Kiørboe (1994)	4	19	range (Temperate Coastal)
	2.9		Fenchel (1968)	8	20	Max. growth
	2.8		Finlay (1977)	10	25	Max. growth
	3.0		Hamilton & Preslan (1969)	15	20	Max. growth
	2.0		Verity (1985)	5	15	Max. growth
	1.5		Verity (1985)	15	25	Max. growth
		Linear increase, slope=0.08 $^{\circ}C^{-1}$	Derived from Montages *et al.* (2003)			Max. growth
	1.96*	$\log10\mu = -0.583 + 0.0293T$	Derived from Rose & Caron (2007)	0	40	n=909 from 71 studies
Dinoflagellates		Linear increase, slope=0.03 $^{\circ}C^{-1}$	Derived from Montages *et al.* (2003)			Max. growth
Nano/microflagellates	2.5		Caron *et al.* (1986)	14	26	Max. growth
	2.66		Choi & Peters (1992)			Single species
	2.72		Choi & Peters (1992)			Single species
	2.48		Caron *et al.* (1986)	14	26	Max. growth for single species
	1.1		Sherr *et al.*(1983)	3	30	Single species
		Linear increase, slope=0.08 $^{\circ}C^{-1}$	Derived from Montages *et al.* (2003)			Max. growth
	2.62*	$Log10\mu = -0.668 + 0.0419T$	Derived from Rose & Caron (2007)	0	30	n=184 from 27 studies

Table 7.2 Continued

Copepods	3.0		Mullin & Brooks (1970)	10	15	Max. growth
(0.1 to 1.0µg C)	3.32	Log10 μ = −1.938 + 0.0521T	Hirst *et al.* (2003)			
(1 to 10µg C)	1.96	Log10 μ = −1.467 + 0.0292T	Hirst *et al.* (2003)			
(100 to 1000µg C)	4.02	Log10 μ = −1.966 + 0.0604T	Hirst *et al.* (2003)			
Adult broadcasters	1.59	μ = −3.751 + 0.0463T	Hirst & Bunker (2003)	−2.3	29.4	*In situ*
Adult sac spawners	1.43	μ = −3.367 + 0.0359T	Hirst & Bunker (2003)	3.0	30.1	*In situ*
Juvenile broadcasters	2.19	μ = −2.898 + 0.0786T	Hirst & Bunker (2003)	7.6	28.2	*In situ*
Juvenile sac spawners	2.41	μ = −3.453 + 0.0881T	Hirst & Bunker (2003)	6.5	28.2	*In situ*
Adult broadcasters	1.59	μ = −3.337 + 0.0994T	Hirst & Bunker (2003)	−1.5	30.0	Food saturated
Adult sac spawners	1.43	μ = −4.328 + 0.1381T	Hirst & Bunker (2003)	1.3	23.8	Food saturated
Juvenile broadcasters	2.19	μ = −2.323 + 0.0623T	Hirst & Bunker (2003)	3.0	30.0	Food saturated
Juvenile sac spawners	2.41	μ = −2.514 + 0.0605T	Hirst & Bunker (2003)	3.0	25.0	Food saturated
	3.03*	μ = 0.0445 e^0.111T	Huntley & Lopez (1992)	−1.7	30.7	
	3.19*	μ = 0.0477 e^0.116T	Huntley & Lopez (1992)	−1.7	30.7	Upper 95% confidence limit)
	2.86*	μ = 0.0415 e^0.105T	Huntley & Lopez (1992)	−1.3	30.7	Lower 95% confidence limit)
Bacteria	3.31*	Log μ = −1.54 + 0.052T	White *et al.* (1991)			Marine
	2.88*	Log μ = −1.30 + 0.046T	White *et al.* (1991)			Estuarine & Coastal
	3.9		White *et al.* (1991)			Salt water
	1.50*	Log μ = −0.949 + 0.0176T	Rivkin *et al.* (1996)			All temperatures
	1.44*	Log μ = −0.918 + 0.0157T	Rivkin *et al.* (1996)			For temperature>4°C

the polar mean was used, above 20°C the tropical mean, with the temperate mean used at all intermediate temperatures.

For nano/microflagellates the majority of studies that reported the temperature dependence of specific growth rate dealt with maximum growth. As these groups were likely to be limited in the natural environment, for instance by food availability, their growth rates are likely be sub-optimal and were therefore deemed too high for inclusion in my study. I derived my own relationships between growth rate and temperature after obtaining temperature and growth rates from the appendix of Rose & Caron (2007) for heterotrophic ciliates (n=909, 71 studies) and nano/microflagellates (n=184, 27 studies). Following a log10 transformation of specific growth rate I performed an ordinary least-square regression using the statistical package MINITAB v.15 for both ciliates ($p<0.001$, R-squared=16.5%, n=909; Appendix 23) and nano/microflagellates ($p<0.001$, R-squared=17.2%, n=184; Appendix 24).

The growth rates of dinoflagellates are typically much lower than other protozoa, whilst sharing comparable temperature dependence of maximum growth (both increase with a slope of $0.03°C^{-1}$; Montagnes *et al.* 2003). Using data from the appendix of Rose & Caron (2007), I found the mean average specific growth rate of dinoflagellates to be approximately one third of that of ciliates, which closely matches the findings of Montagnes *et al.* (2003). In my model I therefore make the assumption that dinoflagellate specific growth is a third of that of ciliates, with an identical temperature (slope).

Although the temperature dependence of bacterial growth has been derived over a large temperature range (White *et al.* 1991), I take a cautious approach to using equations over the full range following evidence by Rivkin *et al.* (1996) that at temperatures below 4°C no clear trend can be determined. I therefore employ the temperature dependence outlined in Rivkin *et al.* (1996) for temperatures greater than 4°C, and use a mean specific growth value for colder temperatures.

The relationship between copepod specific growth rate and temperature has been comprehensively detailed by Hirst & Bunker (2003) where *in situ* growth rates and

temperature dependence was found to be lower than when under food saturated conditions. In my models I use the temperature dependence of adult broadcasters (species that release their eggs), which were derived from a greater data set (n=3081) than sac spawners (those that retain their eggs; n=452) whilst sharing a similar mean (0.15 & 0.16 d^{-1}) and slightly higher temperature dependence (=1.59 & 1.43 respectively).

Results

Production

Of all the suites of GGE values, using a common GGE value for all heterotrophic planktonic groups resulted in the highest production values, relative to total phytoplankton production, for ciliates, and copepods. This was the case for the polar, temperature, and tropical temperature regimes, for LNA and HNA models (Table 7.3).

Ciliate relative production was consistently lowest under all temperature regimes (polar, temperate and tropical) for nutrient poor and rich conditions when using taxon- specific GGEs (suite E), and was significantly lower (no overlap of confidence limits) than values derived using a common GGE (suite D). When taking diet-specific GGEs into account (suite F) ciliate production was intermediate between that of suites D and E, and was not significantly different to either suite. Production in nutrient poor and rich models using suite E was approximately 50% of that estimated using a common GGE (suite D), although when diet specific GGEs are also taken into account (suite F), production was approximately 20% less than using suite D.

Under all temperature regimes copepod relative production was highly similar using suites E and F in the LNA model, and a 25% reduction of values derived using a common GGE for all taxa (Figure 7.1). Across GGE suites, production did not differ significantly, whilst across temperature regimes values remained very consistent within each suite (increase ≤ 5% between polar and tropical environments).

Table 7.3 Production values (as a proportion of total phytoplankton production, % PP) of nano/microflagellates, ciliates, dinoflagellates and copepods using a common GGE value for all taxa (suite D), taxon specific GGEs (Suite E), and taxon and diet type specific GGEs in models of low (LNA) and high (HNA) nutrients. Upper and lower production limits are indicated by – and + respectively, and derived using parameter values (clearance efficiencies, GGEs, specific growth rates, and bacterial input values) 10% above and below that chosen for the central model (see method section of Chapter 6; p. 138). Models were run under polar (3°C), temperate (15°C) and tropical (25°C) regimes.

		Polar (3°C)											
GGE	Trophic	Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite	State	% PP	–	+	% PP	–	+	% PP	–	+	% PP	–	+
D	LNA	8.1	6.6	9.8	8.1	6.6	9.9	2.5	2.0	3.0	7.2	5.8	8.7
	HNA	4.8	3.9	5.9	12.9	10.5	15.6	2.9	2.3	3.5	5.0	4.0	6.0
E	LNA	9.6	7.8	11.6	4.2	3.4	5.1	0.5	0.4	0.7	5.4	4.3	6.5
	HNA	5.7	4.6	6.9	6.4	5.2	7.7	0.6	0.5	0.8	3.5	2.8	4.2
F	LNA	14.5	11.7	17.5	6.8	5.5	8.2	0.2	0.2	0.2	5.5	4.5	6.7
	HNA	8.4	6.8	10.1	10.8	8.7	13.0	0.2	0.2	0.3	3.6	2.9	4.3
		Temperate (15°C)											
GGE	Trophic	Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite	State	% PP	–	+	% PP	–	+	% PP	–	+	% PP	–	+
D	LNA	10.3	8.4	12.5	9.3	7.5	11.2	2.5	2.0	3.0	7.3	5.9	8.8
	HNA	6.9	5.6	8.4	14.0	11.3	16.9	2.9	2.3	3.5	5.1	4.1	6.1
E	LNA	12.2	9.9	14.8	4.8	3.9	5.8	1.6	1.3	1.9	5.5	4.4	6.6
	HNA	8.2	6.6	9.9	7.0	5.7	8.5	1.8	1.5	2.2	3.6	2.9	4.3
F	LNA	16.9	13.7	20.5	7.3	5.9	8.8	1.1	0.9	1.4	5.6	4.5	6.7
	HNA	10.7	8.6	12.9	11.2	9.1	13.6	1.3	1.1	1.6	3.6	2.9	4.4
		Tropical (25°C)											
GGE	Trophic	Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite	State	% PP	–	+	% PP	–	+	% PP	–	+	% PP	–	+
D	LNA	15.4	12.5	18.6	11.9	9.6	14.4	2.5	2.0	3.0	7.5	6.0	9.0
	HNA	11.7	9.4	14.1	16.5	13.4	20.0	2.9	2.3	3.5	5.2	4.2	6.3
E	LNA	18.2	14.7	22.0	6.2	5.0	7.5	3.8	3.0	4.6	5.6	4.6	6.8
	HNA	13.8	11.2	16.7	8.4	6.8	10.1	4.4	3.6	5.3	3.8	3.1	4.6
F	LNA	22.6	18.3	27.4	9.1	7.4	11.0	5.0	4.1	6.1	5.7	4.7	6.9
	HNA	16.0	13.0	19.4	13.0	10.6	15.8	5.9	4.8	7.1	3.8	3.1	4.6

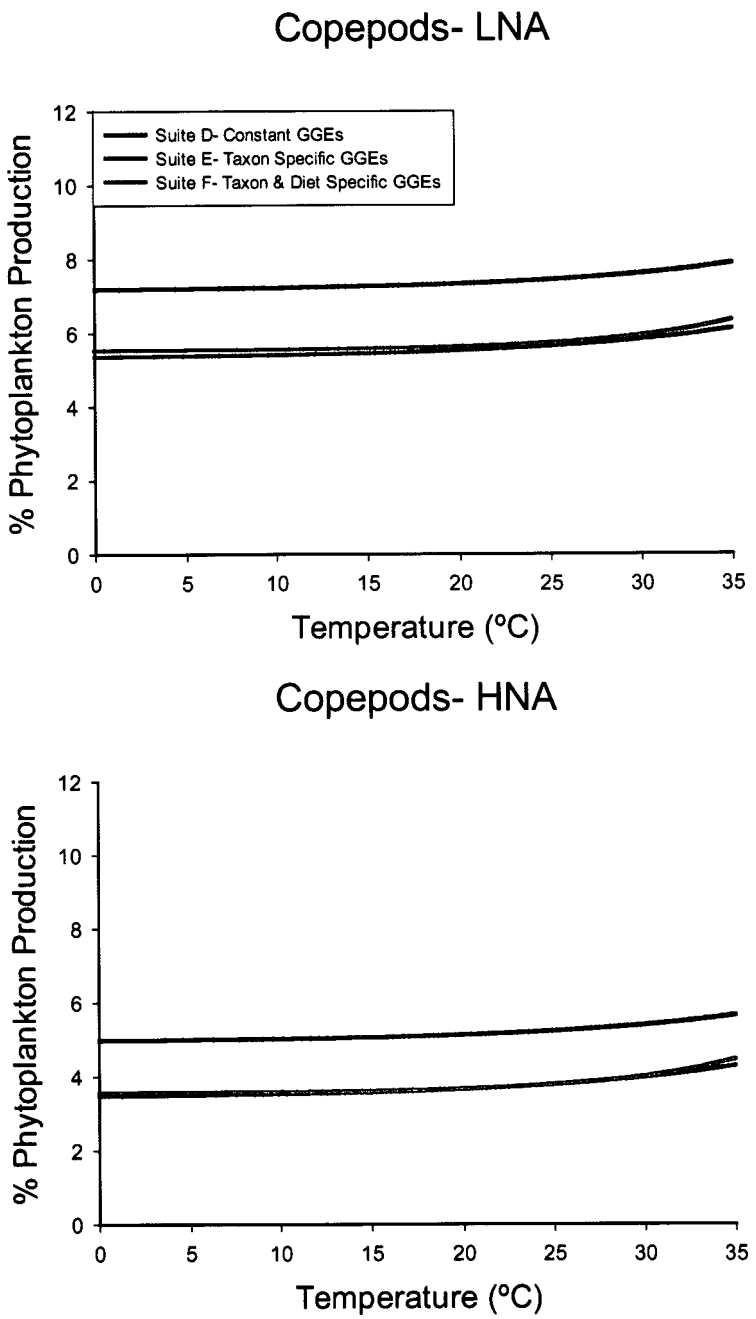


Figure 7.1 Copepod production, expressed as a percentage of total phytoplankton production, in response to temperature in low (LNA) and high (HNA) nutrient environments. Production values are determined using common for all planktonic taxa (suite D), taxon specific (suite E), or both taxon and diet type specific (suite F).

For instance, under the polar temperature regime copepod production was just 7.2% using a common GGE value and 5.4% of that derived using only taxon specific values (Table 7.3). At higher temperatures HNA copepod production was greater using suite F than using suite E, representing 80% of that using suite D, a common GGE.

Using common GGE values provided the lowest estimate of nano/microflagellates relative production, with the highest estimates derived using taxon-and diet-specific GGEs (suite F) in both LNA and HNA models. Under the polar and temperate regimes nano/microflagellate production derived using suite D was significantly lower than that derived using suite F, representing approximately 56% of the production of the latter suite in the polar region, and 70% under the tropical regime for LNA and HNA models. Intermediate values of nano/microflagellate relative production were obtained using only taxon-specific values (suite E), which were not significantly different from other suites, and approximated 66% of production using suite F for polar HNA and LNA models, and 80 and 86% under the tropical regime.

Under the polar and temperate regimes dinoflagellate relative production was lowest using taxon-and diet-specific GGEs (suite F) in both the LNA and HNA models, and significantly lower than the highest estimates derived using suite D (Figure 7.2). Using GGE suite F dinoflagellate production was only 8 and 7% of that using suite D for the LNA and HNA polar models, and 44 and 45% in the temperature model. However, under the tropical regime, using suite F provided estimates of dinoflagellate production significantly greater, and approximately double that of estimates derived using suite D. For instance, dinoflagellate production using taxon and diet type specific GGEs under the tropical regime was twice that using a common GGE. In the polar and temperate models using only taxon-specific GGES (suite E) provide values intermediate of those derived using suites D and F, and significantly lower than values of the former. Under the tropical regime however, dinoflagellate production derived using suite E was significantly greater than using a common GGE value across taxa (suite D), with estimates approximately a third greater in both the LNA and HNA models.

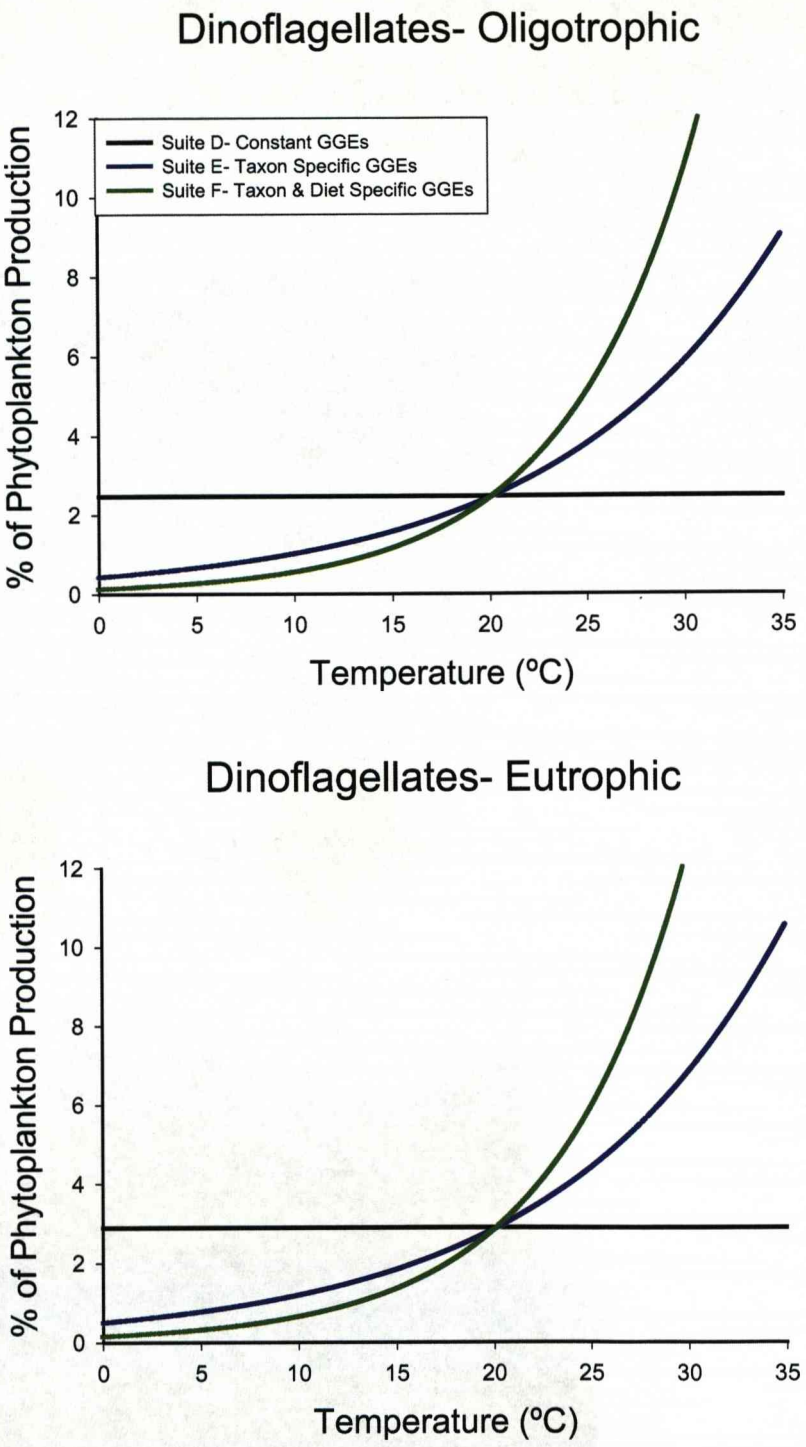


Figure 7.2 Dinoflagellate production, expressed as a percentage of total phytoplankton production, in response to temperature in the LNA and HNA environment. Production values are determined using common for all planktonic taxa (suite D), taxon specific (suite E), or both taxon and diet type specific (suite F).

Thus use of non-temperature dependent, taxa-specific GGEs (suite G) provided production estimates (relative to total phytoplankton production) of nano/microflagellates, that although were higher than those derived using a common GGE (suite D), did not vary significantly within both the LNA (polar=9.6%, temperate=12.2%, tropical=18.2%) and HNA (polar=5.7%, temperate=8.2%, tropical=13.8%) models (Table 7.4).

Using suite G, relative production of copepods (LNA: polar=5.5%, temperate=5.5%, tropical=5.6%, HNA: polar=3.6%, temperate=3.6%, tropical=3.7%), and dinoflagellates (polar, temperate and tropical: LNA=2.2%, HNA=2.6%), although lower than estimates derived using suite D, not decrease below the lower confidence limits for all temperature regimes.

Ciliate relative biomass was far lower using suite G, in comparison to suite D under all temperature regimes and both trophic models (LNA: polar=4.2%, temperate=4.8%, tropical=8.4%, HNA: polar=6.4%, temperate=7.0%, tropical=8.4%).The use of non-temperature dependent, taxa-, and diet-specific GGEs resulted in a nano/microflagellate production significantly greater than estimates derived using suite D in the polar (LNA=14.5%, HNA=8.4%), and temperate (LNA=16.9%, HNA=10.7%) regimes, but did not vary in the tropical regime (LNA=22.6, HNA=16.0%).

Copepod production did not vary significantly from values using suite D in the polar (LNA=6.2%, HNA=4.2), temperate (LNA=6.3%, HNA=4.2%), and tropical regimes (LNA=6.3%, HNA=4.3%), as was the case for dinoflagellates (polar, temperate and tropical: LNA=2.5%, HNA=2.9%).

Estimated ciliate relative biomass meanwhile, although lower using suite H, did not vary significantly from values derived using suite D for polar (LNA=6.8%, HNA=10.8%), temperate (LNA=7.3%, HNA=11.3%) and tropical (LNA=8.5%, HNA=12.4%) regimes.

Table 7.4 **Production values (as a proportion of total phytoplankton production, % PP) of nano/microflagellates, ciliates, dinoflagellates and copepods using using a non-temperature dependent GGEs specific to each taxon (Suite G), and to both taxon and diet type (suite H) in low (LNA) and high (HNA) nutrient models. Upper and lower production limits are indicated by – and + respectively, and derived using parameter values (clearance efficiencies, GGEs, specific growth rates, and bacterial input values) 10% above and below that chosen for the central model (see method section of Chapter 6; p. 138). Models were run under polar (3°C), temperate (15°C) and tropical (25°C) regimes.**

		Polar (3°C)											
GGE	Trophic Model	Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite		% PP	–	+	% PP	–	+	% PP	–	+	% PP	–	+
G	LNA	9.6	7.8	11.6	4.2	3.4	5.1	2.2	1.8	2.7	5.5	4.4	6.6
	HNA	5.7	4.6	6.9	6.4	5.2	7.7	2.6	2.1	3.2	3.6	2.9	4.3
H	LNA	14.5	11.7	17.5	6.8	5.5	8.3	2.5	2.0	3.0	6.2	5.1	7.6
	HNA	8.4	6.8	10.1	10.8	8.8	13.1	2.9	2.3	3.5	4.2	3.4	5.1
		Temperate (15°C)											
GGE	Trophic Model	Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite		% PP	–	+	% PP	–	+	% PP	–	+	% PP	–	+
G	LNA	12.2	9.9	14.8	4.8	3.9	5.8	2.2	1.8	2.7	5.5	4.4	6.6
	HNA	8.2	6.6	9.9	7.0	5.7	8.5	2.6	2.1	3.2	3.6	2.9	4.4
H	LNA	16.9	13.7	20.5	7.3	5.9	8.9	2.5	2.0	3.0	6.3	5.1	7.6
	HNA	10.7	8.6	12.9	11.3	9.2	13.7	2.9	2.3	3.5	4.2	3.4	5.1
		Tropical (25°C)											
GGE	Trophic Model	Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite		% PP	–	+	% PP	–	+	% PP	–	+	% PP	–	+
G	LNA	18.2	14.7	22.0	6.2	5.0	7.5	2.2	1.8	2.7	5.6	4.5	6.7
	HNA	13.8	11.2	16.7	8.4	6.8	10.1	2.6	2.1	3.2	3.7	3.0	4.5
H	LNA	22.6	18.3	27.4	8.5	6.9	10.3	2.5	2.0	3.0	6.3	5.1	7.6
	HNA	16.0	13.0	19.4	12.4	10.1	15.0	2.9	2.3	3.5	4.3	3.5	5.2

Biomass

In comparison to models using a common GGE for all planktonic taxa, those that used either only taxon-specific values (suite E) or both taxon- and diet-specific values (suite F) reduced estimates of the contribution of copepod biomass by approximately 25 and 30% in the LNA and HNA models respectively (Figure 7.3, Table 7.5), although values did were not significantly different i.e. there was overlap in confidence limits between suites. Copepod biomass, relative to phytoplankton biomass, was very similar using suites E and F, with less than 3% difference observed between the two. Under the tropical regime bacterial relative biomasses exceeded that of copepods for LNA and HNA models using all three GGE suites. For LNA models, copepod relative biomass fell within the lower estimates of bacterial biomass, but did not using suites E and F in HNA models.

The relative biomass of nano/microflagellates was lowest using GGE suite D, but not significantly different form other suites. Suite F provided the greatest estimate, with the greatest increase between suites observed in the polar regime where values were 44 and 42% higher than those of suite D for LNA and HNA models respectively. Across temperature regimes, nano/microflagellate relative biomass decreased with increasing temperature for LNA and HNA models using all GGE suites. In LNA models, nano/microflagellates relative biomass under the tropical regime was approximately 32% of that derived in the polar regime using suites D and E, and 27% using suite F. In the HNA models nano/microflagellate relative biomass was 41% of that in the polar environment using suites D and E, and 33% using suite F.

Ciliate relative biomass decreased with increasing temperature, with values derived under the tropical regime less than half that in the polar regime for all GGE suites in LNA and HNA models (Figure 7.4). Estimates of ciliate relative biomass were greatest when using suite D, which were significantly greater than, and approximately twice that of the lowest estimates derived with suite E for LNA and HNA models. The use of taxon- and diet-specific GGEs (suite F), provided relative biomasses of ciliates approximately 20% less than those derived with a common GGE for all taxa (suite D) for LNA and HNA models under all temperature regimes, although there was no significant difference.

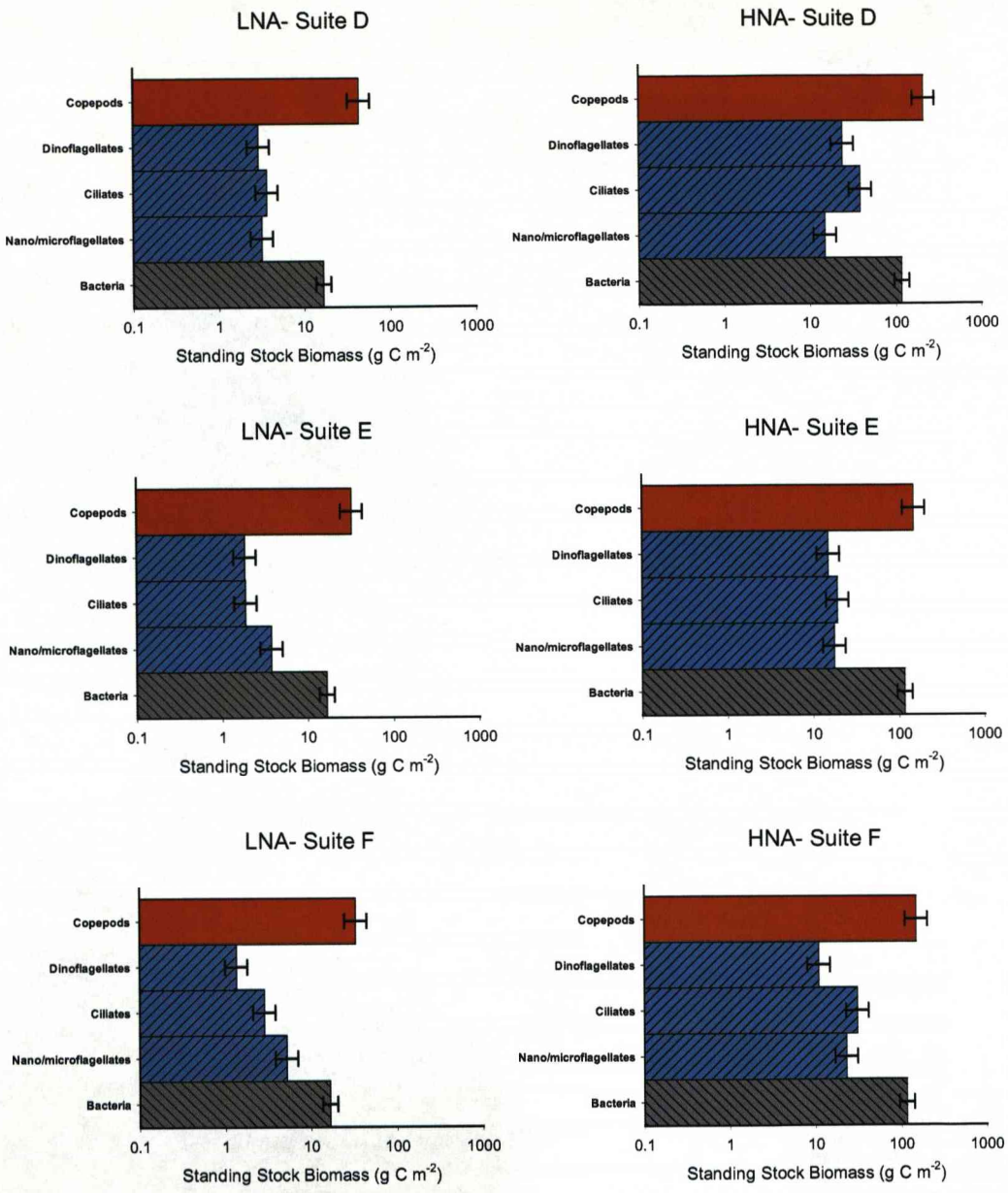


Figure 7.3 Structure of the planktonic food–web in terms of standing stock biomass (g C m^{-2}) in nutrient poor (LNA) and rich (HNA) environments under a temperate regime (15°C). Different GGE values used to derive biomass values were either common for all planktonic taxa (suite D), taxon specific (suite E), or both taxon and diet type specific (suite F). Error bars represent upper and lower biomass limits derived using parameter values (clearance efficiencies, GGEs, specific growth rates, and bacterial input values) 10% above and below that chosen for the central model (see method section of Chapter 6; p. 138).

Table 7.5 **Biomass values (as a proportion of total phytoplankton biomass, % PB) of nano/microflagellates, ciliates, dinoflagellates, copepods and bacteria using a common GGE value for all taxa (suite D), taxon specific GGEs (Suite E), and taxon and diet type specific GGEs in models of low (LNA) and high (HNA) nutrients. Upper and lower production limits are indicated by – and + respectively, the derivation of which is described in the method section (p.138). Models were run under polar (3°C), temperate (15°C) and tropical (25°C) regimes.**

Polar (3°C)

GGE	Trophic	Bacteria			Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite	State	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+
D	LNA	4.7	3.8	5.8	13.1	9.6	17.6	11.8	8.7	15.8	10.7	7.9	14.4	123.3	90.8	165.8
	HNA	4.7	3.8	5.8	7.8	5.7	10.5	18.7	13.7	25.1	12.5	9.2	16.8	85.4	62.9	114.8
E	LNA	4.7	3.8	5.8	15.5	11.4	20.8	6.0	4.5	8.1	2.4	1.7	3.2	91.9	67.7	123.6
	HNA	4.7	3.8	5.8	9.2	6.8	12.4	9.3	6.8	12.4	2.8	2.0	3.7	59.5	43.8	80.0
F	LNA	4.7	3.8	5.8	23.3	17.2	31.4	9.8	7.2	13.2	0.8	0.6	1.1	94.7	69.7	127.3
	HNA	4.7	3.8	5.8	13.5	9.9	18.1	15.6	11.5	20.9	1.0	0.7	1.3	60.9	44.9	81.9

Temperate (15°C)

GGE	Trophic	Bacteria			Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite	State	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+
D	LNA	33.1	27.1	40.5	6.3	4.7	8.5	7.2	5.3	9.7	5.8	4.3	7.8	86.6	63.8	116.4
	HNA	33.1	27.1	40.5	4.2	3.1	5.7	10.9	8.0	14.7	6.7	5.0	9.1	60.2	44.3	80.9
E	LNA	33.1	27.1	40.5	7.5	5.5	10.1	3.7	2.8	5.0	3.7	2.7	4.9	64.9	47.8	87.2
	HNA	33.1	27.1	40.5	5.0	3.7	6.7	5.4	4.0	7.3	4.3	3.1	5.7	42.4	31.2	57.0
F	LNA	33.1	27.1	40.5	10.4	7.6	14.0	5.7	4.2	7.6	2.7	2.0	3.6	66.3	48.8	89.1
	HNA	33.1	27.1	40.5	6.5	4.8	8.8	8.8	6.4	11.8	3.1	2.3	4.2	42.9	31.6	57.7

Tropical (25°C)

GGE	Trophic	Bacteria			Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite	State	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+
D	LNA	69.3	56.7	84.7	4.2	3.1	5.7	5.5	4.1	7.4	3.5	2.5	4.6	65.4	48.1	87.9
	HNA	69.3	56.7	84.7	3.2	2.4	4.3	7.7	5.7	10.3	4.0	3.0	5.4	45.9	33.8	61.6
E	LNA	69.3	56.7	84.7	5.0	3.7	6.7	2.9	2.1	3.9	5.2	3.9	7.1	49.5	36.5	66.6
	HNA	69.3	56.7	84.7	3.8	2.8	5.1	3.9	2.9	5.2	6.1	4.5	8.2	33.1	24.4	44.5
F	LNA	69.3	56.7	84.7	6.2	4.6	8.3	4.2	3.1	5.7	7.0	5.2	9.5	50.4	37.1	67.8
	HNA	69.3	56.7	84.7	4.4	3.2	5.9	6.1	4.5	8.1	8.2	6.0	11.0	33.3	24.5	44.8

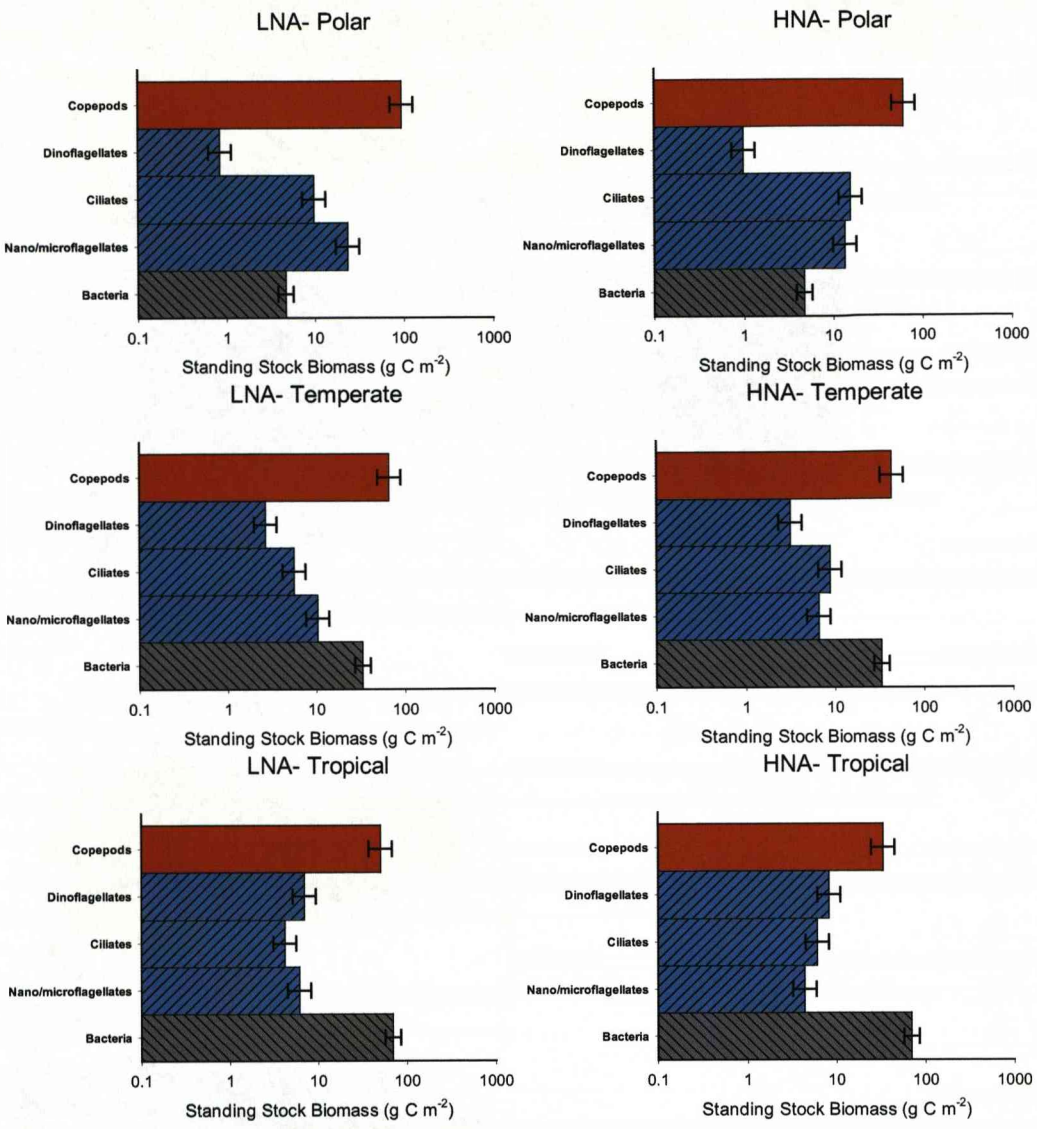


Figure 7.4 Structure of the planktonic food–web in terms of biomass relative to total phytoplankton biomass in the environments of low (LNA) and high (HNA) nutirents under polar (3°C), temperate (15°C) and tropical (25°C) temperature regimes using taxon–, diet– and temperature specific GGEs (suite F). Error bars represent upper and lower limits as described in the Methods section (p.138).

Copepods maintained a superior, and significantly greater biomass than ciliates dinoflagellates and nano/microflagellates in both low and high nutrients under polar, temperate, and tropical regimes. Bacterial relative biomass was consistently lower that copepod relative biomass under all GGE suites in the LNA and HNA polar models.

Under the temperate regime, copepod relative biomass exceeded bacterial relative biomass using all GGE suites in the LNA models, and using suite D in the HNA model. However, whilst bacterial relative biomasses using suites E and F were lower than copepod relative biomass by approximately 12% in temperate HNA models, values fell with the lower limits of estimates of copepod relative biomass. Within the LNA model, I found the distribution of biomass between protozoan groups to be approximately equal, with a high degree of overlap confidence limits, when using a common GGE (suite D) at temperate regimes. However, when taxon–specific GGEs are considered, nano/microflagellates had a superior, and significantly greater biomass than ciliates and dinoflagellates at low temperatures (for instance polar and temperate regimes), with the latter protozoan group having the lowest biomass. As temperature increased, dinoflagellates increased in biomass, having the highest protozoan biomass (although not significant greater) in the tropical regime.

In the HNA model ciliates dominated protozoan biomass under all temperature regimes using a common GGE value for all taxa, with values significantly greater than nano/microflagellates. However, when considering taxon– and also diet–specific GGES both ciliates and nano/microflagellates had comparable biomass with a high degree of overlap of confidence limits, and both were significantly greater than dinoflagellate biomass in polar and temperate regimes. The change in protozoan structure with suites of GGEs differed at the highest temperatures. Under the tropical regime dinoflagellate biomass was significantly greater than that of nano/microflagellates using taxon–specific GGEs and became comparable to ciliate biomass when diet–specific values were also considered.

The use of non-temperature dependent, taxa-specific GGEs (suite G) provided nano/microflagellate biomass estimates (relative to total phytoplankton biomass),

that although greater than those derived using suite D, did not vary significantly in polar (LNA=15.5%, HNA=9.2%) temperate (LNA=7.5%, HNA=5.0%) or tropical (LNA=5.0%, HNA=3.8%) regimes (Table 7.6, Figure 7.5). Ciliate relative biomass was significantly lower in polar (LNA=6.0%, HNA=9.3%) temperate (LNA=3.7%, HNA=5.4%) and tropical (LNA=2.9%, HNA=3.9%) regimes using suite G than in models using suite D.

Dinoflagellates relative biomass, although lower using GGE suite G in polar (LNA=9.7%, HNA=11.5%) temperate (LNA=5.2%, HNA=6.2%) and tropical (LNA=3.1%, HNA=3.7%) regimes, did not exceed the confidence limits of values derived using suite G.

Copepod relative biomass was also lower in polar (LNA=93.4%, HNA=61.3%) temperate (LNA=65.3%, HNA=42.9%) and tropical (LNA=48.8%, HNA=32.3%) regimes using suite G than in models using suite D, but did not exceed confidence limits, and therefore did not vary significantly.

The use of non-temperature dependent, taxa-, and diet-specific GGEs (suite H) provided nano/microflagellate biomass estimates (relative to total phytoplankton biomass), that although greater than those derived using suite D, did not vary significantly in polar (LNA=23.3%, HNA=13.5%) temperate (LNA=10.4%, HNA=6.5%) or tropical (LNA=6.2%, HNA=4.4%) regimes.

Although ciliate relative biomass was lower using suite H than suite D for all temperature regimes (LNA=9.9%, HNA=15.7%) temperate (LNA=5.7%, HNA=5.8%) and tropical (LNA=4.0%, HNA=5.8%), values did not vary significantly. Dinoflagellates relative biomass, although lower using GGE suite G in polar (LNA=10.7%, HNA=12.5%) temperate (LNA=5.8%, HNA=6.7%) and tropical (LNA=3.5%, HNA=4.0%) regimes, did not exceed the confidence limits of values derived using suite H. Copepod relative biomass was also lower in polar (LNA=106.9%, HNA=72.3%) temperate (LNA=74.4%, HNA=50.4%) and tropical (LNA=55.2%, HNA=37.5%) regimes using suite H than in models using suite D, but did not exceed confidence limits, and therefore did not vary significantly.

Table 7.6 **Biomass values (as a proportion of total phytoplankton biomass, % PB) of nano/microflagellates, ciliates, dinoflagellates, copepods and bacteria using a non-temperature dependent GGEs specific to each taxon (Suite G), and to both taxon and diet type (suite H) in low (LNA) and high (HNA) nutrient models. Upper and lower indicated by – and + respectively, and derived using parameter values (clearance efficiencies, GGEs, specific growth rates, and bacterial input values) 10% above and below that chosen for the central model (see method section of Chapter 6; p. 138. Models were run under polar (3°C), temperate (15°C) and tropical (25°C) regimes.**

Polar (3°C)

GGE	Trophic	Bacteria			Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite	State	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+
G	LNA	4.7	3.8	5.8	15.5	11.4	20.8	6.0	4.5	8.1	9.7	7.1	13.0	93.4	68.8	125.6
	HNA	4.7	3.8	5.8	9.2	6.8	12.4	9.3	6.8	12.4	11.5	8.5	15.4	61.3	45.1	82.4
H	LNA	4.7	3.8	5.8	23.3	17.2	31.4	9.9	7.3	13.3	10.7	7.9	14.4	106.9	78.7	143.7
	HNA	4.7	3.8	5.8	13.5	9.9	18.1	15.7	11.5	21.0	12.5	9.2	16.8	72.3	53.2	97.2

Temperate (15°C)

GGE	Trophic	Bacteria			Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite	State	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+
G	LNA	33.1	27.1	40.5	7.5	5.5	10.1	3.7	2.8	5.0	5.2	3.8	7.0	65.3	48.1	87.8
	HNA	33.1	27.1	40.5	5.0	3.7	6.7	5.4	4.0	7.3	6.2	4.6	8.3	42.9	31.6	57.7
H	LNA	33.1	27.1	40.5	10.4	7.6	14.0	5.7	4.2	7.7	5.8	4.3	7.8	74.4	54.8	100.1
	HNA	33.1	27.1	40.5	6.5	4.8	8.8	8.8	6.5	11.8	6.7	5.0	9.1	50.4	37.1	67.7

Tropical (25°C)

GGE	Trophic	Bacteria			Nano/microflagellates			Ciliates			Dinoflagellates			Copepods		
Suite	State	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+	% PB	–	+
G	LNA	69.3	56.7	84.7	5.0	3.7	6.7	2.9	2.1	3.9	3.1	2.3	4.2	48.8	35.9	65.6
	HNA	69.3	56.7	84.7	3.8	2.8	5.1	3.9	2.9	5.2	3.7	2.7	5.0	32.3	23.8	43.4
H	LNA	69.3	56.7	84.7	6.2	4.6	8.3	4.0	2.9	5.3	3.5	2.5	4.6	55.2	40.7	74.2
	HNA	69.3	56.7	84.7	4.4	3.2	5.9	5.8	4.3	7.8	4.0	3.0	5.4	37.5	27.6	50.4

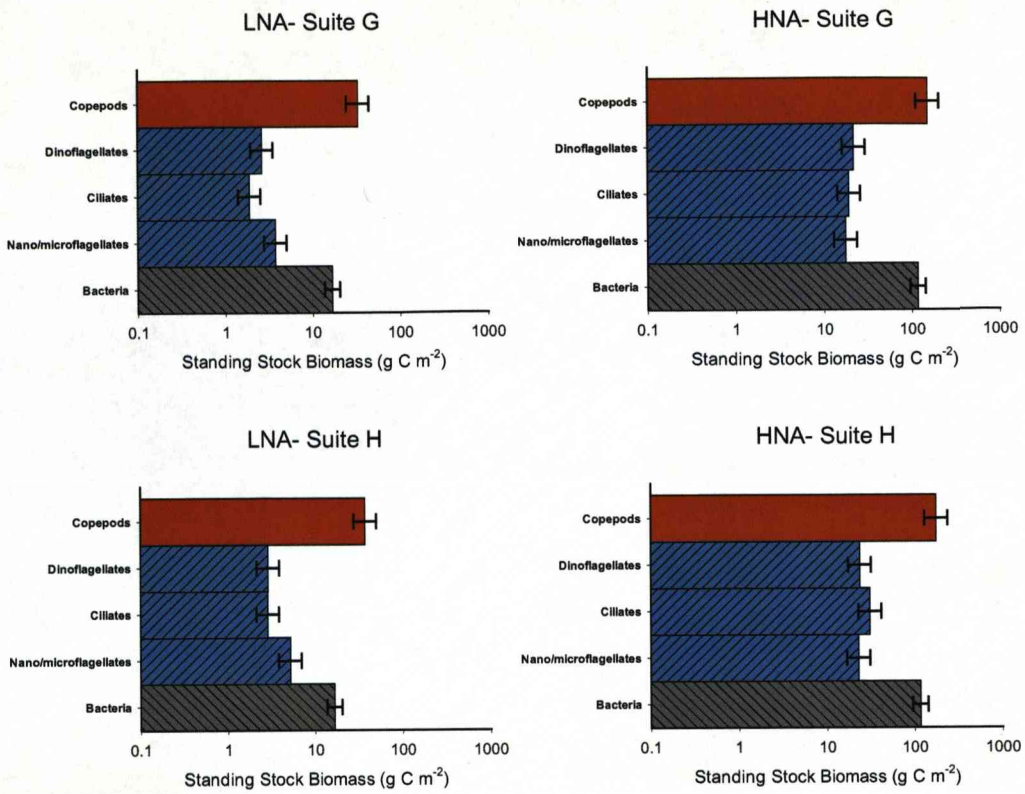


Figure 7.5 Structure of the planktonic food–web in terms of standing stock biomass (g C m^{-2}) in nutrient poor (LNA) and rich (HNA) environments under a temperate regime (15°C). Different GGE values used to derive biomass values were common for all planktonic taxa and either the mean from Straile (1997) (suite G), or from Chapter 3 (suite H). Error bars represent upper and lower biomass limits derived using parameter values (clearance efficiencies, GGEs, specific growth rates, and bacterial input values) 10% above and below that chosen for the central model (see method section of Chapter 6; p. 138).

Discussion

The results shown indicate that ecosystem models using a common GGE for all taxa are prone to inaccuracies, the extent of which may vary with temperature. The use of taxon-specific and diet specific GGEs within LNA and HNA models affected the predicted production and distribution of biomass between taxa of the planktonic food web. Using a common GGE for all planktonic taxa can lead to an overestimation of production and biomass, relative to phytoplankton, for both ciliates and copepods, in comparison to when taxon-specific GGEs are considered. At the highest temperature, such as those illustrated in the tropical regimes, dinoflagellate and nano/microflagellate production was predicted to be much greater using taxon- and diet-specific GGEs. However, my results suggest that dinoflagellate biomass may be overestimated in all but the warmest of environments, whilst nano/microflagellates may be underestimated using a common GGE value by up to 40%.

The effect of different GGE suites on the production of dinoflagellates varied according to temperature. At lower temperatures, including the polar and temperate regimes, the use of suite D appears to overestimate dinoflagellate production. At higher temperatures however, such as that in the tropical regime, dinoflagellate production was estimate to be double when incorporating taxon- and diet-specific GGEs in comparison to a common GGE for all taxa.

A relatively constant contribution of copepod biomass to planktonic biota is consistent with my findings in Chapter 4 (p.91), where copepods, and total mesozooplankton relative biomass did not vary significantly with increasing temperature. Consequently, the grazing pressure of copepods on microzooplankton is also unlikely to vary with temperature, and more likely to vary with levels of primary production due to changes in phytoplankton size structure (Calbet 2001, Calbet *et al.* 2008). Copepods are important contributors to the regeneration of nutrients, providing picophytoplantkon and bacterial with up to 23% of their production requirements (Hernández-León 2008). The extent to which nutrient regeneration by copepods varies with temperature is unlikely to be high as

copepod production remains constant. Therefore copepod nitrogen excretion rates, which were shown to decrease with increasing latitude, from 0.65 gigatons N $year^{-1}$ in tropical waters to 0.05 gigatons N $year^{-1}$ in polar waters (Hernández-León 2008), are likely to be the result of food availability, rather than an change in the efficiency of processing nitrogen.

However, although copepod relative biomass did not vary significant with increasing temperature, there was a general negative trend which may be a product of the absence of temperature dependent clearance efficiencies within the model. In the natural environment copepods are able to switch prey types to that are most abundant (Gismervik & Anderson 1997, Kiørboe et al 1996). For example, in a review of copepod grazing it has been shown that the contribution of ciliates to copepod diet decreases with increasing phytoplankton concentration (Calbet & Saiz 2005). Although my model accounts for changes in phytoplankton size structure between nutrient rich and poor areas, changes as a result of increased temperature are not considered. If increased temperature results in a change in phytoplankton size structure favourable to copepods (e.g. an increased proportion of microphytoplankton), then copepod biomass estimated in this study is likely to be underestimated at higher temperatures.

This model the first step in understanding the effect of using taxa-, diet-specific and temperature dependent GGEs on the planktonic food web. Models of both high and low complexity benefit from the determination and inclusion of accurate parameters, and in particular their response to temperature. Some parameters are well documented, for instance copepod growth rates have been detailed extensively, with robust relationships outlined within the literature (Huntley & Lopez 1992, Hirst *et al.* 2003, Hirst & Bunker 2003). However others likely to benefit our understanding of the food-web dynamics and biogeochemical cycles, such as clearance efficiency (the proportion of available prey consumed by a predator), are in need of further research. Although values of clearance efficiency are available within the literature, they are often reported as single values, single experiments, from small locations or over a narrow time period.

At higher temperatures viscosity of water decreases, giving a greater Reynolds number which has been shown to be important in the feeding mechanism of calanoid copepods which feed by the generating a current with their appendages (Koehl & Strickler 1981, Naganuma 1996). If an overall increase in clearance efficiency results from higher Reynolds numbers then production of copepod may be underestimated at higher temperatures in my model.

The increase in nano/microflagellate and dinoflagellate biomass relative to total phytoplankton production has important implications for understanding the export of carbon from the euphotic zone to the oceans depths (Vèzina *et al.* 2000). As major grazers of the smallest phytoplankton (Kuhn 1997), the increased relative production of nano/microflagellates at higher temperatures indicates that not only is this group likely to provide a greater proportion of material available to secondary consumers, but also have an increased responsibility in the maintaining the microbial loop through the increase in processes such as excretion and lysis of algae which provide dissolved organic carbon to bacteria (Christaki *et al.* 2001). This increased role of nano/microflagellates will be more substantial in nutrient poor areas, which are generally associated with an increased proportion of smaller, picophytoplankton (Uitz *et al.* 2006). In nutrient rich areas larger, micro-sized phytoplankton are exported more readily than smaller species (Legendre and Fèvre 1995, Vèzina *et al.* 2000). As significant grazers of microphytoplankton (Lessard & Swift 1985), dinoflagellates help transfer material from primary producers to secondary consumers such as copepods. As dinoflagellate relative biomass and production is greater at higher temperatures, the proportion of microphytoplankton carbon passed up through the planktonic food web will increase, resulting in a reduction of carbon export out of the euphotic zone, as marine snow for example (Legendre & Fèvre 1995).

My models predict an increase in the contribution of dinoflagellate relative production which is consistent with findings reported in Chapter 4 (p. 91). Understanding changes in the production of dinoflagellate is of ecological importance as the sedimentation of their cysts can represent up to 22% of total pelagic sediment flux out of the euphotic zone (Dale & Dale 1992). Therefore, it is

likely that the contribution of dinoflagellates to biochemical cycles of the marine pelagic environment increases with temperature. The observed dinoflagellate increase, and nano/microflagellate decrease, in relative biomass with increasing temperature is also consistent with my findings in Chapter 4 (p. 91), and supports my suggestion that temperature-dependent taxon- and diet-specific GGEs may be the cause of the observed relative biomass-temperature patterns.

Inaccuracies may also be derived using only taxon-specific GGEs owing to the proportion of different diet types synthesised into predator biomass with different efficiencies. My models suggest that the inclusion of diet-specific GGEs may have a profound impact on accurately determining production of planktonic taxa. I found, for instance, inclusion of diet-specific GGEs predicts dinoflagellate production less than half that of when only taxon-specific values are used, that at low temperature, such as in the polar regime, and underestimations production by around 25% in the tropical regime. In contrast, using taxon-specific GGEs underestimates the production of ciliates and nano/microflagellates in comparison to using taxon- and diet-specific GGES.

The incorporation of temperature dependence into planktonic ecosystem models is of fundamental importance since many key physiological and life history rates vary with temperature (Eppley 1972, Hirst & Bunker 2003, Montagnes *et al.* 2003, Bunker & Hirst 2004). Without temperature-dependence, estimated biomass of nano/microflagellates, ciliates were dinoflagellates using either taxa-specific (suite B; Chapter 6, p.126) or taxa- and diet-specific (suite C) GGEs was significantly lower in comparison to those which did include temperature dependence (suite G and H), under all temperature regimes except tropical. Copepod relative biomass meanwhile was significantly lower using non-temperature dependent models (suite B and C) in comparison to temperature-dependent models (suites G and H), run under all temperature regimes. A comparison of the non-temperature dependent model and temperature dependent model under the polar regime gave biggest differences, using taxa-, and diet-specific suites (C and H), with copepod, ciliate, dinoflagellate, and nano/microflagellate relative biomasses approximately 80%, 65%, 70% and 75% in the LNA temperature-dependent model.

The models utilized in this study are an initial step in understanding how temperature, through its affect on GGE, affects the distribution of biomass among protozoan taxa and can fundamentally influence the flow of material, such as carbon, through the planktonic food web. Protozoan groups are often considered as a single component, such as "microzooplankton" within ecosystem models of low (Landry & Calbet 2004) to high complexity (Buitenhuis *et al.* 2006). However, since my models predict production and relative biomass varies between individual protozoan taxa (nano/microflagellates, ciliates and dinoflagellates) with temperature, and temperature-dependent specific growth rates vary between taxa (Table 7.2), I suggest there is scope for important changes in the magnitude and pathway of biogeochemcial fluxes in the marine environment.

Bacteria play an important role in the remineralisation of dissolved organic carbon in the food-web. Ciliates and nano/microflagellates are important grazers of bacteria (Sanders *et al.* 1992, Callieri *et al.* 2002), and therefore play a pivotal role in the transfer of carbon to higher trophic levels. Although bacteria has been suggested as a prey item of dinoflagellates, (Lessard & Swift 1985, Strom 1991) , the optimum prey size of dinoflagellates is equal to their own size (Hansen *et al.* 1994), suggesting direct grazing impact on bacteria is at best very low in the natural environment. Changes in the relative contribution of bacterial grazers will have knock-on consequences for the trophic transfer of remineralised carbon. My models suggest that, as higher temperatures are associated with increased bacterial and dinoflagellate relative production and biomass, and a decrease in ciliate relative biomass, I may expect a lower proportion of bacterial production to transfer to higher trophic levels.

Importantly, the change in biomass structure as a result of increasing temperature, across different suites of GGEs highlights the variability in predicted production and biomass using common variables across a broad range of taxa. With the pressing issue of climate change the need for a fundamental understanding of factors determining planktonic food web structure and functions over large-scales has never been greater. Just as temperature is highly influential in shaping phytoplankton biomass and community structure (Fiala *et al.* 1998, Gasiunaite *et al.*

2005), I suggest that it may also drive patterns in zooplankton through its impact of taxon-specific processes.

Chapter 8. Discussion

This study has shown the efficiency with which ingested prey biomass is converted into predator biomass (gross growth efficiency, GGE) varies between planktonic taxa, with diet, and is temperature-dependent in some taxa and not others (Chapter 3 p.27). These inherent differences in GGE between taxa are likely to be the result of a combination of different processes and rates that act differently on different taxa. For instance, pico- to mesoplankton may differ in size by up to five orders of magnitude (0.2 to 20 000μm), in locomotion (beating of cilia, flagella or other appendages (Sleigh 1989, Alcaraz & Strickler 1988), in growth form (binary fission, eutely, egg production), in feeding method (raptorial, filter feeding or direct uptake of dissolved organic nutrients; Hansen & Calado 1999, Hansen *et al.* 1994), in mode of prey detection, and diet type. Since temperature may impact these processes differently (e.g. by increasing the rate of enzyme driven reactions, or decreasing the viscosity of the surrounding medium), the ingestion and production of biomass, and therefore GGE, is affected to different degrees between taxa. Such inherent differences are likely to be the reason GGE responds differently with temperature, increasing or decreasing in some taxa, but showing no variation in others.

As a measure of the proportion of material flowing from prey to predator, GGE of heterotrophs also gives an indication of the production and standing stock biomass a taxon is able to maintain. For taxa that were found to possess temperature-dependent GGEs, production and biomass, relative to phytoplankton, are likely to be constrained to differing degrees with increasing temperature. As the temperature-dependence of GGE varied among different taxa either increasing, decreasing, or showing no variation, the flux of carbon and the biomass structure of the planktonic food-web are likely to vary with increasing temperature.

This study has provided evidence to suggest that taxon-, diet-, and temperature-dependent GGEs may underpin, or impose limits upon the structure of the planktonic food-web over a global scale. The incorporation of temperature-dependent, taxon- and diet-specific GGEs into ecosystem models

(Chapter 7 p.163) resulted in several trends that were reflected in the study using biomasses from real world data, most notably and increasing in the proportion of dinoflagellate biomass to total planktonic biomass, and decrease of nano/microflagellates with increasing temperature.

The contribution of different taxa to the planktonic food-web varies, with bacteria and dinoflagellates increasing, ciliates and flagellates decreasing, and mesozooplankton remaining a constant proportion with increasing temperature, and supports suggestions that only can alter the structure of the planktonic food-web (O'Conner *et al.* 2009). In both the low and high nutrient models, total heterotrophic biomass (bacteria, ciliates, nano/microflagellates, dinoflagellates) was greater in the tropical regime (LNA=137.1, HNA=121.3% of phytoplankton production), than in the polar (LNA=133.3, HNA=95.7%). These findings are consistent with those of Müren *et al.* (2005) and O'Conner *et al.* (2009), indicating an overall greater control of primary producers by heterotrophic organisms at higher temperatures. An increased heterotrophic:autotrophic ratio with increased temperature is a key prediction of metabolic theory of ecology. Whilst heterotrophic organisms are constrained by respiration, and autotrophic by photosynthesis, the metabolic theory of ecology predicts that the differential temperature-scaling of these processes results in an increase of heterotrophs:autotrophs with increasing temperature (López-Urrutia *et al.* 2006). Therefore, my results suggest that higher temperatures are associated with an increased domination of heterotrophic organisms, and where community respiration exceeds photosynthesis, net source of . Conversely, low temperature are predicted to decrease heterotrophs:autotrophs, are associated with a reduced control of primary producers by consumers, and net sink of .

Because of these changes in planktonic structure, and the significantly greater GGEs of taxa feeding on algae in comparison to other diet types, the consideration of diet-specific GGEs is an important factor when modelling material flux through the planktonic ecosystem, or for instance calculating the carbon budget of an individual species. For instance, warmer environments were associated with an increase in the relative biomass of bacteria, which play an important role in the marine pelagic

environment by remineralising and recycling dissolved organic matter (Cho & Azam 1988, Cho & Azam 1990), thus making it available for consumption by heterotrophs. As grazers of bacteria (Sanders *et al.* 1992, Šolić & Krstulović 1994), ciliates play an important role in transferring material, recycled by bacteria, up to higher trophic levels (Gifford 1991). However, as bacteria are consumed at a much lower efficiency by ciliates than are algae, average ciliate GGE will decrease if the proportion of bacteria in the diet of ciliates also increases as a result of an increased relative biomass. Unless ingestion by ciliates is increased to such an extent as to compensate for an overall decrease in GGE, then ciliate production and standing stock biomass relative to phytoplankton will also decrease. Therefore, in warmer environments, the proportion of ingested bacterial carbon that is transferred to higher trophic levels is lower when considering diet-specific GGEs. Therefore ecosystem models that assume conversion of both algae and bacteria into ciliate biomass is achieved with equal efficiency may overestimate the contribution of bacterial carbon to higher trophic levels.

This study has demonstrated that differences in GGE among taxa, diets and temperatures, when implemented into ecosystem models, are likely to enhance accuracy in describing the structure of marine food-webs. The parameters used in ecosystem models are often a compromise between increased complexity and increased accuracy, with even the most complex models simplifying the true ecosystem, biota or processes. The compartmentalising of species into broader groups is one such simplification with all protozoan groups frequently grouped together as "microzooplankton" or "protozoa" (Aumont *et al. 2003*, Buitenhuis *et al.* 2006, Daniels *et al.* 2006, Denman *et al.* 2006). Although I found no evidence to suggest total protozoan biomass, relative to total phytoplankton, varies with temperature, significant changes in composition were found to occur *within* protozoa. Ciliates, nano/microflagellates and dinoflagellates are functionally important primary consumers in the marine pelagic environment (Kuuppo-Leinkki 1990, Lignell et al. 1993, Rysgaard *et al.* 1999). In addition to being intermediaries between phytoplankton and secondary consumers such as copepods, the protozoan groups perform important functions influencing biogeochemical cycles.

Dinoflagellates can be a large contributor to flux of sediment out of the euphotic zone (Dale & Dale 1992), whilst ciliate release of ammonium is important in regeneration of nutrients (Ota & Taniguchi 2002). In addition, total protozoa excrete phosphorus at a far greater rate than mesozooplankton despite having a smaller biomass (Johannes 1965), and contribute a large part of total community respiration. Developing a greater understanding differences between protozoa is therefore likely to be key in the goal of developing a comprehensive understanding of how planktonic food-web structure changes geographically and with temperature.

The determination of the extent to which each protozoan group contributes to biogeochemical cycles and trophic transfer of material over large, geographical scales will undoubtedly aid the understanding of local impacts. For instance, some phytoplankton species are toxic, and their consumption, and subsequently accumulation in species of higher trophic levels can result in mortality of marine mammals, and sea birds (Work *et al.* 1993, Turner & Tester 1997). Although harmful phytoplankton are unlikely to have impact on the majority of ecosystems and locations, application of temperature-dependent trends in relative biomass, and gross growth efficiencies of different taxa will undoubtedly help determine the role of protozoan grazers on promoting and reducing toxic blooms in specific locations.

Although there is overlap in the size of phytoplankton grazed by ciliates and dinoflagellates, the latter generally consume larger prey than that consumed by ciliates (Hansen *et al.* 1994). Whilst ciliates are known consumers of bacteria, the tendency for dinoflagellates to be important bacterial grazers is unclear, although most evidence suggests their impact on bacteria is minimal at best (Jakobsen & Hansen 1997, Hansen 1998). Therefore with an increased contribution of dinoflagellates and decreased contribution of ciliates, the structure and flow of material through the food-web may be significantly different in high temperature (e.g. tropical) environments than in cooler ones (e.g. temperate or polar). The ratio between ciliates and dinoflagellate may be particularly important if one group is preferentially predated by metazoan zooplankton. Predator production may be increased through the consumption of preferred prey if the chemical composition

provides essential components, or if the costs associated with its capture are lower than other prey of equal nutritional value. Whilst some experimental evidence suggests copepod species prefer dinoflagellates, whether this can be considered a general trend is unclear. For instance copepods of different feeding modes (ambush and current generating) removed a higher proportion of ciliates than dinoflagellates of the same size, which was suggested to be the result of greater hydromechanical signals (disturbances in the water) by the more mobile ciliates (Buskey *et al.* 1993, Jakobsen *et al.* 2005). However, calanoid copepods were found to clear dinoflagellates at a higher rate than ciliates, which was argued to be a result of the more "jerky motion" of ciliates that enhances predator avoidance (Suzuki *et al.* 1999).

If metazoan zooplankton such as copepods do generally predate dinoflagellates in preference to ciliates in the natural environment the impact of changes in the biomass distribution of protozoan biomass associated with increasing temperature is likely to extend further up the food chain. Determining a general rule for the preferred prey of a whole taxon such as dinoflagellates or copepods may be difficult since there are large differences between species within taxa. For instance the mode of feeding varies between dinoflagellate species (Hansen & Calado 1999) and between copepod species (ambush and current generating), whilst diet may also vary between copepod families (Atkinson *et al.*1996).

Any change in the protozoan structure with increasing temperature is likely to impact mesozooplankton such as copepods, which are a vital component of the food web (Banse 1995, Kiørboe 1998, Calbet 2001). However, since the plankton models in this study uses temperature-dependent copepod parameters determined from robust patterns of physiological and life-history rates (Hirst & Kiørboe 2002, Hirst & Bunker 2003, Bunker & Hirst 2004), and in conjunction with the absence of change in relative biomass with temperature over a large geographical range, I find no reason to have assume this to be incorrect. Although other environmental factors, such as phytoplankton structure and nutrient availability may influence the proportion of copepod biomass in the planktonic food-web, the results suggest an absence of a relationship with temperature, which has important ecological and

economic importance. Copepods are the dominant component of mesozooplankton (up to 80% Kiørboe 1998, Hirst & Bunker 2003), and predators of both primary producers and consumers. My results indicate that across large-scale temperature gradients copepods remain important in the transfer of the global aquatic primary production needed to sustain current removal of fish in the open ocean (Pauly & Christensen 1995). In addition, copepods will also undoubtedly play a key role in supplying energy to fish at high latitudes, the production of which is expected to increase with predicted climate change (Brander 2007).

Although copepod relative biomass does not vary with temperature, there may be significant changes within this, and other zooplankton taxa. For instance, species which have thermal optima closely matching that of the environmental temperature are likely to benefit from reduced energetic costs in comparison species of sup-optimal thermal optima and high costs. As a result of this competitive advantage "optimal" species may be able to increase their biomass and production, achieving populations that are more resistant to local extinction. Although a latitudinal gradient of marine bacterial species richness has been determined, such trends for other planktonic taxa are currently unavailable. Since bacterial species richness was strongly and positively correlated with temperature (Fuhrman *et al.* 2008), a trend mirrored by numerous terrestrial species (Blackburn & Gaston 2003). This gap in the protozoa and mesozooplankton literature of species richness-temperature relationships signifies an opportunity to develop our understanding of determinants of large-scale distribution of marine planktonic species, and I therefore urge research into this area of marine ecology.

The models presented here represent the first step in understanding the effect of using taxa-, diet-specific and temperature dependent GGEs on the planktonic food web. However, models of both high and low complexity benefit from the determination and inclusion of accurate parameters, and in particular their response to temperature. Some parameters are well documented, for instance copepod growth rates have been detailed extensively, with robust relationships outlined within the literature (Huntley & Lopez 1992, Hirst *et al.* 2003, Hirst & Bunker 2003). However others likely to benefit our understanding of the food-web

dynamics and biogeochemical cycles, such as clearance efficiency (the proportion of available prey consumed by a predator), are in need of further research. Although values of clearance efficiency are available within the literature, they are often reported as single values, single experiments, from single locations or over a narrow time period (Varity 1985, Leakey *et al.* 1992, Dam *et al.* 1995).

The advent of models based on the size distribution of plankton can be useful as generally predation is size based, and size fractions of plankton can be collected and quantified with relative ease. However, size-based studies and models may overlook important differences if size categories comprise species and broader groups of taxa that display fundamental physiological and ecological differences. For instance, in addition to predating bacteria, ciliates possess a lower GGE (Chapter 3, p.36), and specific growth rates approximately three times that of dinoflagellates (Montagnes *et al.* 2003). I therefore urge greater consideration of the differences between protozoan taxa, and the implications that changes in their abundance may have. The development of global patterns of plankton has perhaps been hampered by the difficulties associated with large scale sampling and general availability of data. However, the greater availability of distributional data will undoubtedly help in the formation of global patterns of zooplankton. My study has shown that despite local fluctuations, important relationships between biomass and temperature persist examined on a global scale.

Given the importance of plankton in the global carbon cycle (Hays *et al.* 2005) it is imperative that the processes determining large-scale distribution and abundance of planktonic species are established. However, with the increase of macroecological studies of marine biota (Wieters 2001), I urge caution when grouping species into broad taxonomic groups. Only with the understanding of fundamental differences between the protozoan taxa of ciliates and dinoflagellates may the large-scale determinants of food-web structure be established.

Appendices

Appendix 1. Taxonomic classication of phytoplankton, dinoflagellates and flagellates within the MarProd dataset, with the carbon conversion values used within this study. Dinoflagellate values were derived from means of autrophic (auto), mixotrophic (mixo) or heterotrophic (hetero) species

				Carbon Content		
Species	**Phylum**	**Class**	**Taxonomic Grouping**	**Value (pg C cell^{-1})**	**Description**	**Source**
Acanthoica quattrospina	Haptomonada	Prymnesiophyceae	Algae	701.5	Non-diatom algae mean	Mullin *et al.* (1966)
Calcidiscus leptoporus	Haptomonada	Prymnesiophyceae	Algae	701.5	Non-diatom algae mean	Mullin *et al.* (1966)
Emiliania huxleyi	Haptomonada	Prymnesiophyceae	Algae	701.5	Non-diatom algae mean	Mullin *et al.* (1966)
Ophiaster hydroideus	Haptomonada	Prymnesiophyceae	Algae	701.5	Non-diatom algae mean	Mullin *et al.* (1966)
Phaeocystis	Haptomonada	Prymnesiophyceae	Algae	701.5	Non-diatom algae mean	Mullin *et al.* (1966)
Syracosphaera rotula	Haptomonada	Prymnesiophyceae	Algae	701.5	Non-diatom algae mean	Mullin *et al.* (1966)
Asterionellopsis glacialis	Bacillariophyta	Fragilariophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Bacillariophyta	Bacillariophyta		Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Bacteriastrum furcatum	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Biddulphia alternans	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Cerataulina pelagica	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Chaetoceros	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Chaetoceros atlanticus	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Chaetoceros concavicornis	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Chaetoceros debilis	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Chaetoceros decipiens	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Chaetoceros laciniosus	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Chaetoceros simplex	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Corethron criophilum	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Coscinodiscus	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Eucampia groenlandica	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Fragilaria	Bacillariophyta	Fragilariophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)

Guinardia striata	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Hemiaulus hauckii	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Leptocylindrus mediterraneus	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Leptocylindrus minimus	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Licmophora	Bacillariophyta	Fragilariophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Lithodesmium undulatum	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Navicula planamembranacea	Bacillariophyta	Bacillariophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Nitzschia closterium	Bacillariophyta	Bacillariophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Nitzschia delicatissima	Bacillariophyta	Bacillariophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Nitzschia seriata	Bacillariophyta	Bacillariophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Odontella regia	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Pleurosigma planctonicum	Bacillariophyta	Bacillariophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Rhizosolenia alata	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Rhizosolenia calcar-avis	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Rhizosolenia delicatula	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Rhizosolenia fragilissima	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Rhizosolenia hebetata semispina	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Rhizosolenia setigera	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Rhizosolenia shrubsoleii	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Rhizosolenia styliformis	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Skeletonema costatum	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Striatella unipunctata	Bacillariophyta	Fragilariophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Thalassionema nitzschioides	Bacillariophyta	Fragilariophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Thalassiosira	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Thalassiosira angulata	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Thalassiosira delicatula	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Thalassiosira gravida	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Thalassiosira nordenskioeldii	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Thalassiosira polychorda	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Thalassiosira rotula	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Thalassiosira subtilis	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Thalassiothrix frauenfeldii	Bacillariophyta	Coscinodiscophyceae	Diatoms (algae)	12739.6	Diatom mean	Menden-Deuer & Lessard (2000)
Amphidoma caudatum	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Ceratium furca	Dinomastigota	Dinophyceae	Dinoflagellates	5068.8	Mixo dinoflagellate mean	Menden-Deuer & Lessard (2000)
Ceratium fusus	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Ceratium horridum	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Ceratium lineatum	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Cochlodinium	Dinomastigota	Dinophyceae	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Dinophysis acuminata	Sarcomastigophora	Phytomastigophorea	Dinoflagellates	5068.8	Mixo dinoflagellate mean	Menden-Deuer & Lessard (2000)
Dinophysis acuta	Sarcomastigophora	Phytomastigophorea	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Dinophysis hastata	Sarcomastigophora	Phytomastigophorea	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Dinophysis rotundata	Sarcomastigophora	Phytomastigophorea	Dinoflagellates	5068.8	Mixo dinoflagellate mean	Menden-Deuer & Lessard (2000)

Gonyaulax	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Gonyaulax spinifera	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Gymnodinium	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Gymnodinium mikimotoi	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Gyrodinium fusiforme	Dinomastigota	Dinophyceae	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Katodinium	Dinomastigota	Dinophyceae	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Micranthodinium	Dinomastigota	Dinophyceae	Dinoflagellates	5068.8	Mixo dinoflagellate mean	Menden-Deuer & Lessard (2000)
Oxytoxum	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Oxytoxum laticeps	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Podolampas palmipes	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Pronoctiluca	Dinomastigota	Dinophyceae	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Prorocentrum compressum	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Prorocentrum minimum	Dinomastigota	Dinophyceae	Dinoflagellates	5068.8	Mixo dinoflagellate mean	Menden-Deuer & Lessard (2000)
Protoperidinium	Dinomastigota	Dinophyceae	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Protoperidinium bipes	Dinomastigota	Dinophyceae	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Protoperidinium brevipes	Dinomastigota	Dinophyceae	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Protoperidinium divergens	Dinomastigota	Dinophyceae	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Protoperidinium steini	Dinomastigota	Dinophyceae	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Ptychodiscus	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Pyrrophycophyta			Dinoflagellates	5068.8	Mixo dinoflagellate mean	Menden-Deuer & Lessard (2000)
Scrippsiella	Dinomastigota	Dinophyceae	Dinoflagellates	3257.1	Auto dinoflagellate mean	Menden-Deuer & Lessard (2000)
Torodinium	Dinomastigota	Dinophyceae	Dinoflagellates	7697.2	Hetero dinoflagellate mean	Menden-Deuer & Lessard (2000)
Cryptomonadales	Cryptomonada	Cryptophyceae	Flagellates	6.4	Flagellate mean	Holligan *et al.* (1984)

Appendix 2. Taxonomic classication of metazoan zooplankton within the MarProd dataset, with the carbon conversion values used within this study, calculated from values reported in Hirst *et al.* (2003).

Group	Taxonomic Classification						Carbon Content	
	Phylum	Subphylum	Class	Subclass	Order	Family	Value (µg ind^{-1})	Derivation
Aglantha	Cnidaria		Hydrozoa				9585.7	Cnidarian mean
Amphipoda	Arthropoda	Crustacea	Malacostraca				11000	Meszozooplankton mean (mid-range)
Appendicularia	Chordata		Appendicularia				0.3	Appendicularian mean
Beroe	Ctenophora		Nuda				4706.2	Ctenophore mean
Bivalvia	Mollusca						11000	Meszozooplankton mean (mid-range)
Bryozoa	Bryozoa						11000	Meszozooplankton mean (mid-range)
Calanoida copepodite	Arthropoda	Crustacea	Maxillopoda	Copepoda			6.6	Calanoida copepodite mean
Calanoida nauplii	Arthropoda	Crustacea	Maxillopoda	Copepoda			0.2	Calanoida nauplii mean
Calanoida adult	Arthropoda	Crustacea	Maxillopoda	Copepoda			60.0	Calanoida adult mean
Calanus finmarchicus copepodite	Arthropoda	Crustacea	Maxillopoda	Copepoda			35.7	Calanus finmarchicus copepodite mean
Calanus finmarchicus adult	Arthropoda	Crustacea	Maxillopoda	Copepoda			138.1	Calanus finmarchicus adult mean

Calanus finmarchicus/ helgolandicus/glacialis copepodite	Arthropoda	Crustacea	Maxillopoda Copepoda	35.7	Calanus finmarchicus copepodite mean
Calanus finmarchicus/ helgolandicus/glacialis nauplii	Arthropoda	Crustacea	Maxillopoda Copepoda	0.1	Copepod nauplii mean
Calanus finmarchicus/ helgolandicus/glacialis adult	Arthropoda	Crustacea	Maxillopoda Copepoda	182.0	Calanus finmarchicus/helgolandicus/glacialis adult mean
Calanus helgolandicus copepodite	Arthropoda	Crustacea	Maxillopoda Copepoda	6.5	Copepod copepodite mean
Calanus helgolandicus adult	Arthropoda	Crustacea	Maxillopoda Copepoda	75.3	Calanus helgolandicus mean
Calanus hyperboreus copepodite	Arthropoda	Crustacea	Maxillopoda Copepoda	6.5	Copepod copepodite mean
Calanus hyperboreus nauplii	Arthropoda	Crustacea	Maxillopoda Copepoda	0.1	Copepod nauplii mean
Calanus hyperboreus adult	Arthropoda	Crustacea	Maxillopoda Copepoda	2791.9	Calanus hyperboreus mean
Cephalopoda	Mollusca			11000	Meszozooplankton mean (mid-range)
Ceriantharia	Cnidaria		Anthozoa	9585.7	Cnidarian mean
Chaetognatha	Chaetognatha			121.8	Chaetognath mean
Cirripedia nauplii	Arthropoda	Crustacea	Maxillopoda Thecostraca	4100	Meszozooplankton mean (lower-range)
Cirripedia	Arthropoda	Crustacea	Maxillopoda Thecostraca	11000	Meszozooplankton mean (mid-range)
Clio	Mollusca		Gastropoda	632.7	Clione mean

Clione	Mollusca		Gastropoda		632.7	Clione mean
Cnidaria	Cnidaria				9585.7	Cnidarian mean
Copepoda	Arthropoda	Crustacea	Maxillopoda Copepoda		55.0	Copepod mean
Crustacea nauplii	Arthropoda				11000	Meszozooplankton mean (mid-range)
Cyclopoida	Arthropoda	Crustacea	Maxillopoda Copepoda		0.4	Oithona mean
Decapoda adult	Arthropoda	Crustacea	Malacostraca		216.6	Decopod mean
Decapoda+Mysida	Arthropoda	Crustacea	Malacostraca		630.3	Decopod mean
Doliolida	Chordata		Thaliacea		11000	Meszozooplankton mean (mid-range)
Echinodermata	Echinodermata				11000	Meszozooplankton mean (mid-range)
Eukrohnia hamata	Chaetognatha				121.8	Chaetognath mean
Euphausia krohnii	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean
Euphausiidae adult	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean
Euphausiidae calyptopis	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean
Euphausiidae eggs	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean
Euphausiidae furcilia	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean
Euphausiidae juvenile	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean
Euphausiidae juvenile+adult	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean

Euphausiidae nauplii	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Euphausiidae	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Euphausiidae remains	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Evadne	Arthropoda	Crustacea	Branchiopoda	Cladocera		11000	Meszozooplankton mean (mid-range)
Gastropoda larvae	Mollusca		Gastropoda			11000	Meszozooplankton mean (mid-range)
Gymnosomata	Mollusca		Gastropoda			11000	Meszozooplankton mean (mid-range)
Harpacticoida C1-adult	Arthropoda	Crustacea	Maxillopoda Copepoda			6.5	Copepod copepodite mean
Harpacticoida N1-6	Arthropoda	Crustacea	Maxillopoda Copepoda			0.1	Copepod nauplii mean
Hyperia	Arthropoda	Crustacea	Malacostraca	Amphipoda		1219.4	Amphipod mean
Isopoda	Arthropoda	Crustacea	Malacostraca			11000	Meszozooplankton mean (mid-range)
Limacina	Mollusca		Gastropoda			11000	Meszozooplankton mean (mid-range)
Meganyctiphanes norvegica female	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Meganyctiphanes norvegica furcilia	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Meganyctiphanes norvegica	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Metridia C1-5	Arthropoda	Crustacea	Maxillopoda Copepoda			6.5	Copepod copepodite mean
Metridia longa adult female	Arthropoda	Crustacea	Maxillopoda Copepoda			44.4	Metridia mean
Metridia longa adult male	Arthropoda	Crustacea	Maxillopoda Copepoda			44.4	Metridia mean

Metridia lucens adult female	Arthropoda	Crustacea	Maxillopoda Copepoda		26.2	Metridia lucens mean
Metridia lucens adult male	Arthropoda	Crustacea	Maxillopoda Copepoda		26.2	Metridia lucens mean
Microsetella C1-adult	Arthropoda	Crustacea	Maxillopoda Copepoda		6.5	Copepod copepodite mean
Microsetella	Arthropoda	Crustacea	Maxillopoda Copepoda		63.2	Copepod adult mean
Mollusca larvae	Mollusca				4100	Meszozooplankton mean (lower-range)
Mollusca	Mollusca				11000	Meszozooplankton mean (mid-range)
Mormonilla	Arthropoda	Crustacea	Maxillopoda Copepoda		55.0	Copepod mean
Mysida adult	Arthropoda	Crustacea	Malacostraca		883.8	Mysid mean
Mysida juvenile	Arthropoda	Crustacea	Malacostraca		883.8	Mysid mean
Mysida	Arthropoda	Crustacea	Malacostraca		883.8	Mysid mean
Nematobrachion boopis	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean
Nematoscelis megalops	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean
Oithona C1-5	Arthropoda	Crustacea	Maxillopoda Copepoda		0.4	Cyclopoida copepodite mean
Oithona C1-adult	Arthropoda	Crustacea	Maxillopoda Copepoda		0.4	Cyclopoida copepodite mean
Oithona N1-6	Arthropoda	Crustacea	Maxillopoda Copepoda		0.01	Cyclopoida nauplii mean
Oithona adult female	Arthropoda	Crustacea	Maxillopoda Copepoda		0.4	Cyclopoida adult mean
Oithona adult male	Arthropoda	Crustacea	Maxillopoda Copepoda		0.4	Cyclopoida adult mean

Oithona nauplii	Arthropoda	Crustacea	Maxillopoda Copepoda		0.01	Cyclopoida nauplii mean
Oithona	Arthropoda	Crustacea	Maxillopoda Copepoda		0.4	Oithona mean
Oncaea C1-adult	Arthropoda	Crustacea	Maxillopoda Copepoda		6.5	Copepod copepodite mean
Ostracoda	Arthropoda	Crustacea	Ostracoda		11000	Meszozooplankton mean (mid-range)
Paraeuchaeta C1-5	Arthropoda	Crustacea	Maxillopoda Copepoda		16.1	Paraeuchaeta copepodite mean
Paraeuchaeta adult female	Arthropoda	Crustacea	Maxillopoda Copepoda		86.7	Paraeuchaeta adult mean
Paraeuchaeta adult male	Arthropoda	Crustacea	Maxillopoda Copepoda		86.7	Paraeuchaeta adult mean
Paraeuchaeta nauplii	Arthropoda	Crustacea	Maxillopoda Copepoda		0.1	Copepod nauplii mean
Parathemisto	Arthropoda	Crustacea	Malacostraca	Amphipoda	1219.4	Amphipod mean
Periphylla medusae	Cnidaria	Scyphozoa			9585.7	Cnidarian mean
Platyhelminthes-Nemertea	Platyhelminthes	and	Nemertina		11000	Meszozooplankton mean (mid-range)
Pleurobrachia	Ctenophora				4706.2	Ctenophore mean
Pleuromamma C1-adult	Arthropoda	Crustacea	Maxillopoda Copepoda		6.5	Copepod copepodite mean
Pleuromamma	Arthropoda	Crustacea	Maxillopoda Copepoda		63.2	Copepod adult mean
Podon	Arthropoda	Crustacea	Branchiopoda	Cladocera	11000	Meszozooplankton mean (mid-range)
Polychaeta adult	Annelida		Polychaeta		1.0	Polychaete mean
Polychaeta larvae	Annelida		Polychaeta		1.0	Polychaete mean

Sagitta maxima	Chaetognatha					121.8	Chaetognath mean
Siphonophora bracts	Cnidaria		Hydrozoa			9585.7	Cnidarian mean
Siphonophora	Cnidaria		Hydrozoa			9585.7	Cnidarian mean
Siphonophora remains	Cnidaria		Hydrozoa			9585.7	Cnidarian mean
Stylocheiron elongatum	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Stylocheiron longicorne	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Stylocheiron maximum	Arthropoda	Crustacea	Malacostraca		Euhausiidae	7359.8	Euphausiid mean
Thecosomata	Mollusca		Gastropoda			11000	Meszozooplankton mean (mid-range)
Thysanoessa furcilia	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Thysanoessa inermis female	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Thysanoessa inermis juvenile+adult	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Thysanoessa inermis	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Thysanoessa longicaudata female	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Thysanoessa longicaudata juvenile+adult	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Thysanoessa longicaudata male	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean
Thysanoessa longicaudata	Arthropoda	Crustacea	Malacostraca		Euphausiidae	7359.8	Euphausiid mean

Thysanoessa raschii	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean
Thysanopoda acutifrons	Arthropoda	Crustacea	Malacostraca	Euphausiidae	7359.8	Euphausiid mean
Tomopteris	Annelida		Polychaeta		1.0	Polychaete mean

Appendix 3. Taxonomic classication of ciliate within the MarProd dataset, with the carbon conversion values used within this study.

Species	Class	Order	Family	Derivation of carbon value	Volume	Length (µm)	Width (µm)	Carbon Content (fg c cell^{-1})
Acanthostomella gracilis	Polyhymenophora	Oligotrichida	Ascampbelliellidae	Oligotrichida mean	24812.5			4714375
Askenasia sp.	Kinetofragminophora	Haptorida	Didiniidae	Kinetofragminophora mean	43750			8312500
Balanion sp.	Kinetofragminophora	Prostomatida	Didiniidae	*Balanion comatum*	2500	15	10	475000
Ciliatea sp.				Ciliophora mean	39791.7			7560416.7
Codonellopsis ecaudata	Polyhymenophora	Oligotrichida	Codonellopsidae	Oligotrichida mean	24812.5	94	23	4714375
Cyrtostrombidium	Polyhymenophora	Oligotrichida	Strobilidiidae	Strombidiid mean	23290.9			4425272.7
Didinium	Kinetofragminophora		Didiniidae	*Didinium gargantua*	85000	70	50	16150000
Laboea strobila				*Laboea strobila*	60000	85	42	11400000
Leegaardiella ovalis	Polyhymenophora	Oligotrichida	Strobilidiidae	*Leegaardiella ovalis*	7000	20	20	1330000
Leegaardiella sol	Polyhymenophora	Oligotrichida	Strobilidiidae	*Leegaardiella sol*	40000	30	45	7600000
Leegaardiella sp.	Polyhymenophora	Oligotrichida	Strobilidiidae	Strobilidiid mean	23290.9			4425272.7
Lohmaniella oviformis	Polyhymenophora	Oligotrichida	Strobilidiidae	*Lohmanniella oviformis*	6000	20	15	1140000
Myrionecta rubra	Litostomatea	*Cyclotrichida*	*Mesodiniidae*	*Myrionecta rubra*	5000 to 300000	25 to 100	20 to 75	28975000

Parafavella sp.	Polyhymenophora	Oligotrichida	Xystonellidae	Oligotrichida mean	24812.5			4714375
Paratontonia gracillima	Polyhymenophora	Oligotrichida	Strobilidiidae	*Tontonia gracillima*	20000	60	35	3800000
Pelagostrombidium	Polyhymenophora	Oligotrichida	Strobilidiidae	Strombidiid mean	23290.9			4425272.7
Pseudotontonia simplicidens		Oligotrichida		Oligotrichida mean	24812.5			4714375
Ptychocylis minor	Polyhymenophora	Oligotrichida	Ptychocylididae	Oligotrichida mean	24812.5			4714375
Salpingella minutissima	Polyhymenophora	Oligotrichida	Tintinnidae	Oligotrichida mean	24812.5			4714375
Salpingella secata	Polyhymenophora	Oligotrichida	Tintinnidae	Oligotrichida mean	24812.5			4714375
Scuticociliate sp.				Ciliophora mean	39791.7			7560416.7
Spirotontonia	Polyhymenophora	Oligotrichida		Oligotrichida mean	24812.5			4714375
Strombidium capitatum	Polyhymenophora	Oligotrichida	Strobilidiidae	*Strombidium capitatum*	40000	40	40	7600000
Strombidium conicum	Polyhymenophora	Oligotrichida	Strobilidiidae	*Strombidium conicum*	35000	65	35	6650000
Strombidium coronatum	Polyhymenophora	Oligotrichida	Strobilidiidae	Strombidiid mean	23290.9			4425272.7
Strombidium dalum	Polyhymenophora	Oligotrichida	Strobilidiidae	*Strombidium dalum*	500	15	10	95000
Strombidium emergens	Polyhymenophora	Oligotrichida	Strobilidiidae	*Strombidium emergens*	10000	35	20	1900000
Strombidium rhynchum	Polyhymenophora	Oligotrichida	Strobilidiidae	Strombidiid mean	23290.9			4425272.7
Strombidium sp.	Polyhymenophora	Oligotrichida	Strobilidiidae	Strombidiid mean	23290.9			4425272.7
Tintinnina sp.	Polyhymenophora	Oligotrichida		Oligotrichida mean	24812.5			4714375

Urotricha	Ciliatea	*Urotricha cyrtonucleata*	25000	45	32	4750000

Appendix 4. Taxonomic and trophic classication of dinoflagellates present in the MarProd dataset, with the source(s) from which the trophic classication was based.

Species	Phylum	Class	Trophic Classification	Source
Amphidoma caudatum	Dinomastigota	Dinophyceae	Autotrophic	Gribble *et al.* (2007)
Ceratium furca	Dinomastigota	Dinophyceae	Mixotrophic	Ismael (2003)
Ceratium fusus	Dinomastigota	Dinophyceae	Autotrophic	Gribble *et al.* (2007), Menden-Deuer & Lessard (2000)
Ceratium horridum	Dinomastigota	Dinophyceae	Autotrophic	Gribble *et al.* (2007)
Ceratium lineatum	Dinomastigota	Dinophyceae	Autotrophic	Gribble *et al.* (2007)
Cochlodinium	Dinomastigota	Dinophyceae	Heterotrophic	Iwataki *et al.* (2007)
Dinophysis acuminata	Sarcomastigophora	Phytomastigophorea	Mixotrophic	Jacobson & Andersen (1994)
Dinophysis acuta	Sarcomastigophora	Phytomastigophorea	Autotrophic	Gribble *et al.* (2007)
Dinophysis hastata	Sarcomastigophora	Phytomastigophorea	Mixotrophic	Schnepf & Deichgraber (1983)
Dinophysis rotundata	Sarcomastigophora	Phytomastigophorea	Mixotrophic	Hansen (1991)
Gonyaulax	Dinomastigota	Dinophyceae	Autotrophic	Dodge (1993), Gribble *et al.* (2007)

Gonyaulax spinifera	Dinomastigota	Dinophyceae	Autotrophic	Dodge (1993)
Gymnodinium	Dinomastigota	Dinophyceae	Autotrophic	Dodge (1993), Menden-Deuer & Lessard (2000)
Gymnodinium mikimotoi	Dinomastigota	Dinophyceae	Autotrophic	Menden-Deuer & Lessard (2000)
Gyrodinium fusiforme	Dinomastigota	Dinophyceae	Heterotrophic	Ismael (2003)
Katodinium	Dinomastigota	Dinophyceae	Heterotrophic	Tikhonenkov *et al.* (2006)
Micranthodinium	Dinomastigota	Dinophyceae	Mixotrophic	Hansen (1991), Vernal *et al.* (2005)
Oxytoxum	Dinomastigota	Dinophyceae	Autotrophic	Menden-Deuer & Lessard (2000)
Oxytoxum laticeps	Dinomastigota	Dinophyceae	Autotrophic	Menden-Deuer & Lessard (2000)
Podolampas palmipes	Dinomastigota	Dinophyceae	Autotrophic	Gribble *et al.* (2007)
Pronoctiluca	Dinomastigota	Dinophyceae	Heterotrophic	Gribble *et al.* (2007)
Prorocentrum compressum	Dinomastigota	Dinophyceae	Autotrophic	Dodge (1989), Gribble *et al.* (2007)
Prorocentrum minimum	Dinomastigota	Dinophyceae	Mixotrophic	Ismael (2003)
Protoperidinium	Dinomastigota	Dinophyceae	Heterotrophic	Dodge (1989), Gribble *et al.* (2007)
Protoperidinium bipes	Dinomastigota	Dinophyceae	Heterotrophic	Jeong *et al.* (2004), Gribble *et al.* (2007)
Protoperidinium brevipes	Dinomastigota	Dinophyceae	Heterotrophic	Gribble *et al.* (2007)
Protoperidinium divergens	Dinomastigota	Dinophyceae	Heterotrophic	Gribble *et al.* (2007)
Protoperidinium steini	Dinomastigota	Dinophyceae	Heterotrophic	Gribble *et al.* (2007)
Ptychodiscus	Dinomastigota	Dinophyceae	Autotrophic	Raven *et al.* (1998)

Pyrrophycophyta			Mixotrophic	
Scrippsiella	Dinomastigota	Dinophyceae	Autotrophic	Meiners *et al.* (2002), Gribble *et al.* (2007)
Torodinium	Dinomastigota	Dinophyceae	Heterotrophic	Menden-Deuer & Lessard (2000)

Appendix 5. **Regressions of log10 biomass of ciliates, dinoflagellates, flagellates, bacteria, total protozoa and total mesozooplankton, relative to total phytoplankton biomass (μg C L^{-1} / μg C L^{-1}, log10RelBio) derived from chlorophyll-*a* concentration using a constant ratio (Chl*a*:CC) against temperature (°C, T). Biomass values were derived from mean values for each sampling site in the combined dataset. Equations of significant relationships are shown only (p<0.05). Model fit measured by R-squared.**

	P	Model Fit	Equation	Mean Relative Biomass (μg C L^{-1}/μg C L^{-1})	S.E. Mean
Ciliates	<0.001	26.7	log10RelBio= 0.788 – 0.039T		
Dinoflagellates	<0.001	37.5	log10RelBio= –0.373 + 0.061T		
Flagellates	<0.001	88.3	log10RelBio= 2.03 – 0.289T		
Bacteria	<0.001	16.1	log10RelBio= -1.60 + 0.064T	0.50	136
Protozoa	0.599	0.2			
Mesozooplankton	0.446	0.5		5.39	3.09

Appendix 6. **Regressions of log10 biomass of autotrophs, heterotrophs, bacteria, protozoa and mesozooplankton, relative to total phytoplankton biomass (μg C L^{-1} / μg C L^{-1}, log10RelBio) derived from chlorophyll-*a* concentration using a constant ratio (Chl*a*:CC) against temperature (°C, T). Biomass values were derived from mean values for each sampling site in the Gasol dataset. Equations of significant relationships are shown only (p<0.05). Model fit measured by R-squared.**

	P	Model Fit	Equation	Mean Relative Biomass (μg C L^{-1}/μg C L^{-1})	S.E. Mean
Heterotrophs	0.001	13.4	log10RelBio = -1.17 + 0.062T	0.42	0.05
Bacteria	0.004	9.7	log10RelBio = -1.66 + 0.060T	0.15	0.05
Protozoa	0.419	1.0		0.07	0.05
Mesozooplankton	0.001	12.7	log10RelBio = -1.86 + 0.080T	0.10	0.07

Appendix 7. **Regressions of log10 biomass of different planktonic taxa in the MarProd dataset, relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) derived from chlorophyll-*a* concentration using a constant ratio (Chl*a*:CC) against temperature (°C, T). Biomass values were derived from mean values for each sampling site. Only taxa of n>10 are shown and equations are of significant relationships (p<0.05). Model fit measured by R-squared.**

	P	Model Fit	Equation	Mean Relative Biomass (µg C L^{-1}/µg C L^{-1})	S.E. Mean
Ciliates	0.243	4.1		3.50	1.26
Dinoflagellates	0.033	13.1	log10RelBio= 1.27 – 0.196T	0.98	1.30
Algae	0.024	14.6	log10RelBio = 3.54 – 0.365T	14.52	1.60
Flagellates	0.006	20.7	log10RelBio = 1.82 – 0.251T	1.51	1.31
Chaetognaths	0.202	5.2		0.004	1.53
Tunicates	0.135	14.3		0.0002	2.10
Cnidarians	0.842	0.7		0.01	1.70
Copepods	0.134	5.8		0.07	1.48
Crustaceans	0.524	1.1		0.70	1.52

Echinoderms	0.191	20.4		1.01	1.82
Molluscs	0.884	0.1		0.14	2.31
Polychaetes	0.746	0.9		0.00003	1.77
Total Protozoa	0.039	12.3	log10RelBio = 1.91 – 0.165T	6.89	1.26
Total Mesozooplankton	0.403	1.5		0.44	1.58

Appendix 8. **Regressions of log10 biomass of different planktonic taxa in the MarProd dataset, relative to total phytoplankton biomass (μg C L^{-1} / μg C L^{-1}, log10RelBio) derived from chlorophyll-*a* concentration using trophic specific ratios (Chl*a*:CT) against temperature (°C, T). Biomass values were derived from mean values for each sampling site. Only taxa of n>10 are shown and equations are of significant relationships (p<0.05). Model fit measured by R-squared.**

	P	Model Fit	Equation	Mean Relative Biomass (μg C L^{-1}/μg C L^{-1})	S.E. Mean
Ciliates	0.889	0.1		4.26	1.21
Dinoflagellates	0.137	6.6		1.20	1.23
Algae	0.055	10.7		17.70	1.52
Flagellates	0.018	15.9	log10RelBio= 1.34 – 0.165T	1.84	1.22
Chaetognaths	0.347	2.9		0.005	1.47
Tunicates	0.202	10.6		0.0002	1.95

Cnidarians	0.892	0.3	0.011	1.72
Copepods	0.211	4.1	0.08	1.41
Non-copepod crustaceans	0.823	0.1	0.78	1.50
Echinoderms	0.236	17.0	1.21	1.73
Molluscs	0.780	0.5	0.14	2.17
Polychaetes	0.742	0.9	0.00004	1.63
Total Protozoa	0.199	5.0	8.39	1.19
Total Mesozooplankton	0.662	0.4	0.49	1.55

Appendix 9. **Regressions of log10 biomass of different planktonic taxa in the AMT dataset, relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) derived from chlorophyll-*a* concentration using a constant ratio (Chl*a*:CC) against temperature (°C, T). Biomass values were derived from mean values for each sampling site. Only taxa of n>10 are shown and equations are of significant relationships (p<0.05). Model fit measured by R-squared.**

	P	Model Fit	Equation	Mean Relative Biomass (µg C L^{-1}/µg C L^{-1})	S.E. Mean
Ciliates	0.705	1.0		0.99	0.20
Diatom	0.459	3.7		0.09	0.05
Dinoflagellates	0.496	3.1		19.69	3.90
Coccolithophores	0.721	0.9		0.16	0.06
Flagellates	0.399	8.0		0.00003	1.98
Picoplankton	0.031	27.5	log10RelBio = -0.105 + 0.041T	7.92	0.90

Phytoplankton					
0.2-2µm	0.226	7.6		0.21	0.03
2-20µm	0.001	43.1	log10RelBio = 0.159 – 0.061T	0.19	0.08
>20µm	0.000	52.5	log10RelBio = 0.250 – 0.077T	0.11	0.03
Bacteria (leucine)	0.345	5.0		1.81	0.35
Bacteria (thymidine)	0.210	8.1		70.20	10.60
Total Protozoa	0.457	3.7		14.09	1.28

Appendix 10. **Regressions of log10 biomass of different planktonic taxa in the AMT dataset, relative to total phytoplankton biomass (μg C L^{-1} / μg C L^{-1}, log10RelBio) derived from chlorophyll-*a* concentration using trophic specific ratios (Chl*a*:CT) against temperature (°C, T). Biomass values were derived from mean values for each sampling site. Only taxa of n>10 are shown and equations are of significant relationships (p<0.05). Model fit measured by R-squared.**

	P	Model Equation	Mean Relative Biomass (μg C L^{-1}/μg C L^{-1})	S.E. Mean
		Fit		
Ciliates	0.918	0.1	0.61	1.23
Diatom	0.448	3.9	0.01	1.86
Dinoflagellates	0.639	1.5	10.52	1.32
Coccolithophores	0.848	0.3	0.06	1.41
Flagellates	0.356	9.5	0.00002	2.04
Picoplankton	0.202	10.6	5.75	1.19
Phytoplankton				

0.2-2µm	0.058	17.7	log10RelBio= -0.118 – 0.036T	0.15	1.24
2-20µm	0.000	55.9	log10RelBio = 0.448 – 0.078T	0.08	1.30
>20µm	0.000	49.0	log10RelBio = 0.537 – 0.094T	0.05	1.41
Bacteria (leucine)	0.045	20.5	log10RelBio = 0.691 – 0.031T	1.22	1.22
Bacteria (thymidine)	0.846	0.2		51.11	1.13
Total Protozoa	0.608	1.8		11.53	1.30

Appendix 11. **Comparison of log10 biomass of different planktonic taxa in the MarProd dataset, relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) using different chlorophyll-*a* to carbon ratios, constant (Chl*a*:CC) and trophic specific (Chl*a*:CT) using a T-test at 95% confidence level. Biomass values were derived from mean values for each sampling site, with taxa of n>10 are shown only.**

	Chl*a*:CC		Chl*a*:CT		P	N	T	DF
	log10 Relative Biomass		log10 Relative Biomass					
	Mean	S.E. Mean	Mean	S.E. Mean				
Ciliates	0.54	0.10	0.63	0.08	0.516	35	0.65	65
Dinoflagellates	-0.008	0.12	0.078	0.09	0.562	35	0.58	64
Algae	1.16	0.20	1.25	0.18	0.754	35	0.31	67
Flagellates	0.18	0.12	0.264	0.09	0.561	35	0.58	63
Chaetognaths	-2.39	0.18	-2.337	0.17	0.846	33	0.19	63
Tunicates	-3.76	0.32	-3.73	0.29	0.954	17	0.06	31
Cnidarians	-1.95	0.23	-1.964	0.24	0.960	8	-0.05	13

Copepods	-1.16	0.17	-1.084	0.15	0.730	40	0.35	76
Non-copepod crustaceans	-0.15	0.18	-0.11	0.18	0.856	38	0.18	73
Ctenophores	-0.91	0.90	-0.69	0.90	0.878	2	0.17	2
Echinoderms	0.003	0.26	0.082	0.24	0.826	10	0.22	17
Molluscs	-0.86	0.36	-0.86	0.34	0.996	17	-0.01	31
Polychaetes	-4.51	0.25	-4.428	0.21	0.795	14	0.26	25
Total Protozoa	0.84	0.10	0.924	0.08	0.495	35	0.69	62
Total Mesozooplankton	-0.36	0.20	-0.31	0.19	0.847	48	0.19	93

Appendix 12. **Comparison of log10 biomass of different planktonic taxa in the AMT dataset, relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) using different chlorophyll-*a* to carbon ratios, constant (Chl*a*:CC) and trophic specific (Chl*a*:CT) using a T-test at 95% confidence level. Biomass values were derived from mean values for each sampling site.**

	Chl*a*:CC		Chl*a*:CT		N	P	T	DF
	log10 Relative Biomass		log10 Relative Biomass					
	Mean	S.E. Mean	Mean	S.E. Mean				
Ciliates	-0.13	0.08	-0.22	0.09	17	0.488	0.70	31
Diatom	-2.08	0.25	-2.17	0.27	17	0.813	0.24	31
Dinoflagellates	1.11	0.12	1.02	0.12	17	0.608	0.52	31
Coccolithophores	-1.16	0.15	-1.25	0.15	17	0.678	0.42	31
Flagellates	-4.54	0.30	-4.62	0.31	19	0.850	0.19	19
Picoplankton	0.85	0.06	0.76	0.08	17	0.364	0.92	30
Phytoplankton								

0.2-2µm	-0.78	0.08	-0.83	0.10	21	0.679	0.42	38
2-20µm	-1.04	0.10	-1.09	0.12	21	0.743	0.33	39
>20µm	-1.27	0.12	-1.32	0.15	21	0.791	0.27	37
Bacteria (leucine)	0.12	0.08	0.09	0.085	20	0.724	0.36	37
Bacteria (thymidine)	1.76	0.07	1.71	0.052	21	0.543	0.61	38
Total Protozoa	1.15	0.11	1.06	0.11	17	0.582	0.56	31

Appendix 13. **Comparison of log10 biomass of heterotrophs, relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio), using different chlorophyll-*a* to carbon ratios, constant (Chl*a*:CC) and trophic specific (Chl*a*:CT), and standardised to six temperatures (-1.89, 0, 5, 10, 15, 17.5°C). Biomass values were derived from the Gasol dataset and compared using a T-test at 95% confidence level. Biomass values were derived from mean values for each sampling site, D.F.= degrees of freedom, N= number of data.**

	Chl*a*:CC		Chl*a*:CT		N	P	T	DF
Temperature	**log10 Relative Biomass**		**log10 Relative Biomass**					
	Mean	**S.E. Mean**	**Mean**	**S.E. Mean**				
-1.89°C	-1.287	0.051	-0.997	0.049	83	<0.001	4.10	163
0°C	-1.170	0.051	-0.891	0.049	83	<0.001	3.95	163
5°C	-0.862	0.051	-0.611	0.049	83	0.001	3.55	163
10°C	-0.553	0.051	-0.330	0.049	83	0.002	3.16	163
15°C	-0.245	0.051	-0.050	0.049	83	0.006	2.76	163
17.5°C	-0.090	0.051	0.091	0.049	83	0.011	2.56	163

Appendix 14. **Comparison of log10 biomass of bacteria, relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio), using different chlorophyll-*a* to carbon ratios, constant (Chl*a*:CC) and trophic specific (Chl*a*:CT), and standardised to six temperatures (-1.89, 0, 5, 10, 15, 17.5°C). Biomass values were derived from the Gasol dataset and compared using a T-test at 95% confidence level. Biomass values were derived from mean values for each sampling site, D.F.= degrees of freedom, N= number of data.**

	Chl*a*:CC		Chl*a*:CT		N	P	T	DF
Temperature	**log10 Relative Biomass**		**log10 Relative Biomass**					
	Mean	**S.E. Mean**	**Mean**	**S.E. Mean**				
−1.89°C	-1.774	0.060	-1.483	0.060	83	0.001	3.42	163
0°C	-1.660	0.060	-1.380	0.060	83	0.001	3.30	163
5°C	-1.359	0.060	-1.107	0.060	83	0.003	2.97	163
10°C	-1.058	0.060	-0.834	0.060	83	0.009	2.64	163
15°C	-0.757	0.060	-0.561	0.060	83	0.022	2.31	163
17.5°C	-0.606	0.060	-0.425	0.060	83	0.034	2.14	163

Appendix 15. **Comparison of log10 biomass of mesozooplankton, relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio), using different chlorophyll-*a* to carbon ratios, constant (Chl*a*:CC) and trophic specific (Chl*a*:CT), and standardised to six temperatures (-1.89, 0, 5, 10, 15, 17.5°C). Biomass values were derived from the Gasol dataset and compared using a T-test at 95% confidence level. Biomass values were derived from mean values for each sampling site, D.F.= degrees of freedom, N= number of data.**

	Chl*a*:CC		Chl*a*:CT		N	P	T	DF
Temperature	**log10 Relative Biomass**		**log10 Relative Biomass**					
	Mean	**S.E. Mean**	**Mean**	**S.E. Mean**				
-1.89°C	-2.011	0.068	-1.720	0.065	83	0.002	3.08	163
0°C	-1.860	0.068	-1.580	0.065	83	0.003	2.97	163
5°C	-1.460	0.068	-1.208	0.065	83	0.008	2.67	163
10°C	-1.061	0.068	-0.837	0.065	83	0.019	2.37	163
15°C	-0.661	0.068	-0.465	0.065	83	0.039	2.08	163
17.5°C	-0.462	0.068	-0.280	0.065	83	0.055	1.93	163

Appendix 16. **Comparison of log10 biomass of autotrophs, relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio), using different chlorophyll-*a* to carbon ratios, constant (Chl*a*:CC) and trophic specific (Chl*a*:CT), and standardised to six temperatures (-1.89, 0, 5, 10, 15, 17.5°C). Biomass values were derived from the Gasol dataset and compared using a T-test at 95% confidence level. Biomass values were derived from mean values for each sampling site, D.F.= degrees of freedom, N= number of data.**

	Chl*a*:CC		Chl*a*:CT		N	P	T	DF
Temperature	**log10 Relative Biomass**		**log10 Relative Biomass**					
	Mean	**S.E. Mean**	**Mean**	**S.E. Mean**				
-1.89°C	-0.460	0.014	-0.610	0.020	94	<0.001	-6.18	163
0°C	-0.419	0.014	-0.530	0.020	94	<0.001	-4.57	163
5°C	-0.311	0.014	-0.319	0.020	94	0.742	-0.33	163
10°C	-0.203	0.014	-0.108	0.020	94	<0.001	3.91	163
15°C	-0.095	0.014	0.103	0.020	94	<0.001	8.16	163
17.5°C	-0.041	0.014	0.208	0.020	94	<0.001	10.28	163

Appendix 17. **Comparison of the regression slopes of log10 biomass relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) against temperature (°C, T), derived from chlorophyll-*a* concentration using a constant (Chl*a*:CC) and trophic specific ratios (Chl*a*:CT), for each group (autotrophs, heterotrophs, bacteria, protozoa and mesozooplankton). Biomass values were derived from mean values for each sampling site in the Gasol dataset. Slopes and their standard error (Slope S.E.) are given for regressions of Chl*a*:CC and Chl*a*:CT biomasses, with details of the statistical test described in the methods section. Model fit measured by R-squared.**

	Chl*a*:CC		Chl*a*:CT				
	Slope	**Slope S.E.**	**Slope**	**Slope S.E.**	**F**	**P**	**Model Fit**
Autotrophs	0.0216	0.0023	0.0422	0.0034	24.77	<0.001	61.86%
Heterotrophs	0.0617	0.0174	0.0561	0.0165	0.05	0.818	16.49%
Bacteria	0.0602	0.0205	0.0546	0.0203	0.04	0.847	11.63%
Protozoa	−0.0080	0.0098	0.0124	0.0092	2.31	0.131	3.02%
Mesozooplankton	0.0799	0.0232	0.0743	0.0221	0.03	0.863	14.54%

Appendix 18. **Comparison of the regression slopes of log10 biomass relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) against temperature (°C, T), derived from chlorophyll-*a* concentration using a constant (Chl*a*:CC) and trophic specific ratios (Chl*a*:CT), for each planktonic group. Biomass values were derived from mean values for each sampling site in the MarProd dataset. Slopes and their standard error (Slope S.E.) are given for regressions of Chl*a*:CC and Chl*a*:CT biomasses, with details of the statistical test described in the methods section. Model fit measured by R-squared.**

	Chl*a*:CC		Chl*a*:CT				
	Slope	**Slope S.E.**	**Slope**	**Slope S.E.**	**F**	**P**	**Model Fit**
Ciliates	−0.0961	0.0809	−0.0097	0.0687	0.66	0.418	3.06%
Dinoflagellatesl	−0.1959	0.0879	−0.1095	0.0719	0.58	0.449	11.03%
Algae	−0.3646	0.1536	−0.2781	0.1399	0.17	0.679	12.99%
Flagellates	−0.1647	0.0660	−0.1647	0.0660	0.64	0.426	19.39%
Bryozoans							
Chaetognaths	−0.1168	0.1222	−0.1168	0.1222	0.10	0.753	4.20%
Tunicates	−0.2172	0.1628	−0.2172	0.1628	0.07	0.796	12.64%

Cnidarians	0.0328	0.2317	0.0328	0.2317	0.06	0.809	0.54%
Copepods	−0.2016	0.1315	−0.1492	0.1172	0.09	0.767	5.21%
Crustaceans	−0.0908	0.1413	−0.0307	0.1368	0.09	0.761	0.70%
Echino	−0.2285	0.1598	−0.1905	0.1487	0.03	0.864	19.07%
Mollusc	0.0417	0.2805	0.0734	0.2583	0.01	0.934	0.33%
Platyhelminths/ Nemerteans							
Polychaetes	−0.0722	0.2182	−0.0626	0.1861	0.00	0.974	1.18%
Total Protozoa	−0.1646	0.0765	−0.0781	0.0596	0.79	0.376	10.28%
Total Mesozooplankton	−0.1280	0.1517	−0.0640	0.1453	0.09	0.762	1.04%

Appendix 19. **Comparison of the regression slopes of log10 biomass relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) against temperature (°C, T), derived from chlorophyll-*a* concentration using a constant (Chl*a*:CC) and trophic specific ratios (Chl*a*:CT), for each planktonic group. Biomass values were derived from mean values for each sampling site in the AMT dataset. Slopes and their standard error (Slope S.E.) are given for regressions of Chl*a*:CC and Chl*a*:CT biomasses, with details of the statistical test described in the methods section. Model fit measured by R-squared.**

	Chl*a*:CC		Chl*a*:CT				
	Slope	**Slope S.E.**	**Slope**	**Slope S.E.**	**F**	**P**	**Model Fit**
Ciliates	0.0112	0.0289	0.0033	0.0319	0.03	0.857	1.99%
Diatom	−0.0640	0.0843	−0.0718	0.0921	0.00	0.951	3.98%
Dinoflagellates	0.0279	0.0399	0.0201	0.0420	0.02	0.894	3.11%
Coccolithophores	0.0180	0.0495	0.0103	0.0524	0.01	0.915	1.09%
Flagellates	−0.0984	0.1112	−0.1122	0.1152	0.01	0.932	8.97%
Picoplankton	0.0408	0.0171	0.0329	0.0247	0.07	0.796	19.04%
Phytoplankton							

0.2-2µm	−0.0191	0.0152	−0.0363	0.0179	0.73	0.400	14.71%
2-20µm	−0.0609	0.0161	−0.0781	0.0159	2.20	0.148	54.67%
>20µm	−0.0773	0.0169	−0.0944	0.0221	0.91	0.347	50.87%
Bacteria (leucine)	−0.0140	0.0144	−0.0314	0.0146	0.73	0.400	13.82%
Bacteria (thymidine)	0.0159	0.0122	−0.0020	0.0102	1.26	0.268	5.95%
Total Protozoa	0.0283	0.0370	0.0205	0.0391	0.02	0.886	3.6

Appendix 20. **Comparison of log10 biomass relative to total phytoplankton biomass (µg C L^{-1} / µg C L^{-1}, log10RelBio) between taxa (A and B) using a T-test. Biomass values were derived from mean values for each sampling site in the combined dataset, using either a constant chlorophyll-*a* to carbon ratio (Chl*a*:CT) or ratios specific to environmental trophic status (Chl*a*:CT). Model fit measured by R-squared.**

	Taxon A	Taxon B	F	P	Model Fit
Chl*a*:CC	Ciliates	Dinoflagellates	48.21	p<0.001	33.64%
	Ciliates	Flagellates	207.67	p<0.001	85.61%
	Ciliates	Bacteria	35.88	p<0.001	45.76%
	Dinoflagellates	Flagellates	342.76	p<0.001	83.99%
	Dinoflagellates	Bacteria	0.04	p=0.843	47.62%
	Protozoa	Mesozooplankton	0.80	p=0.372	1.97%
	Protozoa	Bacteria	165.70	p<0.001	97.69%
	Bacteria	Mesozooplankton	127.06	p<0.001	31.98%
Chl*a*:CT	Ciliates	Dinoflagellates	65.48	p<0.001	39.67%
	Ciliates	Flagellates	250.47	p<0.001	88.33%
	Ciliates	Bacteria	27.86	p<0.001	46.21%
	Dinoflagellates	Flagellates	439.62	p<0.001	87.37%
	Dinoflagellates	Bacteria	0.57	0.453	46.48%
	Protozoa	Mesozooplankton	0.35	0.557	1.48%
	Protozoa	Bacteria	0.97	0.325	3.70%
	Bacteria	Mesozooplankton	2.45	0.119	1.75%

Appendix 21 **Values of the proportion of pico-, nano- and microphytoplanton to total phytoplankton production reported within the literature and used as a guide for autotrophic input variables in the oligotrophic and eutrophic. Baterial production, given as a measurement of totalphytoplantkon are also reported, and usd to dermine the level of heterotrophic bacteria input**

Taxon	Model Notation	Proportion of Primary Production	Time	Region	Trophic Status	Source	Notes
Picophytoplankton	*PP*	<10%	Daily	Global	Eutrophic	Agawin *et al.* (2000)	
		3 to 28.5%		Brazil- Estuarine	Eutrophic	Teixeira & Gaeta (1991)	
		15.5 to 40.4%		Brazil- Coastal	Eutrophic	Teixeira & Gaeta (1991)	
		2 to 25%		Coastal Waters	Eutrophic	Stockner & Antia 1986)	
		61%	Hourly	50ºN to 50ºS	Eutrophic	Marañón *et al.* (2001)	Mean
		57%	Hourly	50ºN to 50ºS	Oligotrophic	Marañón *et al.* (2001)	Mean
		>50%	Daily	Global	Oligotrophic	Agawin *et al.* (2000)	
		>50%	Daily	NW Mediterranean Sea	Oligotrophic	Agawin *et al.* (2000)	
		57%		50ºN to 50ºS	Oligotrophic	Marañón *et al.* (2001)	
		50 to 80%		Open Ocean	Oligotrophic	Stockner & Antia (1986)	
		6.7 to 100%		Brazil- Oceanic	Oligotrophic	Teixeira & Gaeta (1991)	
		0 to 32%	Hourly	Southern Ocean	Eutrophic	Weber & El-Sayed (1987)	
		8%	Hourly	Southern Ocean	Eutrophic	Weber & El-Sayed (1987)	Mean
		39%	Daily	Global		Agawin *et al.* (2000)	
		<10%	Annual	Global		Raven (1998)	
		56%	Hourly	50ºN to 50ºS		Marañón *et al.* (2001)	Mean
		1 to 90%	Hourly			Stockner (1988)	
		≤48%				Walker & Peterson (1992)	Flagellates dominated
		< 15%				Walker & Peterson (1992)	Diatom dominated
Nanophytoplankton	*PN*	30%	Hourly	50ºN to 50ºS	Oligotrophic	Marañón *et al.* (2001)	Mean
		24%	Hourly	50ºN to 50ºS	Eutrophic	Marañón *et al.* (2001)	Mean

		16 to 92%	Hourly	Southern Ocean	Eutrophic	Weber & El-Sayed (1987)	
		53%	Hourly	Southern Ocean	Eutrophic	Weber & El-Sayed (1987)	Mean
		29%	Hourly	50ºN to 50ºS		Marañón *et al.* (2001)	
		81%	Annual	Gulf of Maine		O'Reilly & Bush (1984)	
		74.2%		Weddell Sea		El-Sayed & Taguchi (1981)	Mean
		54%		Ross Sea		Fay (1973)	
Microphytoplankton	*PM*	13%	Hourly	50ºN to 50ºS	Oligotrophic	Marañón *et al.* (2001)	Mean
		15%	Hourly	50ºN to 50ºS	Eutrophic	Marañón *et al.* (2001)	Mean
Bacteria	*PBac*	8%	Daily	Western North Atlantic 40ºN	Eutrophic	Li *et al.* (1993)	
		18%	Daily	Western North Atlantic 45ºN	Eutrophic	Li *et al.* (1993)	
		8%	Daily	Western North Atlantic 40ºN	Eutrophic	Li *et al.* (1993)	
		47%	Daily	Western North Atlantic 45ºN	Eutrophic	Li *et al.* (1993)	
		9 to 30%	Daily	Northwest Indian Ocean	Eutrophic	Wiebinga *et al.* (1997)	Monsoon
		18%	Daily	Northwest Indian Ocean	Eutrophic	Wiebinga *et al.* (1997)	Mean, Monsoon
		16%		Peru upwelling	Eutrophic	Sorokin (1978)	
		13 to 21%		Equatorial pacific- upwelling	Eutrophic	Murray *et al.* (1994)	
		100%		Tropical pacific	Eutrophic	Vinogradov *et al.* (1972)	
		12 to 39%		40 to 45N North Atlantic	Eutrophic	Harrison *et al.* (1993)	
		9 to 28%	Daily	Northwest Indian Ocean	Oligotrophic	Wiebinga *et al.* (1997)	Mean, Monsoon
		18%	Daily	Northwest Indian Ocean	Oligotrophic	Wiebinga *et al.* (1997)	Mean, Monsoon
		14 to 22%	Daily	Northwest Indian Ocean	Oligotrophic	Wiebinga *et al.* (1997)	Monsoon
		15%	Daily	Northwest Indian Ocean	Oligotrophic	Wiebinga *et al.* (1997)	Mean, Monsoon
		2 to 8%	Daily	Sargasso Sea	Oligotrophic	Carlson *et al.* (1996)	
		5%	Daily	Sargasso Sea	Oligotrophic	Carlson *et al.* (1996)	
		5 to 15%	Daily	Sargasso Sea	Oligotrophic	Carlson *et al.* (1996)	
		6 to 7%	Daily	Sargasso Sea	Oligotrophic	Carlson *et al.* (1996)	
		108%		Tropical pacific	Oligotrophic	Vinogradov *et al.* (1973)	
		1.5 to 32%		Gulf stream ring core	Oligotrophic	Ducklow (1986)	
		12%		Gulf stream ring core	Oligotrophic	Ducklow (1986)	Mean
		21%	Daily	Equatorial Pacific	Oligotrophic	Kirchman *et al.* (1995)	El Niño conditions
		17%	Daily	Equatorial Pacific	Oligotrophic	Kirchman *et al.* (1995)	El Niño year
		22%	Daily	Equatorial Pacific	Oligotrophic	Ducklow *et al.* (1995)	El Niño conditions
		12%	Daily	Equatorial Pacific	Oligotrophic	Ducklow *et al.* (1995)	El Niño year
		5 to 30%	Daily	Coastal and offshore		Azam *et al.* (1983)	
		10 to 34%	Daily	Northwest Indian Ocean		Wiebinga *et al.* (1997)Monsoon	
		19%	Daily	Northwest Indian Ocean		Wiebinga *et al.* (1997)	Mean, Monsoon
		30%		Global		Cole *et al.* (1988)	
		20%	Daily			Cole *et al.* (1988)	Mean value from synthesis
		25%	Daily	North Atlantic			
		26%	Daily	Equatorial Pacific			

11%	Daily	Equatorial Pacific		
22%	Daily	Arabian		
18%	Daily	Bermuda		
4%	Daily	Ross Sea		
4 to 19%	Daily	Subarctic Pacific	Kirchman *et al.* (1993)	
13%	Daily	Subarctic Pacific	Kirchman *et al.* (1993)	Mean
2 to 12%	Daily	Subarctic Pacific	Kirchman *et al.* (1993)	
5%	Daily	Subarctic Pacific	Kirchman *et al.* (1993)	Mean
7 to 16%	Daily	Subarctic Pacific	Kirchman *et al.* (1993)	
12%	Daily	Subarctic Pacific	Kirchman *et al.* (1993)	Mean
6 to 42%	Daily	Subarctic Pacific	Kirchman *et al.* (1993)	
15%	Daily	Subarctic Pacific	Kirchman *et al.* (1993)	Mean
11%	Daily	Subarctic Pacific	Kirchman *et al.* (1993)	Overall mean
15 to 80%	Daily	Eastern North Atlantic	Ducklow *et al.* (1993)	
30%	Daily	Eastern North Atlantic	Ducklow *et al.* (1993)	Mean
18%	Daily	Northwest Indian Ocean		
0.6 to 8.8%	Daily	Arabian Sea		End of monsoon
4.8%	Daily	Arabian Sea	Pomroy & Joint (1999)	End of monsoon
2.1 to 27.4%	Daily	Arabian Sea	Pomroy & Joint (1999)	End of monsoon
10.3%	Daily	Arabian Sea	Pomroy & Joint (1999)	Mean, end of monsoon
3.2 to 21.1%	Daily	Arabian Sea	Pomroy & Joint (1999)	End of monsoon
7.9%	Daily	Arabian Sea	Pomroy & Joint (1999)	Mean, end of monsoon
6 to 44.1%	Daily	Arabian Sea	Pomroy & Joint (1999)	End of monsoon
14.6%	Daily	Arabian Sea	Pomroy & Joint (1999)	Mean, end of monsoon
11%	Daily	NE subarctic Pacific	Sherry *et al.* (1999)	
4%	Daily	NE subarctic Pacific	Sherry *et al.* (1999)	
3%	Daily	NE subarctic Pacific	Sherry *et al.* (1999)	
12%	Daily	NE subarctic Pacific	Sherry *et al.* (1999)	
21%	Daily	NE subarctic Pacific	Sherry *et al.* (1999)	
8%	Daily	NE subarctic Pacific	Sherry *et al.* (1999)	
6.8 to 44%	Daily	Southern Ocean Polar Front	Lochte *et al.* (1997)	
15.5%	Daily	Southern Ocean Polar Front	Lochte *et al.* (1997)	
7.8 to 56.4%	Daily	Southern Antarctic Circumpolar Current	Lochte *et al.* (1997)	
22.4%	Daily	Southern Antarctic Circumpolar Current	Lochte *et al.* (1997)	
4.7 to 27%	Daily	Southern Ocean marginal ice zone	Lochte *et al.* (1997)	
11.9%	Daily	Southern Ocean marginal ice zone	Lochte *et al.* (1997)	
15 to 20%		Global	Ducklow(2000) Values considered normal from synthesis	
10-15%		Global (open ocean)	Anderson & Ducklow(2001) Estimates from steady-state models	
76%		Sea of Japan	Sorokin (1978)	
16 to 165%		Central tropical Indian Ocean	Calculated from Sorokin (1985) & conversion factors (Bratbak & Dundas (1984)	

59%	Central tropical Indian Ocean	Calculated from Sorokin (1985) & conversion factors (Bratbak & Dundas1984) mean
17%	North pacific gyre- open ocean	Cho & Azam (1988)
9 to 46%	Gulf stream rings- open ocean	Ducklow & Carlson ( )
27%	Gulf stream ring- open ocean	Ducklow & Carlson ( )
8 to 104%	Indian ocean- open ocean	Ducklow ( )
40%	Indian ocean- open ocean	Ducklow ( )
8 to 61%	West North Atlantic- open ocean	Li *et al.* (1993)
23%	West North Atlantic- open ocean	Li *et al.* (1993)
19 to 51%	East North Atlantic- open ocean	Ducklow *et al.* (1993)
34%	East North Atlantic- open ocean	Ducklow *et al.* (1993)
4 to 42%	Subarctic Pacific- open ocean	Kirchman *et al.* (1993)
11%	Subarctic Pacific- open ocean	Kirchman *et al.* (1993)
12%	Equatorial pacific- equator	Kirchman *et al.* (1995)
30%	Equatorial pacific- 12N and 12S	Kirchman *et al.* (1995)

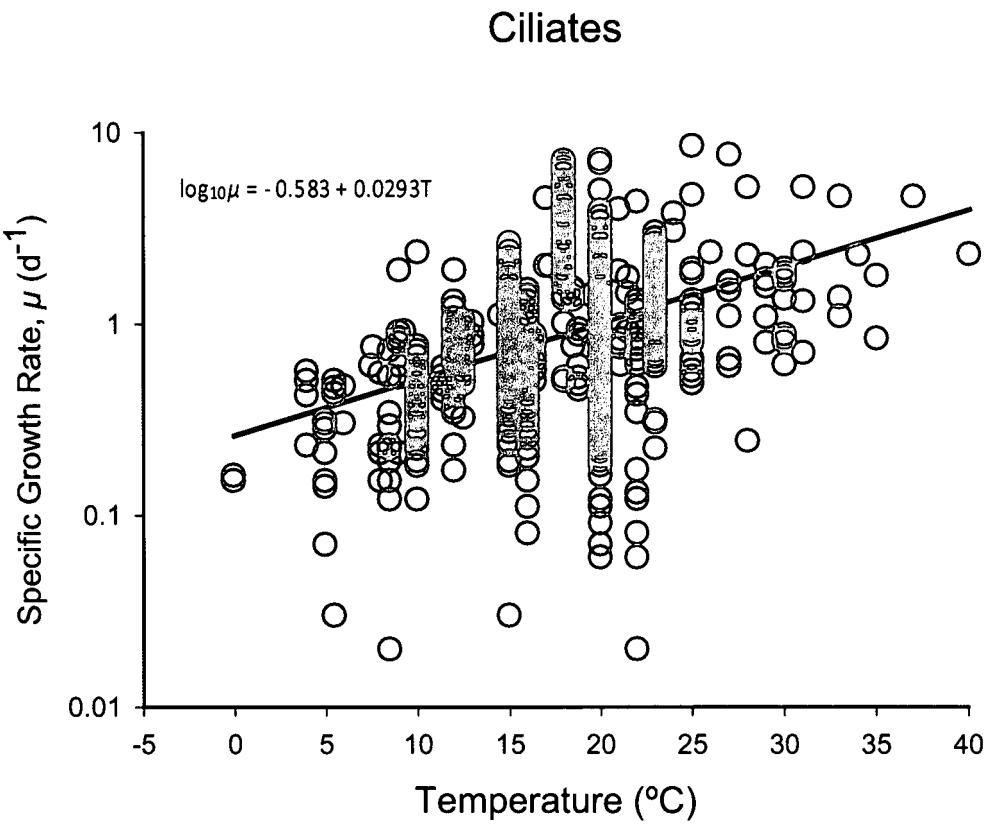
Appendix 22 **Values of clearance efficiency (reported as percentage of prey production consumed) for different taxa of the planktonic food web reported in the literature and used as a guide for the oligotrophic and eutrophic models.**

Taxon	Prey	Model Notation	% Prey Consumed	Time	Region	Trophic Status	Source	Notes
All	Phytoplankton		59.9	Daily	Coastal	Eutrophic	Calbet & Landry (2004)	
			56.6	Daily	Coastal	Eutrophic	Calbet & Landry (2004)	
			74.5	Daily	Tropical	Eutrophic	Calbet & Landry (2004)	
			71.3	Daily	Tropical/subtropical	Eutrophic	Calbet & Landry (2004)	
			68.8	Daily	Temperate/subpolar	Eutrophic	Calbet & Landry (2004)	
			69.6	Daily	Oceanic	Oligotrophic	Calbet & Landry (2004)	
			78.0	Daily	Oceanic	Oligotrophic	Calbet & Landry (2004)	
			59.2	Daily	Polar	Oligotrophic	Calbet & Landry (2004)	
			65.2	Daily	Polar	Oligotrophic	Calbet & Landry (2004)	
Nano/microflagellates	Picophytoplankton	*FCEPP*	39%		Marine		Derived from Stockner (1988)	
	Phytoplankton		2 to 3 %		Coastal	Eutrophic	Lignell *et al.* (1993)	
	Bacteria	*FCEB*	66 to 74 %		Coastal	Eutrophic	Lignell *et al.* (1993)	
			75%				Kuuppo-Leinikki (1990)	
			83%		Baltic Sea		Kuuppo-Leinkki (1990)	
			80%	Annual			Calliari *et al.* (2002)	
			72 to 96%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994)	Mean
			80%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994)	
			23 to 154%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994)	
			78%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994)	Mean
Ciliates	Picophytoplankton	*CilCEPP*	17%		Marine		Derived from Stockner (1988)	
	Nanophytoplankton	*CilCEPN*	52%	Annual	Narragansett Bay	Eutrophic	Verity (1987)	Annual mean
			32%	Annual	Narragansett Bay	Eutrophic	Verity (1985)	
			9 to 52%	Daily	NW Mediterranean	Oligotrophic	Rassoulzadegan *et al.* (1988)	
			22%	Annual	NW Mediterranean	Oligotrophic	Rassoulzadegan *et al.* (1988)	Annual mean

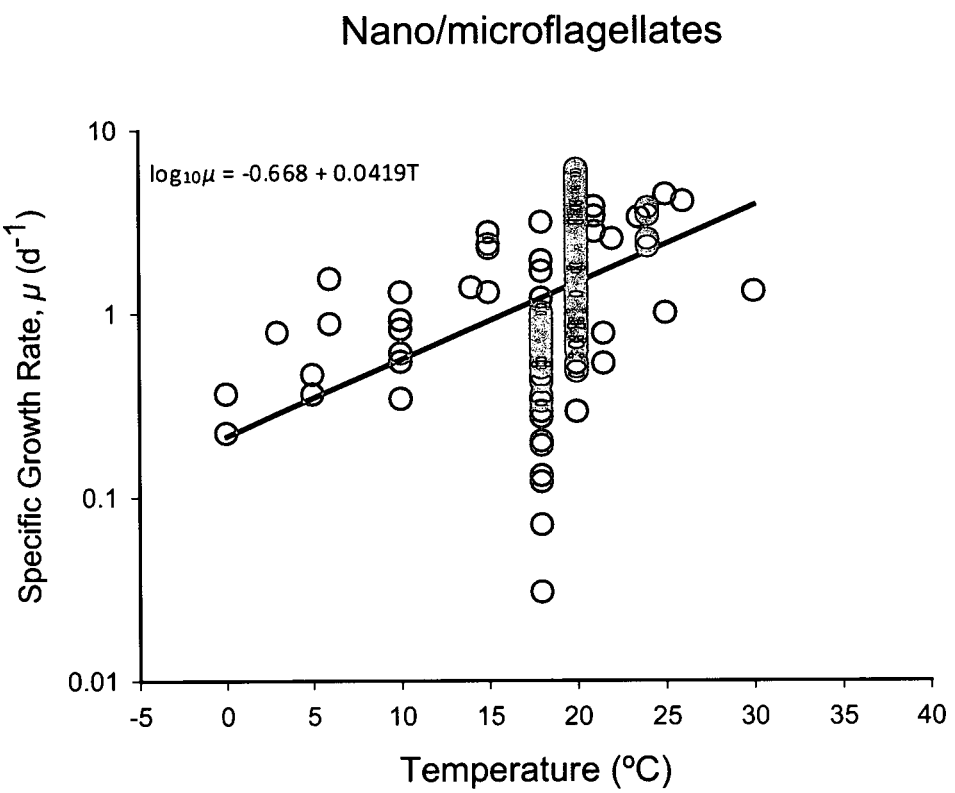
		18 to 99%		Mediterranean-offshore		Rassoulzadegan *et al.* (1988)	
	Phytoplankton	9 to 11%	Annual	Southampton Water	Eutrophic	Leakey *et al.* (1992	Annual Mean
		26%	Annual	Narragansett Bay	Eutrophic	Verity (1987)	Annual
		4 to 23 %		Peruvian upwelling	Eutrophic	Hendrikson *et al.* (1982)	
		5.5%	Daily	California Bight	Eutrophic	Heinbokel and Beers (1979)	Mean values
		26%	Annual	Narragansett Bay	Eutrophic	Verity (1985)	Annual
		16%	Annual	Narragansett Bay	Eutrophic	Verity (1985)	
		49%	Annual	Southern Kattegat	Eutrophic	Nielsen & Kiøboe (1994)	Mean
		8%	Annual	Young Sound	Eutrophic	Rysgaard *et al.* (1999)	Annual Mean
		4.6%	Daily	California Bight	Eutrophic	Heinbokel and Beers (1979)	Mean values
		5.2%	Daily	California Bight	Eutrophic	Heinbokel and Beers (1979)	Mean values
		27%	Annual	Long Island Sound	Eutrophic	Capriulo & Carpenter (1983)	Annual Mean
		24%	Daily	Sanich Inlet	Eutrophic	Takahashi & Hoskins (1978)	
		49%	Annual			Nielsen & Kiørboe (1994)	Mean
	Nano/microflagellates *CilCEF*	100%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994) and Weisse *et al.* (1990))	
		63 to 175%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994)	
		106%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994)	Mean
	Bacteria *CilCEB*	0.8 to 38%		NW Mediterranean	Eutrophic	Rassoulzadegan *et al.* (1988)	
		5 to 27%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994	
		14%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994 Mean	
		4 to 28%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994	
		20%		Adriatic Sea	Eutrophic	Solic & Krstovic (1994 Mean	
		1 to 38%	Daily	NW Mediterranean	Oligotrophic	Rassoulzadegan *et al.* (1988)	
Dinoflagellates	Phytoplankton	6%	Annual	Young Sound	Eutrophic	Rysgaard *et al.* (1999)	
Nanoflagellates & Ciliates	Bacteria	90%				Kuuppo-Leinikki (1990	
Ciliates & Dinoflagellates	Phytoplankton	1 to 5%		Coastal	Eutrophic	Lignell *et al.* (1993)	
	Nanoflagellates	30 to 39%		Coastal	Eutrophic	Lignell *et al.* (1993)	
	Microphytoplankton	14%	Annual			Rysgaard *et al.* (1999)	
Microzooplankton	Picophytoplankton	8 to 29%		Benguela upwelling	Eutrophic	Painting *et al.* (1993)	
	Nanophytoplankton	62%	Annual	Narragansett Bay	Eutrophic	Verity (1986)	Grazing primarily by ciliates
	Phytoplankton	50%		North Atlantic	Eutrophic	Harrison *et al.* (1993)	
		88%		North Atlantic	Eutrophic	Harrison *et al.* (1993)	
		55 to 83%		Equatorial pacific	Eutrophic	Murray *et al.* (1994)	
		0 to 100%	Daily	Halifax Harbour	Eutrophic	Gifford (1988)	Grazing primarily by ciliates
		49.3%	Daily	Halifax Harbour	Eutrophic	Gifford (1988	Grazing primarily by ciliates
		30%	Daily	Sanich Inlet	Eutrophic	Takahashi & Hoskins (1978)	
		40.2 to 113.7%	Daily	Jones Sound, Arctic	Eutrophic	Paranjape (1987)	

			36.7 to 87.8%	Daily	Baffin Bay, Arctic	Eutrophic	Paranjape (1987)	
			31%	Daily	Jones Sound, Arctic	Eutrophic	Paranjape (1987)	
			47%	Daily	Baffin Bay, Arctic	Eutrophic	Paranjape (1987)	
			74%	Daily	Jones Sound, Arctic	Eutrophic	Paranjape (1987)	Mean
			61%	Daily	Baffin Bay, Arctic	Eutrophic	Paranjape (1987)	Mean
			83%		Equator		Landry *et al.* (1995)	
			12%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)	
			16%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)	
			24%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)	
			56%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)	
			39 to 104%		Eastern tropical Pacific		Beers & Stewart (1971)	
			70%		Eastern tropical Pacific		Beers & Stewart (1971)	Mean
			5 to 125%		California		Beers & Stewart (1971)	Mean
			22%		California		Beers & Stewart (1971)	Mean
			7 to 52%		California		Beers & Stewart (1971)	Mean
			23%		California		Beers & Stewart (1971)	Mean
Protists	Phytoplankton		26 to 50%		Coastal upweling	Eutrophic	Neuer & Cowles (1994)	
			39 to 115%		North Atlantic	Eutrophic	Burkhill *et al.* (1993)	
	Bacteria		80%	Annual			Calliari *et al.* (2002)	
Copepods	Picophytoplankton	*CopCEPP*	14%		Marine		Derived from Stockner (1988)	
	Nanophytoplankton	*CopCEPN*	3 to 96%	Daily			Uitto & Hallfors XXXX	
	Microphytoplankton	*CopCEPM*	10.1%			Eutrophic	Calbet & Prairie(2003)	
			15%			Eutrophic	Calbet(2001)	
			40.4%			Oligotrophic	Calbet & Prairie(2003)	
			74%			Oligotrophic	Calbet(2001)	
			81%				Roman & Gauzens (1997)	
			22%				Roman & Gauzens (1997)	
			3%	Annual			Kiørboe & Nielsen (1994)	
			20%				Huskin *et al.* (2006)	Mean
			44%				Huskin *et al.* (2006)	
			0.8%				Huskin *et al.* (2006)	
			22.6%	Annual			Calbet(2001)	Mean
			6%	Annual			Calbet(2001)	Mode
	Phytoplankton		0.02 to 5%		Coastal	Eutrophic	Lignell *et al.* (1993)	
			6 %		Coastal	Eutrophic	Lignell *et al.* (1993)	Quoted value
			1 to 9%		Coastal	Eutrophic	Lignell *et al.* (1993)	
			11 to 41%		Peruvian upwelling	Eutrophic	Hendrikson *et al.* (1982)	
			1 to 2%		North Atlantic	Eutrophic	Verity (1993)	
			44%	Annual	Long Island Sound	Eutrophic	Capriulo & Carpenter (1983)	Annual mean
	Nano/microflagellates	*CopCEF*	8 to 34%		Coastal		Lignell *et al.* (1993)	

	Ciliates and dinoflagellates	63 to 88%		Coastal	Eutrophic	Lignell *et al.* (1993)
Copepods (nauplii)	Phytoplankton	9%	Daily	Sanich Inlet	Eutrophic	Takahashi & Hoskins (1978)
Mesozooplankton	Phytoplankton	1 to 12%		Equatorial Pacific	Eutrophic	Dam *et al.* (1995)
		2 to 12%		Equatorial Pacific	Eutrophic	Zhang *et al.* (1995)
		5%		40N North Atlantic	Eutrophic	Harrison *et al.* (1993)
		9%		45N North Atlantic	Eutrophic	Harrison *et al.* (1993)
		2 to 12%		Equatorial pacific-	Eutrophic	Dam *et al.*, Zhang *et al.*
		10%		Benguela upwelling	Eutrophic	Painting *et al.* (1993)
		18%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)
		41%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)
		38%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)
		24%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)
Bacteria		66%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)
		70%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)
		78%		Tropical Indian Ocean		Calculated from values in Sorokin (1985)



Appendix 23. Response of log10 ciliate specific growth rate in response to temperature. We used heterotrophic ciliate data (n=909) from 71 studies as reported in Rose & Caron (2007). The solid line represents the significant relationship determined by regression ($p<0.001$, R-squared=16.5%, F=179).



Appendix 24. Response of log10 nano/microflagellate specific growth rate in response to temperature. We used heterotrophic ciliate data (n=184) from 27 studies as reported in Rose & Caron (2007). The solid line represents the significant relationship determined by regression ($p<0.001$, R-squared=17%, F=37.68).

Bibliography

Aelion CM, Chisholm SW (1985) Effect of temperature on growth and ingestion rates of *Favella* sp. Journal of Plankton Research 7(6):821-830

Agawin NSR, Duarte CM, Agustí S (2000) Nutrient and temperature control of the contribution of picoplankton biomass and production. Limnology and Oceanography 45(3): 591-600

Altamirano RC, Sierra-Beltrán AP (2008) Biotoxins from freshwater and marine harmgul algal blooms occurring in Mexico. Toxin Review 27(1): 27-77

Amon MW, Benner R (1994) Rapid cycling of high-molecular weight dissolved organic matter in the ocean. Nature 369: 549-552

Anderson TR, Ducklow HW (2001) Microbial loop carbon cycling in ocean environments studied using a simple steady-state model. Aquatic Microbial Ecology 26: 37-49

Anderson TR, Pond DW (2000) Stoichiometric theory extended to micronutients: Comparison of the roles of essential fatty acids, carbon, and nitrogen in the nutrition of marine copepods. Limnology and Oceanography 45: 1162-1167

Anderson TR, Turley CM (2003) Low bacterial growth efficiency in the oligotrophic eastern Mediterranean Sea: a modelling analysis. Journal of Plankton Research 25(9): 1011-1019

Angilletta MJ, Dunham AE (2003) The temperature-size rule in Ectotherms: simple evolutionary explanations may not be general. American Naturalist 162: 332-342

Arendt KE, Jónasdóttir SH, Hansen PJ, Gärtner S (2005) Effects of dietary fatty acids on the reproductive success of the calanoid copepod *Temora longicornis*. Marine Biology 146: 513-530

Arias-González JE, Delesalle B, Salvat B, Galzin R (1997) Trophic functioning of the Tiahura reef sector, Moorea Island French Polynesia. Coral Reefs 16: 231-246

Arndt (2004) Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. Hydrobiologia 1: 231-246

Armstrong RA (1999) Stable model structures for representing biogeochemical diversity and size spectra in plankton communities. Journal of Plankton Research 21(3): 445-464

Atkinson A (1996) Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey populations. Marine Ecology Progress Series 130: 85-96

Atkinson A, Ward P, Murphy EJ (1996) Diel periodicity of Subantarctic copepods: relationships between vertical migration, gut fullness and gut evacuation rate. Journal of Plankton Research 18(8): 1387-1405

Atkinson D (1996) Ectotherm life-history responses to developmental temperature. In: Johnston IA, Bennett AF (eds) Animals and Temperature: Phenotypic and Evolutionary Adaptation Cambridge University Press pp183-204

Augustí S, Enríquez S, Frost-Christensen H, Sand-Jensen K, Duarte CM (1994). Light harvesting among photosynthetic organisms. Functional Ecology 8: 273-279

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The Ecological Role of Water-Column Microbes in the Sea. Marine Ecology Progress Series 10: 257-263

Baird D, McGlade JM, Ulanowicz RE (1991) The comparative ecology of six marine ecosystems. Philosophical Transactions: Biological Sciences 333: 15-29

Båmstedt U, Lane J, Martinussen MB (1999) Bioenergetics of ephyra larvae of the scyphozoan jellyfish *Aurelia aurita* in relation to temperature and salinity. Marine Biology 135: 89-98

Banse K (1994) Grazing and zooplankton production as key controls of the phytoplankton production in the open ocean. Oceanography 7(1): 13-20

Banse K (1995) Zooplankton: Pivotal role in the control of ocean production. ICES Journal of Marine Science 52: 265-277

Beaugrand G, Lindley JA, Helaouet P, Bonnet D (2007). Macroecological study of *Centropages typicus* in the North Atlantic Ocean. Progress in Oceanography 72(2-3): 259-273

Beaver JR, Crisman TL (1982) The trophic response of ciliates protozoans in freshwater lakes. Limnology and Oceanography 27(2): 246-253

Bell T, Kalff J (2001). The contribution of picophytoplanktonin marine and freshwater systems of different trophic status and depth. Limnology and Oceanography 46(5) 1243-1248

Benoît E, Rochet M-J (2004) A continuous model of biomass size spectra governed by predation and the effects of fishing on them. Journal of Theoretical Biology 226: 9-21

Berggreen U, Hansen B, Kiørboe T (1988) Food spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Marine Biology 99: 341-352

Bernard C, Rassoulzadegan F (1990) Bacteria or microflagellates as a major food source for marine ciliates: possible implications for the microzooplankton. Marine Ecology Progress Series 64: 147-155

Bissinger JE, Montagnes DJS, Sharples J, Atkinson D (2008) Predicting marine phytoplankton maximum growth rates from temperature: improving on the Eppley curve using quantile regression. *Limnology and Oceanography* 53(2): 487-493

Booth BC, Lewin J, Postel JR (1993) Temporal variation in the structure of autotrophic and heterotrophic communities in the subarctic Pacific. Progress in Oceanography 32: 57-99

Booth S, Zeller D (2005) Mercury, food webs, and marine mammals: Implications of diet and climate change for human health. Environmental Health Perspectives 113(5): 521-526

Borsheim KY, Bratbak G (1987) Cell volume to cell carbon conversion factors for the bacterivorous *Monas* sp. enriched from seawater. Marine Ecology Progress Series 36: 171-175

Boyd PW, Strom S, Whitney FA, Doherty S, Wen ME, Harrison PJ, Wong CS, Varela DE (1995) The NE subarctic Pacific in winter: I. Biological standing stocks. Marine Ecology Progress Series 128: 11-24

Brander KM (2007) Global fish production and climate change. Proceedings of the National Academy of Sciences of the United States of America 104(50): 19709-19714

Buchary EA (2001) Preliminary reconstruction of the Icelandic marine ecosystem in 1950 and some predictions with time series data. In Fisheries impacts on North Atlantic ecosystems: models and analyses. FCRR 4:198-206

Buck KR, Chavez FP, Campbell L (1996) Basin-wide distributions of living carbon components and the inverted trophic pyramid of the central gyre of the North Atlantic Ocean, summer 1993. Aquatic Microbial Ecology 10: 283-298

Bunker AJ, Hirst AG (2004) Fecundity of marine planktonic copepods: global rates and patterns in relation to chlorophyll *a*, temperature and body weight. Marine Ecology Progress Series 279: 161-181

Buitenhuis E, Le Quéré C, Aumont O, Beaugrand G, Bunker A, Hirst A, Ikeda T, O'Brien T, Piontkovski S, Straile D (2006). Biogeochemical fluxes through mesozooplankton. Global Biogeochemical Cycles 20(2): 18 GB2003, doi:10.1029/2005GB002511

Buskey EJ (1993) Annual pattern of micro- and mesozooplankton abundance and biomass in a subtropical estuary. Journal of Plankton Research 15(8): 907-924

Buskey EJ, Coulter C, Strom S (1993) Locomotory patterns of microzooplankton: potential effects on food selectivity of larval fish. Bulletin of Marine Science 53(1): 29-45

Buskey EJ, Coulter CJ, Brown SL (1994) Feeding, growth and bioluminescence of the heterotrophic dinoflagellate *Protoperidinium huberi*. Marine Biology 121: 373-380

Calbet (2001). Mesozooplankton grazing effect on primary production: A global comparative analysis in marine ecosystems. Limnology and Oceanography 46: 1824–1830

Calbet A, Landry MR (2004). Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. Limnology and Oceanography 49: 51-57

Calbet A, Prairie YT (2003). Mesozooplankton grazing and primary production: Reply to the comment by Laws. Limnology and Oceanography 48: 1359-1362

Calliari D, Tiselius P (2005) Feeding and reproduction in a small calanoid copepod: *Acartia clausi* can compensate quality with quantity. Marine Ecology Progress Series 298:241-250

Calow P (1977) Conversion efficiencies in heterotrophic organisms. Biological Reviews 52: 385-409

Callieri C, Karjalained SM, Passoni S (2002). Grazing by ciliates and heterotrophic nanoflagellates on picocyanobacteria in Lago Maggiore, Italy. Journal of Plankton Research 24(8): 785-796

Capriulo GM, Carpenter AJ (1980). Grazing by 35 to 202 μm micro-zooplankton in Long Island Sound. Marine Biology 56(3): 19-326

Capriulo G, Carpenter EJ (1983) Tintinnid abundance species composition and feeding impact in central Long Island Sound. Marine Ecology Progress Series 10: 277-288.

Carlson CA, Ducklow HW, Hansell DA, Smith WO (1998) Organic carbon partitioning during spring phytoplankton blooms in the Ross Sea polynya and the Sargasso Sea. Limnology and Oceanography 43: 375-386

Caron DA, Goldman JC, Dennett MR (1986) Effect of Temperature on Growth, Respiration, and Nutrient Regeneration by an Omnivorous Microflagellate. Applied and Environmental Microbiology 52(6): 1340-1347

Caron DA, Goldman JC, Dennett MR (1990) Carbon utilization by the omnivorous flagellate *Paraphysomonas imperforata*. Limnology and Oceanography 35(1): 192-201

Carrick HJ, Schelske (1997) Have We Overlooked the Importance of Small Phytoplankton in Productive Waters? Limnology and Oceanography 42(7): 1613-1621

Castellani C, Irigoien X, Harris RP, Lampitt RS (2005) Feeding and egg production of *Oithona similis* in the North Atlantic. Marine Ecology Progress Series 288: 173-182

Cavender-Bares KK, Mann EL, Chisholm SW (1999) Differential response of equatorial Pacific phytoplankton to iron fertilization. Limnology and Oceanography 44(2): 237-246

Chavez, FP (1989) Size distribution of phytoplankton in the central and eastern tropical Pacific. Global Biogeochemical Cycles 3: 27-35

Checkley DM (1980) The egg production of a marine planktonic copepod in relation to its food supply: Laboratory studies. Limnology and Oceanography 25: 430-446

Chigbu P, Sibley TH (1994) Predation by *Neomysis mercedis*: Effects of temperature, *Daphnia magna* size and prey density on ingestion rate and size selectivity. Freshwater Biology 32: 39-48

Cho BC, Azam F (1990). Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. Marine Ecology Progress Series 63: 253-259

Choi JW, Peters F (1992) Effects of Temperature on Two Psychrophilic Ecotypes of a Heterotrophic Nanoflagellate, *Paraphysomonas imperforata*. Applied and Environmental Microbiology 58(2): 593-599

Christaki U, Giannakourou A, van Wambeke F, Grégori G (2001) Nanoflagellate predation on auto- and heterotrophic picoplankton in the oligotrophic Mediterranean Sea. Journal of Plankton Research 23: 1297-1310

Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling 172: 109-139

Christian JR, Karl DM (1994) Microbial community structure at the US-JGOFS station ALOHA: inverse methods for estimating biochemical indicator ratios. Journal of Geophysical Research 99: 14269-14276

Clarke A, Crame JA (1997) Diversity, latitude and time: Patterns in the shallow sea. *In* Ormond RJD, Gage JD, Angel MV (eds) Marine biodiversity: Patterns and processes. Cambridge University Press, Cambridge pp. 122–147

Clarke A, Griffiths HJ, Linse K, Barnes DKA, Crame JA (2007) How well do we know the Antarctic marine fauna? A preliminary study of macroecological and biogeographical patterns in Southern Ocean gastropod and bivalve molluscs. Diversity & Distributions, 13(5): 620-632

Coffin RB, Connolly JP (1997) Bacteria and heterotrophic microflagellate production in the Santa Rosa Sound, Florida. Hydrobiologia 353: 53-61

Cole BE, Cloern JE, Alpine AE (1986) Biomass and productivity of three phytoplankton size classes in San Francisco Bay. Estuaries 9: 117-126

Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Marine Ecology Progress Series 42: 1-10

Colin SP, Dam HG (2002) Testing for toxic effects of prey on zooplankton using sole versus mixed diets. Limnology and Oceanography 47:1430-1437

Conover RJ (1979) Secondary production as an ecological phenomenon. In: van der Spoel, Pierrot-Bults AC (eds) Zoogeography and diversity of plankton. Halsted pp 50-86

Copping AE, Lorenzen CJ (1980) Carbon budget of a marine phytoplankton-herbivore system with carbon-14 as a tracer. Limnology and Oceanography 25: 873-882

Crawford DW (1992) Metabolic Cost of Motility in Planktonic Protists: Theoretical Considerations on Size Scaling and Swimming Speed. Microbial Ecology 24: 1-10

Dalsgaard JPT, Oficial RT (1997) A Quantitative approach for assessing the productive performance and ecological contributions of smallholder farms. Agricultural Systems 55(4): 503-533

Dam HG, Colin SP (2005) *Prorocentrum minimum* (clone Exuv) is nutritionally insufficient, but not toxic to the copepod *Acartia tonsa*. Harmful Algae 4: 575-584.

Dam HG, Lopes RM (2003) Omnivory in the calanoid copepod *Temora longicornis*: feeding, egg production and egg hatching rates. Journal of Experimental Marine Biology and Ecology 292: 119-137

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440: 165-173

de Vernal A, Eynaud F, Henry M, Hillaire-Marcel C, Londeix L, Mangin S, Matthiessen J, Marret F, Radi T, Rochon A, Solignac, Turon J-L (2005) Reconstruction of sea-surface conditions at middle to high latitudes of the Nothern Hemisphere during the Last Glacial Maximum (LGM) based on dinoflagellate cyst assemblages. Quaternary Science Reviews 24: 897-924

Deason EE (1980). Grazing of *Acartia hudsonica* (*A. clausi*) on *Skeletonema costatum* in Narragansett Bay (USA): influence of food concentration and temperature. Marine Biology 60: 101-113

Debs CA (1984) Carbon and nitrogen budget of the calanoid copepod *Temora stylifera*: effect of concentration and composition of food. Marine Ecology Progress Series 15: 213-223

del Giorgio PA, Cole JJ (1998) Bacterial growth efficiency in natural aquatic systems. Annual Review of Ecological Systems 29: 503-541

del Giorgio PA, Williams PJleB (2005) Respiration in Aquatic Ecosystems. Oxford University Press

de Vooys CGN (1979). Primary production in aquatic environments. In: Global Carbon Cycle (Eds. Bolin B, Degens ET, Kempe S, Ketner P) pp259-292. Wiley, New York

Dodge JD (1989) Records of marine dinoflagellates from North Sutherland (Scotland). British Phycological Journal 24: 385-389

Dodge JD (1993) Armoured dinoflagellates in the NE Atlantic during the BOFS cruises, 1988-90. Journal of Plankton Research 15(5): 465-483

Dolan JR (1991). Guilds of ciliate microzooplankton in the Chesapeake Bay. Estuarine, Coastal and Shelf Science 33: 137-152

Dolan JR, Marrase C (1995) Planktonic ciliate distribution relative to a deep chlorophyll maximum: Catalan Sea, N.W. Mediterranean, June 1993. Deep Sea Research 42(11-12): 1965-1987

Donald KM, Scanlan DJ, Carr NG, Mann, NH, Joint I (1997) Comparative phosporus nutrition of the marine cyanobacterium *Synechococcus* WH7803 and the marine diatom *Thalassiosira weissflogii*. Journal of Plankton Research 19: 1793-1813

Duarte CM, Cebrián J (1996) The fate of marine autotrophic production. Limnology and Oceanography 41(8): 1758-1766

Duarte CM, Agustí S, Gasol JM, Vaqué D, Vazquez-Dominguez E (2000) Effect of nutrient supply on the biomass structure of planktonic communities: an experimental test on a Mediterranean coastal community. Marine Ecology Progress Series 206: 87-95

Ducklow HW, Carlson CA (1992) Oceanic bacterial production. Advances in Microbial Ecology 12: 113-181

Eppley RW (1968) An Incubation Method for Estimating the Carbon Content of Phytoplankton in Natural Samples. Limnology and Oceanography 13(4): 574-582

Eppley RW (1972) Temperature and phytoplankton growth in the sea. Fishery Bulletin 70(4): 1063-1085

Evans KL, Warren PH, Gaston KJ (2005) Species-energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews 80(1): 1-25

Evans KL, James NA, Gaston KJ (2006) Abundance, species richness and energy availability in the North American avifauna. Global Ecology and Biogeography 15: 372-285

Falkowski PG, Barber RT, Smetacek V (1998) Biogeochemical controls and feedbacks on ocean primary production. Science 281: 200-206

Fasham MJR (2003) Ocean biogeochemistry: the role of the ocean carbon cycle in global change. Global change- the IGBP series. Springer

Fenchel T (1968) The ecology of marine microbenthos III. The reproductive potential of ciliates. *Ophelia 5*: 123-136

Fenchel T (1982) Ecology of heterotrophic microflagellates. II. Bioenergetics and growth. Marine Ecology Progress Series 8: 225-231

Fenchel T (1987) The Ecology of Protozoa. Madison/Springer-Verlag, Berlin

Feinstein TN, Traslavina R, Sun M, Lin S (2002) Effects of light on photosynthesis, grazing, and population dynamics of the heterotrophic dinoflagellate *Pfiesteria piscicida* (Dinophyceae). Journal of Phycology 38: 659-669

Fiala M, Semeneh M, Oriol L (1998) Size-fractionated phytoplankton biomass and species composition in the Indian sector of the Southern Ocean during austral summer. Journal of Marine Systems 17: 179-194

Finlay BJ (1977) The dependence of reproductive rate on cell size and temperature in freshwater ciliated protozoa. Oecologia 30: 75-81

Fogg GE (1987) Picoplankton. Proceedings IV ISME pp 96-100

Foggo A, Frost MT, Attrill MJ (2003) Abundance-occupancy patterns in British estuarine macroinvertebrates. Marine Ecology Progress Series 265: 297-302

Frost BW (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnolology and Oceanography 17: 805-815

Gaedke U (1993) Ecosystem analysis based on biomass size distributions: A case study of a plankton community in a large lake. Limnology and Oceanography 38(1): 112-127

Gasiūnaitė ZR, Cardoso AC, Heiskanen A-S, Henriksen P, Kauppila P, Olenina I, Pilkaitytė R, Purine I, Razinkovas A, Sagert S, Schubert H, Wasmund N (2005) Seasonality of coastal phytoplankton in the Baltic Sea: Influence of salinity and eutrophication. Estuarine, Coastal and Shelf Science 65: 239-252

Gasol JM, Del Giorgio PA, Duarte CM (1997). Biomass distribution of marine planktonic communities. Limnology and Oceanography 42: 1353-1363

Gaston KJ (2000) Global patterns in biodiversity. Nature 405: 220-227

Gaston, K.J, Blackburn TM (2000) Pattern and Process in Macroecology. Blackwell Science

Gates MA(1984) Quantitative importance of ciliates in the planktonic biomass of lake ecosystem. Hydrobiologia 108(3): 233-238

Gates MA, Lewg UT (1984) Contribution of ciliates protozoa to the planktonic biomass in a series of Ontario lakes: quantitative estimates and dynamical relationships. Journal of Plankton Research 6(3): 443-456

Geider RJ (1987) Light and temperature dependence of the carbon to chlorophyll a ratio in microalgae and cyanobacteria: implications for physiology and growth of phytoplankton. New Phytologist 106: 1–34

Geider R, Leadbeater BSC (1988) Kinetics and energetics of growth of the marine choanoflagellate *Stephanoeca diplocostata*. Marine Ecology Progress Series 47: 169-177

Gibson DM & Paffenhöfer G-A (2000) Feeding and growth rates of the doliolid, *Dolioletta gegenbauri* Uljanin (Tunicata, Thaliacea) Journal of Plankton Research 22: 1485-1500

Gibson DM & Paffenhöfer G-A (2002) Asexual reproduction of the doliolid, *Dolioletta gegenbauri* Uljanin (Tunicata, Thaliacea). Journal of Plankton Research 24: 703-712

Gillooly JF (2000) Effect of body size and temperature on generation time in zooplankton. Journal of Plankton Research 22(2): 241-251

Goericke R (1998) Response of phytoplankton community structure and taxon-specific growth rates to seasonally varying physical forcing in the Sargasso Sea off Bermuda. Limnology and Oceanography 43(5): 921-935

Goldman JC, Caron DA, Dennett MR (1987) Regulation of gross growth efficiency and ammonium regeneration in bacteria by substrate C : N ratio. Limnology and Oceanography 32: 1239-1252

Goldman JC, McCarthy JJ, Peavey DC (1979) Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature 279: 210-215

Gonzalez JM, Sherr EB, Sherr BF (1990) Size-selective grazing on bacteria by natural assemblages of estuarine flagellates and ciliates. Applied Environmental Microbiology 56: 583-589

Grafen A, Hails R (2002) Modern Statistics for the Life Sciences. Oxford University Press

Gribble KE, Nolan G, Anderson DM (2007) Biodiversity, biogeography and potential trophic impact of *Protoperidinium* spp. (Dinophyceae) off the southwestern coast of Ireland. Journal of Plankton Research 29(11): 931-947

Hallegraeff GM (1992) Harmful algal blooms in the Australian region. Marine Pollution Bulletin 25(5-8): 186-190

Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. Trends Ecol Evol 20: 337-344

Hamilton RD, Preslan JE (1969) Cultural characteristics of a pelagic marine hymenostome ciliate, *Uronema* sp. Journal of Experimental Marine Biology and Ecology 4: 90-99

Hansell DA, Bates NR, Gundersen K (1995) Mineralization of dissolved organic carbon in the Sargasso Sea. Marine Chemistry 51: 201-212

Hansen PJ (1991) *Dinophysis* – a planktonic dinoflagellates genus which can act as both prey and predator of a ciliate. Marine Ecology Progress Series 69: 201-204

Hansen B, Bjørnsen PK, Hansen PJ (1994). The size ration between planktonic predators and their prey. Limnology and Oceanography 39(2): 395-403

Hansen PJ (1992) Prey size selection, feeding rates and growth dynamics of heterotrophic dinoflagellates with special emphasis on *Gyrodinium spirale*. Marine Biology 114: 327-334

Hansen PJ, Bjørnsen PK, Hansen BW (1997). Zooplankton grazing and growth: scaling within the 2-2,000- µm body size range. Limnology and Oceanography 42(4): 687-704

Hansen RB, Lowery HK (1983) Nucleic acid synthesis in oceanic microplankton from the Drake Passage, Antarctica: Evaluation of steady-state growth. Marine Biology 73: 79-89

Haq SM (1967) Nutritional physiology of Metridia lucens and M. Longa from the Gulf of Maine. Limnology and Oceanography 12: 40-51

Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M (2000) ICES Zooplankton Methodology Manual. Academic Press, San Diego, CA

Harris RP, 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

Harrison WG, Head EJH, Horne EPW, Irwin B, Li WKW, Longhurst AR, Paranjape MA, Platt T (1993) The western North Atlantic Bloom Experiment. Deep-Sea Research II 40(1-2): 279-305

Harvey CJ, Kareiva PM (2005) Community context and the influence of non-indigenous species on juvenile salmon survival in a Columbia river resevoir. Biological Invasions 7: 651-663

Havens KE, James RT, East TL, Smith VH (2003) Environmental Pollution 122(3): 379-390

Heinbokel JF (1978) Studies on the functional role of tintinnids in the Southern California Bight. I. Grazing and growth rates in the laboratory cultures. Marine Biology 47: 177-189

Helaouët P, Beaugrand G (2007) of *Calanus finmarchicus and C. helgolandicus* in the North Atlantic Ocean and adjacent seas. Marine Ecological Progress Series, : -165

Hendrikson P, Sellner KG, Rojas de Mendiola B, Ochoa N, Zimmermann R (1982) The composition of particulate organic matter and biomass in the Peruvian upwelling region during ICANE 1977 (Nov. 14 – Dec. 2). Journal of Plankton Research 4(1): 163-186

Hewes CD, Sakshaug E, Reid FMH, Holm-Hansen O (1990) Microbial autotrophic and heterotrophic eucaryotes in Antarctic waters: relationships between biomass and chlorophyll, adenosine triphosphate and particulate organic carbon. Marine Ecology Progress Series 63: 27-35

Hirst AG, Bunker AJ (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. Limnology and Oceanography 48: 1988-2010

Hirst AG, Lucas CH (1998) Salinity influences body weight quantification in the scyphomedusa *Aurelia aurita*: important implications for body weight determination in gelatinous zooplankton. Marine Ecology Progress Series 165: 259-269

Hirst AG, Kiørboe T (2002) Mortality of marine planktonic copepods: global rates and patterns. Marine Ecology Progress Series 230: 195-209

Hirst AG, Roff JC, Lampitt RS (2003) A Synthesis of Growth Rates in Marine Epipelagic Invertebrate Zooplankton. Advances in Marine Biology 44: 1-142

Holen DA, Boraas ME (1991) The feeding behavior of *Spumella* sp. as a function of particle size: Implications for bacterial size in pelagic systems. Hydrobiologia 220: 73-88

Holligan PM, Harris RP, Newell RC, Harbour DS, Head RN, Linley EAS, Lucas MI, Tranter PRG, Weekley CM (1984) Vertical distribution and partitioning of organic carbon in mixed, frontal and stratified waters of the English Channel. Marine Ecology Progress Series 14: 111-127

Hopkins TL, Lancraft TM, Torres JJ, Donnelly J (1993) Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988). Deep-Sea Research I 40(1): 81-105

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

Hoppe H-G, Glocke K, Koppe R, Begler C (2002) Bacterial growth and primary production along a north-south transect of the Atlantic Ocean. Nature 416: 168-171

Huntley M, Boyd C (1984) Food-limited growth of marine zooplankton. American Naturalist 124(4): 455-478

Huntley ME, Lopez MDG (1992) Temperature-Dependent Production of Marine Copepods: A Global Synthesis. American Naturalist 140(2): 201-242

Huskin I, Anadon R, Alvarez-Marques F (2000) Ingestion, faecal pellet and egg production rates of *Calanus helgolandicus* feeding coccolithophorid versus non coccolithophorid diets. Journal of Experimental Marine Biology and Ecology 248: 239-254

Huskin I, López E, Viesca L, Anadón R (2006). Seasonal variation of mesozooplankton biomass, abundance and copepod grazing in the central Cantabrian Sea (southern Bay of Biscay). Scientia Marina 70S1: 119-130

Ikeda T, Kanno Y, Ozaki K, Shinada A (2001) Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. Marine Biology 139: 587-596

Ishigaki T, Sleigh MA (2001) Grazing characteristics and growth efficiencies at two different temperatures for three nanoflagellates fed with *Vibrio* bacteria at three different concentrations. Microbial Ecology 41:264–271

Ismael AA (2003) Succession of heterotrophic and mixotrophic dinoflagellates as well as autotrophic microplankton in the harbour of Alexandria, Egypt. Journal of Plankton Research 25(2): 193-202

Iwataki M, Kawami H, Matsuoka K (2007) *Cochlodinium fulvescens* sp. Nov. (Gymnodiniales, Dinophyceae), a new chain-forming unarmoured dinoflagellate from Asian coasts. Phycological Research 55: 231-239

Jacobsen DM, Anderson DM (1993) Growth and grazing rates of *Protoperidinium hirobis* Abé, a thecate heterotrophic dinoflagellate. Journal of Plankton Research 15: 723-736

Jakobsen HH, Halvorsen, Hansen BW, Visser AW (2005) Effects of prey motility and concentration on feeding in *Acartia tonsa* and *Temora longicornis*: the importance of feeding modes. Journal of Plankton Research 27(8): 775-785

Jackobsen HH, Hansen PJ (1997) Prey size selection, grazing and growth response of the small heterotrophic dinoflagellate *Gymnodinium* sp. and the ciliate *Balanion comatum* - a comparative study. Marine Ecology Progress Series 158: 75-86

James MR, Hall JA (1995) Planktonic ciliates protozoa: their distribution and relationship to environmental variables in a marine coastal ecosystem. Journal of Plankton Research 17(4): 659:683

Jeong HJ, Kim JS, Kim JH, Kim ST, Seong KA, Kim TH, Song JY, Kim SK (2005) Feeding and grazing impact of the newly described heterotrophic dinoflagellate *Stoeckeria algicida* on the harmful alga *Hetersigma akashiwo*. Marine Ecology Progress Series 295: 69-78

Jeong HJ, Yoo YD, Kim ST, Kang NS (2004) Feeding by the heterotrophic dinoflagellate Protoperidimium bipes on the diatom Skeletonoma costatum. Aquatic Microbial Ecology 36(2): 171-179

Johannes RE (1965) Influence of marine protozoa on nutrient regeneration. American Society of Limnology and Oceanography 10: 434-442

Johnson, WS, Allen DM (2005). Zooplankton of the Atlantic and Gulf Coasts. A Guide to Their Identifcation and Ecology. Johns Hopkins University Press. Baltimore, Maryland

Jones RH, Flynn KJ & Anderson TR (2002) Effect of food quality on carbon and nitrogen growth efficiency in the copepod *Acartia tonsa*. Marine Ecology Progress Series 235: 147-156

Jonsson PR (1986) Particle size selection, feeding rates and growth dynamics of marine planktonic oligotrichous ciliates (Ciliophora: Oligotrichina). Marine Ecology Progress Series 33-265-277

Kiørboe T, Nielsen TG (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. I. Copepods. Limnology and Oceanography 39: 493-507

Kiørboe T, Mohlenberg F, Hamburger K (1985) Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. Marine Ecology Progress Series 26: 85-97

Kirchman DL (1993) Leucine incorporation as a measure of biomass production by heterotrophic bacteria. In: Kemp PF, Sherr BF, Sheer EB, Cole JJ (eds) Handbook Methods in Aquatic Microbial Ecology. Lewis, Boca Raton, p 509-512

Kirchman DL, Rich JH, Barber RT (1995) Biomass and biomass production of heterotrophic bacteria along 140ºW in the equatorial Pacific: Effect of temperature on the microbial loop. Deep-Sea Research II 42(2-3): 603-619

Klaas C (1997) Microprotozooplankton distribution and their potential grazing impact in the Antarctic Circumpolar Current. Deep-Sea Research II 44(1-2): 375-393

Koblentz-Mishke OJ, Vedernikov VI (1976) Marine Science Communications 2: 357-374

Koehl MAR, Strickler JR (1981) Copepod feeding currents: Food capture at low Reynolds number. Limnology and Oceanography 26(6): 1062-1073

Kozlowsky-Suzuki B, Karjalainen M, Lehtiniemi M, Engström-Öst J, Koski, M, Carlsson P (2003) Feeding, reproduction and toxin accumulation by the copepods *Acartia bifilosa* and *Eurytemora affinis* in the presence of the toxic cyanobacterium *Nodularia spumigena*. Marine Ecology Progress Series 249: 237–249

Kühn SF (1997) Infection of *Coscinodiscus* spp. By the parasitoid nanoflagellate *Pirsonia diadema*: I. Behavioural studies on the infection process. Journal of Plankton Research 19(7): 791-804

Kuuppo-Leinikki (1990). Protozoan grazing on planktonic bacteria and its impact on bacterial population. Marine Ecology Progress Series 63: 227-238

Lalli CM, Parsons TR (1997) Biological Oceanography, An Introduction (2nd edition). The Open University

Lampitt RS, Noji T, von Bodungen B (1990) What happens to zooplankton faecal pellets? Implications for material flux. Marine Biology 104(1): 15-23

Lance VP, Hiscock MR, Hilting AK, Stuebe DA, Bidigare RR, Smith WO, Barber RT (2007) Primary productivity, differential size fraction and pigment composition responses in two Southern Ocean in situ iron enrichments. Deep Sea Research Part I: Oceanographic Research Papers 54(5): 747-773

Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142: 911-927

Landry MR, Constantinou J, Kirshtein J (1995) Microzooplankton grazing in the central equatorial Pacific during February and August, 1992. Deep-Sea Research. II 42: 657-671

Landry MR, Calbet A (2004) Microzooplankton production in the seas. ICES J Mar Sci 61: 501-507

Landry MR, Hassett RP (1982) Estimating the grazing impact of marine micro-zooplankton. Marine Biology 67: 283-288

Landry MR, Haas LW, Fagerness (1984) Dynamics of microbial plankton communities: experiments in Kaneohe Bay, Hawaii. Marine Ecology Progress Series 16: 127-133

Laybourn-Parry J (1984) A functional biology of free-living protozoa. Croom Helm, London

Le Borgne R (1981) Relationships between the hydrological structure, chlorophyll and zooplankton biomasses in the Gulf of Guinea. Journal of Plankton Research 3(4): 577-592

Leakey RJG, Burkill PH, Sleigh MA (1992).Planktonic ciliates in Southampton Water: Abundance, biomass, production, and role in pelagic carbon flow. Marine Biology 114: 67-83

Leakey RJG, Fenton N, Clarke A (1994) The annual cycle of planktonic ciliates in nearshore waters at Signy Island, Antarctica. Journal of Plankton Research 16(7): 841-856

Legendre L, Rivkin RB (2002). Fluxes of carbon in the upper ocean: regulation by food-web control nodes. Marine Ecology Progress Series 242: 95-109

Lessard EJ, Swift E (1985). Species-specific grazing rates of heterotrophic dinoflagellates in oceanic waters, measured with a dual-label radioisotope technique. Marine Biology 87: 289-296

Levinsen H, Turner JT, Nielsen TG, Hansen BW (2000) On the trophic coupling between rotists and copepods in arctic marine ecosystems. Marine Ecology Progress Series 204: 65-77

Lewis MR, Hebert D, Harrison WG, Platt T, Oakey NS (1986). Vertical Nitrate Fluxes in the Oligotrophic Ocean. Science 234: 870-873

Lewis DM (2005). A simple model of plankton population dynamics coupled with a LES of the surface mixed layer. Journal of Theoretical Biology 234: 565-591

Li WKW (2002) Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. Nature 419: 154-157

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

Lignell R, Heiskanen A-S, Kuosa H, Gundersen K, Kuuppo-Leinikki P, Pajuniemi R, Uitto A (1993) Fate of a phytoplankton spring bloom: sedimentation and carbon flow in the planktonic food web in the northern Baltic. Marine Ecology Progress Series 94: 239-252

Lin H-J, Shao K-T, Hwang J-S, Lo W-T, Cheng I-J, Lee L-H (2004) A Trophic model for Kuosheng Bay in Northern Taiwan. Journal of Marine Science and Technology 12(5): 424-432

Linley EAS, Newell RC, Lucas MI (1983) Quantitative relationships between phytoplankton, bacteria and heterotrophic microflagellates in shelf waters. Marine Ecology Progress Series 12: 77-89

López-Urrutia A, Acuña JL, Irigoien X, Harris R (2003) Food limitation and growth in temperate epipelagic appendicualrians (Tunicata). Marine Ecology Progress Series 252: 143-157

López-Urrutia A, San Martin E, Harris RP, Irigoien X (2006) Scaling the metabolic balance of the oceans. Proceedings of the National Academy of Science of the United States of America 103: 8739-8744

Lu S, Hodgkiss IJ (2004) Harmful algal bloom causative collected from Hong Kong. Hydrobiologia 512(1-3): 231-38

Lucas MI, Painting SJ, Muir DG (1986). Estimates of carbon flow through bacterioplankton in the S. Benguela upwelling region based on -thymidine incorporation and predator-free incubations. In: Deuxième Colloque International de Bactériologie marine, Brest, CNRS pp375-383

Marañón E, Behrenfeld MJ, González N, Mouriño B, Zubkov MV (2003). High variability of primary production in oligotrophic waters of the Atlantic Ocean: uncoupling from phytoplankton biomass and size structure. Marine Ecology Progress Series 257: 1-11

Marañón E, Holligan PM, Barciela R, González N, Mouriño B, Pazó, Varela M (2001). Patterns of phytoplankton size structure and productivity in contrasting open-ocean environments. Marine Ecology Progress Series 216: 43-56

Marine Zooplankton Colloquium 2 (2001). Future marine zooplankton research – a perspective. Marine Ecology Progress Series 222: 297-308

Martin ES, Harris RP, Irigoien X (2006) Latitudinal variation in plankton size spectra in the Atlantic Ocean. Deep-Sea Research II 53:1560-1572

Massana R, Stumm, CK, Pedrós-Alió C (1994) Effects of temperature, sulfide and food abundance on growth and feeding of anaeorobic ciliates. Applied Environmental Microbiology 60: 1317-1324

Mathes J, Arndt H (1995) Annual cycle of protozooplankton (ciliates, flagellates and sarcodines) in relation to phyto- and metazooplankton in Lake Neumühler See (Mecklenburg, Germany) Archiv für Hydrobiologie 134(3): 337-358

Matsuyama Y, Uchida T, Honjo T (1999) Effects of harmful dinoflagellates, *Gymnodinium mikimotoi* and *Heterocapsa circularisquama*, red-tide on filtering rate of bivalve mollusks. Fisheries Science 65(2): 248-253

Meiners K, Fehling J, Granskog MA, Spindler M (2002) Abundance, biomass and composition of biota in Baltic sea ice and underlying water (March 2000). Polar Biology 25: 761-770

Menden-Deuer S, Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnology and Oceanography 45(3) 569-579

Metz *C,* Schnack-Schiel SB (*1995*) *Observations* on carnivorous *feeding in Antarctic* calanoid *copepods*. Marine Ecology Progress Series 129:71-75

Mironova EI, Telesh IV, Skarlato SO (2009) Planktonic ciliates of the Baltic Sea (a Review). InlandWater Biology 2(1) 13-14

Mitchell BG, Brody EA, Holm-Hansen O, McClain C, Bishop J (1991) Light limitation of phytoplankton biomass and macronutirent utilization in the Southern Ocean. Limnology and Oceanography 36(8): 1662-1677

Møller EF, Nielsen TG (2001) Production of Bacterial Substrate by Marine Copepods: Effect of Phytoplankton Biomass and Cell Size. Journal of Plankton Research 23(5): 527-536.

Moloney CL, Field JG (1991) The size-based dynamics of plankton food webs. I. A simulations model of carbon and nitrogen flows. Journal of Plankton Research 13(5): 1003-1038

Moloney CL, Field JG, Lucas MI (1991) The size-based dynamics of plankton food webs. II. Simulations of three contrasting southern Benguela food webs. Journal of Plankton Research 13(5): 1039-1092

Montagnes DJS, Franklin DJ (2001) Effect of temperature on diatom volume, growth rate, and carbon and nitrogen content: Reconsidering some paradigms. Limnology and Oceanography 46(8): 2008-2018

Montagnes DJS, Kimmance SA, Atkinson D (2003) Using : Can growth rates increase linearly with temperature? Aquatic Microbial Ecology 32: 307-313

Montagnes DJS, Lynn DH, Roff JC, Taylor WD (1988). The annual cycle of heterotrophic planktonic ciliates in the waters surrounding the Isles of Shoals, Gulf of Maine: an assessment of their trophic role. Marine Biology 99: 21-30

Montagnes DJS, Lessard EJ (1999) Population dynamics of the marine planktonic ciliate *Strombidinopsis multiauris*: its potential to control phytoplankton blooms. Aquatic Microbial Ecology 20: 167-181

Montagnes DJS, Lynn DH, Roff JC & Taylor WD (1988) The annual cycle of heterotrophic planktonic ciliates in the waters surrounding the Isles of Shoals, Gulf of Maine: an assessment of their trophic role. Marine Biology 99: 21-30

Müller H (1991) *Pseudobalanion planctonicum* (Ciliphora, Prostomatida): ecological significance of an algivorous nanociliate in a deep meso-eutrophic lake. Journal of Plankton Research 13: 247-262

Müller H, Geller W (1993) Maximum growth rates of aquatic ciliated protozoa: the dependence on body size and temperature reconsidered. Archiv fuer *Hydrobiologie* 126:315-327

Mullin MM, Brooks ER (1970) The effect of concentration of food on body weight, cumulative ingestion, and rate of growth of the marine copepod *Calanus helgolandicus*. Limnology and Oceanography 15: 748-755

Mullin MM, Sloan PR, Eppley RW (1996) Relationship Between Carbon Content, Cell Volume, and Area in Phytoplankton. Limnology and Oceanography 11(2): 307-311

Murray JW, Barber RT, Roman MR, Bacon MP, Feely RA (1994) Physical and Biological Controls on Carbon Cycling in the Equatorial Pacific. Science 266: 58-65

Müren U, Bergland J, Samuelsson K, Andersson A (2005) Potential effects of elevated sea-water temperature on pelagic food webs. Hydrobiologia 545: 153-166

Naganuma T (1996) Calanoid copepods: linking lower-higher trophic levels by linking lower-higher Reynolds numbers. Marine Ecology Progress Series 136: 311-313

Nakano S (1994) Estimation of phosphorus release rate by bacterivorous flagellates in Lake Biwa. *Japanese* Journal of *Limnology*. 55:201-211

Nandini S, Rao TR (1998) Somatic and population growth in selected cladoceran and rotifer species offered the cyanobacterium *Microcystis aeruginosa* as food. Aquat Ecol 31: 283-298

Nielson TG, Kiørboe T (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 2. Ciliates. Limnology and Oceanography 39(3): 508-519

Nielson TG, Kiørboe T (1991) Effects of a storm event on the structure of the pelagic food web with special emphasis on planktonic ciliates. Journal of Plankton Research 13(1): 35-51

Nielsen TG, Løkkegaard B, Richardson K, Pedersen FB, Hansen L (1993) Structure of plankton communities in the Dogger Bank area (North Sea) during a stratified situation. Marine Ecology Progress Series 95: 115-131

O'Connor MI, Piehler MF, Leech DM, Anton A, Bruno JF (2009) Warming and resource availability shift food web structure and metabolism. Public Library of Science Biology 7(8): e10000178

O'Reilly JE, Bush DA (1984) Phytoplankton primary production on the northwestern Atlantic shelf. Rapport et Proces-Verbaux Réunions. Conseil International pour l'Exploration de la mer 183: 255-268

Odum EP (*1971*) *Fundamentals* of Ecology. 3rd edition. Saunders, Philadelphia

Ohman MD, Snyder RA (1991) Growth kinetics of the omnivorous oligotrich ciliate *Strombidium* sp. Limnology and Oceanography 36(5): 922-935

Ortner PB, Wiebe PH, Cox JL (1980). Reltiopnships between oceanic epizooplankton distributions and the seasonal deep chlorophyll maximum in the Northwestern Atlantic ocean. Journal of Marine Research 38: 507-531

Ota T, Taniguchi A (2003) Standing crop of planktonic ciliates in the East China Sea and their potential grazing impact and contribution to nutrient regeneration. Deep Sea Research Part II: Topical Studies in Oceanography 50(2): 423-442

Paffenhöfer G (1976) Feeding, growth, and food conversion of the marine planktonic copepod *Calanus helgolandicus*. Limnology and Oceanography 21: 39-50

Paranjape MA(1987) The seasonal cycles and vertical distribution of tintinnines in Bedford Basin, Nova Scotia, Canada. Canadian Journal of Zoology 65: 41-48

Pauly D, Christensen V (1996). Mass-balance model of Alaska gyre. In Purcell J, Arai M, Jarre-Teichmann A, Huato L, Purcell J, Livingston P, Trites A, Heise K, Kelson J, Wada Y, Speckmann S, Buckworth R, Walters C, Polovina JJ, Fisheries Centre Research Reports. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada. Vol 4(1)

Peña MA, Lewis MR, Harrison WG (1990) Primary productivity and size structure of phytoplankton biomass on a transect of the equator at 135ºW in the Pacific Ocean. Deep-Sea Research 37: 295-315

Peters RH, Downing JA (1984) Empirical analysis of zooplankton filtering and feeding rates. Limnology and Oceanography 29(4): 763-784

Peterson, WT, Dam HG (1996) Pigment ingestion and egg production rates of the calanoid copepod *Temora longicornis*: implications for gut pigment loss and omnivorous feeding. Journal of Plankton Research 17: 2275-2294

Pitchford J, Brindley J (1999) Iron limitation, grazing pressure and oceanic high nutrient-low chlorophyll (HNLC) regions. Journal of Plankton Research 21: 525-547

Polis GA, Holt RD, Menge BA, Winemiller KO (1996) Time, space, and life history: Influences on food webs. In: Polis GA, Winemiller KO (eds) Food webs: Integration of Patterns and Dynamics. New York pp 435-460

Pomeroy LR (2000). Food web connections: links and sinks. Microbial systems: new frontiers. Proceedings of the 8th International Symposium on Microbial Ecology (eds. Bell CR, Brylinsky M, Johnson-Green P) pp. 81–87, Halifax, Canada: Atlantic Canada Society for Microbial Ecology

Putt M, Stoecker DK (1989) An experimental determined carbon-volume ratio for marine oligotrichous ciliates from estuarine and coastal waters. Limnology and Oceanography 34: 1097-1103

Raimbault P, Rodier M, Taupier-Letage I (1988) Size fraction of phytoplankton in the Ligurian Sea and the Algerian Basin (Mediterranean Sea): size distribution versus total concentration. Marine Microbial Food webs 3(1): 1-7

Rassoulzadegan F (1982) Dependence of grazing rate, gross growth efficiency and food size range on temperature in a pelagic oligotrichous ciliate Lohmanniella spiralis Leeg., fed on naturally occurring particulate matter. Annales de l'Institut Oceanographique 58(2): 177-184

Rassoulzadegan F, Laval-Peuto M, Sheldon RW (1988) Partioning of the food ration of marine ciliates between pico- and nanoplankton. Hydrobiologia 157: 75-88

Raven JA (1998). The twelfth Tansley lecture. Small is beautiful: The picophytoplankton. Functional Ecology 12: 503-513

Rey C, Harris R, Irigoien X, Head R, Carlotti F. (2001) Influence of algal diet on growth and ingestion of *Calanus helgolandicus* nauplii. Marine Ecology Progress Series 216: 151-165

Rey-Rassat C, Irigoien X, Harris R, Head R, Carlotti F (2002) Growth and development of *Calanus helgolandicus* nauplii reared in the laboratory. Marine Ecology Progress Series 238: 125-165

Richards KJ *et al.* (2002), Marine Productivity Cruise Report No. 2. RRS "Discovery" Cruise 262. British Oceanographic Data Centre

Riser CW, Reigstad M, Wassmann P, Arashkevich E, Falk-Petersen S (2006) Export or retention? Copepod abundance, faecal pellet production and vertical flux in the marginal ice zone through snap shots from the northern Barents Sea. Polar Biology 30(6): 2007

Rivkin RB (1990). Seasonal patterns of planktonic production in McMurdo Sound, Antarctica. American Naturalist 31: 5-16

Rivkin RB, Anderson MR, Lajzerowicz C (1996) Microbial processes in cold oceans. I. Relationship between temperature and bacterial growth rate. Aquatic Microbial Ecology 10: 243-254

Rivkin RB, Legendre L (2001) Biogenic carbon cycling in the upper ocean: effects of microbial respiration. Science 291: 2398-2400

Robins () AMT 2 cruise report. Plymouth, UK: Centre for Coastal and Marine Sciences, Plymouth Marine Laboratory

Roman MR, Gauzens AL (1997). Copepod grazing in the equatorial Pacific. Limnology and Oceanography 42: 623-634

Rose JM, Caron DA (2007) Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters. Limnology and Oceanography 52(2): 886-895

Rysgaard S, Nielsen TG, Hansen BW (1999). Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. Marine Ecology Progress Series 179: 13-25

Saiz E, Alcaraz M & Paffenhöfer G-A (1992) Effects of small-scale turbulence on feeding rate and gross-growth efficiency of three *Acartia* species (Copepoda: Calanoida). Journal of Plankton Research 14: 1085-1097

Salomon AK, Waller NP, McIlhagga C, Yung RL, Walters C (2002) Modeling the trophic effects of marine protected area zoning policies: A case study. Aquatic Ecology 36: 85-95

Sanders RW, Caron DA, Berninger U-G (1992) Relationships between bacteria and heterotrophic nanoplankton in marine and fresh waters: an inter-ecosystem comparison. Marine Ecology Progress Series 86: 1-14

Schnepf E, Deichgraber G (1983) 'Myzocytosis', a kind of endocytosis with implications to compartmentation in endosymbiosis. Observations in *Paulsenella* (Dinophyta). Naturwiss 71: 218-219

Sharma PC, Pant MC (1984) An energy budget for *Simocephalus vetulus* (O. F. Muller) (Crustacea : Cladocera). Hydrobiologia 111: 37-42

Sheldon RW, Prakash A, Sutcliffe WHJ (1972) The size distribution of particles in the ocean. Limnology and Oceanography 17(3): 327-340

Sherr EB, Rassoulzadegan F, Sherr BF (1989) Bacterivory by pelagic choreotrichous ciliates in coastal waters of the NW Mediterranean Sea. Marine Ecology Progress Series 55: 235-240

Sherr EB, Sherr BF (1987) High rates of consumption of bacteria by pelagic ciliates. Nature 325: 710-711

Sherr EB, Sherr BF, Fallon RD, Newell SY (1986) Small aloricate ciliates as a major component of the marine heterotrophic nanoplankton. Limnology and Oceanography 31: 177-183

Silvert W, Platt T (1978) Energy flux in the pelagic ecosystem: a time-dependent equation. Limnology and Oceanography 23(4): 813-816

Šimek K, Bobková J, Macek M, Nedoma J (1995) Ciliate grazing on picoplankton in a eutrophic reservoir during the summer phytoplankton maximum: A study at the species and community level. Limnology and Oceanography 40(6): 1077-1090

Snyder RA, Hoch MP (1996) Consequences of protist-stimulated bacterial production for estimating protist growth efficiencies. *Hydrobiologia* 341: 113–123

Šolić M, Krstulović N (1994). Role of predation in controlling bacteria and heterotrophic nanoflagellate standing stocks in the coastal Adriatic Sea: seasonal patterns. Marine Ecology Progress Series 114: 219-235

Sprules WG & Munawar M (1986) Plankton size-spectra in relation to ecosystem productivity, size and perturbation. Canadian Journal of Fisheries and Aquatic Sciences 43: 1789-1794

Steinberg DK, Carlson CA, Bates NR, Goldthwait SA, Madin LP, Michaels AF (2000) Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. Deep-Sea Research I 47: 137-158

Stenseth NC, Ottersen G, Hurrell (2005) Marine ecosystems and climate variation: the North Atlantic : a comparative perspective. Oxford Univerity Press

Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere, Princeton university press p183-185.

Stock CA, Powell TM, Levin SA (2008) Bottom-up and top-down forcing in a simple size-structured aquatic ecosystem model. Journal of Marine Systems 74 (1-2): 134-152

Stockner JG (1988) Phototrophic picoplankton: An overview from marine and freshwater ecosystems. Limnology and Oceanography 33(4): 765-775

Stoecker DK, Capuzzo (1990) Predation on Protozoa: its importance to zooplankton. Journal of Plankton Research 12(5): 891-908

Stoecker DK, Egloff DA (1987) Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. *Journal* of Experimental Marine *Biology* and *Ecology* 110: 53-68

Stoecker DK, Evans GT (1985) Effects of protozoan herbivory and carnivory in a microplankton food web. Marine Ecology Progress Series 25: 159-167

Støttrup JG, Jensen J (1990) Influence of algal diet on feeding and egg-production of calanoid copepod *Acartia tonsa* Dana. Journal of Experimental Marine Biology and Ecology 141: 87-105

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 (1998) Biomass allocation and carbon flow in the pelagic food web of Lake Constance. Advances in Limnology 53: 545:563

Strom SL (1991) Growth and grazing rates of the herbivorous dinoflagellate *Gymnodinium* sp. from the open subarctic Pacific Ocean. Marine Ecology Progress Series 78-103-113

Suzuki K, Nakamura Y, Hiromi J (1999) Feeding by the small calanoid copepod *Paracalanus* sp. on heterotrophic dinoflagellates and ciliates. Aquatic Microbial Ecology 17: 99-103

Teixeira C, Gaeta SA (1991) Contribution of picoplankton to primary production in estuarine, coastal and equatorial waters of Brazil. Hydrobiologia 209: 117-122

Thomas WH (1970) Effect of ammonium and nitrate concentrations on chlorophyll increase in natural tropical Pacific phytoplankton populations. Limnology and Oceanography 30: 1268-1282

Tikhonenkov DV, Mazei YA, Mylnikov AP (2006) Species diversity of heterotrophic flagellates in White Sea littoral sites. European Journal of Protistology 42: 191-200

Toda H, Arima T, Takahashi M, Ichimura S (1987) Physiological evaluation of temperature effect on the growth processes of the mysid, *Neomysis intermedia* Czerniawsky. Journal of Plankton Research 9(1): 51-63

Tremblay J, Legendre L (1994) A model for the size-fractionated biomass and production of marine phytoplankton. Limnology and Oceanography 39: 2004-2014

Turner JT, Tester PA (1997) Toxic marine phytoplankton, zooplankton grazers, and pelagic food webs. Limnology and Oceanography 42(5, part 2): 1203-1214

Uitz J, Claustre H, Morel A, Hooker S (2006). Vertical distribution of phytoplankton communities in open ocean: An assessment based on surface chlorophyll. Journal of Geophysical Research 111: C08005

Ulanowicz RE (1998) A phenomenology of evolving networks. Systems *Research and Behavioral Science* 15:373-383

Uye S, Iwamoto N, Ueda T, Tamaki H, Nakahira K (1999) Geographical variations in the trophic structure of the plankton community along a eutrophic-mesotrophic-oligotrophic transect. Fisheries Oceanography 8(3): 227-237

Uye S, Nagano N, Tamaki H (1996) Geographical and Seasonal Variations in Abundance, Biomass and Estimated Production Rates of Microzooplankton in the Inland Sea of Japan. Journal of Oceanography 52: 689-703

Vega-Cendejas ME & Arreguín-Sánchez F (2001) Energy fluxes in a mangrove ecosystem from a coastal lagoon in Yucatan Peninsula, Mexico. Ecological Modelling 137: 119-113

Verity PG (1985) Grazing, respiration, excretion, and growth rates of tintinnids. Limnology and Oceanography 30(6): 1268-1282

Verity PG (1986a). Growth rates of natural tintinnid populations in Narragansett Bay, Rhode Island. Marine Ecology Progress Series 29: 117-126

Verity PG (1986b) Grazing of phototrophic nanoplankton by microzooplankton in Narragansett Bay. Marine Ecology Progress Series 29: 105-115

Verity PG (1987). Abundance, community composition, size distribution, and production rates of tintinnids in Narragansett Bay, Rhode Island. Estuarine, Coastal and Shelf Science 24: 671–690

Vézina F, Platt T (1988) Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. Marine Ecology Progress Series 42: 269-287

Vézina, AF, Savenkoff C, Roy S, Klein B, Rivkin R, Therriault J-C, Legendre L (2000). Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 2. Inverse analysis. Deep-Sea Research II 47: 609-635

Vrede T, Persson J, Aronsen G (2002) The influence of food quality (P:C ratio) on RNA:DNA ratio and somatic growth rate of Daphnia. Limnology and Oceanography 47: 487:494

Wang D, Neurotoxins from marine dinoflagellates: a brief review. Marine Drugs 6(2): 349-371

Watson R, Alder J, Walters C (2000) A dynamic mass-balance model for marine protected areas. Fish and Fisheries 1: 94-98

Weber LH, El-Sayed SZ (1987). Contributions of the net, nano- and picoplankton to the phytoplankton standing crop and primary productivity in the Southern Ocean. Journal of Plankton Research 9(5): 973-944

Weisee T, Karstens N, Meyer VCL, Janke L, Lettner S, Teichgräber K (2001) Niche separation in common prostome freshwater ciliates: the effect of food and temperature. Aquatic Microbial Ecology 26: 167-179

Weisse T, Müller H, Pinto-Coelho RM, Schweizer A, Springman D & Baldringer G (1990) Response of the microbial loop to the phytoplankton spring bloom in a large prealpine lake. Limnology and Oceanography 35: 781-794

Weisse T, Kartens N, Meyer VCL, Janke L, Lettner S, Teichgräber K (2001) Niche separation in common prostome freshwater ciliates: the effect of food and temperature. Aquatic Microbial Ecology 26: 167-179

Weisse T (2004) *Meseres corlissi*: a rare oligotrich ciliate adapted to warm water and temporary habitats. Aquatic Microbial Ecology 37: 75-83

Welschmeyer N, Goericke R, Strom S, Peterson W (1991) Phytoplankton growth and herbivory in the subarctic Pacific: a chemotaxonomic analysis, Limnology and Oceanography 36: 1631–1649.

White PA, Kalff J, Rasmussen JB, Gasol JM (1991) The Effect of Temperature and Algal Biomass on Bacterial Production and Specific Growth Rate in Freshwater and Marine Habitats 21: 99-118

Wieters (2001) Marine macroecology. Trends in Ecology & Evolution 16(2): 67-69

Work TM (1993) Epidemiology of domoic acid poisoning in brown pelicans (*Pelecanus ocidentalis*) and Brandt's cormorants (*Phalacrocorax penicillatus*) in California. Journal of Zoo and Wildlife Medicine 24(1): 54-62

Zhang X, Dam HG, White JR, Roman MR (1995) Latitudinal variations in mesozooplankton grazing and metabolism in the central tropical Pacific during the U.S. JGOFS EqPac study. Deep-Sea Research II 42(2-3): 695-714

Zucchetta M, Libralato S, Granzotto A, Pranovi F, Raicevich S, Torricelli P (2003) Modelling approach for the evaluation of the efficacy of MPA in the Northern Adriatic Sea. In E Zhan (Ed), Sixth International Conference on the Mediterranean Coastal Environment. MEDCOAST 03, Ravenna, Italy pp 433-443