The Effect of Temperature and Food on Zooplankton Gross Growth Efficiency

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Gross Growth Efficiency

- The ratio or fraction of biomass ingested that is converted to biomass by a predator in a given time interval

$$GGE = \frac{\Delta B}{\Delta I}$$

- Where ΔI is amount of prey biomass ingested and ΔB is the amount of new biomass produced by the predator over time

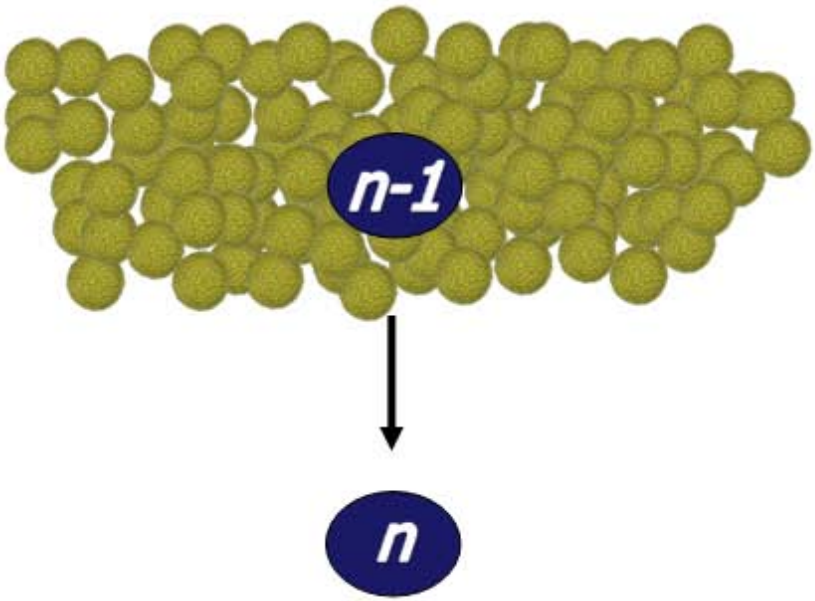
Gross Growth Efficiency

- Important measurement for detailing the flow of material from prey to predator
- Also allows the calculation of the proportion of material lost (through respiration, excretion and egestion)

Gross Growth Efficiency

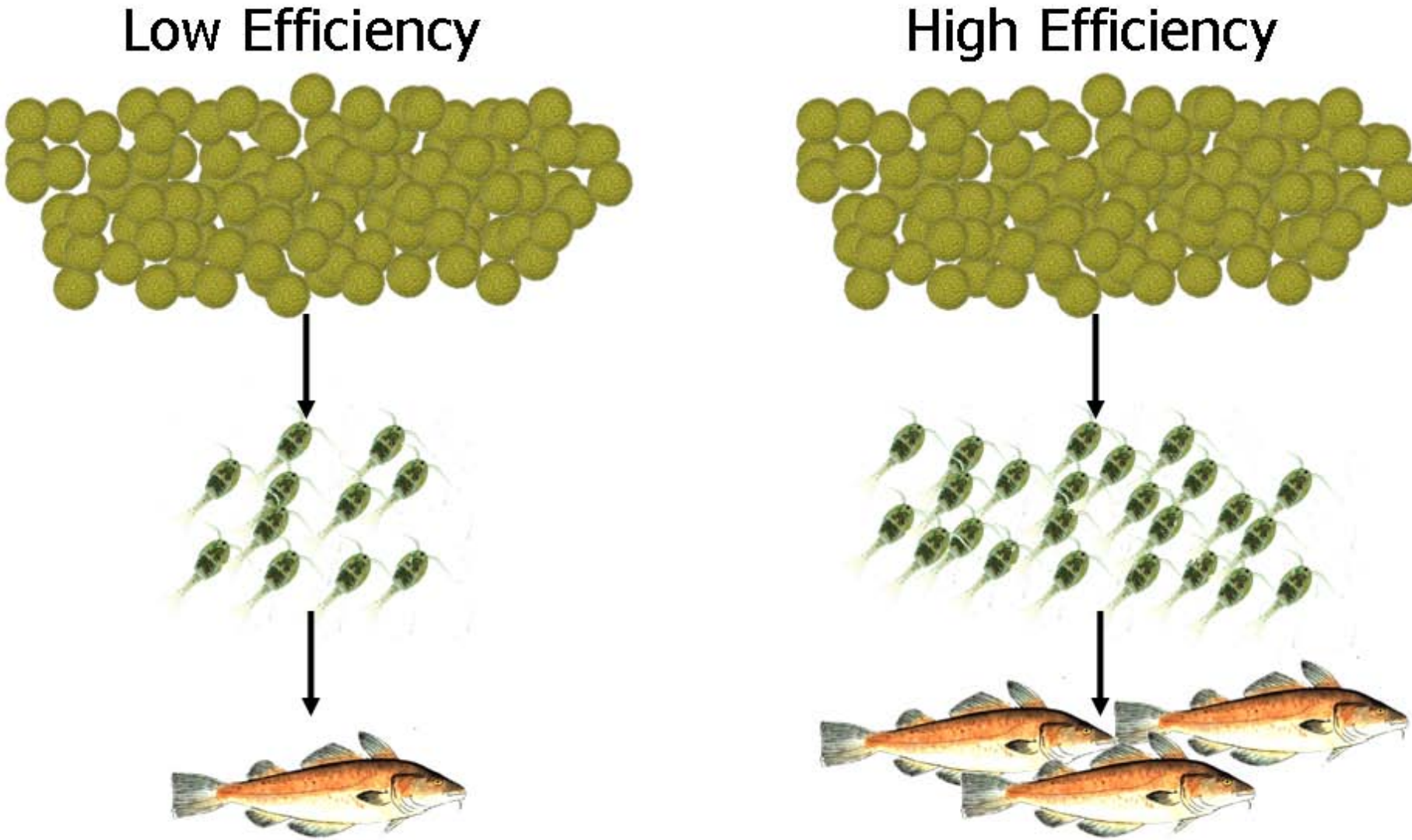
- A composite of growth and ingestion
- The relationship GGE has with independent variables is therefore a composite of how they influence both ingestion and growth
- May vary with e.g. temperature, food concentration and food quality

Effect of GGE on food-web



GGE plays an important role in determining the amount of biomass transferred from one trophic level (*n-1*) to the next (*n*)

Effect of GGE on food-web



Application of GGE

- Ecosystem models have often assumed:
  - A constant GGE value for all types of zooplankton (approximately 30%)
  - No temperature dependence

E.g. Stoecker & Evans (1985), Pomeroy (1999), Anderson & Turley (2003), Calbet & Landry (2004), Lewis (2005), Buitenhuis *et al.* (2006)

Previous findings and predictions

- Similar means found across different zooplankton groups (GGE = 20-30%) (Straile 1997)
- Metazoans to achieve higher efficiencies than protozoans (Calow 1977, Azam *et al.* 1984, Fasham 1985)
- Protozoan GGE values to fall within the range of 30-60% (Caron *et al.* 1990)

Aims

- Provide a new database, correcting GGE values miscalculated by authors
  - Organism growth during the experiment not taken into account when calculating ingestion
  - Incorrectly used the slope of growth vs. ingestion

- Detail the effect of temperature and food concentration on the GGE of:
  - Ciliates, scyphozoans, cladocerans, adult and juvenile copepods, nano/microflagellates, ctenophores, dinoflagellates and rotifers

Questions to be answered

- Does GGE vary with temperature within and between taxonomic groups?
- How does GGE vary with food concentration within taxonomic groups?
- Do mean GGE values vary between taxa?
- How does diet type affect mean GGE within taxonomic groups?

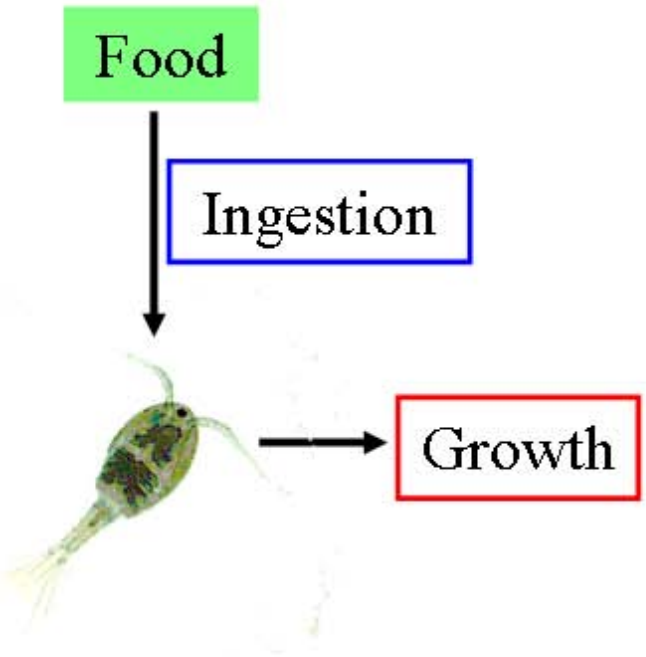
Methods

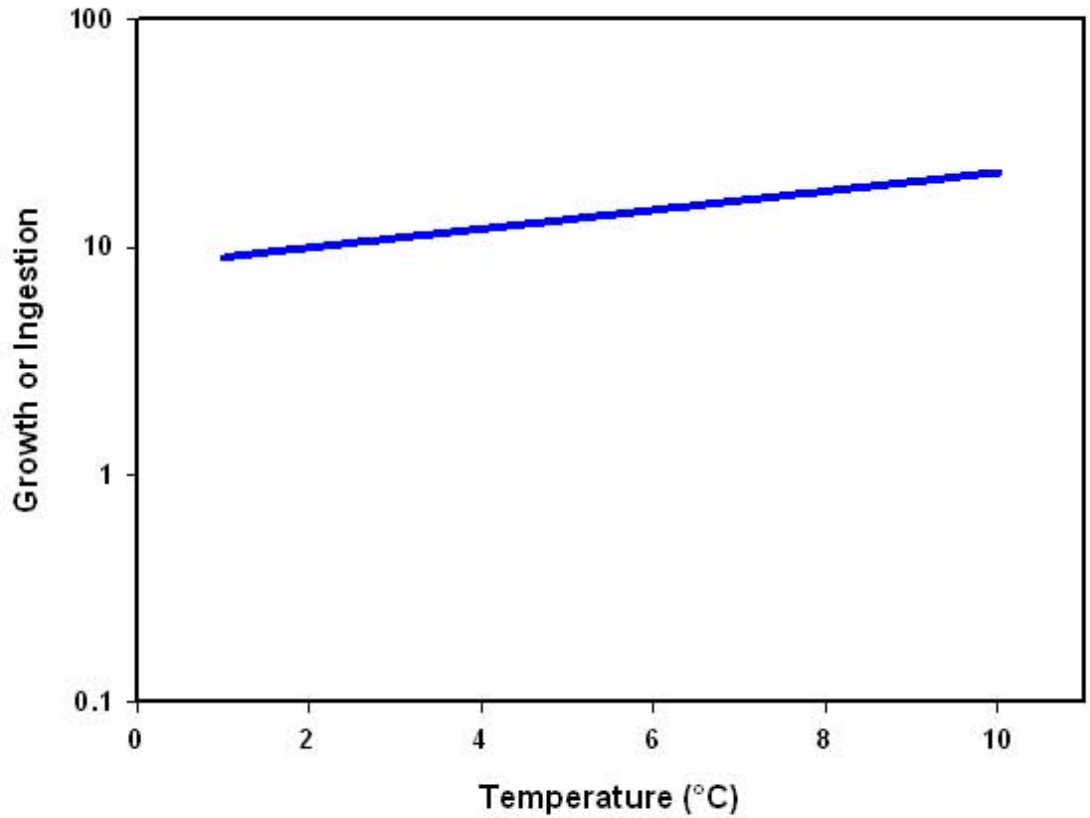
- An extensive literature search was conducted to obtain planktonic GGE data
- n = 1700 from 76 papers
  - Approximately 2.5 times that of previous syntheses on GGE
- Global spatial distribution
- In cases where an incorrect term was used re-calculated the value
- All values converted to carbon (growth and ingestion)

General Linear Models

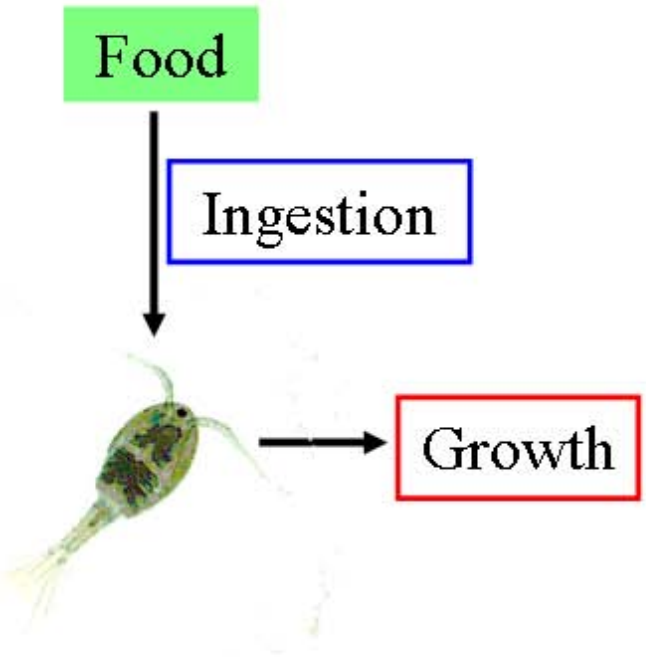
- Assumed an approximately linear relationship between $\log_{10}$ GGE and both temperature and $\log_{10}$ food concentration

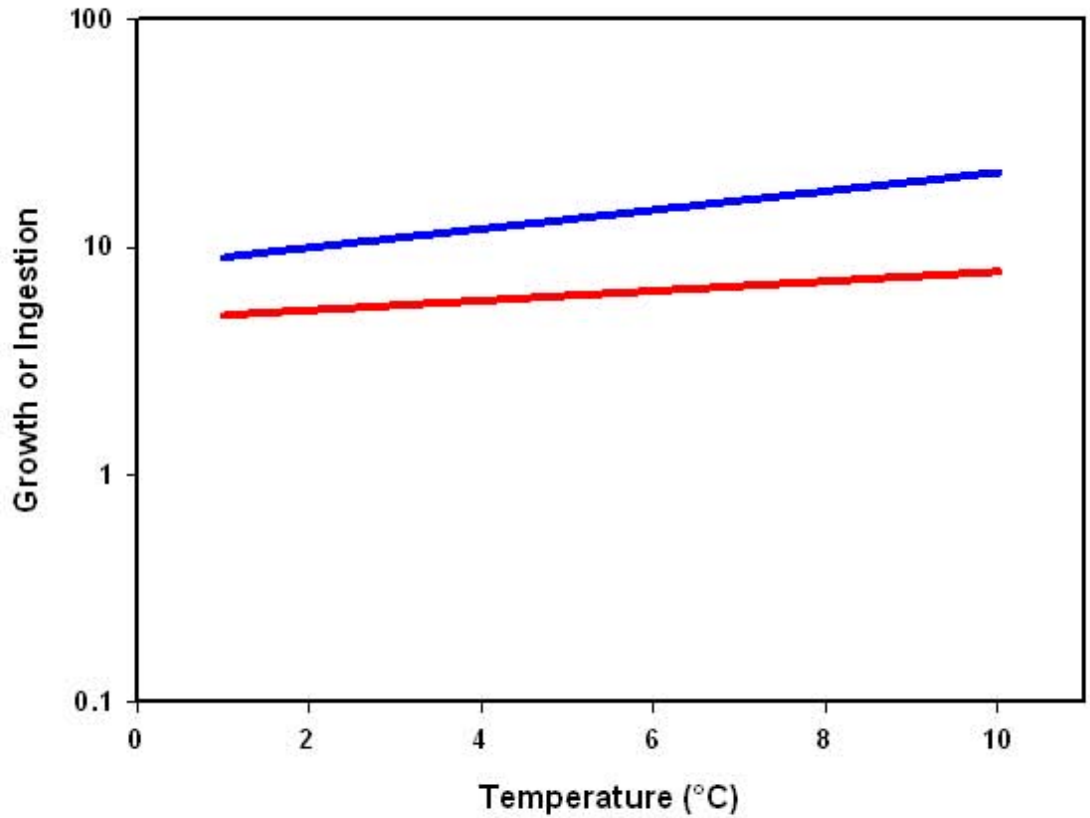
Assuming both ingestion and growth increase with increasing temperature





Assuming both ingestion and growth increase with increasing temperature



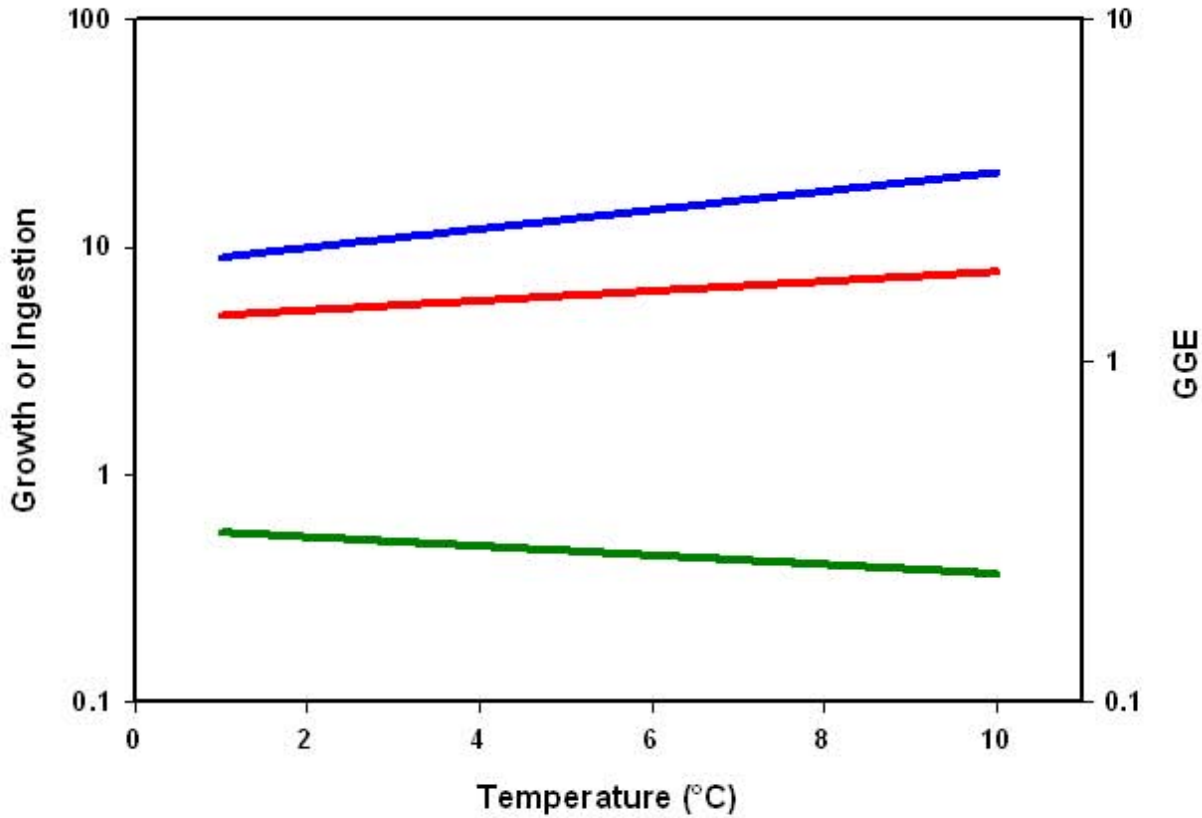


$$\text{GGE} = \frac{\text{Growth}}{\text{Ingestion}}$$

Food

Ingestion

Growth

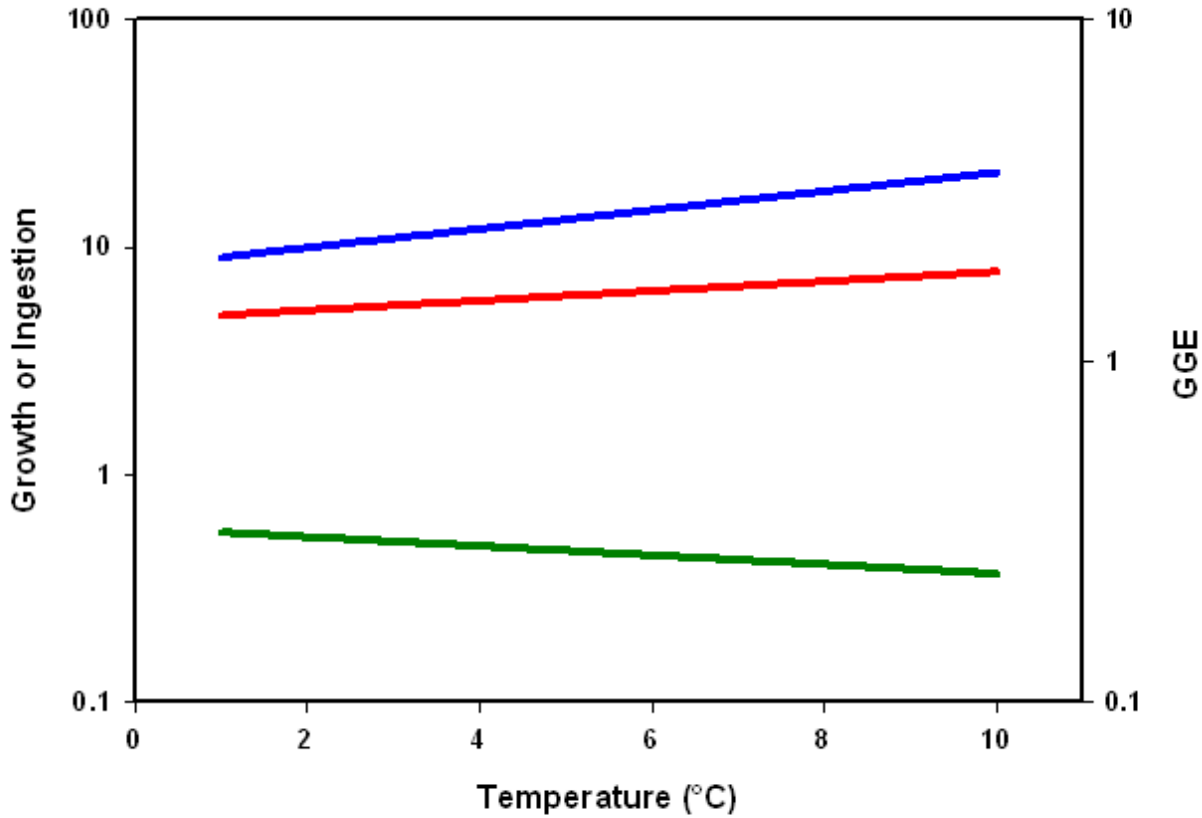


Therefore we assume $\log_{10}$ GGE has a linear relationship with temperature

$$GGE = \frac{\text{Growth}}{\text{Ingestion}}$$

Where temperature dependence of ingestion > temperature dependence of growth:

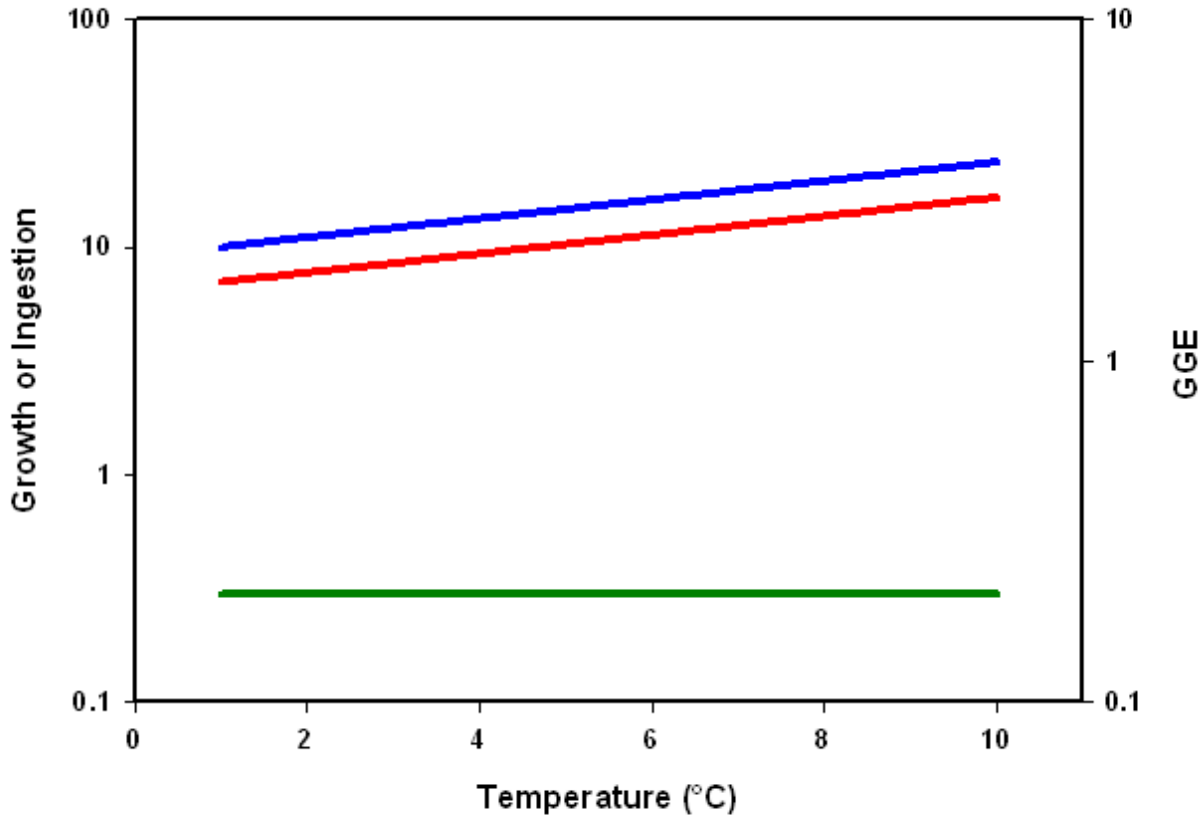
GGE decreases with increasing temperature



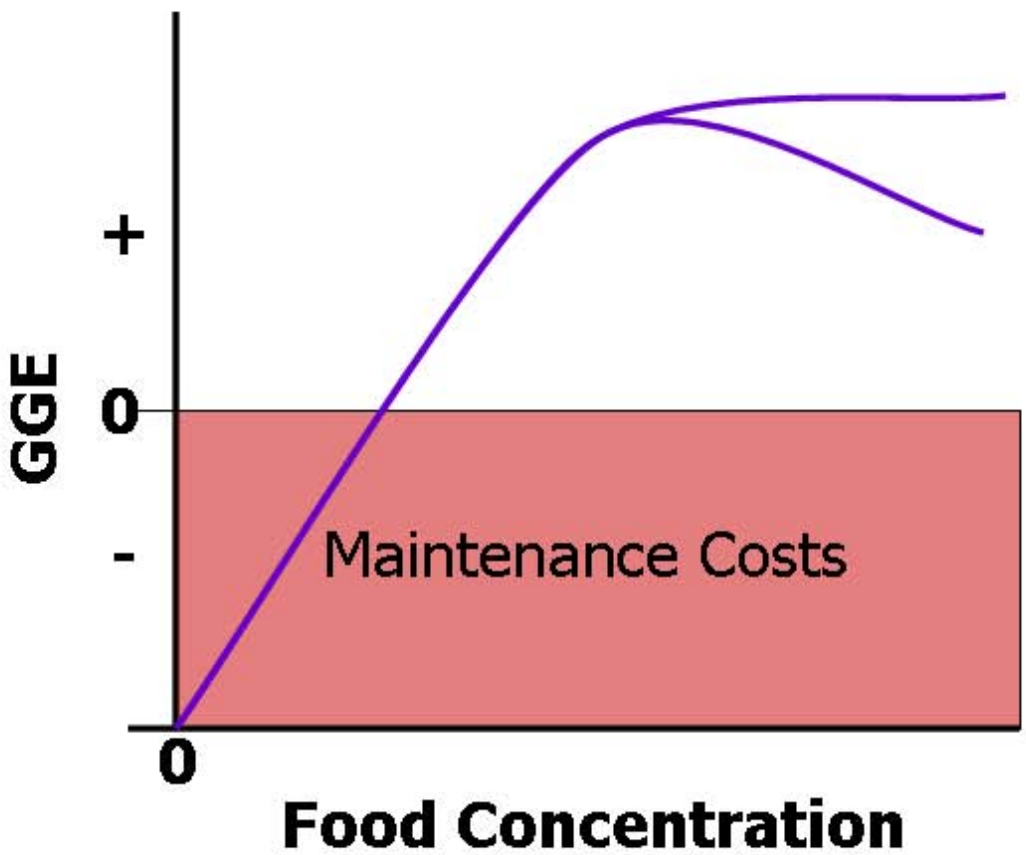
$$GGE = \frac{\text{Growth}}{\text{Ingestion}}$$

Where temperature dependence of ingestion = temperature dependence of growth:

GGE is constant with increasing temperature

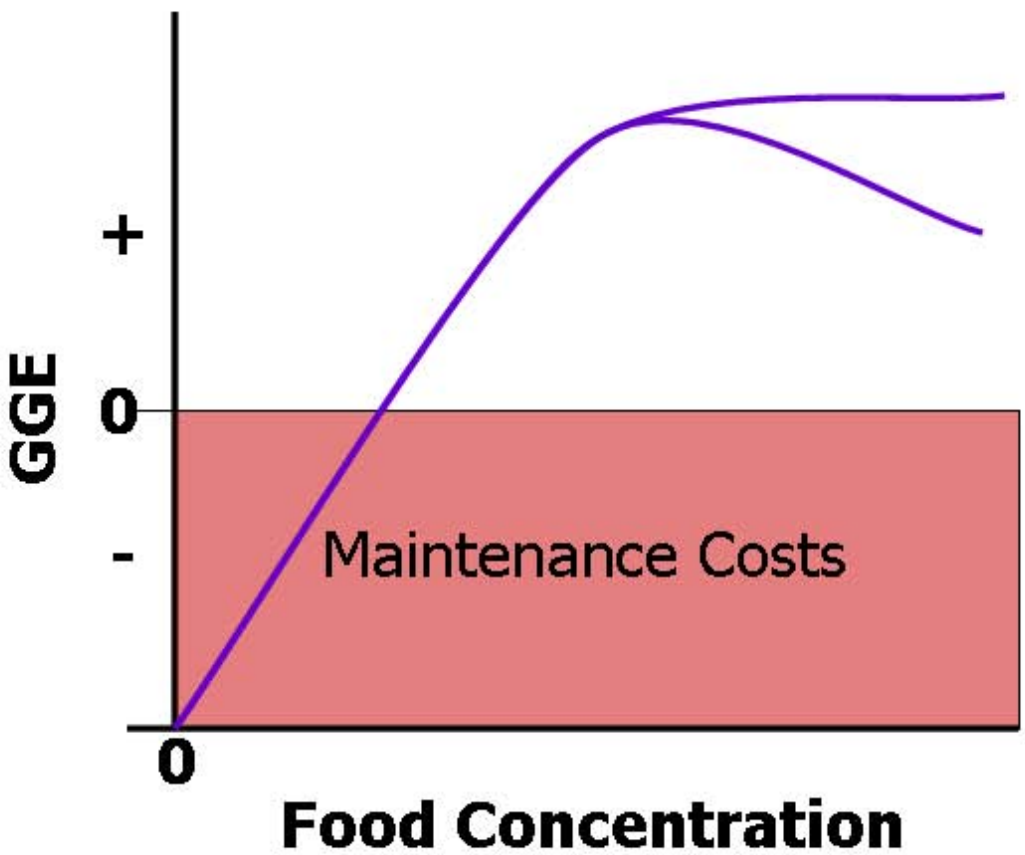


Food Concentration



- Where food concentration = zero, ingestion = zero, growth < zero
- At low food concentrations, ingestion < maintenance costs and therefore GGE is negative
- Higher food concentrations allow ingestion > maintenance costs resulting in positive growth and GGE
- At very high food concentrations GGE may decrease, for example as a result of superfluous feeding

Food Concentration



- Assumed a type II functional relationship between GGE and food concentration
- $\log_{10}$ transformation of food concentration and GGE was applied to provide a greater approximation to a linear relationship for use in general linear models
- Where high food concentrations were associated with a decrease in GGE these were excluded from analyses

General Linear Models

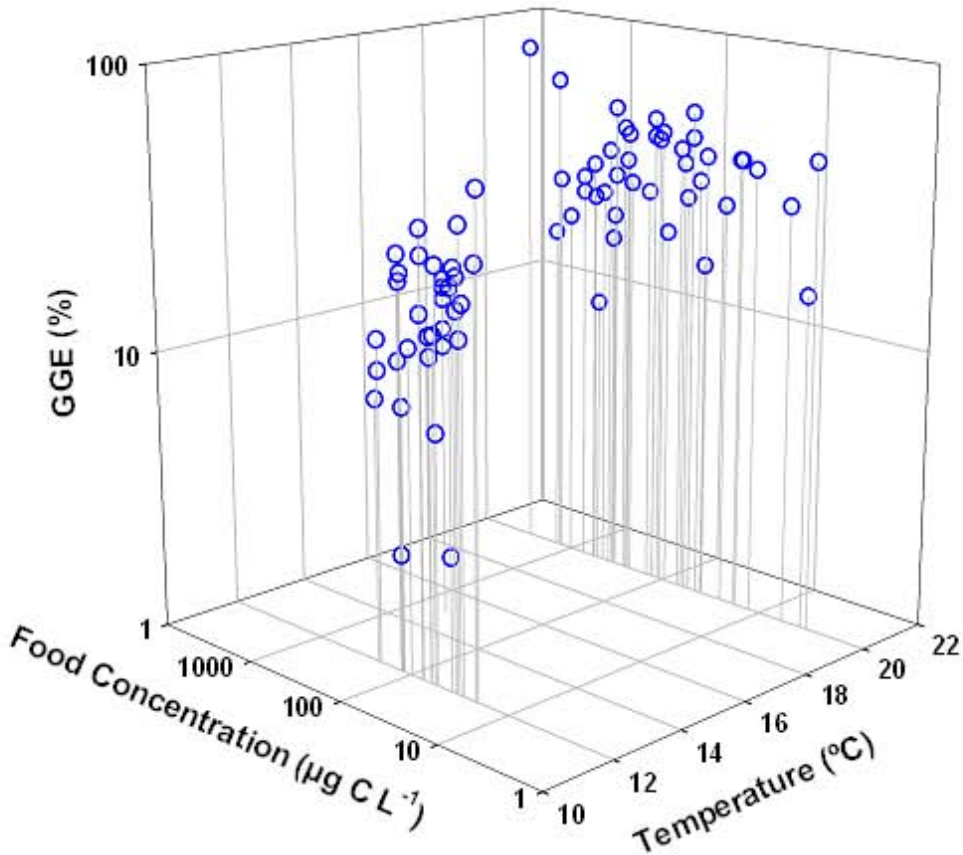
- For each taxonomic group:
- Tested effect of temperature, $\log_{10}$ food concentration and an interaction term on $\log_{10}$ GGE
- Temperature and food concentration may co-vary especially from experiments where food concentration was not controlled
- Minimum Adequate Models (MAMs) arrived at by backwards selection ($P<0.05$)

Differences between and within taxa

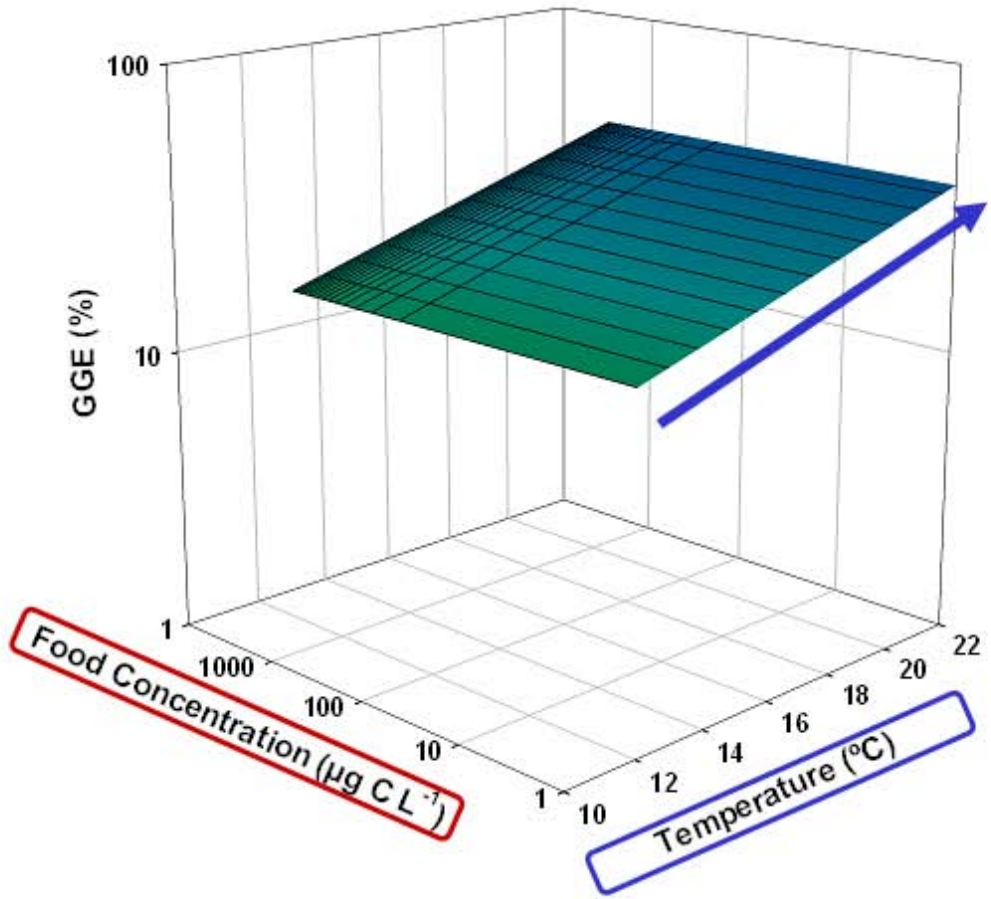
- GGEs compared with all others via a simultaneous Tukey test at a 95% confidence level (P= 0.05)

- Data were separated according to diet type for ciliates, nano/microflagellates, dinoflagellates and copepods
  - Diets classified as bactivorous, herbivorous, carnivorous, and mixed (n=1366)
  - GGE values were compared between diet types within taxa using one-way ANOVA at a 95% confidence level

Dinoflagellates



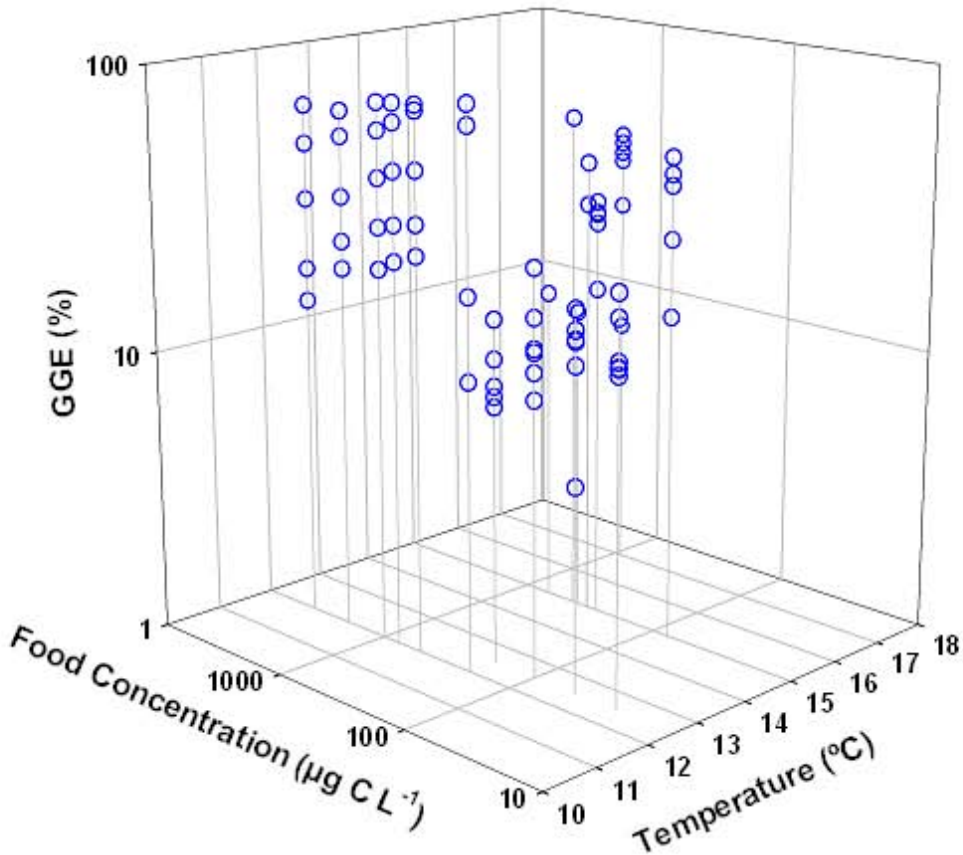
Dinoflagellates



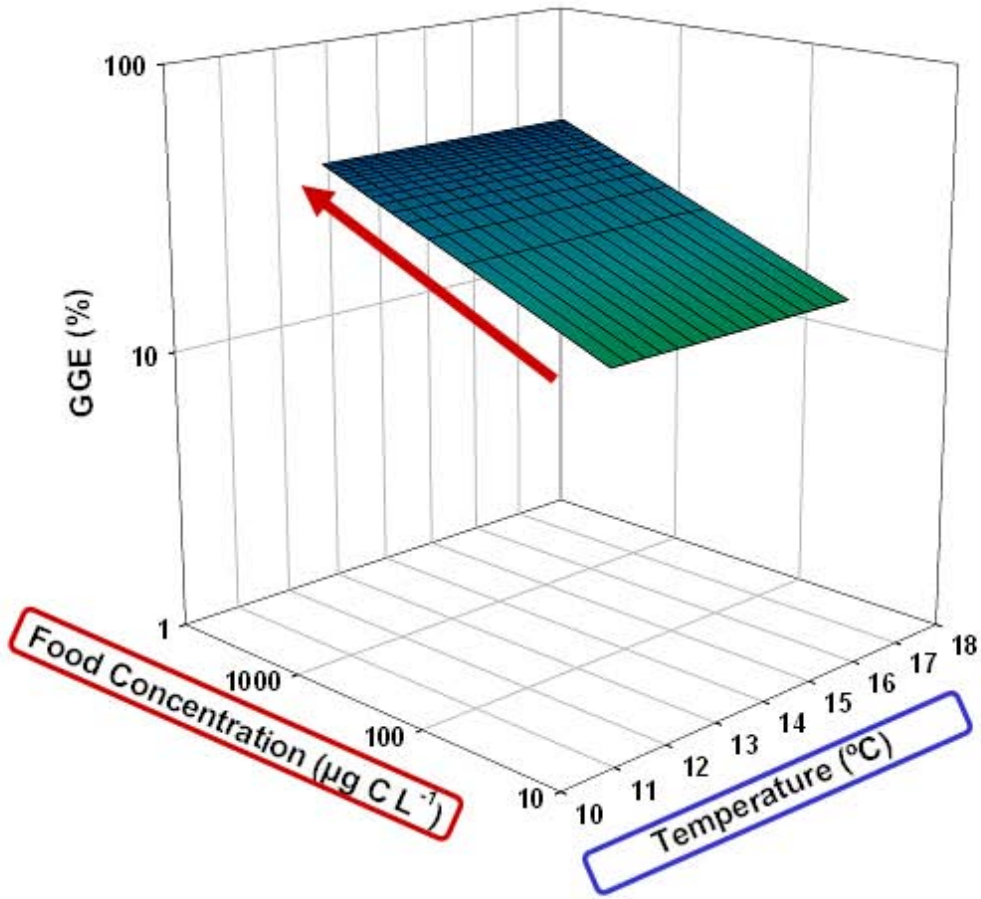
$\log_{10}$ GGE has no relationship with $\log_{10}$ food concentration ($P>0.05$)

$\log_{10}$ GGE has a positive relationship with temperature ($P<0.001$, $n=81$, $r^2=28\%$)

Juvenile Copepods



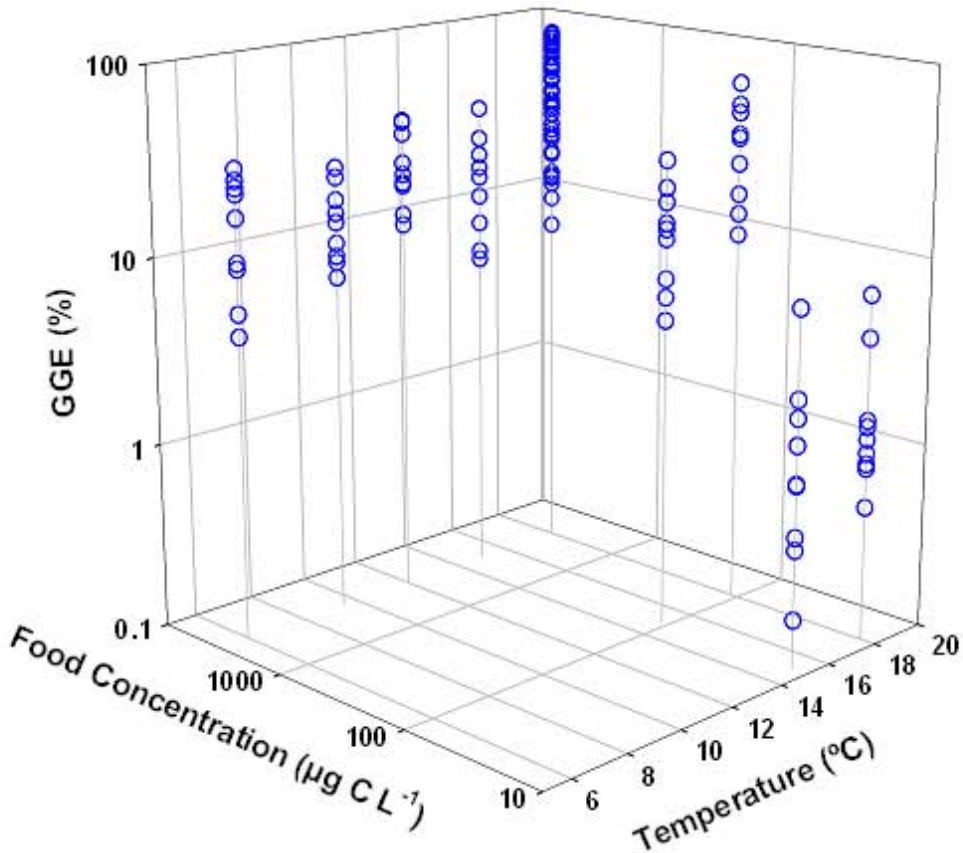
Juvenile Copepods



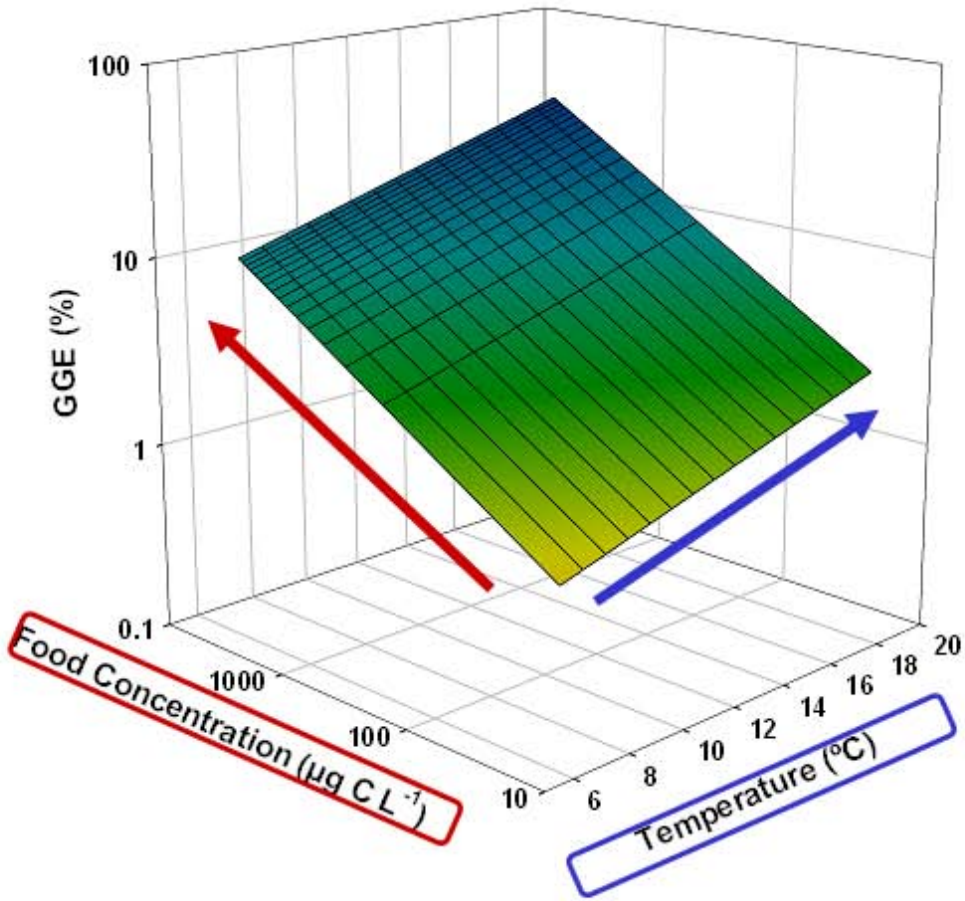
$\log_{10}$ GGE has a positive relationship with $\log_{10}$ food concentration ($P<0.001$, $n=73$, $r^2=18\%$)

$\log_{10}$ GGE has no relationship with temperature ($P>0.05$)

Scyphozoans



Scyphozoans



$\log_{10}$ GGE has a positive relationship with $\log_{10}$ food concentration ($P<0.001$)

$\log_{10}$ GGE has a positive relationship with temperature ($P<0.001$, $n=121$, $r^2=58\%$)

Temperature Dependence

Dinoflagellates	$\log_{10}$ GGE = 0.75 + 0.038T
Ctenophores	$\log_{10}$ GGE = 0.17 + 0.045T
Scyphozoans	$\log_{10}$ GGE = –0.86 + 0.045T + 0.46$\log_{10}$F
Cladocerans	$\log_{10}$ GGE = 3.24 – 0.048T – 0.358$\log_{10}$F
Bacteria	$\log_{10}$ GGE = 1.56 – 0.020T

T = temperature

F = food concentration

Temperature Dependence

Dinoflagellates	$\log_{10}$ GGE = 0.75 + 0.038T
Ctenophores	$\log_{10}$ GGE = 0.17 + 0.045T
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Bacteria	$\log_{10}$ GGE = 1.56 – 0.020T

T = temperature

F = food concentration

Questions to be answered

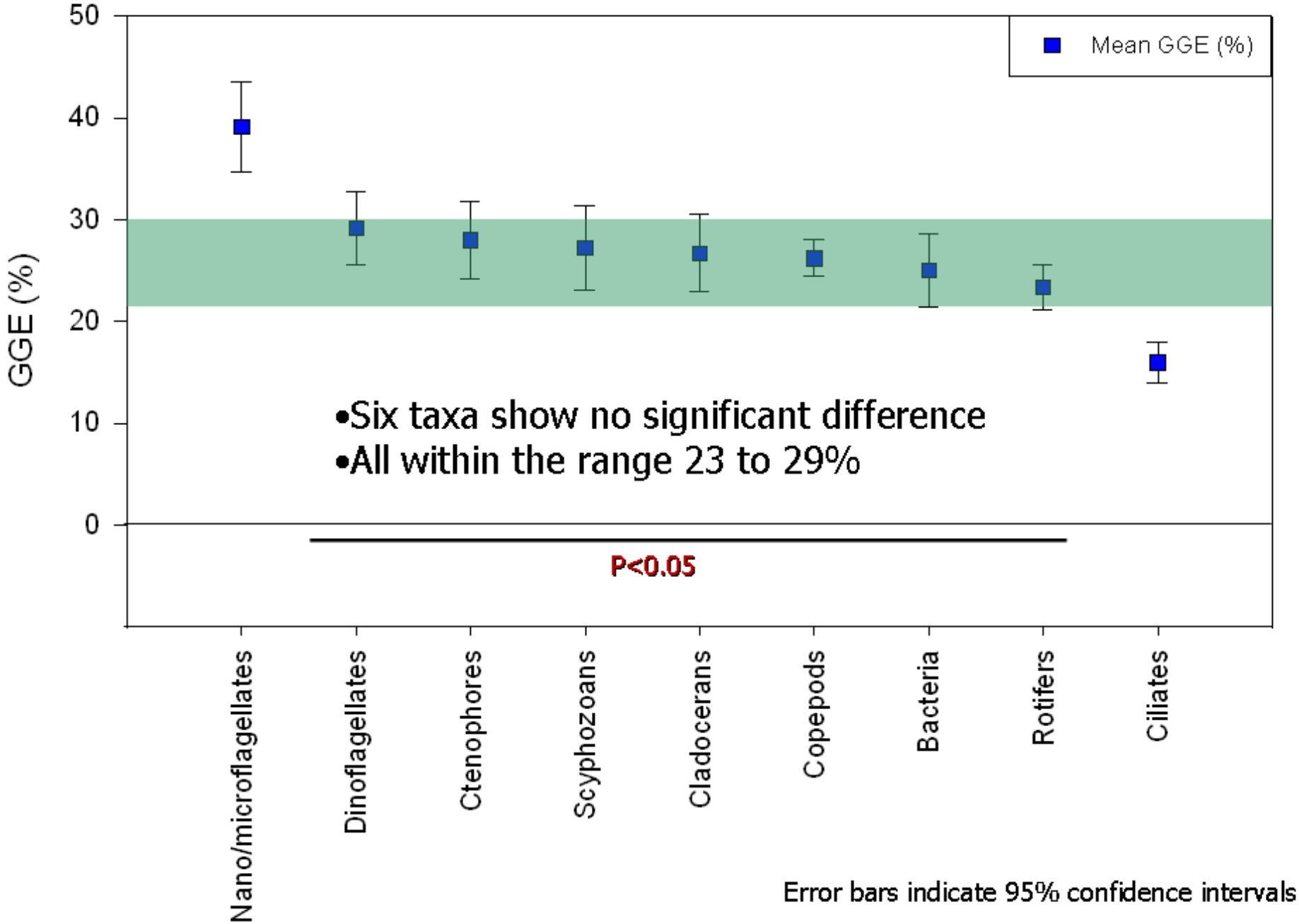
- Does GGE vary with temperature within and between taxonomic groups?
- How does GGE vary with food concentration within taxonomic groups?
- Do mean GGE values vary between taxa?
- How does diet type affect mean GGE within taxonomic groups?

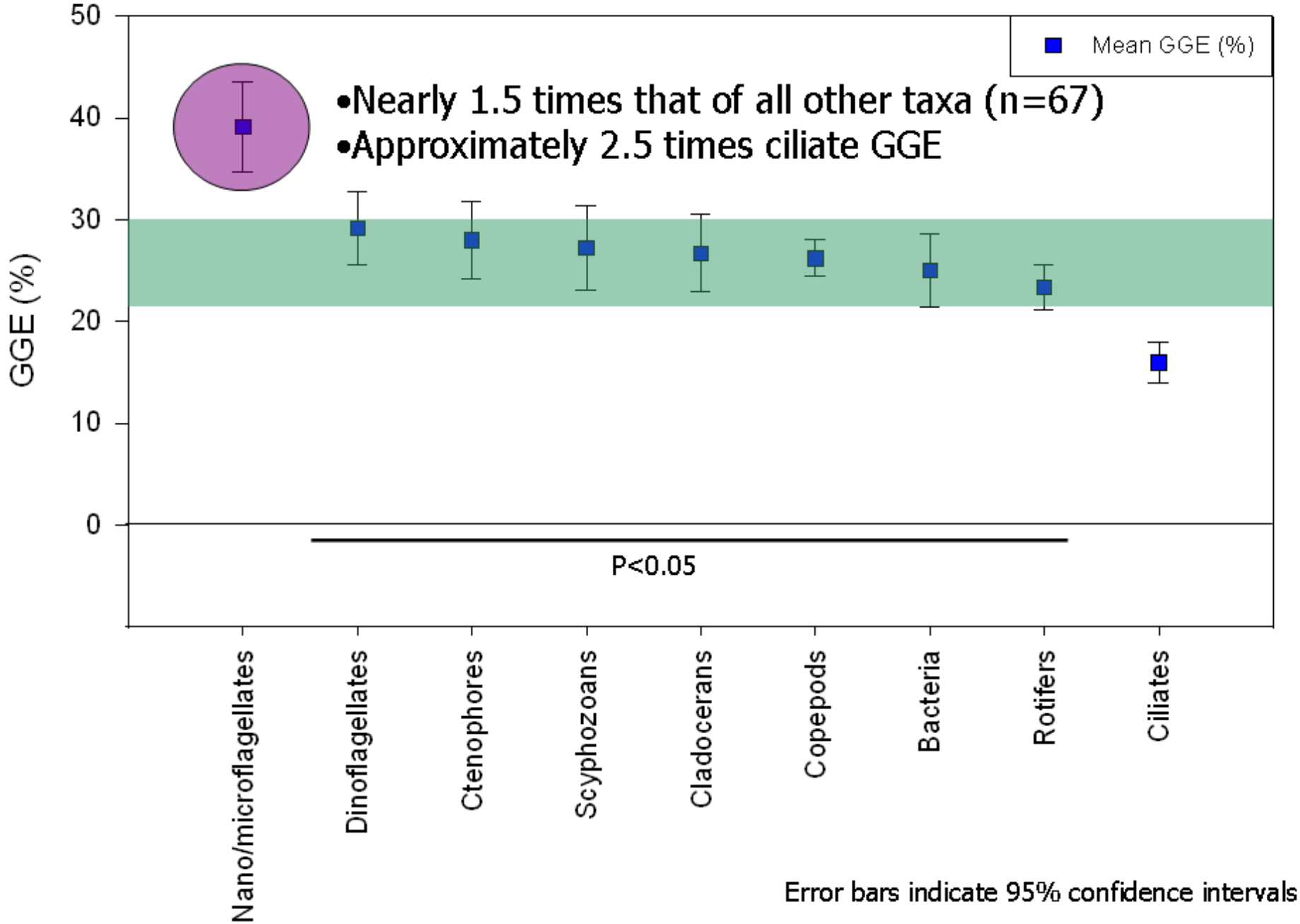
- Dinoflagellate, ctenophore and scyphozoan GGEs increase with temperature
  - Suggests growth has a higher temperature dependence than ingestion
- Cladocean GGEs decrease with temperature
  - Suggests ingestion has a higher temperature dependence than growth
- No temperature dependence was found in:
  - Cilates, nano/microflagellates, rotifers, adult and juvenile copepods

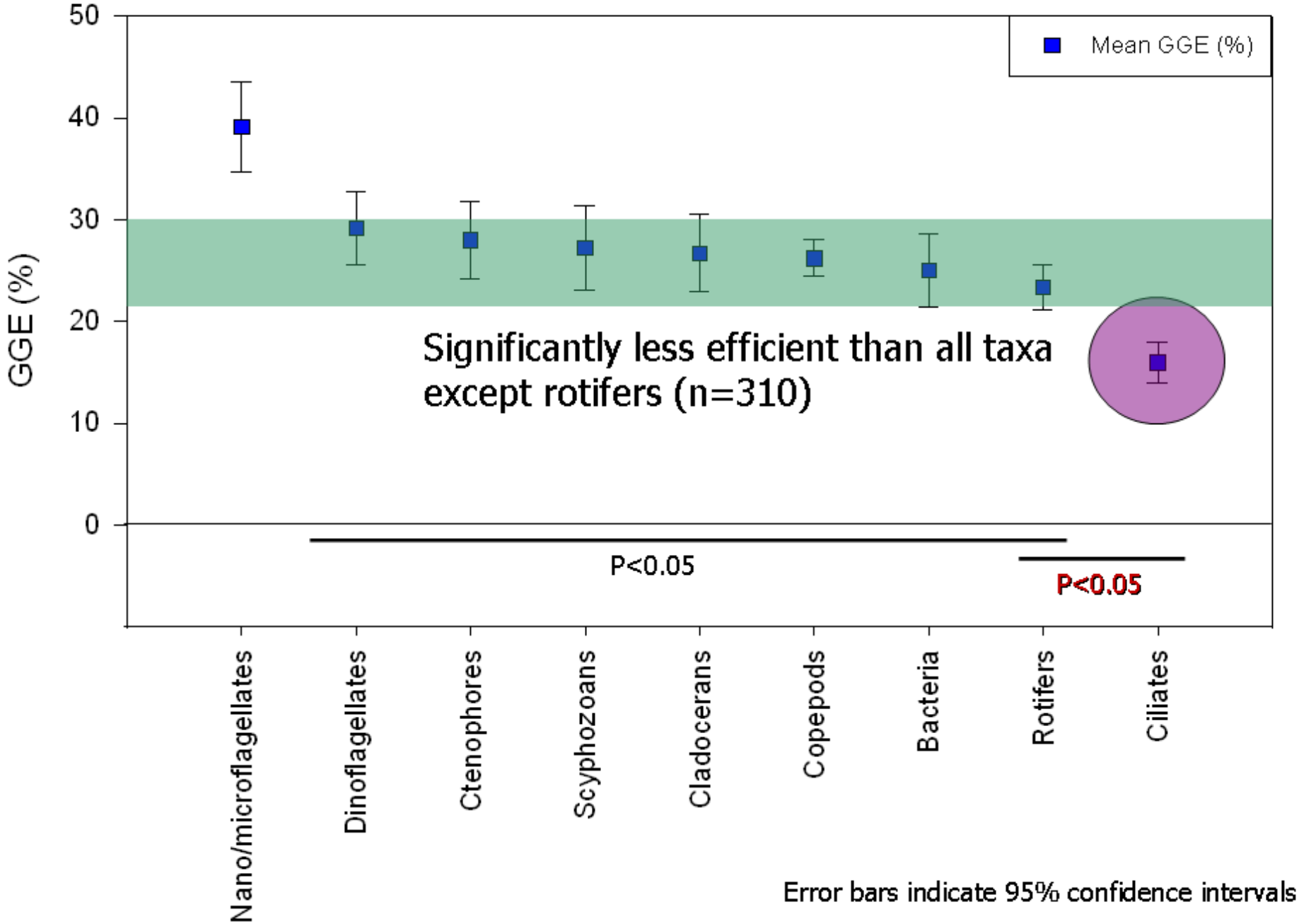
Questions to be answered

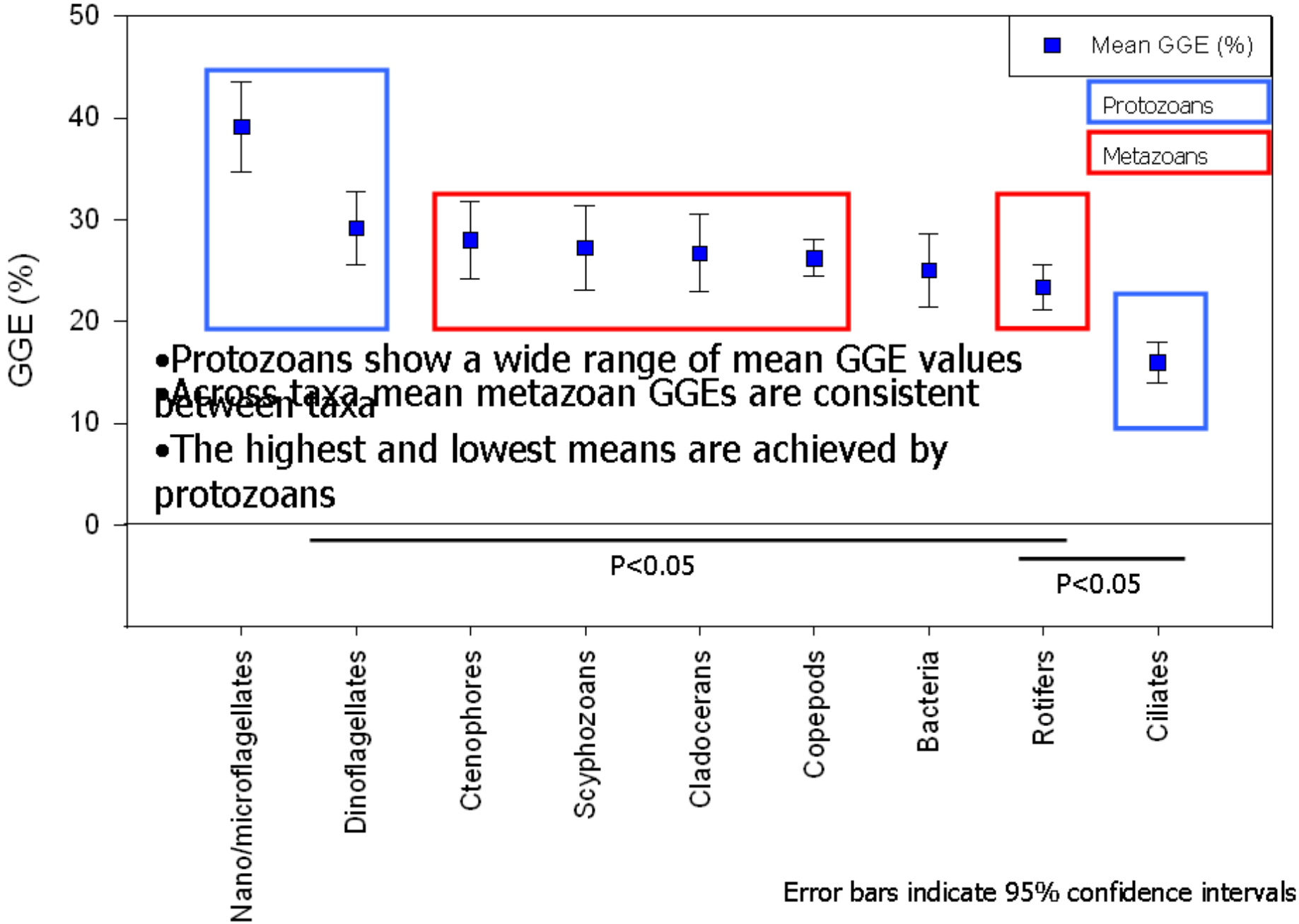
- Does GGE vary with temperature within and between taxonomic groups?
- How does GGE vary with food concentration within taxonomic groups?
- Do mean GGE values vary between taxa?
- How does diet type affect mean GGE within taxonomic groups?

- GGE increased with food concentration in scyphozoans and juvenile copepods
- GGE decreased with food concentration in ciliates and cladocerans
- No relationship was found for the remaining 4 taxa
  - Prey type / food quality?
  - Species-specific food saturation points?


Mean GGE (%)
GGE (%)
50
40
30
20
10
0
•Six taxa show no significant difference
•All within the range 23 to 29%
P<0.05
Nano/microflagellates
Dinoflagellates
Ctenophores
Scyphozoans
Cladocerans
Copepods
Bacteria
Rotifers
Ciliates
Error bars indicate 95% confidence intervals


Mean GGE (%)
•Nearly 1.5 times that of all other taxa (n=67)
•Approximately 2.5 times ciliate GGE
GGE (%)
50
40
30
20
10
0
P<0.05
Nano/microflagellates
Dinoflagellates
Ctenophores
Scyphozoans
Cladocerans
Copepods
Bacteria
Rotifers
Ciliates
Error bars indicate 95% confidence intervals


Mean GGE (%)
GGE (%)
50
40
30
20
10
0
Significantly less efficient than all taxa except rotifers (n=310)
P<0.05
P<0.05
Nano/microflagellates
Dinoflagellates
Ctenophores
Scyphozoans
Cladocerans
Copepods
Bacteria
Rotifers
Ciliates
Error bars indicate 95% confidence intervals


50
40
30
20
10
0
GGE (%)
Mean GGE (%)
Protozoans
Metazoans
•Protozoans show a wide range of mean GGE values
•Across taxa mean metazoan GGEs are consistent between taxa
•The highest and lowest means are achieved by protozoans
P<0.05
P<0.05
Nano/microflagellates
Dinoflagellates
Ctenophores
Scyphozoans
Cladocerans
Copepods
Bacteria
Rotifers
Ciliates
Error bars indicate 95% confidence intervals

Questions to be answered

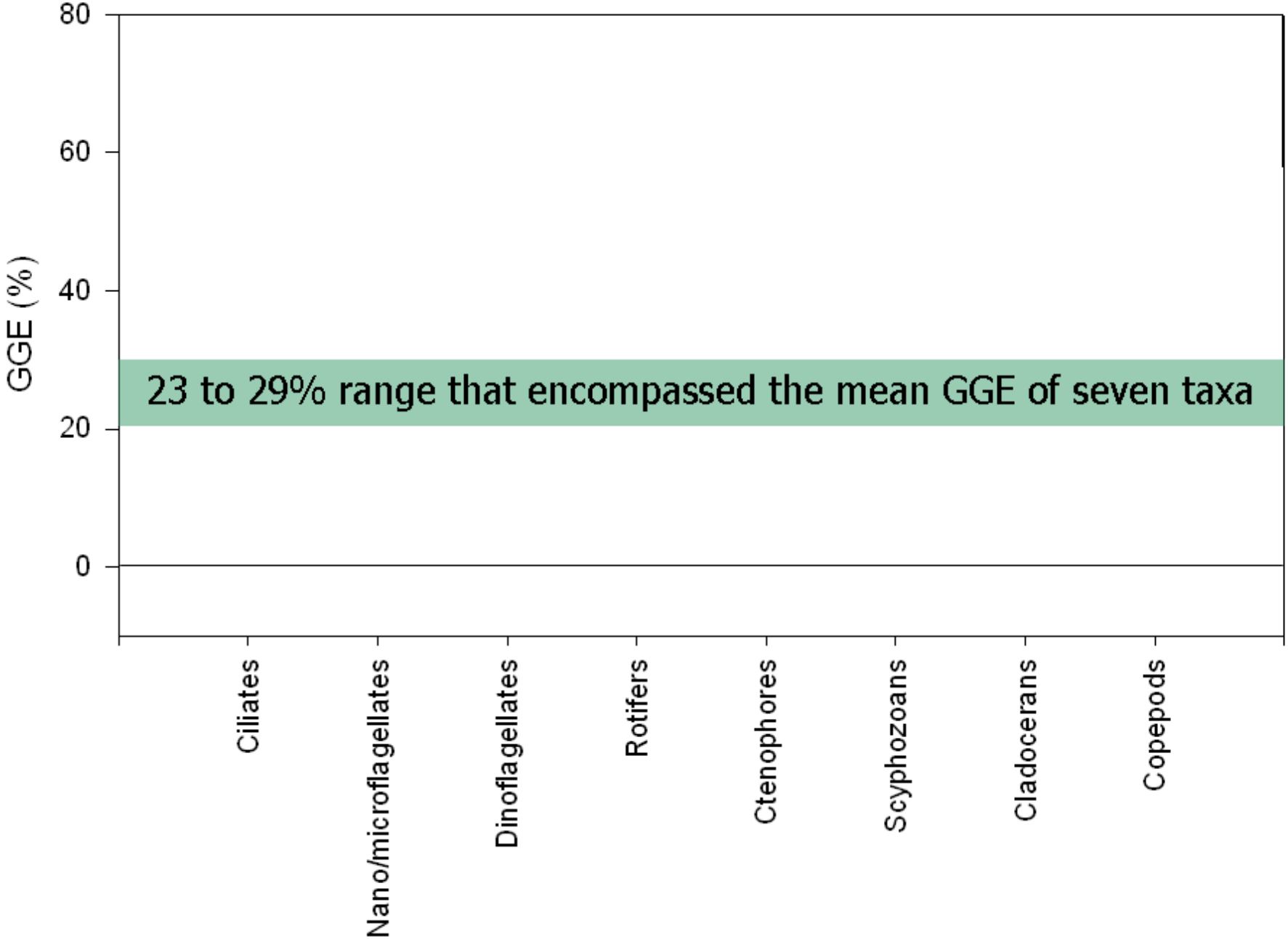
- Does GGE vary with temperature within and between taxonomic groups?
- How does GGE vary with food concentration within taxonomic groups?
- Do mean GGE values vary between taxa?
- How does diet type affect mean GGE within taxonomic groups?

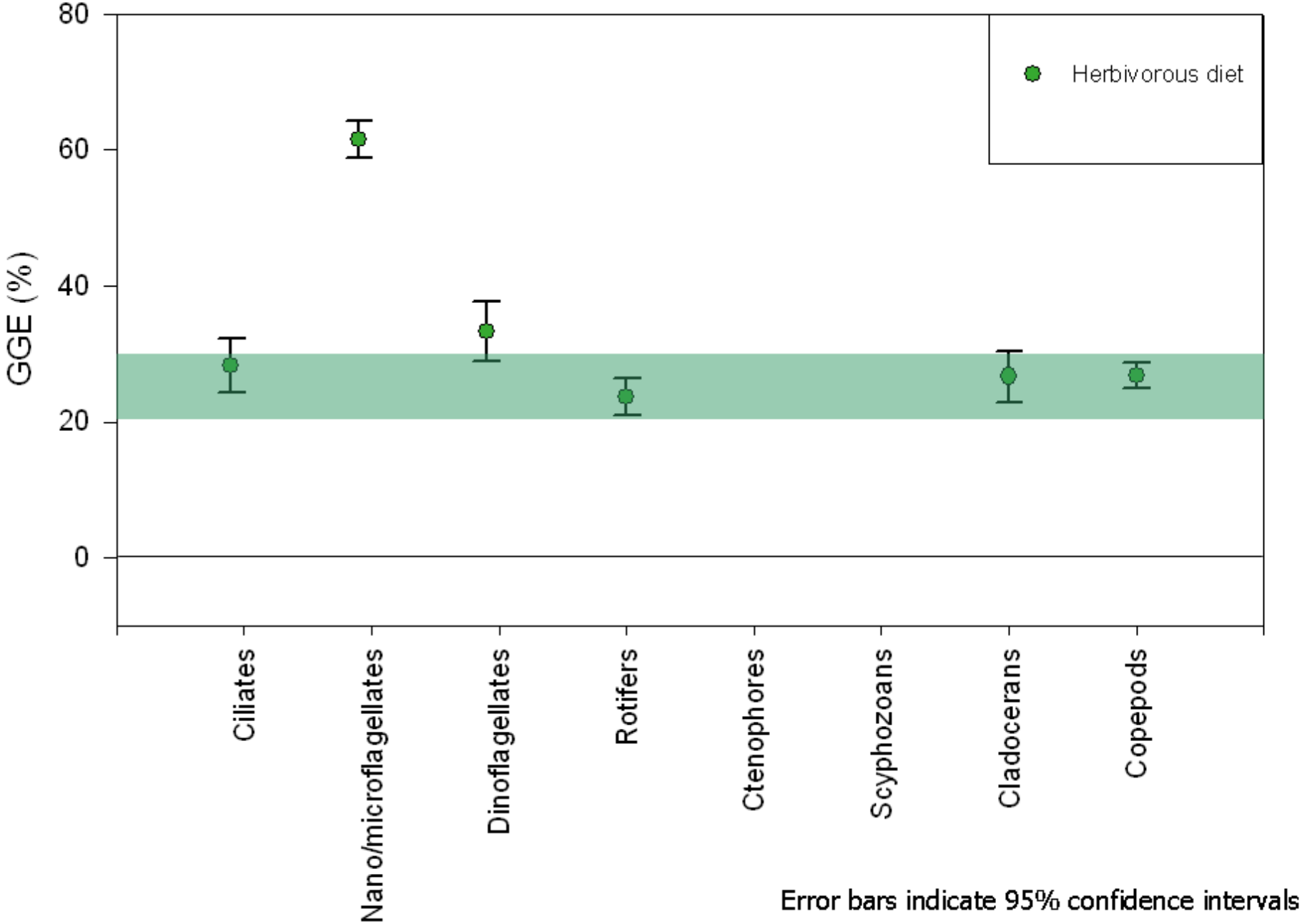
- Mean GGEs across six taxa did not differ significantly from one another
- In contrast to Straile (1997), the mean GGE of two groups were significantly different
- Nano/microflagellates had a significantly higher mean GGE
- Ciliates achieved a significantly lower mean GGE

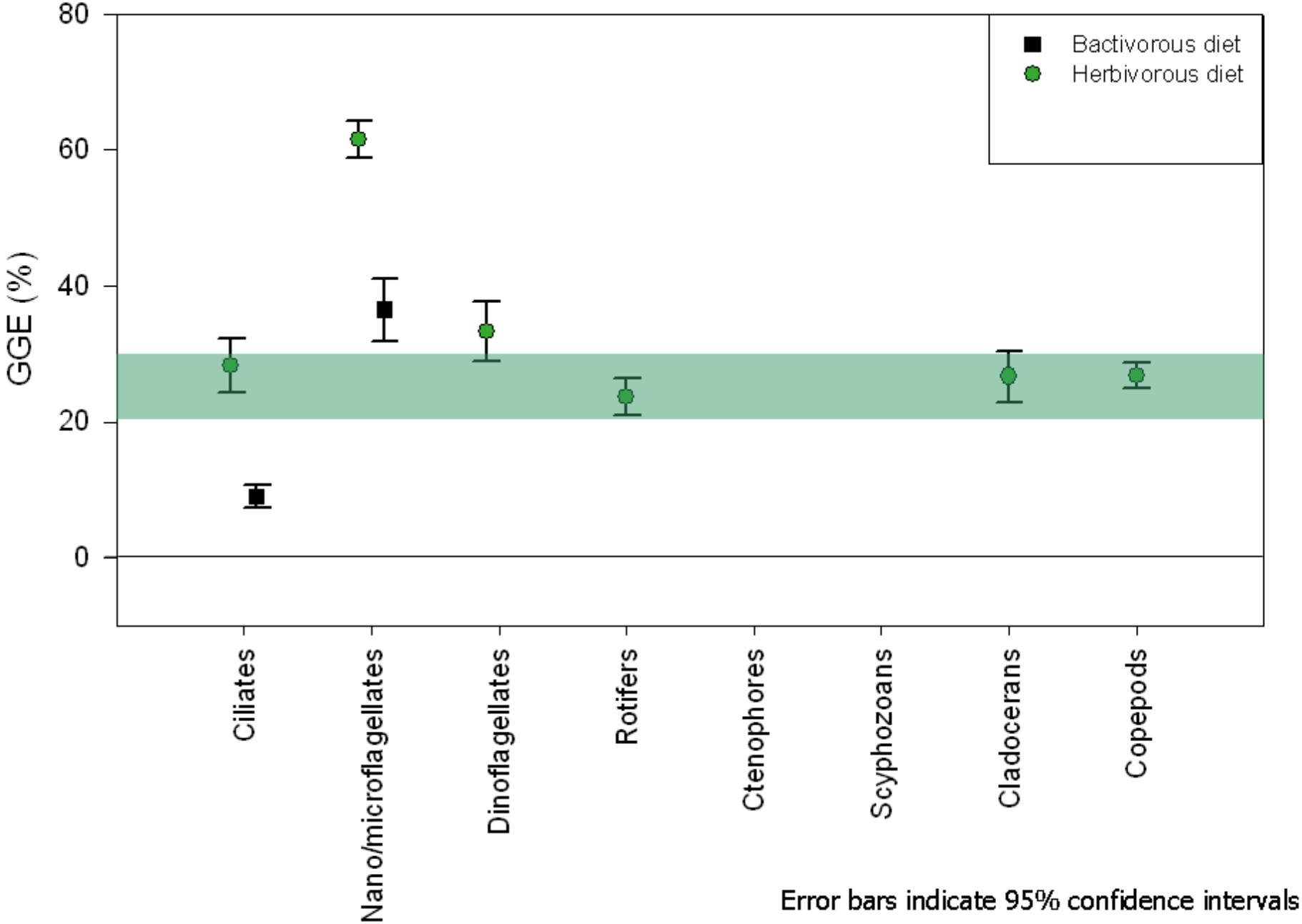
- Metazoans did not show consistently higher efficiencies than protozoans
  - Protozoans achieved higher and lower mean GGEs

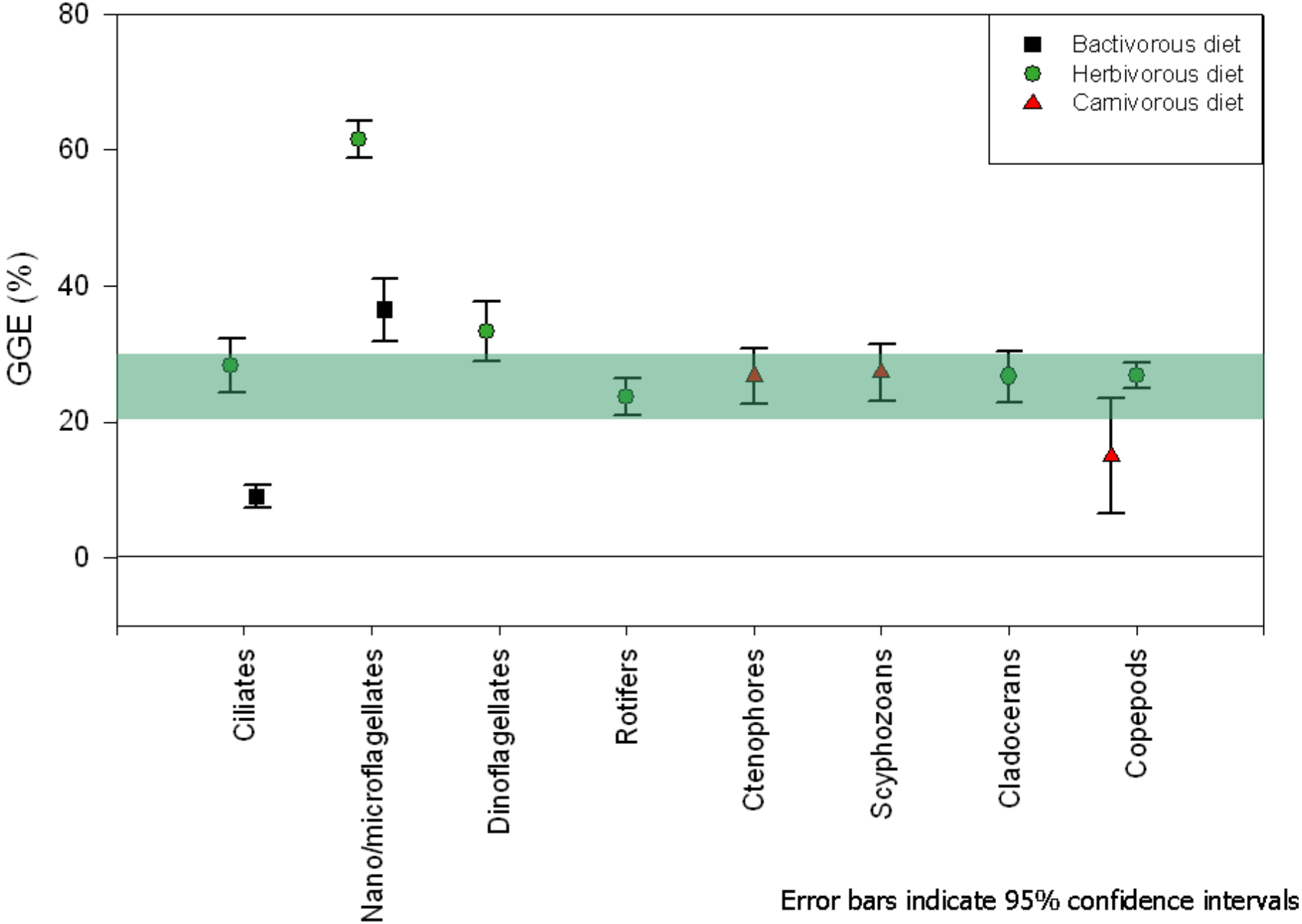
- Nano/microflagellate mean GGE is the only protozoan taxon to fall within the range of 30-60% predicted by Caron *et al.* (1990)

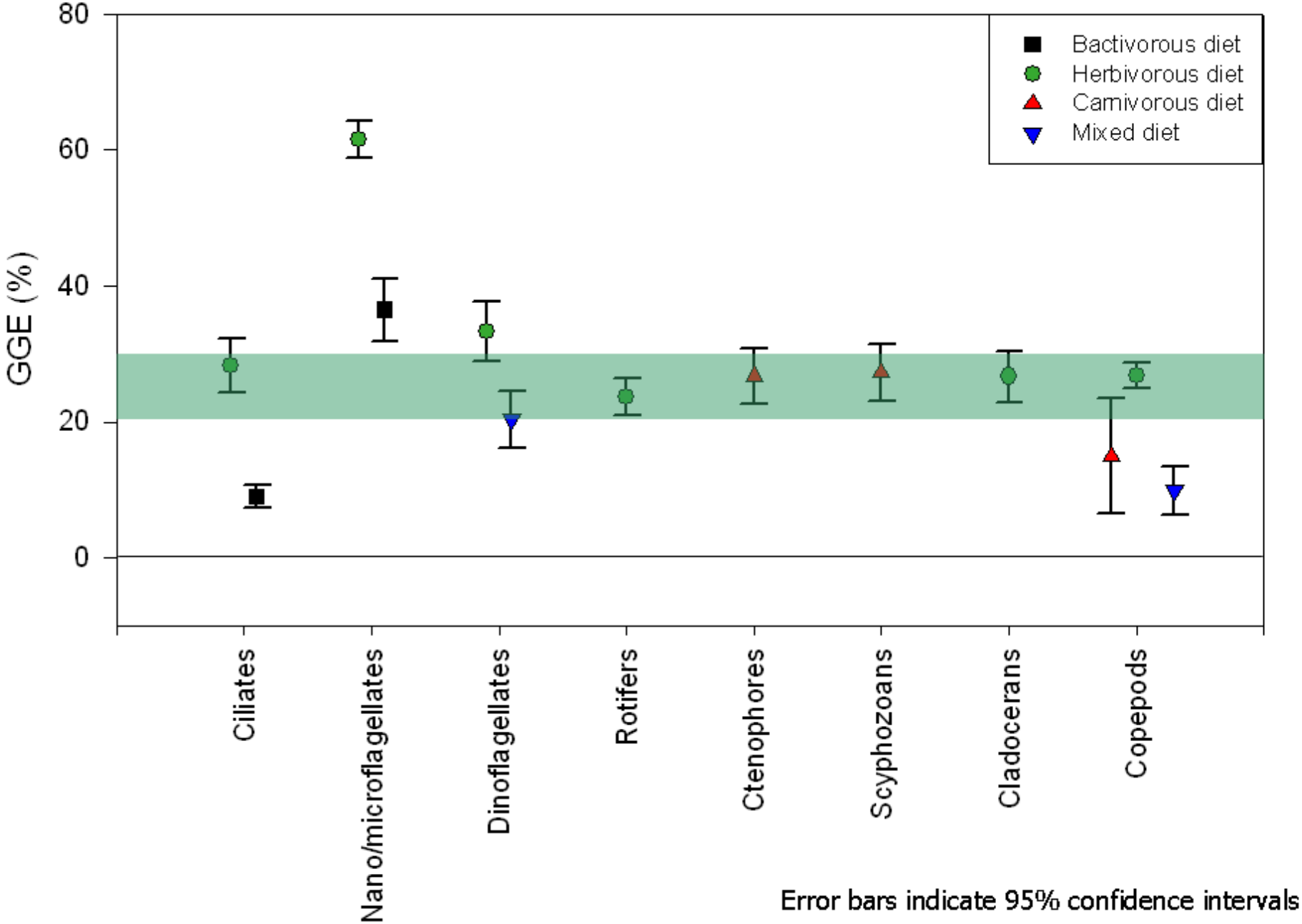
- The mean GGE of all taxa, with the exception of nano/microflagellates, were below 30%

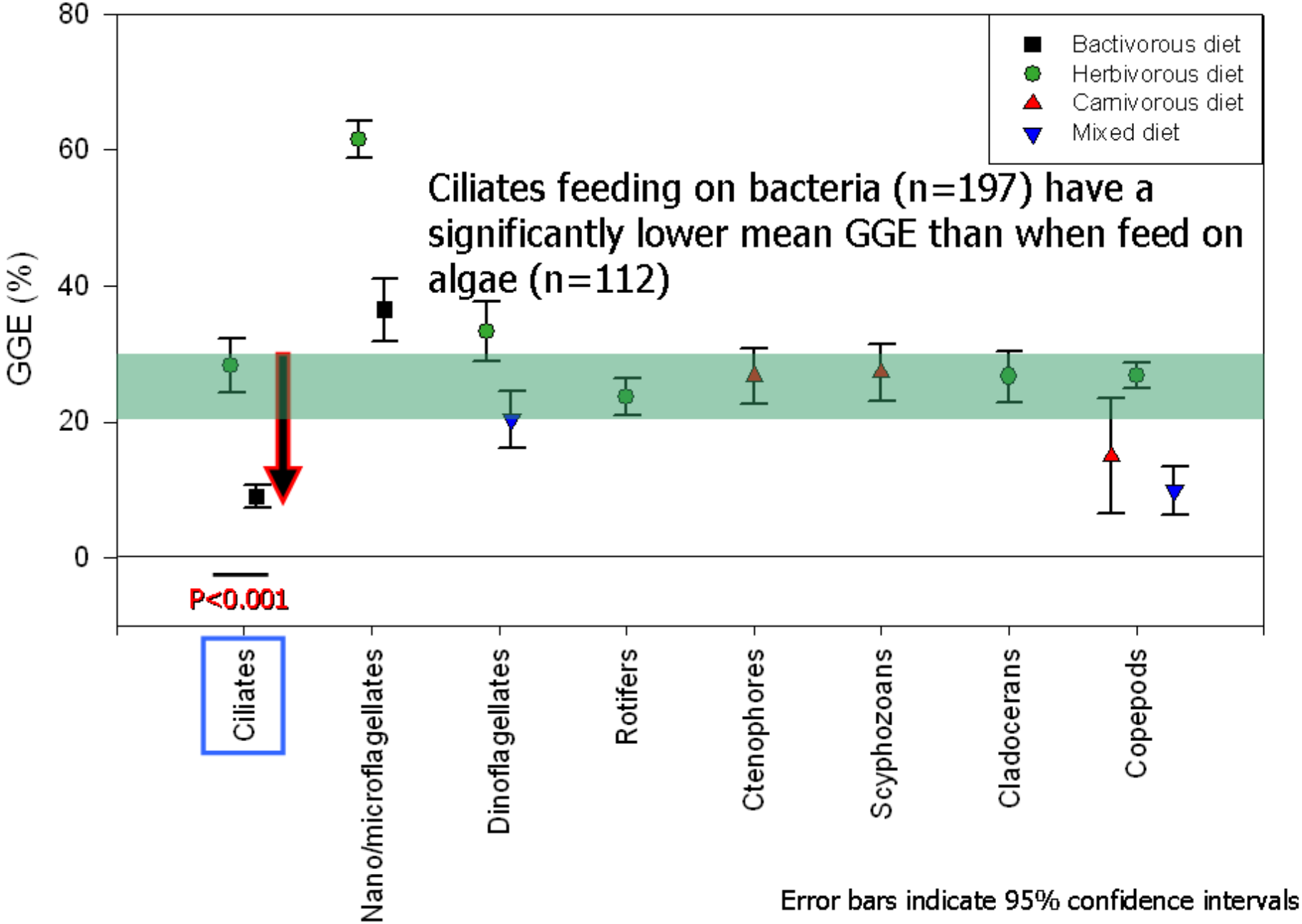

80
60
40
20
0
GGE (%)
23 to 29% range that encompassed the mean GGE of seven taxa
Ciliates
Nano/microflagellates
Dinoflagellates
Rotifers
Ctenophores
Scyphozoans
Cladocerans
Copepods

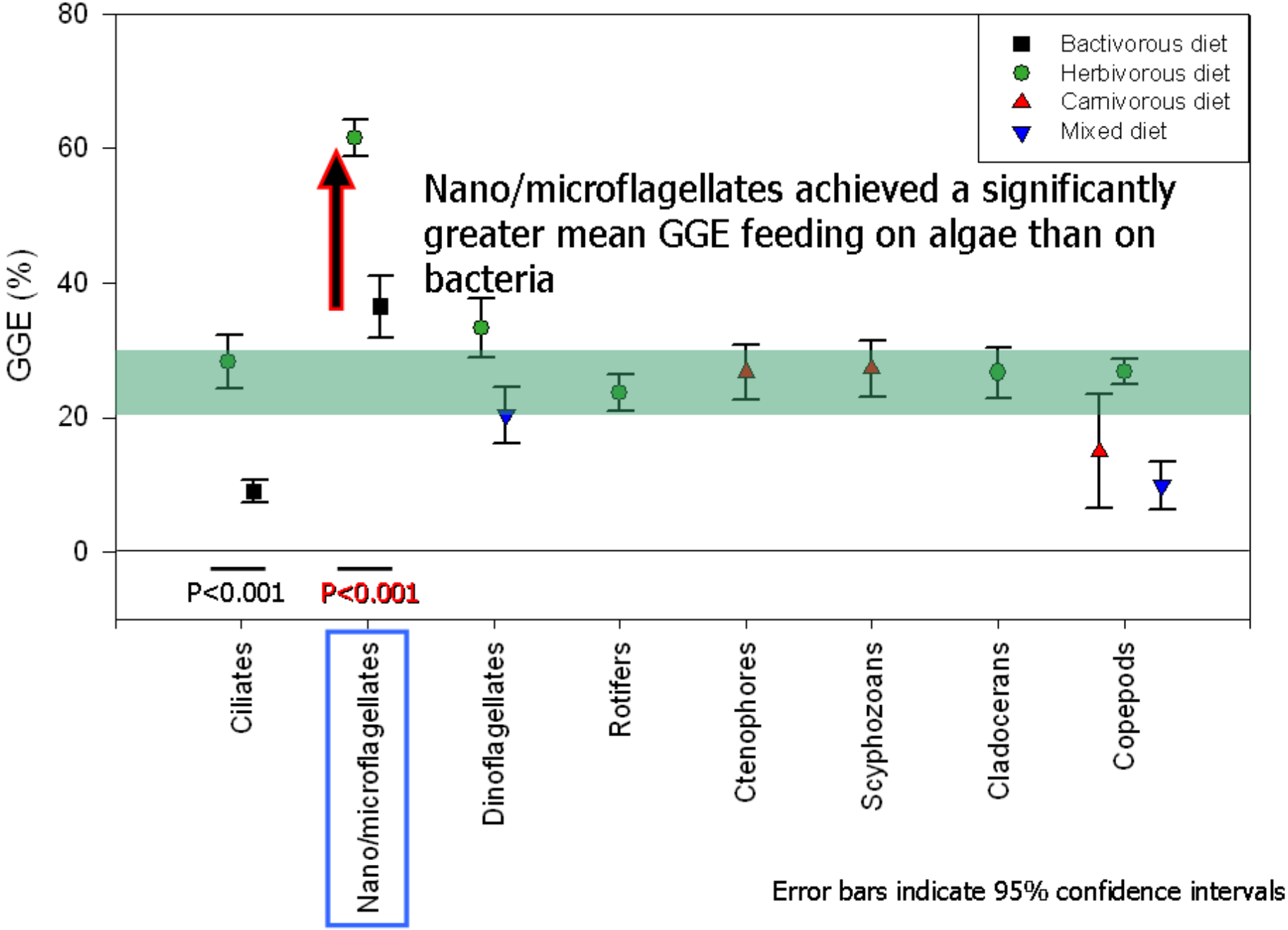

80
60
40
20
0
GGE (%)
Herbivorous diet
Ciliates
Nano/microflagellates
Dinoflagellates
Rotifers
Ctenophores
Scyphozoans
Cladocerans
Copepods
Error bars indicate 95% confidence intervals

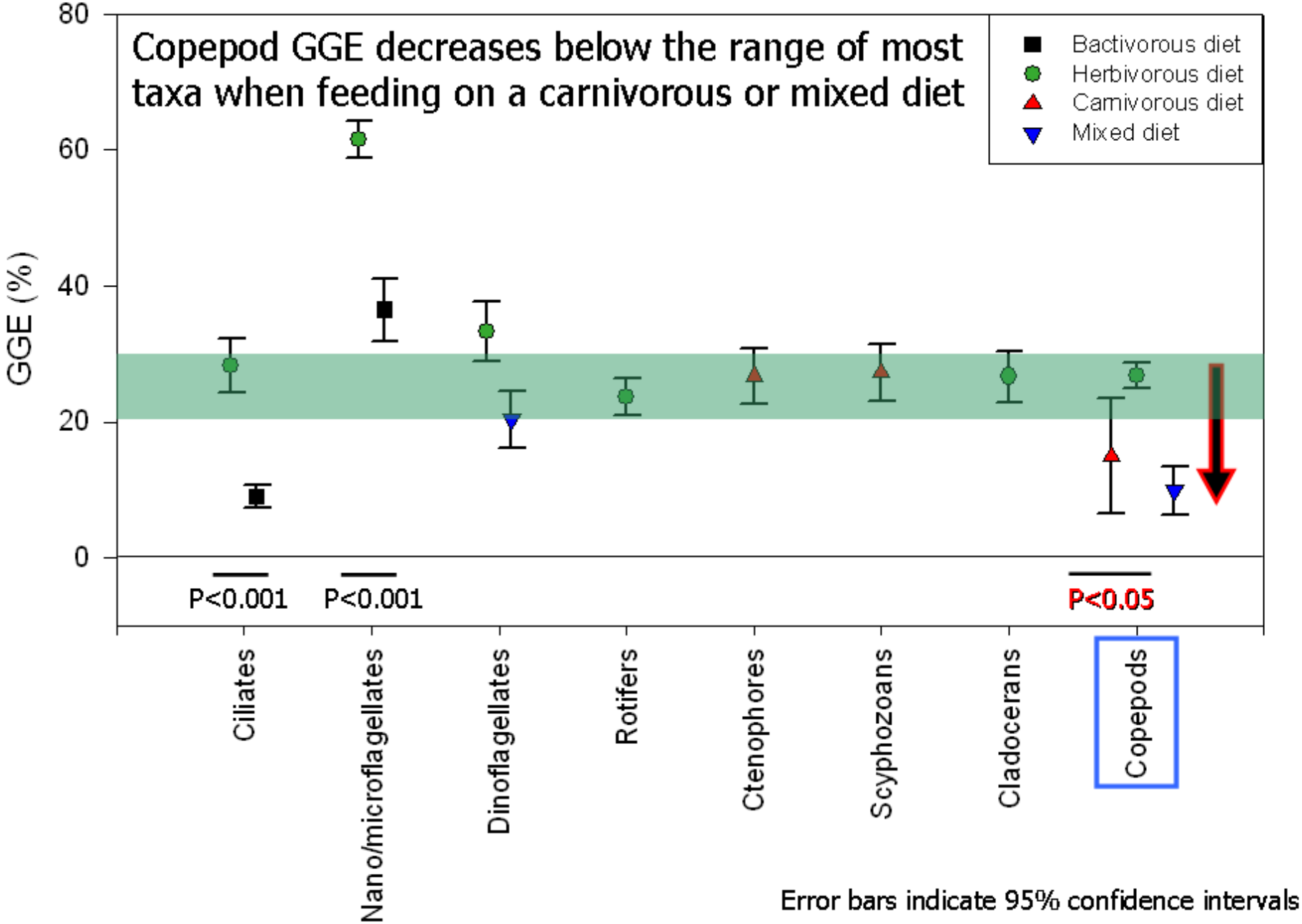

80
60
40
20
0
GGE (%)
Bactivorous diet
Herbivorous diet
Ciliates
Nano/microflagellates
Dinoflagellates
Rotifers
Ctenophores
Scyphozoans
Cladocerans
Copepods
Error bars indicate 95% confidence intervals


80
60
40
20
0
GGE (%)
Bactivorous diet
Herbivorous diet
Carnivorous diet
Ciliates
Nano/microflagellates
Dinoflagellates
Rotifers
Ctenophores
Scyphozoans
Cladocerans
Copepods
Error bars indicate 95% confidence intervals


80
60
40
20
0
GGE (%)
Bactivorous diet
Herbivorous diet
Carnivorous diet
Mixed diet
Ciliates
Nano/microflagellates
Dinoflagellates
Rotifers
Ctenophores
Scyphozoans
Cladocerans
Copepods
Error bars indicate 95% confidence intervals


80
60
40
20
0
GGE (%)
Bactivorous diet
Herbivorous diet
Carnivorous diet
Mixed diet
Ciliates feeding on bacteria (n=197) have a significantly lower mean GGE than when feed on algae (n=112)
P<0.001
Ciliates
Nano/microflagellates
Dinoflagellates
Rotifers
Ctenophores
Scyphozoans
Cladocerans
Copepods
Error bars indicate 95% confidence intervals


80
60
40
20
0
GGE (%)
Bactivorous diet
Herbivorous diet
Carnivorous diet
Mixed diet
Nano/microflagellates achieved a significantly greater mean GGE feeding on algae than on bacteria
P<0.001
P<0.001
Ciliates
Nano/microflagellates
Dinoflagellates
Rotifers
Ctenophores
Scyphozoans
Cladocerans
Copepods
Error bars indicate 95% confidence intervals


Copepod GGE decreases below the range of most taxa when feeding on a carnivorous or mixed diet
Bactivorous diet
Herbivorous diet
Carnivorous diet
Mixed diet
GGE (%)
80
60
40
20
0
P<0.001
P<0.001
P<0.05
Ciliates
Nano/microflagellates
Dinoflagellates
Rotifers
Ctenophores
Scyphozoans
Cladocerans
Copepods
Error bars indicate 95% confidence intervals

Questions to be answered

- Does GGE vary with temperature within and between taxonomic groups?
- How does GGE vary with food concentration within taxonomic groups?
- Do mean GGE values vary between taxa?
- How does diet type affect mean GGE within taxonomic groups?

- All four taxa that could be separated by diet type had a greater mean GGE when feeding on algae
- Ciliates and nano/microflagellates were significantly less efficient when feeding on bacteria
- Copepods were significantly less efficient when feeding carnivorously
- Prey compostion and size may be an important factors

Conclusions

- GGE is influenced by temperature, with the nature and extent of this relationship differing between taxa
- Taxonomic groups differ in their inherent GGE values (in contrast to findings by Straile 1997) which are heavily influenced by diet type
- Diet type is therefore an important consideration when considering GGE and applying them within ecosystem models

Conclusions

- Therefore temperature, through its affect on GGE is likely to have a significant impact on the structure of the planktonic food-web
- In order to improve accuracy, ecosystem models should take into account the different efficiencies of taxa, temperature and food dependence of GGE
- We aim to incorporate our findings into simple and complex planktonic ecosystem models

Acknowledgements

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British Antarctic Survey

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