Food web efficiency under different scenarios of resource availability and predation pressure

By

NGUYEN VAN KHANH

Promotor: Prof. Dr. Colin Janssen
Co-promotor & Tutor: Dr. Frederik De Laender

Thesis submitted in partial fulfillment of the requirements for the academic degree of Master of Science in Aquaculture
COPYRIGHT

The author and promoter give permission to put this thesis to disposal for consultation and to copy parts of it for personal use. Any other use falls under the limitations of copyright, in particular the obligation to explicitly mention the source when citing parts out of this thesis.

May 17th, 2011

Promoter ______________________

Prof. Dr. Colin Janssen

Tutor ______________________

Dr. Frederik De Laender

Author ______________________

Nguyen Van Khanh
ACKNOWLEDGEMENTS

It is a pleasure to thank the many people who made this thesis possible

It is difficult to overstate my gratitude to my promoter Prof. Dr. Colin Janssen and especially Dr. Frederik De Laender who worked not only as my co-promoter but also as my tutor. With their enthusiasm, inspiration and great efforts to explain things clearly and simply, they helped to make modeling work fun for me. Throughout my thesis-writing period, they provided encouragement, sound advice, good teaching and lots of good ideas. I would have been lost without them.

I would like to express my gratitude to the colleagues in Norway charged by Prof. Olav Vadstein and Prof. Yngvar Olsen for providing me the valuable raw datasets as the inputs for the models.

I would like to deeply thank the many people in the Laboratory of Aquaculture & Artemia reference Centre (ARC) and the Centre for Environmental Sanitation (CES) (especially Prof. Dr. Patrick Sorgeloos, Prof. Dr. ir. Peter Bossier) for teaching activities and other administrative supports. I am grateful to the MSc-Aquaculture-Team: Bart Van Delsen, Sebastian Vanopstal and Mieke Eggermont for helping to solve problems not only in study but also in the life since the first day I arrived at Gent. I am also indebted to my many student colleagues for providing a stimulating and fun environment in which to learn and grow.

I would like to thank the teachers who made me love mathematics and biology: my high school teachers (especially Nguyen Van Tien, Nguyen Thi Tinh), my undergraduate teachers at Hanoi Agriculture University (especially Prof. Dr. Nguyen Thuong Hien, Prof. Dr. Vu Trung Tang and Assoc Prof. Dr. Nguyen Mong Hung) and my lecturers in the Master course (especially Prof. Dr. Oliver Thas, Dr. Nancy Nevejan, Dr. Gilbert Van Stappen, Dr. Marleen De Troch).

I would like to say thanks to Belgian Technical Cooperation (BTC) for the financial support. Lastly, and most importantly, I wish to thank my family members, especially my parents, my wife and my daughter who always supported and loved me. To them I dedicate this thesis.

Nguyen Van Khanh, May 27, 2011
# TABLE OF CONTENTS

INTRODUCTION ................................................................................................................... 1

1. LITERATURE REVIEW ............................................................................................... 3

1.2. CARBON IN ECOSYSTEMS ..................................................................................... 3

1.2.1. Ecosystems and components in ecosystems ...................................................... 3

1.2.2. Ecological concepts on food chains and food webs .......................................... 5

1.2.3. Carbon flows and food web efficiency (FWE) .................................................... 8

1.2.4. Research on FWE in fisheries and Aquaculture .............................................. 11

1.3. FOOD WEB MODELING ...................................................................................... 14

1.3.1. Modeling in general .......................................................................................... 14

1.3.2. Modeling of ecosystems .................................................................................. 15

2. MATERIALS AND METHODOLOGY ...................................................................... 17

2.1. THE USED MESOCOSM DATA ........................................................................... 17

2.2. LINEAR INVERSE MODELLING ........................................................................... 18

2.2.1. What is Linear Inverse Modelling? .................................................................. 18

2.2.2. Conceptual food web: food web topology ....................................................... 20

2.2.3. Collecting the experimental data and the constraints from literature ............... 22

2.2.4. Solving the model ............................................................................................ 23

2.3. CALCULATING FOOD WEB EFFICIENCY ......................................................... 24

3. RESULTS .................................................................................................................... 25

3.1. CARBON FLOWS ................................................................................................. 25

3.2. PRIMARY PRODUCTION ...................................................................................... 27

3.3. CILIATE AND COPEPOD PRODUCTION .............................................................. 30

3.4. DIETS FOR CILIATES AND COPEPODS ............................................................. 31

3.5. FOOD WEB EFFICIENCY BASED ON CILIATE PRODUCTION ......................... 33

3.6. FOOD WEB EFFICIENCY BASED ON COPEPOD PRODUCTION ....................... 35

3.7. INTERACTIONS BETWEEN CILIATES AND COPEPODS IN THE FOOD WEBS ... 36

4. DISCUSSION .............................................................................................................. 38
LIST OF FIGURES

Figure 1: Antarctic food chain and food web................................................................. 5
Figure 2: Herbivorous and microbial food chains......................................................... 7
Figure 3: Carbon and energy transferred and heat loss in the food chain..................... 8
Figure 4: Carbon pathway in ecosystems.................................................................... 10
Figure 5: Modeling strategy ......................................................................................... 20
Figure 6: Food web topology ....................................................................................... 21
Figure 7: Carbon flows at the starting stage of the experiment (day 2) ......................... 25
Figure 8: Carbon flows at the end stage of the experiment (day 8) ............................. 26
Figure 9: Production of phytoplankton factions............................................................. 28
Figure 10: Production of ciliate and copepod during the time course of the experiment.. 30
Figure 11: Diet of ciliates during the time course of the experiment.............................. 31
Figure 12: Diet of copepods during the time course of the experiment ....................... 32
Figure 13: Food web efficiency of ciliate during the time course of the experiment ........ 34
Figure 14: Food web efficiency of copepod during the time course of the experiment .... 35
Figure 15: Correlation of copepod production and ciliate production......................... 36
Figure 16: Correlation of the ciliate (solid) and copepod (filled) production and their carbon flow .................................................................................................................. 37
LIST OF TABLES

Table 1: Components in ecosystems................................................................. 3
Table 2: Comparison of the herbivorous food chain and the microbial loop .......... 7
Table 3: Estimated Production of Harvestable Fish......................................... 12
Table 4: Mesocom codes used in the experiment ............................................ 17
Table 5: The parameters were measured and used in modelling...................... 17
Table 6: Constraints used for LIM................................................................. 22
<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>APP</td>
<td>Appendicularia</td>
</tr>
<tr>
<td>BAC</td>
<td>Bacteria</td>
</tr>
<tr>
<td>CIL</td>
<td>Ciliates</td>
</tr>
<tr>
<td>COP</td>
<td>Copepods</td>
</tr>
<tr>
<td>DET</td>
<td>Detritus</td>
</tr>
<tr>
<td>DIC</td>
<td>Dissolved inorganic carbon</td>
</tr>
<tr>
<td>DOC</td>
<td>Dissolved organic carbon</td>
</tr>
<tr>
<td>FWE</td>
<td>Food web efficiency</td>
</tr>
<tr>
<td>GRO</td>
<td>Copepod growth</td>
</tr>
<tr>
<td>HNA</td>
<td>Heterotrophic nano-flagellates</td>
</tr>
<tr>
<td>LIM</td>
<td>Linear inverse models</td>
</tr>
<tr>
<td>PHY2</td>
<td>Phytoplankton fraction size 0.8-2µm</td>
</tr>
<tr>
<td>PHY20</td>
<td>Phytoplankton fraction size; 2-20 µm</td>
</tr>
<tr>
<td>PHY200</td>
<td>Phytoplankton fraction size &gt; 20µm</td>
</tr>
<tr>
<td>SED</td>
<td>Sediment</td>
</tr>
</tbody>
</table>
ABSTRACT

The mass balance principle was used to examine food web efficiency (FWE) of 6 different food web types that differed in top predator (copepod) density and nutrient addition. This was done by combining data from a mesocosm experiment that lasted for 10 days and a carbon flow model.

The models indicated that FWE decreased with increasing nutrient concentration but did not change with predator density. Most FWE values (production of copepods / primary production and production of ciliates / primary production) varied between 0 and 0.2. There were some exceptions such as very high FWE values (around 1) based on copepod production due to a collapse of primary production and extensive support of the microbial loop to copepod production. Also negative FWE values were found in case of ciliate production because of higher metabolic costs than uptake. The cause for average values between 0 and 0.2 was that an increase in primary production was not always matched by an increase in consumer production which reduced the food web efficiency.

Both bottom-up and top-down effects controlled the relations of ciliates and copepods in the food web. Which effect dominated depended on the period: top-down at start vs. bottom-up at end of the experiment. It was concluded that the use of carbon flow models may clarify patterns of resource use in cultured systems. Future research should therefore focus on actively modifying the structure of food webs in order to reduce loss of energy and obtain higher production of cultured species.
INTRODUCTION

Aquaculture continues to be the fastest growing animal food-producing sector and to outpace population growth with production of less than 1 million tons per year in 1950s to more than 50 million tons was reported at the middle of 2000s (Subasinghe 2005). Besides intensifying yield of cultured species to obtain higher production for human demands, the sustainable development and environmental issues are also indicated seriously (De Silva 2001). The sustainable development can be solved by the replacement of man-made habitat by natural aquaculture farms with using of natural resources in farm inputs (particularly feed) (De Silva 2001). There are many other examples of sustainable aquaculture: ecosystem approach in aquaculture which mainly based on the self-provided of ecosystems (Soto et al., 2008) or poly-culture can also be considered to be a sound and effective sustainable system for the use of environmental resources or the shrimp-mangrove-forestry farming systems are also a good example for sustainable use of primary resources (Johnston et al. 1999).

It is clear that to obtain sustainable development in aquaculture, understanding properties in cultured ecosystems such as trophic relation of species (food web structure), transferring of nutrient between compartments in the food web (nutrient flows) and especially efficiency of using nutrient (food web efficiency) is necessary. Thereafter, research on nutrient inputs and conversion efficiency between trophic levels in the food web of aquaculture ponds (ecosystems) has come under increased scrutiny because of increased nutrient use efficiency and decreased environmental impact (Wang et al. 2009).

The efficiency of aquaculture ponds is determined by the capacity of the food web to recycle carbon, nutrients and energy. Enhancement of food web efficiency in aquaculture plays a very important role in aquaculture because of reasons as follows:

- It lowers nutrient inputs and thus decreases loading of waste materials to environment.
- It reduces dependence on fossil energy inputs
- It maximizes the sustainable yield gained per unit of input, thus increase economical benefits.

Goal of this thesis:

The goal of this study is to use food web models to calculate the food web efficiency (FWE) of cultured systems at varying nutrient levels and densities of copepods. The models use the
mass balance principle and a data set is used from a mesocosm experiment to investigate the structure of the food web and to quantify carbon flows between the different food web compartments. Finally, these carbon flows are used to calculate FWE in these ecosystems and examine the influence of predator density and nutrient availability. Additionally, the relationships between two important grazers (copepods and ciliates) are inspected at the different combinations of predator density and nutrient availability.

After all, base on the study results some suggestions will be drawn up in order to obtain higher efficiency of using nutrient in aquaculture.
1. LITERATURE REVIEW

1.2. CARBON IN ECOSYSTEMS

1.2.1. Ecosystems and components in ecosystems

The term “ecology” originates from the Greek word “oikos” meaning “a place to live”. It can be considered as the study of organisms “biotic” within their “abiotic” place to live (Smith & Smith 2001). The combination of all the organisms living in a particular area and all the nonliving, physical components of the environment forms an ecosystem. In Table 1, some examples of abiotic and biotic components are given. In this ecosystem, living organisms not only interact with the physical environment but also exchange carbon with other organisms (biological community) through predator-prey relationships (Campbell et al. 2009).

The way in which ecosystems are categorized is diverse. Natural ecosystems operate by themselves without any major interference by man while artificial ecosystems - also called man-engineered ecosystems or man-made ecosystems are made and maintained by man by the addition of carbon (Jones et al. 2000). Alternatively, according to Smith and Smith (2001) ecosystems can be categorized as aquatic or water based and terrestrial or land based with more than 20 ecosystem types have been characterized. However, commonly one ecosystem can includes components as mentioned in Table 1.

Table 1: Components in ecosystems

<table>
<thead>
<tr>
<th>Examples of abiotic components</th>
<th>Examples of biotic components</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sunlight</td>
<td>Primary producers</td>
</tr>
<tr>
<td>Temperature</td>
<td>Herbivores</td>
</tr>
<tr>
<td>Precipitation</td>
<td>Carnivores</td>
</tr>
<tr>
<td>Water or moisture</td>
<td>Omnivores</td>
</tr>
<tr>
<td>Soil or water chemistry (e.g., P, NH₄⁺)</td>
<td>Detritivores</td>
</tr>
<tr>
<td>Natural disturbances</td>
<td>Decomposers</td>
</tr>
</tbody>
</table>

In aquatic or water based ecosystems, two main categories can be subdivided as freshwater and marine-water ecosystems (Alexander & Fairbridge 1999, Ghosh 2010) with characters in detail need to consider as follows:

- For abiotic components: Water current, tide, salinity, flow, transparency, heavy metal, dissolved oxygen concentration, nutrient concentrations. The levels of these
components varies with the type of aquatic ecosystem (Loeb & Spacie 1994, Dobson & Frid 2008).

- For biotic components: Which encompass all living organisms found in aquatic ecosystems, are either autotrophic or heterotrophic (Manahan 2001). Three main categories of living organisms are defined based on their ability to move in water: plankton (moving with the water current), nekton (have the ability to move against the water current) and benthos (bottom dweller - attached or crawling) (Levinton 1982, Levinton 2008).

As for ecosystems, also biotic components in an ecosystem can be classified in various ways. One way is based on their mode of feeding. Based on this mode of feeding, organisms can be classified into a number of trophic groups (Brenchley & Harper 1998) which include:

- Primary producers - produce organic matter from sunlight (photosynthesis) or chemical reactions in water. These are often referred to as algae or water plants.
- Herbivores - feed on living primary producers.
- Carnivores / predators - feed on live prey.
- Omnivores - feed on various food items including primary producers and herbivores.
- Scavengers - consume dead and/or partially decayed organisms.
- Parasites - feed on another (usually larger) organism without (usually) killing it.
- Suspension feeders (also called filter feeders) - collect particulate matter or microorganisms from suspension in the water.
- Detritivores - feed on decaying organic matter.
- Deposit-feeders - collect particulate matter from the sediment.
- Decomposer - break down decaying organic matter - e.g. Fungi, bacteria

Ecosystem components are not independent from each other. They not only interact with their environment (chemical and physical) but also with other organisms (biological). Organisms in a trophic group may feed on several ones in different trophic groups for example an organism in the carnivorous group may eat organisms in the groups of herbivores, detritivores and/or even carnivores. Thus, carbon in biomass of organisms is transferred from one trophic group to the next in the form of food. The total of all carbon
pathways from producers to top predators composes the food chain or food web and these concepts will be discussed in the next part.

1.2.2. Ecological concepts on food chains and food webs

The dictionary of Cambridge (Elizabeth 2008) gives a definition of “food chain" as a series of organism groups feeds on one other group while the term “food web" was defined as an assembly of multiple interrelated food chains in an ecological community. Such food webs are highly interwoven with linkages representing a wide variety of species interactions (Smith & Smith 2001). A food chain is largely a theoretical idea and one should realize that the feeding relationships of organisms in the real world is almost always more complex than suggested by a food chain. For that reason, the concept of a food web probably more accurately describes biological communities than the food chain concept. Differences between a food web and a food chain are demonstrated in Figure 1.

![Figure 1: Antarctic food chain and food web](http://www.coolantarctica.com/Antarctica%20fact%20file/wildlife/whales/food%20web.htm)
Food webs are organized into three main categories, depending on the kinds of organisms or trophic levels they consider. The three primary trophic levels are producers, consumers and decomposers. Some consumers occupy a single trophic level, but many others such as omnivores, occupy more than one trophic level. The direction of carbon flow presents the feeding relationships in the ecosystem (Smith & Smith 2001). Those flows are not stable through time but vary with the season (Bradford et al. 1999, Leigh et al. 2010), the presence of carbon inputs, species migration and habitat size (Spencer et al. 1996).

The carbon flows in the food web (from one compartment to the next) are reduced gradually with increasing trophic level. This is because carbon flowing through the ecosystem is reduced by a magnitude of 10 from one trophic level to the next (Levinton 2008). Thus the amount of carbon available to the second and third trophic level is so small that few organisms can be supported if they depended. Therefore, each food chain within a food web has three to four links, rarely five (Pimm 1980).

According to Smith and Smith (2001), carbon flows via two main pathways: the grazing or herbivorous food chain or and the detrital or microbial loop. The differences between these two pathways are based on the carbon sources. In the herbivorous food chain, the primary carbon source is primary production and the initial consumers are herbivores (Bradford et al. 1999). In the microbial food chain, primary carbon sources are dead organic matter and detritus with bacteria and fungi as initial consumers (Barettabekker et al. 1995, Bradford et al. 1999). The herbivorous food chain is easy to understand: cattle grazing on pastureland, deer browsing in the forest, insect pest feeding on crops, and zooplankton feeding on phytoplankton are examples of the grazing food chain. However, although highly noticeable, the herbivorous food chain is not the major food chain in ecosystems, only in some aquatic ecosystems, the herbivorous food chain plays a dominant role in carbon flow (Smith & Smith 2001).

On the other hand, the microbial loop is common in many ecosystems. Especially in terrestrial and littoral areas it is the major pathway of carbon flow. However, the carbon flow through a microbial loop is more difficult to measure because the flow of carbon in each of trophic level is recycled and waste is returned as food for microbial organisms at the beginning of the loop (Smith & Smith 2001). The differences between the herbivorous food chain and the microbial loop are shown in Figure 2 and Table 2.
Figure 2: Herbivorous and microbial food chains
(adopted from Smith and Smith (2001, page 497))

Table 2: Comparison of the herbivorous food chain and the microbial loop

<table>
<thead>
<tr>
<th>Criteria</th>
<th>Herbivorous food chain</th>
<th>Microbial food chain</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon sources</td>
<td>Inorganic</td>
<td>Organic</td>
</tr>
<tr>
<td>Energy</td>
<td>Solar radiation</td>
<td>The breakdown of organic matter</td>
</tr>
<tr>
<td>Carbon flow</td>
<td>Unidirectional</td>
<td>Cyclic</td>
</tr>
<tr>
<td>Species composition</td>
<td>Primary consumers</td>
<td>Detritus consumers</td>
</tr>
<tr>
<td>Timing domination</td>
<td>In the beginning to produce</td>
<td>Later when organic matter is</td>
</tr>
<tr>
<td></td>
<td>organic matters for ecosystems</td>
<td>available in ecosystems.</td>
</tr>
</tbody>
</table>

In reality, it is impossible to separate the herbivorous food chain and the microbial loop because the two types will always be present in any ecosystem (Smith & Smith 2001).
Depending on the time of year, the microbial food chain or the herbivorous food chain may dominate in an ecosystem (De Laender et al. 2010a).

1.2.3. **Carbon flows and food web efficiency (FWE)**

The concept of carbon flows in ecological systems is one of the cornerstones of ecology (Smith & Smith 2001). It is known that the food which contains energy in the form of carbon-carbon bonds flows in the food chain. Thus carbon also flows from one organism to the next and to the next and so on. This process is called “flows of carbon”. It denotes that not all the carbon from one trophic level is transferred perfectly to the next (Levinton 2008). In addition, at each trophic level of the food chain, this form of carbon is broken to release energy for living activities such as respiration, digestion, excretion, moving or eventually loss in the form of heat (Figure 3).

![Figure 3: Carbon and energy transferred and heat loss in the food chain](http://www.biologie.uni-hamburg.de/b-online/library/marietta/0eco99.htm)

As a result, when carbon flows to the top of a food chain or food web, the numbers and biomass of organisms are normally reduced significantly (Levinton 2008). It means that the magnitude of carbon flows is decreased quickly from the beginning toward the end of food chain and food web, except for certain aquatic ecosystems with a rapid turnover of small aquatic consumers (Smith & Smith 2001).
As mentioned above, the trophic links in a food web are very complex that results in complexity of carbon flows in the food web. However, because the carbon budget of the food web always obeys the mass balance rule (Stone et al. 1993, Walters et al. 1997, Pinnegar & Polunin 1999) and the carbon flow is dimensional, the carbon use efficiency can be estimated in ecological systems (Smith & Smith 2001). The ecological efficiency of a food web - called food web efficiency (FWE) - can be estimated as the ratio between the productivity of the highest trophic level and the productivity at the lowest trophic level (Rand & Stewart 1998). In other word, the FWE can be estimated without explicitly quantifying carbon flows at the middle trophic levels.

It has been shown that species composition of predators and seasonal variations in light and temperature can cause temporal and spatial variations in magnitude of carbon flows in the food web since then lead to variations in the FWE. For example, De Laender et al. (2010) found that in the Barents Sea the FWE based on copepod production was 1.5 times higher in summer than in spring. Additionally, fishing activities can also impact the FWE. When comparing food webs of protected and exploited areas in the Adriatic Sea, transfer efficiency was consistently higher in the exploited food webs than in the protected ones (Libralato et al. 2008).

The size, structure and components of the food webs also affect to their magnitude of carbon flow and FWE. In oligotrophic and strongly eutrophic ecosystems, the FWE is much lower than that in the moderate nutrient-rich ecosystems (Sommer et al. 2002). In the oligotrophic water, primary producers are mainly pico-phytoplankton (Takamura & Nojiri 1994, Fernandez et al. 2004). More trophic levels are typically needed to transfer the carbon to the highest trophic levels. In moderately nutrient-rich systems, the primary productivity may be dominated by nano-phytoplankton, which can be directly consumed by meso-zooplankton (Koshikawa et al. 1999) which means that carbon can be quickly transferred to the highest trophic level. In eutrophic systems the lower FWE is explained by an increased abundance of inedible or toxic algae which may reduce energy flows in the food web and/or affect to the productivity of the top predator (Sommer et al. 2002).

It is clear that the FWE can be estimated but the question is how to estimate it. According to Smith and Smith (2001), the most useful method for estimation is by using assimilation efficiencies, growth efficiencies, and utilization efficiencies. In the case of measuring
efficiency in carbon transfers, Libralato et al (2008) also formulated three ways to estimate this:

- Mean Transfer Efficiency (calculated as a geometric average of all transfer efficiencies for the whole food web)
- The geometric average transfer efficiency for the microbial loop
- The geometric average transfer efficiency for the herbivorous food chain

According to the book of Ecology by Ricklefs and Miller (2000) the carbon flows of through trophic levels in an ecosystem can be described as Figure 4.

<table>
<thead>
<tr>
<th>Carbon Pathway through Trophic Levels</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trophic level 1</td>
</tr>
<tr>
<td>Net Production at Trophic Level 1 (P1)</td>
</tr>
<tr>
<td>1/2 Non-predatory Death</td>
</tr>
<tr>
<td>Trophic level 2</td>
</tr>
<tr>
<td>Ingested (I)</td>
</tr>
<tr>
<td>1/2</td>
</tr>
<tr>
<td>Defecation</td>
</tr>
<tr>
<td>1/2</td>
</tr>
<tr>
<td>Respiration</td>
</tr>
<tr>
<td>1/2</td>
</tr>
<tr>
<td>Assimilation (A)</td>
</tr>
<tr>
<td>1/2</td>
</tr>
<tr>
<td>Growth &amp; Reproduction</td>
</tr>
<tr>
<td>1/2</td>
</tr>
<tr>
<td>Net Production at Trophic Level 2 (P2)</td>
</tr>
<tr>
<td>1/2 Non-predatory Death</td>
</tr>
<tr>
<td>Next trophic levels (Pn)</td>
</tr>
</tbody>
</table>

**Figure 4: Carbon pathway in ecosystems**

In this book, the authors also defined and formulated to calculate carbon used efficiency and FWE as follows (Ricklefs & Miller 2000):
- Exploitation efficiency is the amount of food ingested divided by the amount of prey production (I / Pn)
- Assimilation efficiency is the amount of assimilation divided by the amount of food ingestion (A / I)
- Net production efficiency is the amount of consumer production divided by the amount of assimilation (Pn + 1 / A)
- Gross production efficiency is the assimilation efficiency multiplied by the net production efficiency, which is equivalent to the amount of consumer production divided by amount of ingestion (Pn + 1 / I)
- Ecological efficiency is the exploitation efficiency multiplied by the assimilation efficiency multiplied by the net production efficiency, which is equivalent to the amount of consumer production divided by the amount of prey production (Pn + 1 / Pn)

The ecological efficiency of a food web or the FWE has been calculated by Berglund et al. (2007) considering organic and inorganic nutrient inputs in the microbial and herbivorous pathways, respectively:

\[ FWE = \frac{MZp}{PP + BP} \]

where MZp is net productivity of the top predator (copepod) in their experimental systems; PP is the net primary productivity; and BP is net bacterial productivity.

It was found that the FWE in a herbivorous food chain and a microbial loop dominated system were always relatively inefficient; 22% in the phytoplankton-based food web and 2% in the bacteria-based food web due to the attribution inedible autotrophs and pass to 1-2 extra trophic levels (Berglund et al. 2007). However, it has also been shown that bacteria in a microbial loop dominated system are able to recycle carbon and thus increase the FWE (Kamiyam 2004, Pavés & González 2008, De Laender et al. 2010a).

1.2.4. Research on FWE in fisheries and Aquaculture

1.1.4.1. In fisheries management

Understanding trophic interactions allows the quantification of production losses in and provides an ecological framework for biomass synthesis that takes into account ecosystem
properties. Ecological models, which will be discussed in the next section, have used this information to provide a basis for estimating the maximum allowable catches, thus give directional advice for fisheries management and support ecosystem-based management of fisheries as well (Libralato et al. 2008).

It is well known that there is a strong relationship between primary production and fish yield (Iverson 1990, Gargett 1997, Hakanson & Boulion 2001). In monitoring fish stocks as a support for exploitation allowances, satellites have been used to detect the phytoplankton density on the sea surfaces to assess fish production, migration of fish stocks or to find fishing grounds (Chassot et al. 2011). In addition, the principle of the relation between primary production and fish production has also been used to indentify food web structure, efficiency and the harvestable production in marine ecosystems as shown in Table 3.

<table>
<thead>
<tr>
<th>Table 3: Estimated Production of Harvestable Fish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open Ocean</td>
</tr>
<tr>
<td>Nutrient concentration</td>
</tr>
<tr>
<td>Primary Production</td>
</tr>
<tr>
<td>Food Chain Length</td>
</tr>
<tr>
<td>Ecological Efficiency</td>
</tr>
<tr>
<td>Fish Production</td>
</tr>
</tbody>
</table>

(Source: http://www.globalchange.umich.edu/globalchange2/current/lectures/fisheries/fisheries.html)

Research on the FWE and food web structure helps to identify species that affect FWE in ecosystems. For example, plankton-feeding pelagic fish as intermediate trophic level in upwelling ecosystems increase FWE (Cury et al. 2000).

By integration of data on catches, trophic levels and carbon and energy flows in food webs, scientists can identify problems like an unbalance status of ecosystems. For example, the overexploitation of economically valuable species has led to a huge increase in jellyfish in the Black Sea (Pauly et al. 1998). Also, by fishing down larger and commercially valuable species in marine food webs has created impoverished and less valuable ecosystems (Pauly et al. 1998).
2.1.4.1. In aquaculture

While the ecosystems in fisheries are natural, the ecosystems in aquaculture are mainly artificial because nutrients and stocks are added to the system (Jones et al. 2000). In general Aquaculture can be classified in three types: extensive, semi intensive and intensive, depending on the level on nutrient input (Landau 1992, FAO 1999).

In the intensive system, one single species is used and carbon supply only comes from artificial feed (Tacon 1995, Boonyaratpalin 1997). The feed conversion ratio (FCR) is to calculate the efficiency of converting feed mass into increased body mass:

$$ FCR = \frac{Feed}{Total \ biomass \ of \ harvested} $$

Generally, less than 1/3 of the nutrients added through feed result in harvestable fish in intensive fish farming. For intensive shrimp pond farming it is even less, ranging between 6 and 21%. (Troell et al. 1999). This single-species model thus increases the waste disposal to the environment.

In contrast, in extensive and semi-intensive cultured ponds where artificial feed is partly or none used for growing of cultured species, feed is also based on natural resources (Landau 1992, Tacon 1995, FAO 1999). There is a strong linear relationship between natural food availability (beginning with phytophankton) and fish yields. Using fish species that feed low in the food chain can obtain up to 9 ton/ha without any supplementary feed. Thus, it is concluded that the approaches to manipulating natural food can increase the productivity and efficiency of aquaculture production systems (Azim & Little 2006).

In the same way with extensive and semi-intensive aquaculture systems, a new approach has been introduced to aquaculture as “ecosystem culture” in order to promote sustainable development, equity, and resilience of interlinked social and ecological systems (Soto et al. 2008, Munang et al. 2009). To enhance the cycling capacity of nutrients to reduce waste based on nature of the food web is the most important goal in this approach (Soto et al. 2008).

There are several ways to develop aquaculture ecosystems that minimize environmental impact and improve the production of the cultured species. For example, a better selection of suspension-feeding organisms like mollusks so that particles are removed more efficiently
(Li et al. 2009). Also, the introduction of alien species to decrease in the mean trophic level of the ecosystem has shown to increase the total yield, throughput and efficiency (Jiang & Gibbs 2005). The integration of filter-feeding fish and enhancement of primary productivity of phytoplankton to obtain higher fish productivity has also reduced the food supply in fish ponds (Honglu 1993). Lastly, bacteria have been supplied to the cultured system to improve water quality, nutrient cycling, growth factors and efficiency of the food chain (Moriarty 1997, Neori 2011)

These examples show that a better understanding of ecosystem functioning will help aquaculturists to better manage farming. Aquaculture based on an ecosystem approach with a good understanding of food web efficiency benefits sustainable development of aquaculture and increases economical benefits.

1.3. FOOD WEB MODELING

1.3.1. Modeling in general

Scientific modeling is the process of generating abstract, conceptual, graphical or mathematical models from reality. A model contains a set of assumptions which are often formulated in a mathematical way, called model equations (Freudenthal 1961, Smith & Smith 2001).

In ecology, models are defined as mathematical representations of ecosystems. Typically they simplify complex food webs to their major components or trophic levels, and quantify these as either numbers of organisms, biomass, concentration of chemical elements and energy flows. The first ecological model was developed by Raymond Lindeman in 1942 and was based on the energy balance rule to study the trophic dynamic structure of Lake Mendota in Wisconsin. In this study, the trophic dynamic concept was based on a hypothesis that plants and animals can be arranged into at least three feeding groups or trophic levels: producers, herbivores and carnivores. The energy content of one trophic level is passed on to the next one and the total energy in the system is in equilibrium (Smith & Smith 2001).

Another way of modeling in ecological network is based on the rule of mass (material) balance using measurements of chemical substances to infer the true state of nature (Chiu & Gould 2010). Furthermore, mass-balance modeling is also able to quantify the food web structure and trophic interactions of the major functional groups (Tadesse et al. 2011). The equation for mass balance can be described as an equation below:

\[ \text{Input} = \text{Output} + \text{Change in storage} \]
In this equation input is considered as total carbon inflows, output is total carbon outflows such as respiration, excretion and change in storage is the amount of carbon remained in the biomass of organisms.

The question is whether the constructed model can reflect the real-life situation, which can only be examined through validation, the last but very important stage of modeling. To validate a model, the investigators must collect field data and determine how well the model agrees with the data collected (Jefferies 1988). However, because of one or more reasons many ecological models have remained invalidated (Smith & Smith 2001).

1.3.2. **Modeling of ecosystems**

Since the first model developed in 1942 by Raymond Lindeman, there have been a lot of models constructed for aquatic ecosystems. In general, the models concentrate to investigate two types of aquatic ecosystems: fresh-water (lake and river) and marine (sea and ocean).

For the lake ecosystem, a large number and a wide variety of models have been developed and published during the past four decades with products like CAEDYM, CE-QUAL-W2, Delft 3D-ECO, LakeMab, LakeWeb, MyLake, PCLake, PROTECH and SALMO. The models for lake systems are categorized into static models, complex dynamic models, structurally dynamic models, minimal dynamic models and various individual-based models (Mooij et al. 2010).

River models have been developed to assess ecosystem health, forecast algal blooms and eutrophication, or investigate food web structure (Donner et al. 2002, Kennard et al. 2006, Delong 2010, Jia et al. 2010, Zhang et al. 2010). Furthermore, models have also been built to assess contaminant flows in freshwater ecosystems (De Laender et al. 2010b).

Research on modeling in marine ecosystems has also been often implemented. At least 20 approaches exist, e.g., whole ecosystem models, biogeochemical ecosystem models, dynamic ecosystem models and dynamic multispecies models (Plagányi 2007). Modeling has been applied to estimate habitat and immigration of marine organisms under effects of physical, chemical and climatic conditions, i.e. to estimate the change of ecological communities by physical disturbance like wave force, light, water velocity (Denny 1995, Salacinska et al. 2010), surface salinity, mixed layer depth and chlorophyll a (Bellier et al. 2010) or by climate change (Regular et al. 2010, Lenoir et al. 2011).
Other models in marine areas concentrate inferring the biological relations between compartments in ecosystems. Mass balance models have been applied widely to investigate ecosystem structure, interactions between trophic groups, the effects of predation in the ecosystem and the variation of biomass with nutrients concentration (Walters et al. 1997, Savenkoff et al. 2009, Waska & Kim 2011). Mass balance models are also used to characterize the relation between prey and predator species while accounting for toxic effects of chemicals (Libralato et al. 2006, De Laender at al. 2008, Kooi et al. 2008, Rennie et al. 2010). In addition, modeling has been done in the context of fisheries research. There are a number of models which have been developed to assist the ecosystem approaching in the fisheries management (Plagányi 2007). The models in fisheries research concentrate on feeding relationships, effects on non-target species and the effects of fishing and predation on the fish populations in general.

In fisheries research, an internationally recognized simulation package is ECOPATH. ECOPATH models have been developed based on the mass balance principle for many different ecosystems over the world, ranging from small estuaries to oceans. Authors and locations of model applications are listed on the ECOPATH website, http://www.Ecopath.org. Since the first publications of ECOPATH in 1984 (Polovina 1984), two other additional packages have been developed and integrated with: ECOSIM (Walters et al. 1997) and ECOSPACE (Walters et al. 1999). An advantage of ECOPATH models is that all trophic levels can be taken into account, from primary producers to top predators. However, a limitation of ECOPATH is that many parameters are uncertain which causes difficulties in decision making although this problem is being solved gradually in more recent versions (Plagányi 2007).

Finally, it is necessary to indicate that modeling has been applied in aquaculture systems to investigate the effects of water temperature, photoperiod, dissolved oxygen, unionized ammonia and food availability on the growth of fish (Yi 1999, Ferreira et al. 2007), the impact of nutrients (nitrogen and phosphorus) on the cultured species (Lefebvre et al. 2001), to determine the fertilization rate to produce natural food in aquaculture ponds (Knud-Hansen 2003) or to predict the waste come from the culture activities (Lupatsch & Kissil 1998, Paez-Osuna 1999). However, the number of study to develop models for whole aquaculture food webs and estimate the food web efficiency is still limited. There are several models reported by Lin et al. (1999), Jiang & Gibbs (2005) or Ren et al. (2010), but these models are mainly developed for opened ecosystems with nutrients from natural resources (lagoon or shellfish culture areas). This study aims to develop models and estimate FWE for closed-artificial ecosystems (mesocosms) to investigate deeply material flows in aquaculture ecosystems.
2. MATERIALS AND METHODOLOGY

2.1. THE USED MESOCOSM DATA

The used mesocosm datasets came from a published experiment carried out in Hapovangen, Norway that used mesocosms (artificial ecosystems) of 4 m³ (Sundt-HansenVadstein et al. 2004, 2006). In the experiment, there were two experimental factors: nutrient supply rate (2 levels of N, P, Si) and copepod density (3 levels). These 6 treatments are indicated here in Table 4:

<table>
<thead>
<tr>
<th>Nutrient concentration</th>
<th>COP density</th>
<th>Normal</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C+</td>
<td>C+/N</td>
<td>C+/N+</td>
</tr>
<tr>
<td>Abundant (C+)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regular (C)</td>
<td></td>
<td>C/N</td>
<td>C/N+</td>
</tr>
<tr>
<td>Low (C-)</td>
<td></td>
<td>C-/N</td>
<td>C-/N+</td>
</tr>
</tbody>
</table>

The collected data included standing stocks, primary and bacterial production and these are listed in Table 5. For phytoplankton, stocks were given as ‘µg Chl a / l’. These were converted to units of carbon (‘µg C/l’) by using appropriate conversion factors (Table 5). For micro and mezo-zoo plankton, stocks were given as counts (numbers/l). These were converted to units of carbon (µg C/l) by using appropriate conversion factors (Table 5).

<table>
<thead>
<tr>
<th>No.</th>
<th>Parameters</th>
<th>Codes</th>
<th>Original unit</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Standing stock of micro-phytoplankton</td>
<td>CHLA&lt;200_C</td>
<td>µg Chl a / l</td>
<td>Converted from chlorophyll a using factor of 50 for high nutrient concentration and 30 for normal concentration (Riemann et al. 1989)</td>
</tr>
<tr>
<td>2</td>
<td>Standing stock of nano-phytoplankton</td>
<td>CHLA&lt;20_C</td>
<td>µg Chl a / l</td>
<td></td>
</tr>
<tr>
<td>No</td>
<td>Standing stock of</td>
<td>Symbol</td>
<td>Unit</td>
<td></td>
</tr>
<tr>
<td>----</td>
<td>------------------</td>
<td>--------</td>
<td>------</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>pico-phytoplankton (0.8µm &lt; size &lt; 2µm)</td>
<td>CHLA&lt;2_C</td>
<td>µg Chl a/l</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>heterotrophic bacteria</td>
<td>Hbact_C</td>
<td>µg C/l</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>heterotrophic nano-flagellates</td>
<td>HNF_C</td>
<td>µg C/l</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>ciliates</td>
<td>CILIAT_C</td>
<td>numbers/l</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>appendicularia</td>
<td>APP_C</td>
<td>numbers/l</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>copepod</td>
<td>INITIALCOPC</td>
<td>numbers/l</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>total organic carbon</td>
<td>TOC</td>
<td>µg C/l</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>dissolved organic carbon</td>
<td>DOC</td>
<td>µg C/l</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>particle organic carbon &lt; 200µm</td>
<td>POC&lt;200µm</td>
<td>µg C/l</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>micro-phytoplankton</td>
<td>largeGPP</td>
<td>µg C/l/d</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>nano-phytoplankton</td>
<td>mediumGPP</td>
<td>µg C/l/d</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>pico-phytoplankton</td>
<td>smallGPP</td>
<td>µg C/l/d</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>detritus</td>
<td>SS_DET</td>
<td>µg C/l/d</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>Bacteria</td>
<td>BACprod</td>
<td>µg C/l/d</td>
<td></td>
</tr>
</tbody>
</table>

### 2.2. LINEAR INVERSE MODELLING

#### 2.2.1. What is Linear Inverse Modelling?

The term “linear” refers to the food web model is described as a linear function of the flows (here was flows of carbon) and “inverse” means that these flows are derived from the observed data. The LIM incorporates the mass balance(s) of each compartment and a set of quantitative data. The data contain the experimental measurements as listed in Table 5. These are high-quality data because they are measured in the specific food web that is used.
in experiment. Low-quality data are also included and these are constraints from literatures that apply to food webs in general (Table 6).

Mathematically, a LIM consists of three sets of linear equations (Van Oevelen et al. 2009b): equalities that have to be met as closely as possible (1), equalities that have to be met exactly (2) and inequalities (3).

\[
\begin{align*}
A.x & \sim b \\
E.x & = f \\
G.x & \geq h
\end{align*}
\]

The vector \(x\) contains the unknown flows (that is, \(x_1, \ldots, x_n\)). Often the problem originally only contains the latter two types of equations (2-3), and the approximate equalities (equation 1) are added to single out one solution. Each row in the equality equation (2) imposes a “hard” constraint which is linear functions of the flows, contains the mass balance over the different compartments and the measured values. Numerical data enter \(f\) which are the rates of change of each compartment or the measured data by sampling in the food webs (Table 5).

For the inequalities equations (3), less strict data constraints are used. This kind of equations extracts the upper and/or lower bonds on the flows. The inequalities appeare to accept only lower bounds, but upper bound constraints can be implemented after converting them to lower bound constraints through multiplication of both sides of equation with -1. The absolute values of bounds are in \(h\). The inequality coefficients, quantifying how much a flow contributed to the inequality, are in \(G\). A default set of inequalities is that \(x \geq 0\), which is for sure that flows have directions that are the same with the food web topology (for example, predators can eat prey, but not the other way around).
2.2.2. **Conceptual food web: food web topology**

Defining the number of compartments and their connections is termed the topology of the food web (Pimm et al. 1991) which needs to be quantified first in linear inverse models (LIM). The food web topology was constructed with 10 model compartments: Detritus DET,
primary producers (pico, nano, micro-phytoplankton marked as PHY2, PHY20, PHY200), merozooplankon (copepods and appendicularia marked as COP and APP), microzooplankton (CIL), Heterotrophic nanoflagellates (HNA) and heterotrophic bacteria (BAC) an three external compartments SED (sedimentation), dissolved organic carbon (DOC), and growth of copepods (GRO). The relation between compartments by flows or the food web topology is shown in the Figure 6. The flow between two compartments may be one direction $A \rightarrow B$ or both directions $A \leftrightarrow B$. A flow from $A$ to $B$ means that carbon is flowing from $A$ to $B$.

Figure 6: Food web topology

In detail the food web topology can be described as follows:

The primary producers (PHY2, PHY20 and PHY200) play a role to generate organic carbon from inorganic carbon for the food web, and are the starting point of the herbivore food chain. BAC takes up organic carbon directly (as DOC) and form the base of the microbial loop.
The top predator in the food web (COP) is known as a particle feeder with the optimum ratio of predator: prey of 18:1 (Hansen et al. 1994). It can graze particles from nano size such as PHY20, PHY200, APP (Sommer et al. 2003), CIL, HNA, DET, and BAC. Bacterial grazing occurs due to association of BAC with DET and other particles (Ustach 1982, Hall & Meyer 1998). CIL graze on both pico and nano particles (BAC, HNA, PHY2 and PHY20) (Bernad & Rassoulzadegan 1990). APP (‘Oikopleura dioica’) is larger than CIL and feeds on particles with pico size like bacteria (Nakamura et al. 1997) due to their ability to trap the food. APP can also ingest particles with sizes up to 30 µm (Alldredge 1981) thus their diets include BAC, all kinds of phytoplankton and HNA. The HNA have a predator: prey ratio of 3:1 (Hansen et al. 1994) and can feed on pico size organisms (BAC and PHY2) as well as ingest a part of PHY20.

The DIC and DOC are the products of respiration and excretion, respectively, and these are done by all organisms. DET is produced as faeces by many groups and is lost through sedimentation.

2.2.3. Collecting the experimental data and the constraints from literature

The data used for the linear inverse model (LIM) included two types; standing stock and rates of change as taken from the dataset (Table 5) and constraints taken from literature (Table 6). The equalities and inequalities formed by integration of the experimental dataset and the constraints (see appendix).

<table>
<thead>
<tr>
<th>Compartments</th>
<th>Characteristic</th>
<th>Unit</th>
<th>Constraints</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Phytoplankton</td>
<td>Excretion rate</td>
<td>Fraction of net primary production</td>
<td>0.05 – 0.6</td>
<td>(Vezina &amp; Platt 1988)</td>
</tr>
<tr>
<td>All Phytoplankton</td>
<td>Respiration rate</td>
<td>Fraction of Gross primary production</td>
<td>0.05 – 0.3</td>
<td>(Vezina &amp; Platt 1988)</td>
</tr>
<tr>
<td>Total Phytoplankton</td>
<td>Sedimentation rate</td>
<td>Fraction of standing stock</td>
<td>0.07</td>
<td>(Tamelander et al. 2004)</td>
</tr>
<tr>
<td>Ciliates</td>
<td>Max ingestion</td>
<td>% body weight/d</td>
<td>0.11</td>
<td>(Bernard &amp; F 1990)</td>
</tr>
<tr>
<td>Heterotrophic</td>
<td>Max ingestion</td>
<td>% body weight/d</td>
<td>0.47</td>
<td>(Eccleston-Parry &amp; Leadbeater 1994)</td>
</tr>
<tr>
<td>nanoflagellates</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ciliates</td>
<td>Biomass-specific</td>
<td>d⁻¹</td>
<td>&gt;0.08</td>
<td>(Vezina &amp; Platt 1988)</td>
</tr>
<tr>
<td></td>
<td>respiration rate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fraction of respiration rate</td>
<td>(Reference)</td>
<td></td>
</tr>
<tr>
<td>----------</td>
<td>----------------------------------------</td>
<td>-------------------------------</td>
<td>-------------</td>
<td></td>
</tr>
<tr>
<td>Ciliates</td>
<td>Excretion</td>
<td>0.33 - 1</td>
<td>(Vezina &amp; Platt 1988)</td>
<td></td>
</tr>
<tr>
<td>Ciliates</td>
<td>Max uptake rate</td>
<td>Proportion of body weight/d</td>
<td>7</td>
<td>(Vezina &amp; Platt 1988)</td>
</tr>
<tr>
<td>Appendicularia</td>
<td>Max uptake rate</td>
<td>Proportion of body weight/d</td>
<td>2.15</td>
<td>(López et al. 2003)</td>
</tr>
<tr>
<td>Appendicularia</td>
<td>Assimilation efficiency</td>
<td>0.39 - 0.84</td>
<td>(López et al. 2003)</td>
<td></td>
</tr>
<tr>
<td>Appendicularia</td>
<td>Excretion rate</td>
<td>Fraction of respiration rate</td>
<td>0.3 - 1</td>
<td>(López et al. 2003)</td>
</tr>
<tr>
<td>Appendicularia</td>
<td>Respiration rate</td>
<td>Proportion of body weight/d</td>
<td>0.4 - 2</td>
<td>(López et al. 2003)</td>
</tr>
<tr>
<td>Copepods</td>
<td>Assimilation efficiency</td>
<td>0.5 - 0.9</td>
<td>(Besiktepe &amp; Dam 2002)</td>
<td></td>
</tr>
<tr>
<td>Copepods</td>
<td>Respiration rate</td>
<td>$d^{-1}$</td>
<td>0.015 – 0.038</td>
<td>(Drits et al. 1993)</td>
</tr>
<tr>
<td>Copepods</td>
<td>Gross production efficiency</td>
<td>&lt; 0.4</td>
<td>(Vezina &amp; Platt 1988)</td>
<td></td>
</tr>
<tr>
<td>Copepods</td>
<td>Excretion rate</td>
<td>Fraction of respiration rate</td>
<td>0.33 - 1</td>
<td>(Vezina &amp; Platt 1988)</td>
</tr>
<tr>
<td>Copepods</td>
<td>Growth rate</td>
<td>% body weight/d</td>
<td>&lt;1.25</td>
<td>(Durbin &amp; Durbin 1981)</td>
</tr>
<tr>
<td>Bacteria</td>
<td>Gross production efficiency</td>
<td>0.1 - 0.5</td>
<td>(del Giorgio &amp; Cole 1998)</td>
<td></td>
</tr>
<tr>
<td>Bacteria</td>
<td>Sedimentation rate</td>
<td>Fraction of bacterial production rate</td>
<td>&lt; 0.02</td>
<td>(Donali et al. 1999)</td>
</tr>
<tr>
<td>Bacteria</td>
<td>Viral mortality of bacteria</td>
<td>Fraction of production rate</td>
<td>0.1 – 0.4</td>
<td>(Fuhrman 2000)</td>
</tr>
<tr>
<td>Detritus</td>
<td>Dissolution</td>
<td>Dissolution as fraction of standing stock</td>
<td>&lt;0.02</td>
<td>(Bever et al. 2010)</td>
</tr>
<tr>
<td>Detritus</td>
<td>Sedimentation</td>
<td>As fraction of standing stock</td>
<td>&lt;0.38</td>
<td>(Bever et al. 2010)</td>
</tr>
</tbody>
</table>

### 2.2.4. Solving the model

For every day of the experiment and for every treatment (i.e. for every cell in Table 5), the LIM was solved. In this way, carbon flows were obtained for every combination of treatment and day.
The model were solved in the R environment for statistical computing, version 2.11.1 published 31/5/2010 (R Development Core Team 2010), with specific packages for LIM (Soetaert & Van Oevelen 2009) and diagram (Soetaert 2008).

Because the data that was used to solve the LIM include low quality - and thus uncertain - literature data, the food web flows were uncertain as well. These were because they cannot be estimated precisely and were therefore quantifiable within ranges only. The ranges were derived using the function Xranges available in the R package ‘limSolve’ (Soetaert et al. 2009) which found the possible ranges (min, max) for each unknown flow. The function ‘isei’ in the same package using the least squares method (least squares with equality and inequality constraints) which minimized some set of linear equations (A.x \geq b) to find the most probable value within that range. From the complete range of values also a user-defined number of random samples can be drawn using a Markov Chain Monte Carlo procedure by the R function ‘xsample’ (Van den Meersche et al. 2009a). The number of samples was set at a value of 3000 with a step of (max(ranges)-min(ranges))/4 which was large enough to cover the solution ranges given by the Xranges function.

2.3. CALCULATING FOOD WEB EFFICIENCY

Because only inorganic nutrients were supplied to the system, only NPP was considered as basal input for food web (Berglund et al. 2007), the FWE was thus calculated by the formula:

\[
FWE \text{ of COP} = \frac{\text{COP growth}}{\text{NPP}}
\]

\[
FWE \text{ of CIL} = \frac{\sum \text{flows to CIL} - \text{respiration} - \text{excretion}}{\text{NPP}}
\]

In which ‘COP growth’ was calculated as the flow from COP to GRO. NPP was total production of primary production.
3. RESULTS

3.1. CARBON FLOWS

Figures 7 and 8 show the structure of the six food webs for the six treatments (mesocombs) of nutrient concentration and predator (copepod) density at the start (Figure 7) and at the end of the experiment (Figure 8). In general, there were 51 carbon flows that linked 13 compartments in each food web. The arrows represent the direction of the carbon transfer and the thickness represents its magnitude (µg C/l/day).

Figure 7: Carbon flows at the starting stage of the experiment (day 2)
The longest pathway of carbon in the food webs included 4 compartments; Phytoplankton < 2 µm (PHY2) $\rightarrow$ heterotrophic nanoflagellates (HNA) $\rightarrow$ ciliates (CIL) $\rightarrow$ copepods (COP) (top predator) which represents the herbivore food chain and bacteria (BAC) $\rightarrow$ HNA $\rightarrow$ CIL $\rightarrow$ COP which represents the microbial loop. However, note that carbon was probably transferred directly from primary producers or BAC to the top predator without any intermediate step.

The magnitude of the carbon flows varied within and between the food webs. It can be seen that carbon flows in all 6 food webs increased over time (e.g. 470.50 µg C/l/day as maximum...
on the last day at treatment C+/N vs. 228.71 µg C/l/day as maximum on day 2 at the same treatment). At the beginning of experiment, the magnitude of the carbon flows in the high nutrient treatments was higher than in the low nutrient treatments. However, this pattern was not found any more at the end of the experiment.

At the start of the experiment, the carbon flow from DOC to BAC ranged from 145.90 to 228.72 µg C/l/day. This was the highest carbon flow in the following treatments: C+/N, C/N, C-/N and C-/N+. The magnitude of flows from BAC to bacteria consumers such as HNA, CIL and COP in these 4 treatments was also higher than that in the other treatments. By the end of experiment, the magnitude of the flows from DOC to BAC (223.02 µg C/l/day as maximum) decreased over time in these treatments while the flows from DIC to PHYs (up to 470.49 µg C/l/day in C-/N+) increased over time (except in the C-/N treatment). It can thus be said that a temporal shift occurred from a microbial loop dominated to a herbivore loop dominated food web structure in these treatments.

3.2. PRIMARY PRODUCTION

Production of 3 size classes of phytoplankton is presented in Figure 9: Pico-phytoplankton (0.8 - 2µm), nano-phytoplankton (2 - 20 µm) and micro-phytoplankton (20 - 200 µm) marked as PHY2, PHY20 PHY200, respectively. In general, the production of phytoplankton in the food webs that had high nutrient concentrations was slightly higher than in the food webs with low nutrients. For example, PHY20 mostly produced at rates > 100 µg C/l/day in the high nutrient treatments (except day 8 of C+/N+) while this was less than 100 µg C/l/day on many occasions in the normal nutrient treatments, e.g. on days 2, 3, 6 of C+/N, days 2, 5 of C/N and days 2, 8 of C-/N.
In general, the primary production increased overtime, for example the PHY20 production at the start of experiment, the values obtained on average were only 94.27 µg C/l/d for day 2 and 103.15 µg C/l/d for day 3, while toward the end of experiment they were up to 248.11 µg C/l/d and 290.33 µg C/l/d for day 7 and day 8, respectively. In the treatments of regular and low COP density, the production of phytoplankton seemed to increase continuously for a week and then slightly fell back towards the end of the experiment. In the C+/N+ treatment,
the production of phytoplankton only increased and reached a peak of 600 µg C/l/d on day 6 and then decreased quickly on days 7 & 8.

PHY20 dominated primary production in all the treatments and during the whole course of the experiment. In contrast, the contribution of PHY200 to the total primary production was quite limited. In 29 out of the 41 treatment-day combinations for which a model could be built, production of PHY200 was less than 50 µg C/l/d, especially on days 8 (C+/N+), 9 (C+/N) where PHY200 production was 2.31 and 3.50 µg C/l/d respectively. However, by the end of the experiment in the food webs with regular and low COP densities and with high nutrients added, the contribution of PHY200 to total primary production was relatively high compared to the other phytoplankton size classes. It reached to 344.56 µg C/l/day in day 8 of the C-/N+.

In some days like day 5 for C/N, days 3 & 6 for C+/N, day 8 for C+/N+ the primary production was very low. The values obtained for all size classes were comparable and were less than 50 µg C/l/day.
3.3. CILIATE AND COPEPOD PRODUCTION

The daily created production of CIL and COP which was calculated in the unit of µg C/l/d is presented in Figure 10.

**Figure 10: Production of ciliate and copepod during the time course of the experiment**

The production of CIL and COP normally ranged between no production at all (zero) to about 40 µg C/l/day as maximum. The COP’s production was mostly higher than the CIL’s.
The temporal variability of the production differed between COP and CIL. The production of COP stayed constant with the average value of about 30 µg C/l/d. The production of CIL varied through time, with the maximal value of 32.82 µg C/l/d (day 7 of C/N+) and the minimal value of -11.37 µg C/l/d (day 6 of C+/N+).

3.4. DIETS FOR CILIATES AND COPEPODS

The proportion of food items which were consumed by CIL and COP is showed in Figures 11 and 12, respectively.

Figure 11: Diet of ciliates during the time course of the experiment
The fragments consumed by CIL must be < 20 µm in size (Bernard & Rassoulzadegan 1990). Thus, the composition in their diets included BAC, PHY2, PHY20, HNA and DET. From figure 11, it is not easy to infer what diet item contributed most in the diet of COP. The contribution of BAC to the diet of CIL was sometimes over 80% such as day 8 (C+/N+), day 5 (C/N). Switching from BAC to PHY2 or PHY20 as dominant food items was common in all treatments, but the contribution of these two items in the diet was normally less than 80%. The DET contribution to the diet of CIL never exceeded 10% in all the treatments while grazing on HNA by CIL was more important, especially for day 3 of the C/N treatment, 28.18% of the CIL diet was HNA.

Figure 12: Diet of copepods during the time course of the experiment
The food spectrum for COP in the experiment included 7 items: APP, BAC, CIL, DET, HNA, PHY20 and PHY200. Due to the wide food spectrum, the variation of the diet composition of COP was much more than it was for CIL. In some days like days 2, 3 (C+/N), day 8 (C+/N+) and days 2 of regular COP density treatments grazing on BAC dominated, more than 50% in the COP diet. It is necessary to note that in these days the primary production was very low (Figure 9). On the other hand, in days such as day 5 (C+/N), day 7 (C/N+) and day 8 (C-/N+), BAC contributed less than 2%. In these days, PHY20 and PHY200 were important food items for COP. Especially in the treatments of low copepod density, the proportion of PHY200 was mostly higher than other items and up to 97.22% of the diet on day 8 of the C-/N+ treatment, indicating that PHY200 was the most favorable food for COP because of low production of PHY200 (see Figure 9). Similar to DET in the diet of CIL, the contribution of DET to the diet of COP was below 2%. The proportion of APP was almost zero throughout the experiment.

3.5. FOOD WEB EFFICIENCY BASED ON CILIATE PRODUCTION

Figure 13 shows the food web efficiency (FWE) based on CIL production. FWE values varied between -0.1 and 0.35. In some days like day 3 for C/N, C-/N+ and C+/N, the FWE was closed to 0.2. In contrast, on day 5 (C/N), day 6 (C+/N+, C/N+), day 8 (C+/N+, C-/N) and day 9 (C-/N+) the FWE values were smaller than zero, thus indicating that on the ingestion by the CIL population was smaller than its metabolic costs on these days.

Except in the C+N+ treatment, FWE decreased over time. From day 2 to 4, the FWE was around 0.1 to and after day 5 the FWE approached zero. The minimal value was observed in days 5, 6 or 8 in the treatments.

No consistent differences in the FWE were found between the low and high nutrient treatments (Figure 13). In the case of abundant COP density (C+), the FWE in the high nutrient treatment was higher than at the low nutrient concentration on day 5, but the opposite was found on day 6. The same result was found for the regular and low COP densities.

In the normal nutrient concentration treatments (N), the FWE on day 5 was the same for normal and high COP densities but clearly lower than in the low COP density. The opposite was found for day 7. Thus it was also not possible to make a general conclusion about the changes in FWE as a function of COP densities.
Figure 13: Food web efficiency of ciliate during the time course of the experiment
3.6. FOOD WEB EFFICIENCY BASED ON COPEPOD PRODUCTION

The FWE based on COP production is illustrated in Figure 14:

![Food web efficiency of copepod during the time course of the experiment](image)

**Figure 14: Food web efficiency of copepod during the time course of the experiment**

The FWE for COP was mostly smaller than 0.2 except on some days like day 2 (C-/N, C+/N, C-/N), day 5 (C/N), days 3 & 6 (C+/N) and day 8 (C+/N+). The FWE values for abundant COP density treatments in some days reached values up to 0.6 on average and 1 as maximum. Although these values seem unrealistically high, we will discuss later on why these are possible (see discussion section). However, if calculated for the whole experimental period (10 days), the FWE was only 0.15 and 0.1 for normal and high nutrient
regimes, respectively. As found for the FWE based on CIL production, the FWE decreased over time in all treatments except in the C+N+ treatment.

The FWE that was found for the normal nutrient treatments was 1.5 times higher than in the high nutrient treatments. In the case of abundant COP densities, the FWEs on days 2 and 6 at the normal nutrient concentrations were 2 and 10 times higher than that at high nutrient concentrations. In addition, FWE values on days 2, 5 (regular copepod treatments) and day 2 (low copepod treatments) in low nutrient concentration treatments were also higher than that in high nutrient concentration treatments. No difference in the FWE between COP density treatments was apparent.

3.7. INTERACTIONS BETWEEN CILIATES AND COPEPODS IN THE FOOD WEBS

Figure 15 displays the trophic interaction between CIL and COP. The top predator (COP) probably controlled the development of their prey (CIL) or vice versa.

![Figure 15: Correlation of copepod production and ciliate production](image)

On days 2, 3 and 5, CIL production and COP production was negatively correlated. This means that when the production of COP increased, the production of CIL decreased. This effect illustrated top-down control in the food webs at the beginning of the experiment. This is also shown in Figure 16, where COP production is shown to be positively correlated to the carbon flow from CIL to COP, and a negative correlation between CIL production and this carbon flow.
However, towards the end of the experiment, the CIL production was positively correlated with the COP production (Figure 15), indicating that CIL production seemed to drive food web dynamics. This was confirmed by one of two feeding activity scenarios (Figure 16).

- The CIL production decrease led to reductions of the flow from CIL to COP (days 6, 7 & 8).
- The increase in CIL production promoted the grazing rate of COP on CIL (days 4 & 9).

Figure 16: Correlation of the ciliate (solid) and copepod (filled) production and their carbon flow
4. **DISCUSSION**

4.1. **PRIMARY PRODUCTION**

Primary production is driven by nutrients, light and temperate (Delgiorgio & Peters 1994, Field et al. 1998, Hill et al. 2010). The primary production was higher in the high nutrient (N+) than the normal nutrient (N) mesocosms and increased over time in all treatments except C+/N+. Besides nutrients, light also has strong effects on both gross primary production and respiration rates of plants (Lasslop et al. 2010). The overdevelopment of algae creates a barrier (self-shading effect) to prevent the light penetrate to the deeper layer of water column (Vincent & Hill 1996, Hameed 2007, Briassoulis et al. 2010). It is very clear that in the C+/N+ on the day 6 the primary production reached a peak of 600 µg C/l/d (the maximum value obtained) indicating that a self-shading effect probably had happened which resulted in the reduction of gross primary production and increase of respiration cost of phytoplankton after day 6. This caused high FWE values for CIL and COP in this food web which will be discussed later.

4.2. **CILIATE AND COPEPOD PRODUCTION**

While the COP production was stable, the CIL production varied quickly through time. This reflects the fact that the life cycle of CIL (generation time of CIL varied from 6.38 hours (Finlay 1977) to 88 hours (Perez et al. 1997) is much shorter than that of COP (varies from 18 to 50 days (Reeve & Walter 1972). Indeed, the short life cycle of CIL allows them to change population biomass in a matter of hours to days while it takes weeks for COP population size to change.

The production of CIL in some days was smaller than zero which displays a situation that the carbon proportion lost by respiration, excretion or consumption by their predator (COP) was more than the new creation (flows from preys to CIL).

4.3. **DIETS OF CILIATES AND COPEPODS**

The high proportion of bacteria (BAC) in CIL’s diet shows that this item is quite important in the diet of CIL. Also the contribution of HNA and PHY20 in the diet was quite high. This can be confirmed by Simek et al. (1995) who found that the contribution of particles with size > 2 µm may exceed 57%.
In the case of COP, one thing need to take into account is that this group is filter-feeding. Thus, the size, shape, density of particles in the water and the average size of the COP population will determine the feeding rate. The phytoplankton with class size > 20 µm (PHY200) seemed to be more favorable food for COP than the size of 2 – 20 µm (PHY20). This result suites with the finding by Hansen, Bjornsen et al (1994) that the optimal prey for COP is 18:1.

CIL and COP shared some groups of prey such as PHY20, DET, BAC and HNA. As a top predator, the diet of COP was more diverse with 7 types of prey. COP not only used the same preys of CIL but also grazed on CIL and APP which are known as their competitors.

4.4. FOOD WEB EFFICIENCY BASED ON CILIATE PRODUCTION

Food web efficiencies are mostly between 0.1 to 0.2 in the natural ecosystems (Levinton 2008). In the case of CIL, according to Elaine & Peter (2001) depending on the nutrient concentrations in the food web, the FWE of CIL is ranged between 0 and 0.33. Thus most FWE values in treatments fell within the range expected from literature.

A negative FWE values based on CIL production were found on day 5 (C/N), day 6 (C/N+, C+/N+), day 8 (C-/N, C+/N+) and day 9 (C-/N+). This can be explained by a reduction in standing stock of CIL and therefore a negative production and thus a negative FWE. Population decline can be explained by ingestion rates (carbon flows from preys to CIL) that are smaller than the respiration rate (CIL → DIC) and the excretion rate (CIL → DOC). This phenomenon is defined as negative assimilation efficiency and negative population growth rate which have been observed elsewhere, e.g. in Elaine & Peter (2001), Jormalainen et al. (2005) and Deardorff & Stark (2011).

When based on CIL production, FWE was not different between nutrient regimes. This reflects a fact that CIL efficiently responded to the higher primary production in the high nutrient treatment. FWE based on CIL production decreased over time, most notably in the regular and low copepod densities. The most sensible explanation for this observation is that the proportion of PHY200 (size > 20 µm) in the total primary production became dominant (up to 50 % of the total primary production). This size fraction is too large to be grazed by CIL (Bernard & Rassoulzadegan 1990) resulting in up to 50 % of the total primary production that cannot be used by CIL. The increase in primary production did thus not result in a proportional increase in CIL production and therefore in a FWE decrease over time.
4.5. FOOD WEB EFFICIENCY BASED ON COPEPOD PRODUCTION

From the results extracted from all models, 82% (34/41) of FWE values based on COP production in this study varied between 0.03 and 0.2. These agreed well with the FWE based on the production of mesozooplankton as obtained by other authors. For example, FWE (defined as the production of mesozooplankton per summed phytoplankton and bacteria production) was 0.22 in a phytoplankton-based food web and 0.02 in a bacteria-based food web (Berglund et al. 2007). This result also agrees with results reported by authors like Levinton (2008) and (Xu et al. 2011).

The COP’s FWE decreased toward the end of experiment in all food webs except C+/N+, this could be explained by a stable copepod production combined with an increasing primary production over time. We can thus conclude that COP was not able to benefit from the increasing primary production. The explanation for this case is the generation time of COP (period needed to reach 50% fertilized females) of about 18-50 days (Reeve & Walter 1972) which made it impossible for the copepods to respond to an increase in food availability (primary production) in the time frame of the experiment.

FWE values based on COP production estimated by the inverse models were much higher than 0.2 for some days reaching values of 1. These values seem to be impossible but there are a number of sound scientific facts that can explain these estimates. The life cycle of the copepod species used in the mesocosm experiment on which this work was based is much longer than the duration of the experiment. This resulted in a relatively stable copepod production over time which was largely supported by bacterial production (Figure 12) and therefore independent of phytoplankton production. When observing the diets (Figure 12) and primary production (Figure 9), it is clear that the extremely high FWE values corresponded to sudden minima in primary productions combined with intense feeding on BAC or other prey (days 2 & 6 (C+/N), days 7 & 8 (C+/N+), days 2 & 5 (C/N)). This illustrates that the microbial loop in the food web may enhance the FWE (Azam et al. 1983, Kamiyam 2004, Carrillo et al. 2006, Pavés & González 2008, De Laender et al. 2010a).

4.6. INTERACTIONS BETWEEN CILIATES AND COPEPODS IN THE FOOD WEBS

Both bottom-up and top-down effects between ciliates and copepod were reported by author such as Nielsen & Levinsen (2002) and Gaedke & Wickham (2004). Thus switching
between two types of effect causes by factors like seasonal variation, temperature, especially food source availability and concentration.

Link to the study results, it can be seen that at the start of experiment (days 2, 3 and 5), the top-down effect controlled the relation between COP and CIL that was related to the low primary production period. COP feed on other items than primary producers - including ciliates - and therefore controlled the development of CIL.

At the end of experiment (days 6 to 9), the production of primary producers in the environment was high. COP consumed more algae in their diet thus reduced predation pressure on the CIL. By the way, the bottom-up effect dominated in this period.
5. CONCLUSIONS AND RECOMMENDATIONS

5.1. CONCLUSIONS

From the results of study, the following conclusions can be drawn:

1. The metabolic costs (energy for respiration and excretion) may be higher than the amount of energy uptake by animals that caused negative production rates and negative values of food web efficiency.

2. The proportion of bacteria in diets of both ciliates and copepods was high, especially when the primary production decreased. This illustrates that the microbial loop in the food web may enhance the food web efficiency.

3. In the short time course of experiment, the production of copepods was stable and not affected by nutrient addition.

4. An increase in the primary production did not always benefit the consumers which resulted in reduction of the food web efficiency over time. Ciliates reacted to the change of primary production more rapidly than copepods.

5. The food web efficiencies based on ciliate and copepods production were mostly smaller than 0.2 and higher than 0.

6. The food web efficiency in the mesocosms supported by normal rates of nutrient may be higher than that in mesocosms with high rates of nutrient supplied.

7. Both bottom-up and top-down effects controlled the relations of ciliates and copepods in the food web. Which effect dominated depended on the period: start vs. end of the experiment.

5.2. RECOMMENDATIONS

There are also suggestions and implications for aquaculture and further study as follows:

1. In semi-intensive, extensive and eco-culture systems used in aquaculture where natural food is used as the main input for cultured species, the input of nutrients
should be tailored bearing in mind the density of consumers and their generation time.

2. Besides known benefits as improvement of cultured water quality, the inhibition of harmful bacteria, the role of bacteria in ecosystems should be further studied as they can enhance the food web efficiency.

3. The use of carbon flow models may clarify patterns of resource use in cultured systems. Future research should therefore focus on actively modifying the structure of food webs in order to reduce loss of energy, obtain higher production of cultured species and aim to sustainable development of cultured systems.
6. REFERENCES


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


Jiang WM & Gibbs MT (2005) Predicting the carrying capacity of bivalve shellfish culture using a steady, linear food web model. *Aquaculture*, 244, 171-185.


---

52


APPENDIX

Equations used for the food web models, where A → B denotes a food web flow from compartment A to B (µg C/l/day) and SS_X denote the standing stock of compartment X (µg C/l/day).

Phytoplankton

Respiration is between 5 and 30% of the gross primary production

PHY2 → DIC > 0.05 x DIC → PHY2
PHY2 → DIC < 0.3 x DIC → PHY2
PHY20 → DIC > 0.05 x DIC → PHY20
PHY20 → DIC < 0.3 x DIC → PHY20
PHY200 → DIC > 0.05 x DIC → PHY200
PHY200 → DIC < 0.3 x DIC → PHY200

Excretion is between 5 and 60% of the net primary production

PHY2 → DOC > 0.05 x (DIC → PHY2 - PHY2 → DIC)
PHY2 → DOC < 0.5 x (DIC → PHY2 - PHY2 → DIC)
PHY20 → DOC > 0.05 x (DIC → PHY20 - PHY20 → DIC)
PHY20 → DOC < 0.5 x (DIC → PHY20 - PHY20 → DIC)
PHY200 → DOC > 0.05 x (DIC → PHY200 - PHY200 → DIC)
PHY200 → DOC < 0.5 x (DIC → PHY200 - PHY200 → DIC)

Sedimentation is smaller than 7% of standing stocks

PHY2 → SED < 0.07 x SS_PHY2
PHY20 → SED < 0.07 x SS_PHY20
PHY200 → SED < 0.07 x SS_PHY200

Protozoa

Respiration is higher than 8% of standing stock per day

CIL → DIC > 0.08 x SS_CIL
HNA → DIC > 0.08 x SS_HNA

Excretion is between 33 and 100% of respiration
CIL → DOC > 0.33 x CIL → DIC
CIL → DOC < 1 x CIL → DIC
HNA → DOC > 0.33 x HNA → DIC
HNA → DOC < 1 x HNA → DIC

Ingestion is smaller than 700% of standing stock per day
BAC → CIL + HNA → CIL + DET → CIL + PHY2 → CIL + PHY20 → CIL < 7 x SS_CIL
BAC → HNA + DET → HNA + PHY2 → HNA + PHY20 → HNA < 7 x SS_CIL

**Copepod**

Ingestion is between 0.8% and 400% of standing stock per day
DET → COP + BAC → COP + PHY20 → COP + PHY200 → COP + APP → COP + HNA → COP + CIL → COP > 0.008 x SS_COP
DET → COP + BAC → COP + PHY20 → COP + PHY200 → COP + APP → COP + HNA → COP + CIL → COP < 4 x SS_COP

Respiration is between 1.5% and 3.8% of standing stock per day
COP → DIC > 0.015 x SS_COP
COP → DIC < 0.038 x SS_COP

Excretion is between 33% and 100% of respiration
COP → DOC > 0.33 x COP → DIC
COP → DOC < 1 x COP → DIC

Assimilation efficiency is between 50% and 90%
DET → COP + BAC → COP + PHY20 → COP + PHY200 → COP + APP → COP + HNA → COP + CIL → COP > 0.5 x (DET → COP + BAC → COP + PHY20 → COP + PHY200 → COP + APP → COP + HNA → COP + CIL → COP)
DET → COP + BAC → COP + PHY20 → COP + PHY200 → COP + APP → COP + HNA → COP + CIL → COP < 0.9 x (DET → COP + BAC → COP + PHY20 → COP + PHY200 → COP + APP → COP + HNA → COP + CIL → COP)

Gross growth efficiency is lower than 40% of total uptake
COP → GRO < 0.4 DET → COP + BAC → COP + PHY20 → COP + PHY200 → COP + APP → COP + HNA → COP + CIL → COP

Gross growth is lower than 125% of standing stock
COP → GRO < 1.25 x SS_COP
**Bacteria**

Gross growth efficiency is between 10% and 50% of total uptake.

DOC $\rightarrow$ BAC - BAC $\rightarrow$ DIC $> 0.1 \times$ DOC $\rightarrow$ BAC

DOC $\rightarrow$ BAC - BAC $\rightarrow$ DIC $< 0.5 \times$ DOC $\rightarrow$ BAC

Sedimentation is below 2% of bacterial production

BAC $\rightarrow$ SED $< 0.02 \times$ (DOC $\rightarrow$ BAC - BAC $\rightarrow$ DIC)

Viral mortality of bacteria is between 10% and 40% of production rate

BAC $\rightarrow$ DOC $> 0.1 \times$ (DOC $\rightarrow$ BAC - BAC $\rightarrow$ DIC)

BAC $\rightarrow$ DOC $< 0.4 \times$ (DOC $\rightarrow$ BAC - BAC $\rightarrow$ DIC)

**DET**

Dissolution is lower than 2% of standing stock per day

DET $\rightarrow$ DOC $< 0.02 \times$ SS_DET

Sedimentation is lower than 38% of standing stock per day

DET $\rightarrow$ SED $< 0.38 \times$ SS_DET

**Appendicularia**

Ingestion is smaller than 215% of standing stock per day

BAC $\rightarrow$ APP + PHY2 $\rightarrow$ APP + PHY20 $\rightarrow$ APP + PHY200 $\rightarrow$ APP + HNA $\rightarrow$ APP $< 2.15 \times$ SS_APP

Respiration is between 40% and 200% of standing stock per day

APP $\rightarrow$ DIC $> 0.4 \times$ SS_APP

APP $\rightarrow$ DIC $< 2 \times$ SS_APP

Excretion is between 33% and 100% of respiration

APP $\rightarrow$ DOC $> 0.33 \times$ APP $\rightarrow$ DIC

APP $\rightarrow$ DOC $< 1 \times$ APP $\rightarrow$ DIC

Assimilation efficiency is between 39 % and 84% of total uptake

BAC $\rightarrow$ APP + PHY2 $\rightarrow$ APP + PHY20 $\rightarrow$ APP + PHY200 $\rightarrow$ APP + HNA $\rightarrow$ APP - APP $\rightarrow$ DET $< 0.39 \times$ BAC $\rightarrow$ APP + PHY2 $\rightarrow$ APP + PHY20 $\rightarrow$ APP + PHY200 $\rightarrow$ APP + HNA $\rightarrow$ APP

BAC $\rightarrow$ APP + PHY2 $\rightarrow$ APP + PHY20 $\rightarrow$ APP + PHY200 $\rightarrow$ APP + HNA $\rightarrow$ APP - APP $\rightarrow$ DET $> 0.84 \times$ BAC $\rightarrow$ APP + PHY2 $\rightarrow$ APP + PHY20 $\rightarrow$ APP + PHY200 $\rightarrow$ APP + HNA $\rightarrow$ APP