Diploma course of study

"Marine Environmental Science"

Diploma thesis

Effects of prey type and morphology on growth and grazing in two dinoflagellate species.

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1 ABSTRACT

In the present study it is reported that the thecate dinoflagellate *Peridiniella cf. danica* which had been previously thought to be autotrophic is a mixotrophic species. The species needs particular food and cannot live without light as sole energy source. Netherless it showed better growth in light than under dark conditions.

All offered prey species were ingested by both algal predators, but *P. cf. danica* only grew with the prey species *Rhodomonas sp.* while *Gyrodinium spirale* did not grow with it. Maximum ingestion rates of the preferred prey had the same curve shape in mixed and single prey diets. The maximal ingestion rates in mixed prey cultures are lower. *P. cf. danica* is able to feed 2 *Rhodomonas sp.* d^{-1} in mixed diet and 6 *Rhodomonas sp.* d^{-1} in single diet. The species *G. spirale* is able to feed 3 *T. rotula* d^{-1} in mixed diet and 13 *T. rotula* d^{-1} in single diet.

The predators preferred prey species which were approximately of their own size. *P. cf. danica* mainly ingested the small cryptophyte *Rhodomonas sp.* while *G. spirale* did not show a preference for the diatoms *Chaetoceros debilis* and *Thalassiosira rotula* but discriminated the cryptophyceae.

Based on these grazing rates the species have a potentially respectable grazing impact on the prey populations at the Helgoland Roads.

2 INTRODUCTION

Dinoflagellates are ubiquitous marine protozoans (Lessard, 1991). Species without chloroplasts comprise approximately 50% of all known dinoflagellate species (Gaines and Elbrächter, 1987; Lessard, 1991; Schnepf and Elbrächter, 1992). Dinoflagellates have a pattern of distribution in space and time. While heterotrophic dinoflagellates can be found in non-illuminated depths, photosynthectic active dinoflagellates are restricted to illuminated areas. Consequently autotrophic dinoflagellates are often found in tropical regions of the oceans whereas heterotrophics are found more in neritic zones of temperate and polar regions (Gaines and Elbrächter, 1987; Lessard, 1991). In general, the heterotrophic dinoflagellate blooms follow the diatom spring bloom in temperated and arctic waters (Taylor and Pollingher, 1987; Levinsen et al., 1999).

The role of heterotrophic dinoflagellates in marine foodwebs

In marine food webs heterotrophic/ mixotrophic dinoflagellates are intermediate with respect to prey size spectra between ciliates and copepods (Jacobson and Anderson, 1986; Schnepf and Elbrächter, 1992; Hansen and Calado, 1999). As Jacobson (1986) showed pallium and peduncle feeders in particular form a new trophic link in marine food webs, because they are able to feed like copepods on large diatoms. That means they can handle similarly large prey and are potential competitors. Heterotrophic dinoflagellates are consumers of a large range of phytoplanktonic species, additionally they feed on bacteria,

heterotrophic protist and mesozoa (Jeong, 1999). However they are also prey for several zooplanktonic consumers (Klein Breteler, 1980; Gifford and Dagg, 1991). On the other hand they can feed on zooplankton, e.g. copepod eggs and nauplier stages (Joeng, 1994).

Interestingly, some species are known to feed on conspecific prey or have reciprocal predation (Jeong, 1999). The species *Oblea rotunda* (Jacobson and Anderson, 1986), *Protoperidinium spp.* (Joeng and Latz, 1994) and *Diplopsalis lenticula* (Naustvoll, 1998) for example can be cannibalistic and the species *Protoperidinium cf. divergens* and *Fragilidium cf. mexicanum* feed on each other (Jeong et al., 1997). Today we have some knowledge of the potential importance of heterotrophic/ mixotrophic dinoflagellate in the food webs (Margalef, 1967; Hansen, 1991; Strom, 1991), but little is still known about the feeding quantities and behaviour or prey selection.

Feeding types

For dinoflagellates different feeding types are known. They can feed by direct engulfment, by ingesting prey with a pallium or by using a peduncle. The direct engulfment also called phagotrophy of whole prey is widespread in naked dinoflagellates, but some thecate species are also capable of feeding in this way for instance *Prorocentrum micans* (Jeong, 2005; see also Skovgaard, 1996; Joeng et al., 1999) . The prey is ingested through the sulcal region. The feeding strategy using a pallium is the solution for most thecate dinoflagellates which use it to ingest large prey. The digestion essentially takes place in a food vacoule outside the main cell body (Jacobson and Anderson, 1986). The third feeding behaviour myzocytosis i.e. feeding by way of a feeding tube (also called peduncle) and is found in many dinoflagellates. In the species *Gymnodinium fungiforme* (Spero, 1982) and *Peridiniopsis berolinensis* (Calado and Moestrup, 1997) this structure was found for instance. In this type of feeding

the peduncle is inserted into the prey, cell contents are sucked out with a narrow flagellar tube and transferred to food vacoules that are formed inside the predator cell (Schnepf and Elbrächter, 1992). The structures described above give dinoflagellates the ability to feed on a wide range of phytoplankton of different taxonomic groups and size (Jacobson and Anderson, 1986; Naustvoll, 1998).

Mixotrophic dinoflagellates have also been known for a long time, but only recently have they been investigated in more detail (Bockstahler and Coats, 1993; Jacobson and Anderson, 1996; Li et al., 1996; Hansen and Nielsen, 1997; Smalley et al., 2003). In this context different dinoflagellate species were discovered to be mixotrophic that had been regarded as autotrophic before (Jacobson and Andersen, 1994; Jeong et al., 2005). A knowledge about the feeding types of species which are regarded in data-series is important because such data form the basis for ecological models.

The situation on the Helgoland Roads

Helgoland is a particularly good location for such a study because it has one of the longest running and most detailed phytoplankton data series in the world that can provide the backround data for the present study. Since 1962, phytoplankton has been counted on a work daily basis (Wiltshire and Dürslen, 2004). Additionally, since 2002 a large scale food web project has been carried out at the Helgoland Roads in the context of which a detailed survey of different plankton groups and the interactions between them has been conducted. On the Helgoland Roads where this study was carried out, some of the abundant species in summer are heterotrophic dinoflagellates, for instance *Gyrodinium spirale* (Bergh) Kofoid et Swezy 1921 and *Noctiluca scintillans* (Macartney) Kofoid et Swezy 1921. In the Helgoland long-term data series some key species are counted every working day. However, most of the species that can be

identified to species level are larger dinoflagellates (ESD = estimated spherical diameter over 20 μm). *Gyrodinium spirale* for instance is continually present on the Helgoland Roads with an abundance maximum in summer (pers. com. Silvia Janisch). Unfortunately the majority of dinoflagellates is of a size < 20μm and while these dinoflagellates were also recorded, they are difficult to identify with standard inverted microscopes and therefore rarely identified to species level.

In summer 2005, during a detailed survey of heterotrophic dinoflagellates and their feeding behaviour at the Helgoland Roads, one component of this group of small dinoflagellates was identified as *Peridiniella cf. danica* (Paulsen) Okolodkov et Dodge 1995. Until recently *Peridiniella cf. danica* was mostly known as an autotrophic species. However, in cells from the field structures, interpreted as food vacuoles, were observed (Grayek, 2006) which lead us assume that the species might be mixotrophic. Previously, structures resembling a feeding tube were also observed in *P. cf. danica* (Karlson and Kuylenstierna, 1998). This species belongs to the smaller dinoflagellate size fraction rarely identified in routine phytoplankton counts for long-term data series. If more of such small mixotrophic/ heterotrophic dinoflagellates will be discovered there might have to be a change in our view of the interactions in food webs. Especially in terms of modeling a knowledge of the trophic mode and the interactions is important. As other experimental works have shown, microzooplankton organisms may play an important role feeding on phytoplankton blooms (Naustvoll, 1998; Strom et al., 2001). Including the feeding impact and interactions of these smaller species could considerably increase the total estoimated grazing impact of the microzooplankton community.

Grazing and prey selection

Because of the important role of feeding on algae blooms and of their wide prey spectrum, heterotrophic dinoflagellates must be included in marine food web models. Dinoflagellates are able to ingest big prey because of the tube or sack-like structures they use. Even naked forms are able to ingest prey which is three times bigger than themselves (Hansen, 1992), although dinoflagellates have shown the highest growth rates while feeding on prey of their own size (Hansen et al., 1994). However, until recently only a few studies have focused on aspects of feeding behaviour and prey size selection of mixotrophic and heterotrophic dinoflagellates (Naustvoll, 1998, 2000a,b; Drebes and Schnepf, 1998). In existing North Sea models of food webs (e.g. ERSEM), dinoflagellates are usually considered as part of the microzooplankton compartment (Baretta-Bekker et al., 1995; Broekhuizen et al., 1995). This may be a problem, because the groups contained in this compartment have totally different prey size spectra and grazing rates. As an example ciliates do not feed on prey bigger than a predator:prey ratio of approximately 10:1 and dinoflagellates prefer predator:prey ratios around 1:1 (Hansen et al., 1994). Moreover ciliates can have higher feeding rates than heterotrophic dinoflagellates. For example big ciliates are able to consume up to 35 cells ind.$^{-1}$ h^{-1} (Montagnes and Lessard, 1999) while feeding rates reported for dinoflagellates are in the range of 0.8 cells ind.$^{-1}$ h^{-1} (Hansen, 1992) to 4.5 cells ind.$^{-1}$ h^{-1} (Joeng, 1994). In addition dinoflagellates may compete with copepods, because they feed on the same prey range (e.g. *Gyrodinium spirale*). Some are able to graze up to 17 times more than copepods in the same phytoplankton community (Calbet et al., 2003; Jeong et al., 2004; Umani et al., 2005) and have faster growth rates (Levinsen and Nielsen, 2002). Therefore unlike copepods, dinoflagellates have growth rates which allow them to respond in their abundances rapidly to fluctuations in phytoplankton numbers (Hansen, 1992).

Aims of this study

The present study was carried out to examine the interaction between dinoflagellates and different forms and size classes of phytoplankton. It was investigated which size classes of microalgae were ingested by dinoflagellates of specific species and which would be preferred. In single and mixed prey diet grazing experiments the growth and ingestions rates on the different food types were measured as an indicator for the ability to efficiently use these species as food items. Finally the grazing impact on phytoplankton blooms was estimated.

3 MATERIAL AND METHODS

3.1 Isolation and culturing of organisms

The present study is based on two dinoflagellate species and on three diatom species. All organisms were collected on the "Helgoland Roads" 54° 10' 0" northern latitude and 7° 52' 60" longitude during 2004 and 2005: *Gyrodinium spirale* and *Peridiniella cf. danica*. Organisms were isolated by capillary isolation from net or bucket samples. Seawater was collected with a bucket and sterile filtered over a 10 μm glass fibre filter (GF 93, Schleicher & Schuell, Microscience) and a 0.2 μm membrane filter (mixed cellulose ester, Schleicher & Schuell, Microscience). The water was filled into autoclaved bottles (Schott) under sterile conditions and was stored in an illuminated cold-storage room at 14.5° C. All predators were cultured in sterile filtered seawater without nutrient suppliments. Seawater was collected on May 10th, 2005, June 23rd, 2005 and August 12th, 2005. These will hereafter be referred to as May, June and August seawater, respectively.

3.1.1 Predators

For this study the species *G. spirale* and *P. cf. danica* were chosen. *G. spirale* is known as a heterotrophic dinoflagellate and as a phagotrophic grazer. The species has the ability to engulf prey its own size or even larger (Hansen (1992). In *Peridiniella cf. danica*, although pigmented, microscopy observa-

tions of the cells have shown a structure that has been interpreted as a peduncle (Karlson and Kuylenstierna, 1998).

The dinoflagellates were cultured on a vertically positioned plankton wheel rotating at about 1 rpm and exposed to irradiance at averaging 30 μmol photons m^2 s^{-1} at a 14 h:10 h light:dark cycle. The wheel was a modification of an existing plankton wheel where wooden boards holding the cultures were replaced with Perspex sheets to avoid shading and therefore changes in light intensity between samples. A photograph of the modified plankton wheel is shown in Figure 3.1.

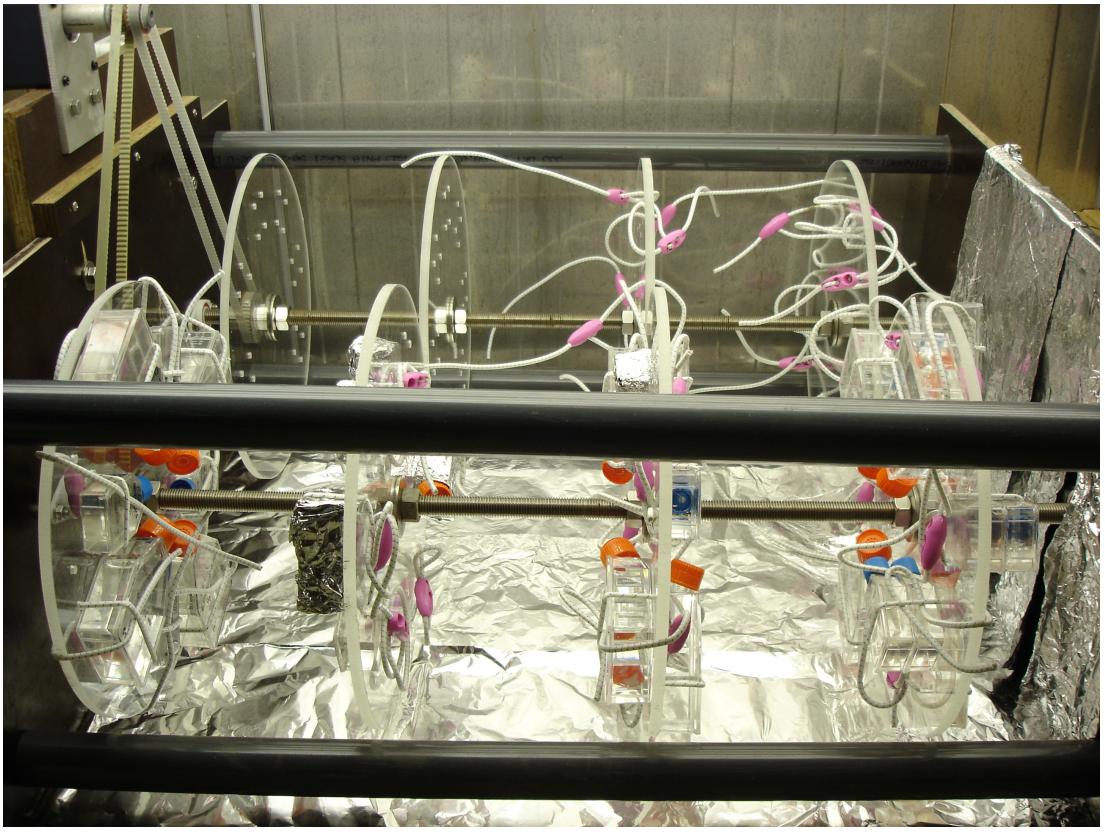

Figure 3.1: Photography of the plankton wheel.

Until July, the temperature was adapted weekly to the ambient temperature at the Helgoland Roads. From July, when the temperature had reached 14.3 $\pm$ 1°C the temperature was held constant for the experiments.

Peridiniella danica

This dinoflagellate species was discovered in one of the culture flasks of *Ceratium fusus* which had been collected with a net sample on May 24th, 2005 . The species was so abundant that *Ceratium fusus* was displaced. This species was identified as *Peridiniella cf. danica*.

During the first time of growing the dinoflagellate cultures received fresh medium (sterile filtered May seawater) and food once a week (*Rhodomonas sp.*).

It was attempted to establish clonal cultures with different methods. First a dilution method was tested but failed. For a capillary isolation the species was too motile. To slow down cells they were dazed with CO_2. During the culturing process the cultures were several times infected with *Cylindrotheca sp.*, but finally a pure but non-clonal culture was established.

Gyrodinium spirale

This species was discovered in cultures of *Protoperidinium steinii* and became abundant in the culture. Cells of *G. spirale* were isolated with a pasteur pipette and transferred to a new culture flask (Orange Scientific 75 cm^2). Every second day the culture was fed with 20 ml of a dense *Thalassiosira rotula* culture, subsequently the *G. spirale* was kept under saturated food conditions. 50 ml of the culture medium was replaced once a week by fresh sterile filtered June seawater.

3.1.2 Prey

As prey organisms the species *Chaetoceros debilis*, *Thalassiosira rotula* and *Rhodomonas sp.* were chosen.

The diatom species were grown in sterile filtered June seawater or in f/2 with Si in culture flask (BD Falcon 25cm^2) at a temperature of about 14.5°C, an irradiance of 15 - 20 μmol photons m^2 s^{-1} and a light:dark cycle of 12:12 h.

The *Chaetoceros debilis* and *Thalassiosira rotula* cultures were clonal cultures, isolated on April 30th, 2004 and March 11th, 2004.

The non-clonal culture of the cryptophyte *Rhodomonas sp.* was grown in f/2 without silica in a conical flask and under the same conditions as the diatoms. The medium was ventilated with air and half of the culture medium including organisms was replaced with fresh medium every third day. After a while the culture became contaminated, so some cells were obtained with a Pasteur pipette and were washed with sterile filtered seawater. The cells were taken to a 270 ml culture flask. Because of contamination by *Cylindrotheca sp.* a breeding container was built. It was a filtering flask with hose connection. The flask was closed with a rubber stopper with two holes through which small glass tubes were passed, so that no spores could get out and nothing could contaminate the culture.

3.2 Preliminary Experiment: Effects of light and prey type on growth in *Peridiniella danica*

This pilot study was designed to determine whether this species is really autotrophic or mixotrophic and to estimate its growth. So far nothing was published on heterotrophic growth in this species. Therefore three treatments were set up.

- light, no prey
- light, prey
- dark, prey

Prior to these experiments the organisms were cultured for some time in light and June seawater. Before the experiment was started the cultures were transferred to dark conditions, to allow the species to graze down the prey. The

experiment was carried out three times. The first and the second were preliminary experiments to estimate the best prey concentration for the main experiment. Each treatment and the prey control were run in triplicate.

In the first experiment the predator:prey ratio was between 1:100 and 1:150 and it was carried out for 96 h. After 48 h and 96h subsamples were taken which were fixed with neutral lugol´s iodine and counted in Segdewick-Rafter chambers. From the stock cultures 20 ml of the predators were transferred to the culture flask with a pipette (BD Falcon 25cm^2). Additionally, 15 ml from the *Rhodomonas sp.* stock culture were transferred to the culture flasks of the treatments light/prey and dark/prey and subsequently all flasks were topped up with fresh sterile filtered June seawater. The experiment was run under an irradiance of $\approx$30 μmol photons m^2 s^{-1} (average).

In the second run of the experiment the irradiance was reduced to approximately 15 μmol photons m^2 s^{-1} (average) to ensure a low growth of the prey during the experiments. The start ratio of predator and prey were 1:10. (*P. cf. danica* had a density approximately 50 cells ml^{-1} and *Rhodomonas sp.* 500 cells ml^{-1}). Into the three replicate flasks of the different treatments the predator and the prey were filled with a pipette, so that the starting concentration were 35 cells ml^{-1} for *P. danica* and 700 cells ml^{-1} for *Rhodomonas sp.*. The duration of the experiment was 24 h.

The third experiment lasted 72 hours and a subsample was taken every 12 h. The experimental conditions were the same as in the second experiment, apart from the predator:prey ratio which was approximately 1:50. This corresponded to 50 predators and 2500 cells of prey ml^{-1}. The prey species was transferred to a new culture flask containing June seawater twelve hours before the start of the experiment.

For every subsample 6 ml were taken from each culture flask and fixed with five drops of Lugol‘s iodine. The flasks were refilled with fresh medium. The dilution and growth rate were calculated with the formulas described in section 3.5.

3.2.1 The effect of starvation and prey on the cell size of *Peridiniella cf. danica*

The size of *P. cf. danica* was measured, because during the counting process it appeared that the cell size decreased from the beginning to the end of the "prey size selection experiment". The cells were taken from the treatments "starvation" and "fed with *Rhodomonas sp.*", and cell size was determined for cells that had been fixed with lugol´s iodione. To measure the length and the width of the dinoflagellate photographs were taken in an inverted microscope (Axio Vert 135) at 400x magnification and with an Axio cam HRc (Zeiss, Germany) and the software Axio Vision Release 3.1 (Zeiss, Germany). The photographs were analysed using the program Image/J (SCION Coperation). From the *Peridiniella cf. danica* treatments with *Rhodomonas sp.* and starvation at time 0 and 72 hours photographs of 30 cells were taken. The replicates were pooled because in the starvation treatments there were not enough cells for measurements.

For this species it was assumed that the cell volume could be estimated by a sphere. The formula that was used is described in equation 3.1. As values of r the average from the width and the length were used. The average was calculated because the species deviated slightly from the shape of sphere.

$$V_s = \frac{4}{3} r^3 \pi \tag{3.1}$$

Where V_s is the body volume in cm^3 and r the average of the width and length of *Peridiniella danica*.

Based on cell volume the ESD (estimated spherical diameter) was calculated. The ESD was calculated to have literature conform data Naustvoll (1998).

$$ESD = \left(\frac{cellvolume}{0.523}\right)^{0.333} \tag{3.2}$$

3.3 Experiment 1: Effects of prey density on growth and grazing in *Peridiniella cf. danica*

This experiment was designed to estimate the effects of different prey concentrations on the growth and grazing of *P. cf. danica*. A clonal culture of the predator cultured in August seawater and under a light:dark cycle of 12:12 h of 20 μmol photons m^2 s^{-1} on the plankton wheel was used. The prey used was the cryptophyte *Rhodomonas sp.*, growing in f/2 medium without silica under the same conditions as the predator. From the prey culture a definite volume with a specific number of cells was filled into culture flasks which contained August seawater as medium. Then the predator was added. The initial concentration of the *P. cf. danica* was 20 cells ml^{-1}. The different concentrations of the algae were set to 800, 1500, 2000, 3000, 5000, 8000 and 16000 cells ml^{-1}. For each density triplicate flasks were filled with prey and predator and triplicate flasks without predators were controls for algal growth. To determine the actual predator concentration 6 ml aliquots were fixed with lugol´s iodine at the beginning of the experiment and after 48 h (end of the experiment). The predator´s growth and the ingestion rate was calculated using the formulas described in chapter 3.5.

3.4 Experiment 2: Effects of prey morphology on growth and grazing in heterotrophic/ mixotrophic dinoflagellates

In these experiments three different prey species were offered to two dinoflagellate species. The prey species covered the size range from a small motile flagellate to a medium sized, chain forming diatom. Each experiment was carried out for 72 hours. Every 12 h subsamples of 6 ml were taken and fixed and the flasks were then refilled with fresh medium. The dilution factor was considered in the calculation of the growth rate of predators (μ) and the ingestion rate (I) which are described in section 3.5. In all treatments which contained food the prey concentration was estimated to be saturating at all times. The experiments were carried out on the plankton wheel under 14:10 h light:dark cycle of 15 μmol photons m^2 s^{-1} with June seawater. Every treatment and the control were done in triplicate. The carbon content of the prey algae should be the same in every treatment, it was not because of wrong CHN measurements. In the experiments each of the dinoflagellates was combined with every prey organism and with a mixture of them. The chart shown in figure 3.2 describes the combination of the experiments.

Twelve hours before beginning the experiments some millilitres of the dense prey species cultures were transferred to new culture flask and topped up with June seawater.

3.4.1 Effects of monocultures

Peridiniella cf. danica cells were transferred with a micropipette to flasks containing the prey algae. The start concentration was 50 cells ml^{-1} and was combined with *Thalassiosira rotula* with approximately 280 cells ml^{-1} ($\approx$ 0.37 μg C)

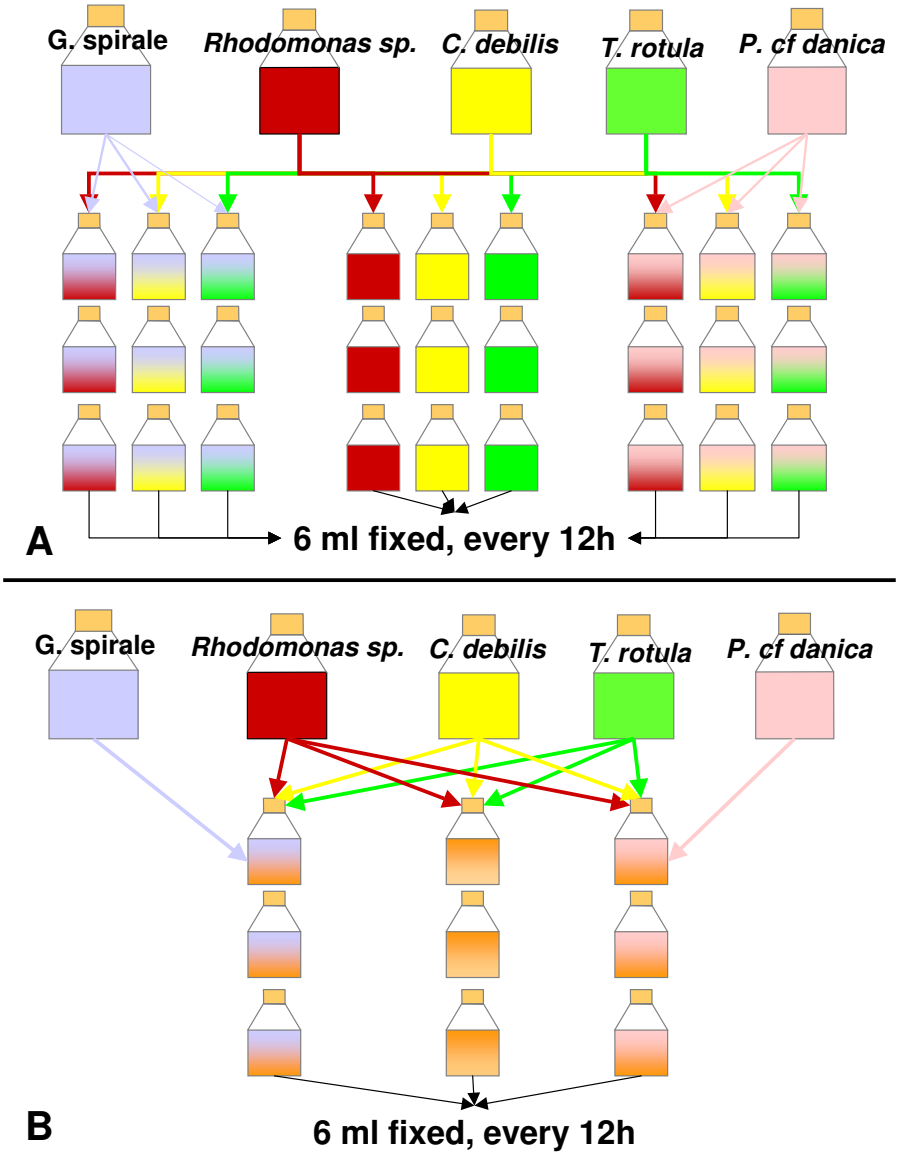

Figure 3.2: The scheme of the experimental design of the prey size selection experiment. (A) Combination of monocultures with the predators. (B) Combination of mixed prey cultures with the predator.

or *Chaetoceros debilis* ($\approx$ 38 ng C) with 540 cells ml^{-1} or 4000 ($\approx$ 76 ng C cells of *Rhodomonas sp.* gCl^{-1}.

Approximately 20 cells of *G. spirale* ml^{-1} were transferred to the culture flasks and combined with every prey species according to the same carbon content based on *T. rotula*. The number of *T. rotula* cells ml^{-1} were approximately 5,500 (7.4 μg C ml^{-1}) and *C. debilis* were taken with 14,600 cells ml^{-1} (1.05 μg C ml^{-1}) to flasks and *Rhodomonas sp.* according to 80,000 cells ml^{-1} which corresponds to a carbon content of 1.5 ng C l^{-1}. The carbon contents were calculated from the biovolume of the species and data for calculation were based on literature (pers. com. Simon Dittami, and CHN measurements).

CHN Measurements

For the CHN measurements a defined volume of the medium containing the algae was filtered on a glass microfibre filters (GF/C, Whatman). The filters were stored at -24 $\circ$C and measured by gaschromatography elemantary analysis (Elemental Analyzer 1108, FISONS.). The carbon content of the sample which was measured had been to the single-cell carbon content.

3.4.2 Effects of mixed cultures

For this experiment the same treatments as for the monoculture grazing experiments were used. Each dinoflagellate species was offered a mixture of the three microalgae that were also used in the previous grazing experiments. In the treatment with mixed prey the absolute cell numbers corresponded to the cell numbers in the treatments with monocultures. But the ratio between the three species based on the carbon content was not the same. For *Peridiniella cf. danica* the total carbon content was 129.8 ng C ml^{-1} and for *Gyrodinium spirale* it was approximately 4.57 μgCl^{-1}. The carbon contents for the different prey species are shown in table 3.1.

Table 3.1: Carbon contents of the different prey species in mixed prey cultures

	P. cf. danica	***G. spirale***
T. rotula	107.8 ng ml$^{-}1$	3.9 μg ml^{-1}
C. debilis	20.2 ng C ml$^{-}1$	324 ng C ml^{-1}
Rhodomonas sp.	1.9 ng C ml$^{-}1$	340 ng C ml^{-1}

3.5 Counting and calculations

After addition of the fixative all organisms or cells were counted in 1 ml Sedgewick-Rafter chambers using an optical microscope (Olympus, CX 41). Each subsample was enumerated three times. Squares in the chamber were counted until 400 cells had been counted. Where densities were too low the whole chamber was counted.

Every subsample removal caused a dilution of the organisms in cultures, because of the refilling of the culture flask (Jeong et al., 2004). The formula which was used to recalculate is given in equation 3.3:

$$N_0 = N_t \left(\frac{f_v}{F_v - n * t_V} \frac{f_v}{f_v - t_v} \right) \tag{3.3}$$

Where N_0 is number of cells calculated in respect to numbers at the start, fv is volume of culture flask, tv volume taken as subsample, n numbers of subsamples and N_t counted cells at subsample dates.

Dinoflagellate growth rates were calculated by averaging the three counts of each subsample and the specific growth rate was estimated by the average

over the growth rate for each subsample interval.

$$D_t = D_0 e^{(\mu * t)} \quad \Longleftrightarrow \quad \mu = \frac{lnD_t - lnD_0}{t} \tag{3.4}$$

Where D_0 and D_t are the observed concentrations of dinoflagellates (dinoflagellates ml^{-1} at the beginning and the end of the time interval t [hours].

The ingestion rates were calculated by using separate coefficients for the growth of the algae in the control flask and flaks with the grazer. The growth constant k (Frost, 1972) for algal growth was calculated from algal control culture flasks.

$$A_2 = A_1 e^{k(t_2 - t_1)} \quad \Longleftrightarrow \quad k = \frac{ln\frac{A_2}{A_1}}{t_2 - t1} \tag{3.5}$$

Where A_1 and A_2 are cell concentration (cells ml^{-1}) at t_1 and t_2.

The grazing coefficient (Frost, 1972) was calculated from

$$A_2^* = A_1^* e^{(k-g)(t_2 - t_1)} \quad \Longleftrightarrow \quad g = \frac{k * (t_2 - t_1) - ln\frac{A_2^*}{A_1^*}}{t_2 - t_1} \tag{3.6}$$

Where $A^*{}_1$ and $A^*{}_2$ are cell concentration of microalgaes in culture flasks with predators at time t_1 and t_2.

For each dinoflagellate the average cell concentration was calculated from (Frost, 1972), using values of g and k:

$$G = \frac{A_1^*[e^{(k-g)(t_2 - t_1)} - 1]}{(t_2 - t_1)(k - g)} [cells ml^{-1}] \tag{3.7}$$

Where G is the average cell concentration of prey for each grazer during the time interval t_1 and t_2.

To estimate the ingestion rate the average concentration of dinoflagellates (3.8) (Heinboekel, 1978) and the volume that was swept clear (3.9) was calculated

during the time interval.

$$N = \frac{D_t - D_0}{lnD_t - lnD_0}[cellsml^{-1}] \tag{3.8}$$

The volume which was swept clear C (Harvey, 1937) was calculated as follows:

$$C = g/N \qquad [ml\ \ dinoflagellate^{-1}h^{-1}] \tag{3.9}$$

In this formula N is the number of dinoflagellates in the culture during the time interval.

The ingestion rate was calculated as:

$$I = G * C \qquad [cells\ eaten\ by\ dinoflagellate\ h^{-}1] \tag{3.10}$$

Prey selection on specific phytoplankton groups in the mixed prey cultures was quantified using the selectivity index (SI) α (Chesson, 1978):

$$\alpha_i = \frac{\frac{r_i}{p_i}}{\frac{r_j}{p_j} + \frac{r_k}{p_k}} \tag{3.11}$$

where r_i is the frequency of prey i in the diet, p_i is the frequency of prey i in the environment, r_j and r_k is the frequency of other prey in the diet and p_j and p_k is the frequency of other prey in the environment. This index, α, varies between 0 and 1 with α_i = $0.\bar{3}$ (in case of three prey species) indicating nonselective feeding towards the prey i, α_i > $0.\bar{3}$ indicates a preference for the prey i and α_i < $0.\bar{3}$ indicates discrimination against the prey i.

3.6 Statistical analysis

All of the experiments had the same design. The data were originally set up in a nested design with 3 replicate samples from the triplicated experimental flasks

for each treatment. The data of the experiments were structured as shown in table 3.1. The values from the replicated samples were averaged. For all data of the experiments "effects of prey morphology on growth and grazing in the both dinoflagellates" and "effects of prey or starvation" a repeated measure ANOVA (α= 0.05) was performed. To prove the homogeneity of the variances a test for sphericity and to prove for normality a Lillifors test was carried out. The parameters of these test are assumptions for the repeated measurement ANOVA (Rees, 1992). Additionally a Student-Newman-Keuls (SNK) post hoc test was performed to estimated between which treatments were significant differences. P-values in the text refer to this post hoc test. In contrast to growth and single diet experiments for the grazing experiments with mixed prey no statistics were done because the variables were not independent. For these the selective predation index (SI) was calculated.

Table 3.2: Design table of the growth and grazing experiments presented in this study

		time 0 h	...	time 72 h
	flask replicates	1 | 2 | 3	1 | 2 | 3	1 | 2 | 3
	count replicates			
treatment 1	1	y_{11} | y_{12} | y_{13}	y_{11} | y_{12} | y_{13}	y_{11} | y_{12} | y_{13}
	2	y_{21} | y_{22} | y_{23}	y_{21} | y_{22} | y_{23}	y_{21} | y_{22} | y_{23}
	3	y_{31} | y_{32} | y_{33}	y_{31} | y_{32} | y_{33}	y_{31} | y_{32} | y_{33}
treatment 2	1	y_{11} | y_{12} | y_{13}	y_{11} | y_{12} | y_{13}	y_{11} | y_{12} | y_{13}
	2	y_{21} | y_{22} | y_{23}	y_{21} | y_{22} | y_{23}	y_{21} | y_{22} | y_{23}
	3	y_{31} | y_{32} | y_{33}	y_{31} | y_{32} | y_{33}	y_{31} | y_{32} | y_{33}
treatment n	...			

For the experiment "effects of prey density" a univariate ANOVA (alpha = 0.05) with a Levenes test for homogeneity of the variances and Lillifors test of normality of the data was performed. All analyses were carried out with STATISTICA Release 6 (StatSoft Inc., Tulsa, USA).

4 RESULTS

4.1 Preliminary Experiment: Growth at different treatments: *Peridiniella danica*

These first experiments were designed to determine the prey concentration and light conditions for these and the other experiments with *P. cf. danica* as well as the time interval for taking subsamples. In the first run of the experiment growth in the treatment "dark and prey" was higher compared with all others. The specific growth rate in this was 1.4 cells d^{-1} and in all the other runs with light the growth rates did not exceed 1 cells d^{-1}. The growth rate in the three runs were 0.33 cells d^{-1} in the 1^{st}, 0.62 in the 2^{nd} run and in the last run growth rate was approximately 0.36 cells d^{-1}. Owing to these results *Peridiniella cf. danica* was used for the growth and grazing experiments with the different morphology types of prey as we were sure now that the species was mixotrophic.

In the treatment "light and prey" the 1^{st} run was terminated after 96 hours because of the high number of *Cylindrotheca sp.* and *Rhodomonas sp.*. Until 48 h the species showed the highest growth in the treatment "light and prey". The prey concentration increased to approximately 87,000 cells of *Rhodomonas sp.* ml^{-1} and the cell numbers of *Cylindrotheca sp.* rose to 61,500 cells ml^{-1} at 96 h. At this time the predator cell concentration decreased to cells numbers which were similar to the number of cells under starvation conditions. In the

treatment "light and no prey" *P. cf. danica* showed positive growth over the whole interval. The predator cell number increased to 20 ml^{-1} (96 h) and the prey was also detected at the end of the experiment. In the treatment "dark and prey" the predator showed little growth until 48 h and then the cell number rose to 404 ml^{-1} at 96 h. The prey concentration decreased. The cell numbers of the prey and the predator are shown in Table 4.1.

Table 4.1: Cell concentrations in the 1^{st} run of prelimnary experiment "Effects of light and prey type". Data are treatment means (n = 3) with the standard derivation.

predator growth	**0h**	**48h**	**96h**
light and prey	107 ±8	210 ±30	14 ±6
light and no prey	57 ±5	11 ±2	20 ±4
dark and prey	94 ±13	99 ±10	404 ±120
growth prey with predator			
light and prey	16664 ±195	11813 ±2410	87840 ±80877
↪Cylindrotheca sp.			61490 ±25769
light and no prey	0	0	6649 ±1798
dark and prey	9993 ±634	3338 ±1430	2210 ±2387
growth prey control	11844 ±6125	16688 ±8085	112034 ±47725

2. run

In the second run the prey in treatments with prey was grazed down completely during the first time interval, so that the experiment was stopped. During this short period of 24 hours the cells of *P. cf. danica* with "light and prey" showed the highest growth (Tab. 4.2). In the treatment "dark and prey" the predator displayed no growth at all. In the third treatment "in light without prey" a negative growth was detected. At 0 h in the subsample a small amount of prey was counted, but grazed down during the first time interval.

Table 4.2: Cell concentrations in the 2^{nd} run of prelimnary experiment "'Effects of light and prey type"'. Data are treatment means (n = 3) with the standard derivation.

predator growth	**0h**	**24h**
light and prey	28 ±10	50 ±9
light and no prey	31 ±12	26 ±305
dark and prey	44 ±5	42 ±12
growth prey with predator		
light and prey	800 ±551	15 ±9
light and no prey	196 ±8	0
dark and prey	636 ±506	6 ±7
growth prey control	333 ±109	414 ±94

3. run

In the third run growth was maintained over a period of 72 hours. The highest growth of *P. danica* in this run occurred in the treatment "light and prey", in which cell numbers rose from 49 to 152 ml^{-1}. In the treatment "dark and prey" the trend in growth was nearly the same compared with the "light and prey" treatment. At 60 h the difference in the cell concentration increased (Fig. 4.1). In the flasks of this treatment the prey cells ml^{-1} rapidly decreased after 48 h. Until 24 h only very small growth rates was detected in the treatments. *P. cf. danica* showed growth under the conditions light and no prey. The cell concentration increased from 54 cells ml^{-1} in the beginning of the experiment to 86 cells ml^{-1} in the end.

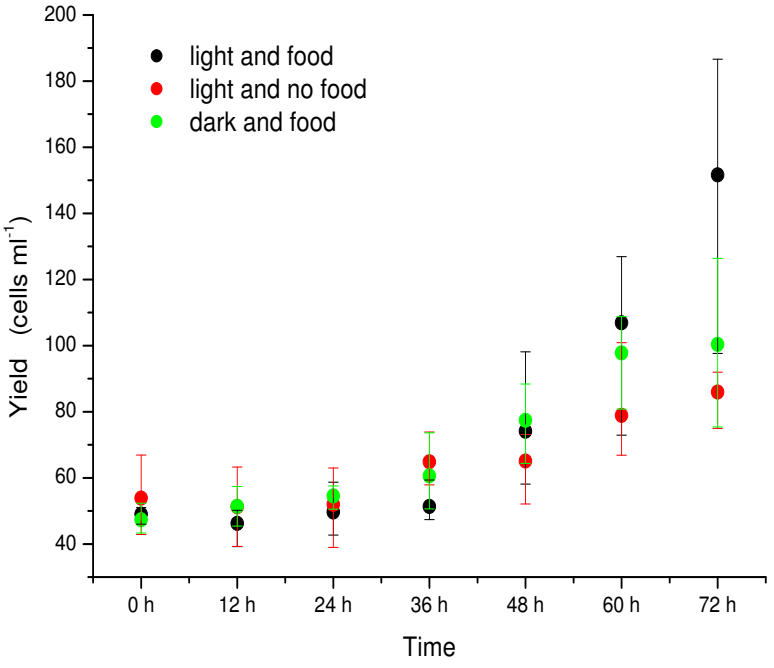

Figure 4.1: Growth in *Peridiniella danica* under the conditions light/prey, light/no prey and dark/ prey. Data points represent treatment means (n = 3) and bars indicate range.

4.1.1 The effect of starvation and prey on the cell size of *Peridiniella cf. danica*

A significant difference in the ESD (estimated spherical diameter) between the treatments "fed" and "starvation" in the subsamples at 72 hours (p = 0.0019) were detected. The cells from the treatment "with prey" were approximately 2.4 μm larger than the cells under starvation. In the beginning the cells in the different treatments showed no significantly difference (p = 0.8551). The effect of starvation and feeding on ESD of *P. cf. danica* is shown in table 4.3.

Table 4.3: Differences in cell size as an effect of prey type. The data represent means over 30 measurements and the standard deviation

	ESD (μm)
starved 0h	33,2 $\pm$4,2
fed 0h	35,2 $\pm$4,0
starved 72h	32,7 $\pm$4,4
fed 72h	28,6 $\pm$6,0

4.2 Experiment 1: Effects of prey density on growth and grazing in *Peridiniella cf. danica*

The shape of the growth curve has the form of a logistic function, but The growth rates *P. cf. danica* were all negative during the experiment. In the grazing rates no dependency on prey density corresponding to a logistic function was detected. All ingestion rates were around -1 apart from the ingestion rate at the concentration 16,000 cells ml^{-1} which was significantly higher then all other concentrations. The results for the growth and grazing rates are shown in Figure 4.2 and 4.3.

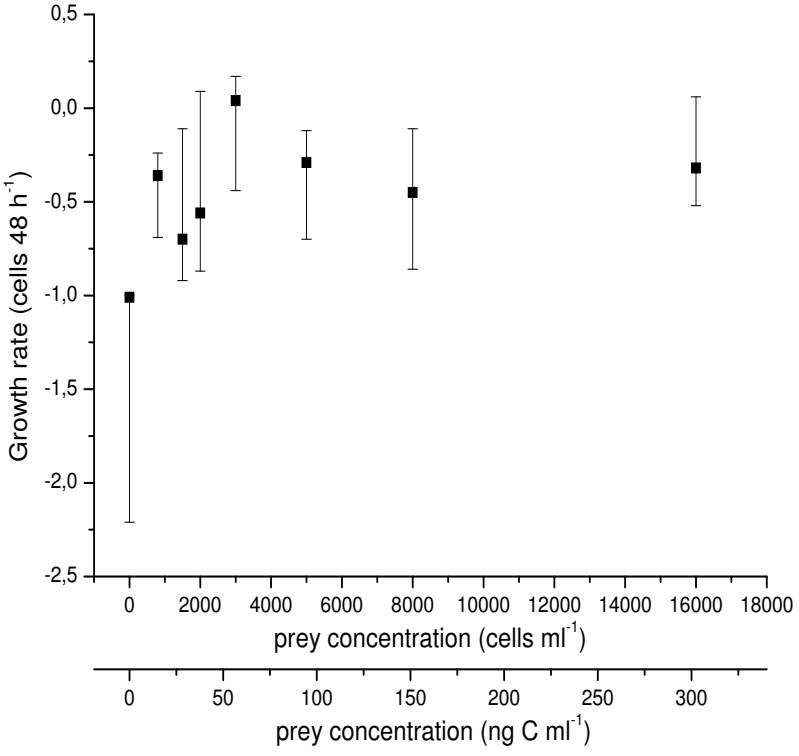

Figure 4.2: Growth rates of *P. cf. danica* on the cryptophyte *Rhodomonas sp.* as a function of mean prey concentration. Data points represent replicate median (n = 3) and bars indicate range.

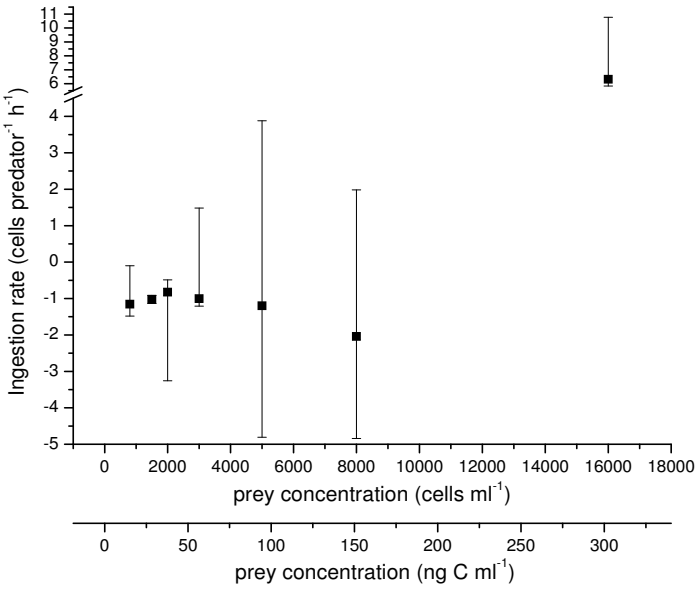

Figure 4.3: Ingestion rates of *P. danica* on the crypophyte *Rhodomonas sp.* as a function of mean prey concentration. Data points represent replicate median (n = 3) and bars indicate range.

4.3 Experiment 2: Effects of prey morphology on growth and grazing in *Gyrodinium spirale and Peridiniella danica*

Three autotrophic species were offered as prey to the two dinoflagellates. The prey species tested ranged from a small motile chryptophyte to chain-forming diatoms, including one with spines. Both species showed the best growth on prey species which were similar to their own size.

In the following sections the results of experiment for each prey treatment with respect to the differences in time and between the treatments are shown. In the four repeated measurement ANOVA´s of the grazing and growth rates of *P. cf. danica* and *G. spirale* significant results were detected. Both factors, the main factor "prey type" and the within "time" and for the interaction were significant. From the significant results only some important aspects were chosen for presentation. The complete results of the Student-Newman-Keuls (SNK) post hoc test are shown in Tables 6.1, 6.2 6.3 and 6.4 in the appendix.

4.3.1 *Peridiniella cf. danica*

Growth

Single diets

This species showed growth under all conditions apart from the cultures with *C. debilis*, but often with a small lag phase. The abundances were highest in the treatment "fed with *Rhodomonas sp.*" (see Fig. 4.4). The cell concentrations with the diatom *T. rotula* were slightly lower than the growth during starvation. In the growth rates no clear trend in the preference for particular species was detected.

In the treatment "fed with *Rhodomonas sp.* the grazing rates rose over time of the experiment. There appeared to be an increase within this treatment over

time, but the ANOVA revealed no significant differences. However the predator showed significant differences in growth rates while feeding on this species to growth rates while feeding on *Chaetoceros debilis* and *T. rotula* in a few subsamples. For example the growth rates ingesting *T. rotula* (F see table 4.4, p = 0.018) and *C. debilis* (F see table 4.4, p = <0.001) were significantly lower than ingestion of *Rhodomonas sp.*.

Table 4.4: Repeated measures ANOVA with one dependent factor for the differences in growth rates of *P. cf. danica* for 6 measurements every 12 h.

source of variation	**df**	**MS**	**F**	**p-value**
Intercept	1	1.156	334.845	<0.001
Prey type	4	0.150	43.475	<0.001
Error	10	0.003		
Time	5	0.602	10.3291	<0.001
Interaction	20	0.119	2.0402	0.021
Error	50	0.058		

The growth in the experimental flasks with *Chaetoceros debilis* as prey was the lowest. Cell numbers of *P. cf. danica* decreased slowly until 60 h. Only in the last subsample the growth rate increased. The growth rate at 72 h was significantly higher than at the points of 12 h, 36 h and 60 h (F see table 4.4, p = 0.021; p = 0.045; p = <0.001 respectively).

The cell numbers (ml^{-1}) in the treatment "fed with *T. rotula*" rose from 56 to 88. The growth rates at 72 h were significantly higher than the growth rate at 12 h (F see table 4.4, p = 0.021).

Mixed prey

The second highest abundance the predator had shown in the "mixed prey" treatment compared to the treatments with single diets and starvation. In this treatment the predator concentration increased to 156 cells ml^{-1} which was slightly less than in the treatment "fed with *Rhodomonas sp.*" (186 cells ml^{-1}). In these experimental treatments no growth during the first 24 h was detected.

Starvation

In the treatment "starvation" the predator concentration increased from 54 to 86 cells ml^{-1}, i.e. similar growth rates to cells fed with *T. rotula*. Within the treatment no significant differences were detected. For this treatment the grazing rates were significant higher than for the treatment "fed with *T. rotula*" at 12 and 36 h and significant lower at 72 h (F see table 4.4, p = 0.013; p = 0.006; p = 0.008). The data of the growth rates are shown in table 4.5.

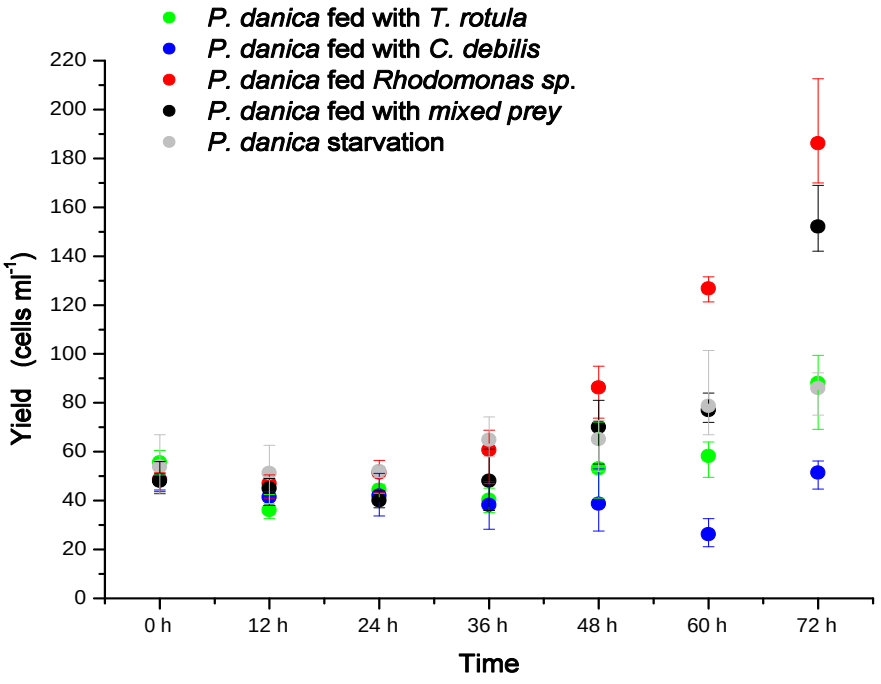

Figure 4.4: The growth of *P. cf danica* on prey of different sizes, fed with *Rhodomonas sp.*, *T. rotula*, *C. debilis*, mixed prey and starvation. Data points represent treatment means (n = 3) and bars indicate range.

Table 4.5: Growth rates of *P. cf. danica* with different prey types. Data are treatment means (n = 3) with the standard derivation.

	Rhodomonas sp.	*C. debilis*	*T. rotula*	mixed prey	starvation
12 h	0.0 ±0.3	-0.2 ±0.3	-0.5 ±0.3	0.0 ±0.3	-0.1 ±0.4
24 h	0.0 ±0.2	0.0 ±0.5	0.2 ±0.3	-0.2 ±0.4	0.0 ±0.3
36 h	0.2 ±0.4	-0.1 ±0.4	-0.1 ±0.2	0.2 ±0.3	0.2 ±0.3
48 h	0.4 ±0.2	0.0 ±0.3	0.2 ±0.5	0.4 ±0.4	0.0 ±0.4
60 h	0.4 ±0.2	-0.4 ±0.6	0.1 ±0.6	0.1 ±0.2	0.2 ±0.3
72 h	0.4 ±0.3	0.6 ±0.7	0.4 ±0.4	0.7 ±0.4	0.1 ±0.5

Grazing

Although there were clear trends in the growth rates, grazing rates were more variable. No clear dependence on prey could was detected.

Single diets

The highest ingestion was reached at 24 h in the cultures fed with *Rhodomonas sp.*. The grazing rate at 36 h on this prey was significant lower than at the other subsamples (F see table 4.6, p = <0.001 for all). At this time the grazing rate was also significantly lower compared to the other treatments (F see table 4.6, p = <0.001 for all). The grazing rates when feeding on *Rhodomonas sp.* were positive at the first two subsamples and at 60 h. In the other subsamples the ingestion was negative. The values for the positive rates were 1.2 (12 h), 2.9 (24 h) and 0.16 (60 h). Maybe the negative data point (36 h) results from the number of cells ml^{-1} counted in the control flasks of *Rhodomonas sp.* at 24 h than it was expected. Perhaps a mistake was made while counting the samples.

With the species *C. debilis* the grazing rates were positive over the whole experiment apart from the first subsample at 12 h. The lowest positive ingestion was detected at 24 h (0.2). The other ingestion rates differed between 0.16 and 0.23 cells $predator^{-1}$ h^{-1}) after 36 h. The data are shown in figure 4.5(A). Within the treatment no significant differences between the grazing rates were detected. For differences between the treatments a significantly lower ingestion rate between feeding on this species and *Rhodomonas sp.* at 36 h was detected (F see table 4.6, p = <0.001 for all).

The grazing on *Thalassisira rotula* was generally the lowest in this experiment. There appeared to be a decrease in this treatment, but the ANOVA revealed no significant differences. Only the first two subsamples were positive and with the values of 0.1 cells $predator^{-1}$ h^{-1} the highest in the experiment, grazing rates were negative thereafter.

When the grazing rates (cells ml^{-1}) were expressed as carbon contents of the

prey cells, *P. cf. danica* ingested higher quantities with cells of the species *T. rotula* at the first both subsamples than feeding on *Rhodomonas sp.*. After 36 h the species had the highest ingestion rate of approximately 15 pg C individium^{-1} h^{-1} while feeding on *C. debilis*.

Table 4.6: Repeated measures ANOVA with one dependent factor for the differences in grazing rates of *P. cf. danica* for 6 measurements every 12 h.

source of variation	**df**	**MS**	**F**	**p-value**
Intercept	1	1.053	5.146	0.0638
Prey type	2	1.221	5.971	0.037
Error	6	0.205		
Time	5	9.573	10.925	<0.001
Interaction	10	9.701	11.071	<0.001
Error	30	0.876		

Mixed prey

The results for *P. cf. danica* feeding on a mixed prey culture show the similar trends to the results for grazing on monocultures. In general the ingestion rates were lower than in monocultures. The grazing rate for feeding on *T. rotula* was negative for all subsamples apart from the subsample 24 and 36 h with an ingestion of 0.01 cells predator^{-1} h^{-1}. For grazing on *Rhodomonas sp.* grazing was only negative during the first subsample but positive thereafter. At 24 h the grazing rate was 0.96 and then decreased to 0.02 in the end of the experiment. When feeding on *C. debilis* on the other hand, grazing rates were always negative apart from the last two subsamples where they were slightly positive, i.e. almost the opposite to grazing rates on *C. debilis* in monocultures. The ingestion was compared to 0.06 and 0.01 cells predator^{-1} h^{-1} at 60 and 72 h. The grazing rate data for feeding on a mixed prey culture are shown in figure 4.5(B).

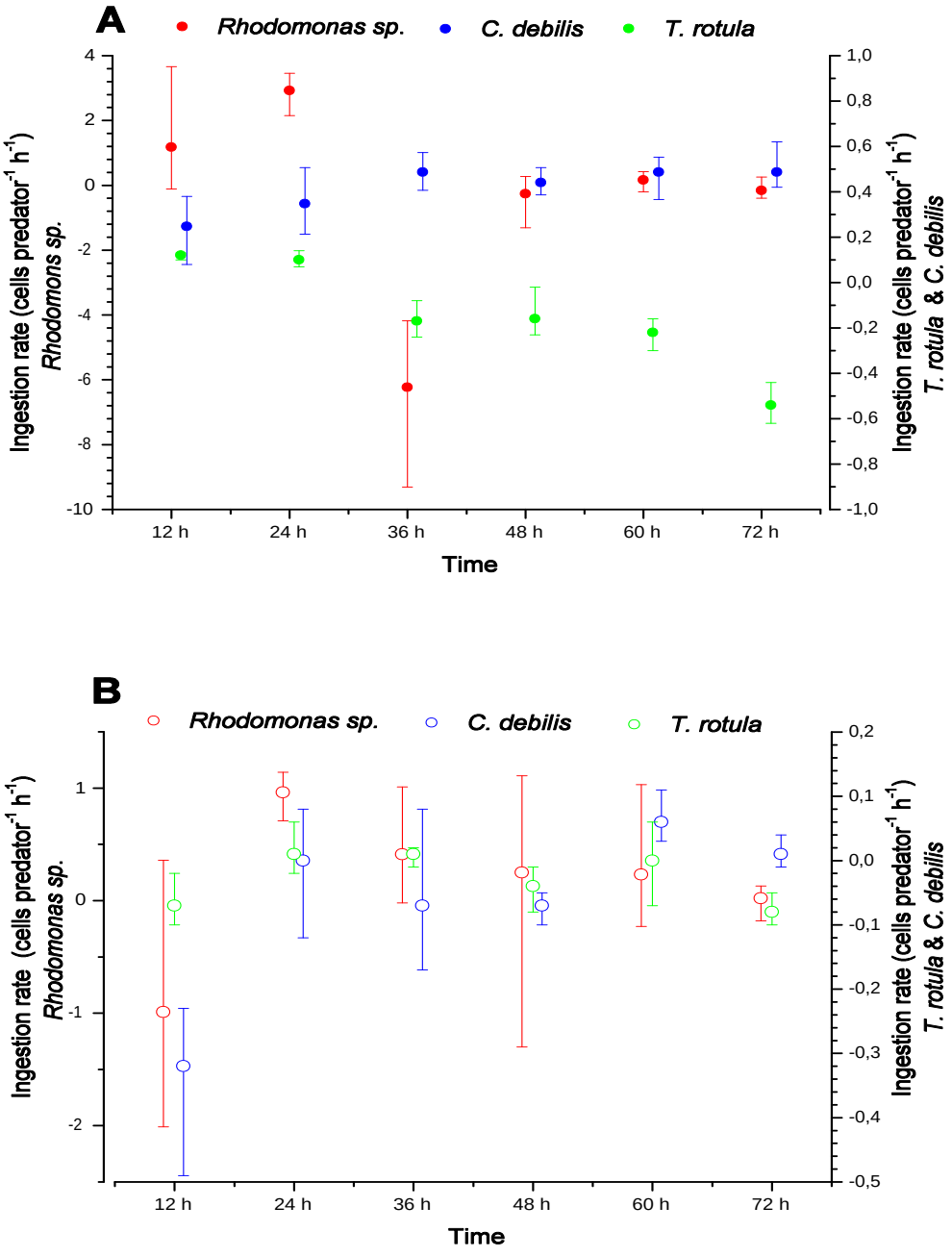

Figure 4.5: The grazing rates of *P. cf. danica* on monocultures (A) and a mixed prey culture (B) with prey algae *Rhodomonas sp.*, *T. rotula*, *C. debilis*. Data points represent treatment means (n = 3) and bars indicate range.

Selective predation

In selective feeding behaviour a clear preference for *Rhodomonas sp.* was detected and for the others mostly discrimination. For the first point no grazing was recognized. In the last two subsamples *P. cf. danica* showed no preference for *C. debilis* or *Rhodomonas sp.*. The big diatom *T. rotula* when fed was always discriminated. In figure 4.6 the selective predation index is shown.

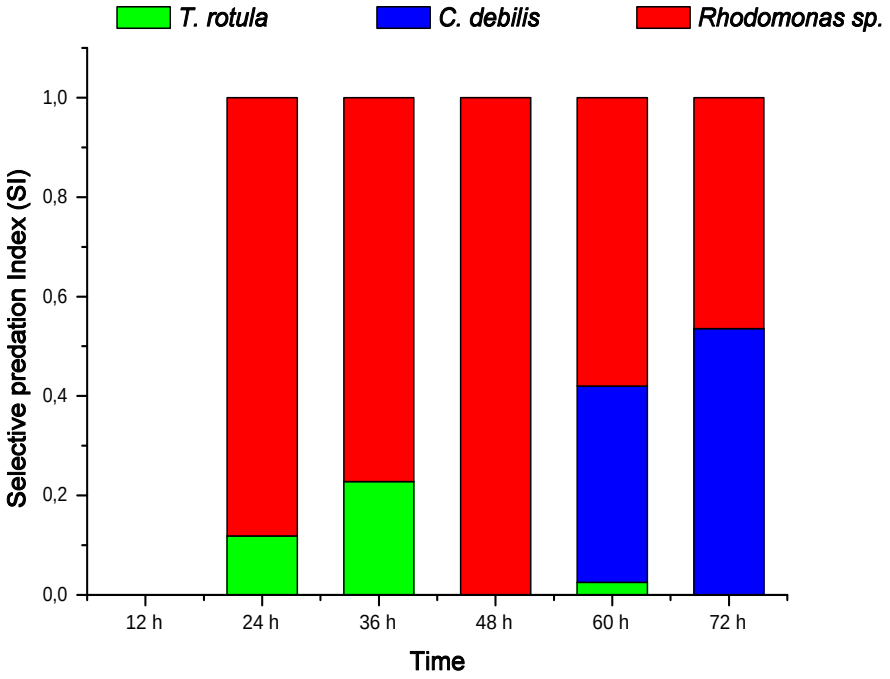

Figure 4.6: Selective predation of *P. cf. danica* feeding on a mixture *Rhodomonas sp.*, *T. rotula*, *C. debilis*. Bars represent treatment means (n = 3) of relative grazing rates.

4.3.2 *Gyrodinium spirale*

Growth

Single diet

Growth in *G. spirale* was very variable over the course of the experiment. *G. spirale* showed significant growth with two of the offered diets (*C. debilis* and *T. rotula*) as well as the mixed diet, but did not grew with *Rhodomonas sp.* or when starved. For all treatments there was a lag phase, but after 36 hours *G. spirale* began to grow faster in three of the five treatments, namely "fed with *T. rotula*", "fed with mixed prey" and "fed with *C. debilis*". The species had the highest growth with *T. rotula* as prey (see Table 4.8). The concentration increased from 16 to 160 cells ml^{-1} in 72 h. Over the course of the experiment for this prey species significant differences in growth rates were detected. The rate at 24 h for instance was significantly higher than the rates at 60 and 72 h (F see Table 4.7, p = 0.029; p = 0.008). Compared for example to the treatment "fed with *Rhodomonas sp.*", significantly higher values in growth for feeding on *T. rotula* occured at the two last subsamples (F see Table 4.7, p = <0.001 (60 and 72 h)). With the treatment "fed with *C. debilis* it was the same.

Table 4.7: Repeated measures ANOVA with one dependent factor for the differences in growth rates of *G. spirale* for 6 measurements every 12 h.

source of variation	df	MS	F	p-value
Intercept	1	5.157	359.231	<0.001
Prey type	4	0.412	28.696	<0.001
Error	10	0.014		
Time	5	0.410	4.037	0.004
Interaction	20	0.316	3.112	0.001
Error	50	0.102		

Mixed prey

The growth on mixed prey was second best compared to single diets and starvation, the increase in cell numbers were slightly lower than for fed with *T. rotula* (Fig. 4.7), with significantly lower values at 48 and 60 h (F see Table 4.7, p = 0.01; p = 0.023). The cell abundances did not exceed a concentration of 20 cells ml^{-1}.

Starvation

The predator in the treatment "starvation" had the lowest growth in cell numbers ml^{-1}. The growth rates differ between -0.3 ($12h^{-1}$) in the beginning and 0.6 ($12h^{-1}$) in the end. In the growth rates no significant difference between these treatments and "fed with *Rhodomonas sp.*" was observed.

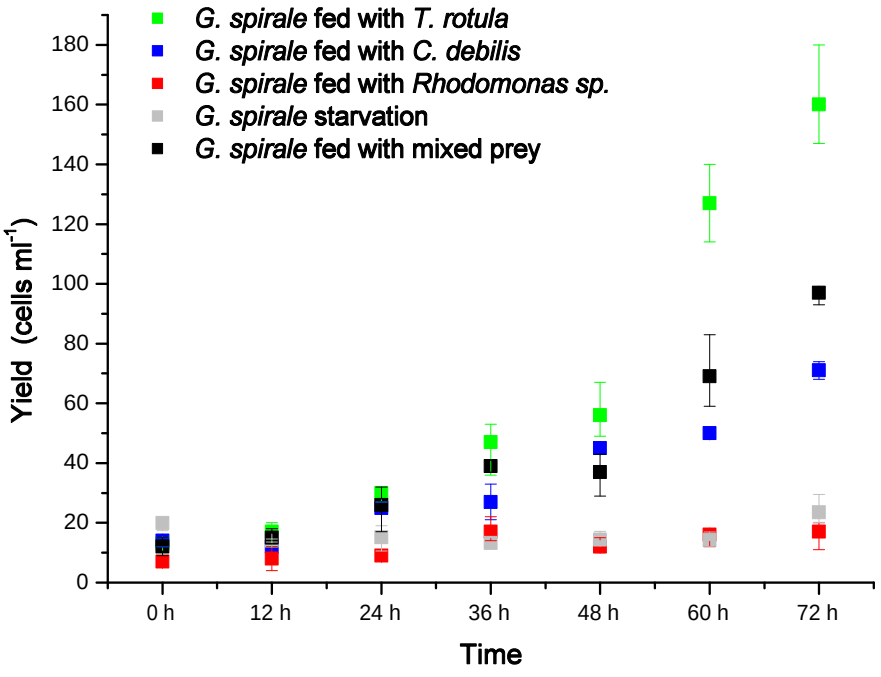

Figure 4.7: The growth of *G. spirale* on prey of different sizes (*Rhodomonas sp.*, *T. rotula*, *C. debilis*) mixed prey and starvation. Data points represent treatment means (n = 3) and bars indicate range.

Table 4.8: Growth rates of *G. spirale* with different prey types. Data are treatment means (n = 3) with the standard derivation.

	Rhodomonas sp.	*C. debilis*	*T. rotula*	mixed prey	starvation
12 h	0.0 ±0.7	0.0 ±0.9	0.2 ±0.6	0.3 ±0.5	-0.3 ±0.3
24 h	0.2 ±0.7	0.8 ±0.4	-0.2 ±0.4	0.5 ±0.6	0.0 ±0.8
36 h	0.7 ±0.6	0.1 ±0.6	0.0 ±0.3	0.5 ±0.4	-0.1 ±1.0
48 h	-0.4 ±0.4	0.5 ±0.4	0.2 ±0.6	-0.1 ±0.3	0.1 ±0.8
60 h	0.3 ±0.7	0.1 ±0.2	0.8 ±0.4	0.6 ±0.5	-0.1 ±0.9
72 h	0.1 ±0.5	0.3 ±0.3	1.1 ±0.2	0.4 ±0.3	0.6 ±0.8

Grazing

The variability which was seen in the growth rates was also reflected in the grazing rates on monocultures and mixed prey cultures.

Single diets

In contrast to *P. danica* there was no evidence of substantial grazing of *G. spirale* on a monoculture of *Rhodomonas sp.*, with the exception of the measurement at 24 h where the grazing rate was positive. The rates in the following subsamples were negative with considerable error between replicates. The grazing on *Rhodomonas sp.* was significantly lower at 48 - 72 h than feeding on *T. rotula* and *C. debilis* (F see table 4.7, p = <0.001 for all). The ingestion rates feeding on the big sized diatom *T. rotula* were positive in the whole experimental period (see Graph 4.8(A)). The grazing on this species had their highest value with 6.5 cells predator^{-1} h^{-1} at 24 h. After this point the rate decreased and fluctuated between 1.7 and 0.02 cells predator^{-1} h^{-1}. For the predator feeding on *C. debilis* the grazing rate was positive in the subsamples at 24, 36, 48 and 72 h. The values were between 34.5 cells predator^{-1} h^{-1} at 24 h and 0.4 cells predator^{-1} h^{-1} at 72 h. Between the treatments "fed with *T. rotula*" and "fed with *C. debilis*" the ANOVA revealed no significant difference. With respect to the carbon content the ingestion of *T. rotula* provides

the predator with the highest carbon content. The starvation treatment like all the other treatments had a contamination with *Cylindrotheca sp.*. A grazing on *Cylindrotheca sp.* was detected.

Table 4.9: Repeated measures ANOVA with one dependent factor for the differences in grazing rates of *G. spirale* for 6 measurements every 12 h.

source of variation	**df**	**MS**	**F**	**p-value**
Intercept	1	52264.3	600.07	<0.001
Prey type	2	66036.7	758.20	<0.001
Error	6	87.1		
Time	5	66507.5	9.69	<0.001
Interaction	10	64070.2	9.34	<0.001
Error	30	6859.2		

Mixed prey

In the mixed prey cultures there was no grazing on *Rhodomonas sp.* during the experiment apart from the first subsample (11 cells predator^{-1} h^{-1}). It is nearly the same trend as in monocultures, but the number of ingested cells was lower. For *C. debilis* a positive grazing rate was detected at 60 h with a value of 2.2 cells predator^{-1} h^{-1} which decreased to 1.0 at 72 h. For grazing on *T. rotula* the same trend as in the monocultures was detected. The grazing rates were lower and the first and the last subsamples had negative rates. The highest ingestion was 1.5 cells predator^{-1} h^{-1} at 24 h. Then the rate decreased from 0.4 and 0.2 cells predator^{-1} h^{-1}.

For the prey species *T. rotula* and *Rhodomonas sp.* the highest carbon ingestions was detected at 24 h. Thereafter the ingestion rates decreased. Ingestion rates were three times higher when feeding on *T. rotula* than feeding on *Rhodomonas sp.*

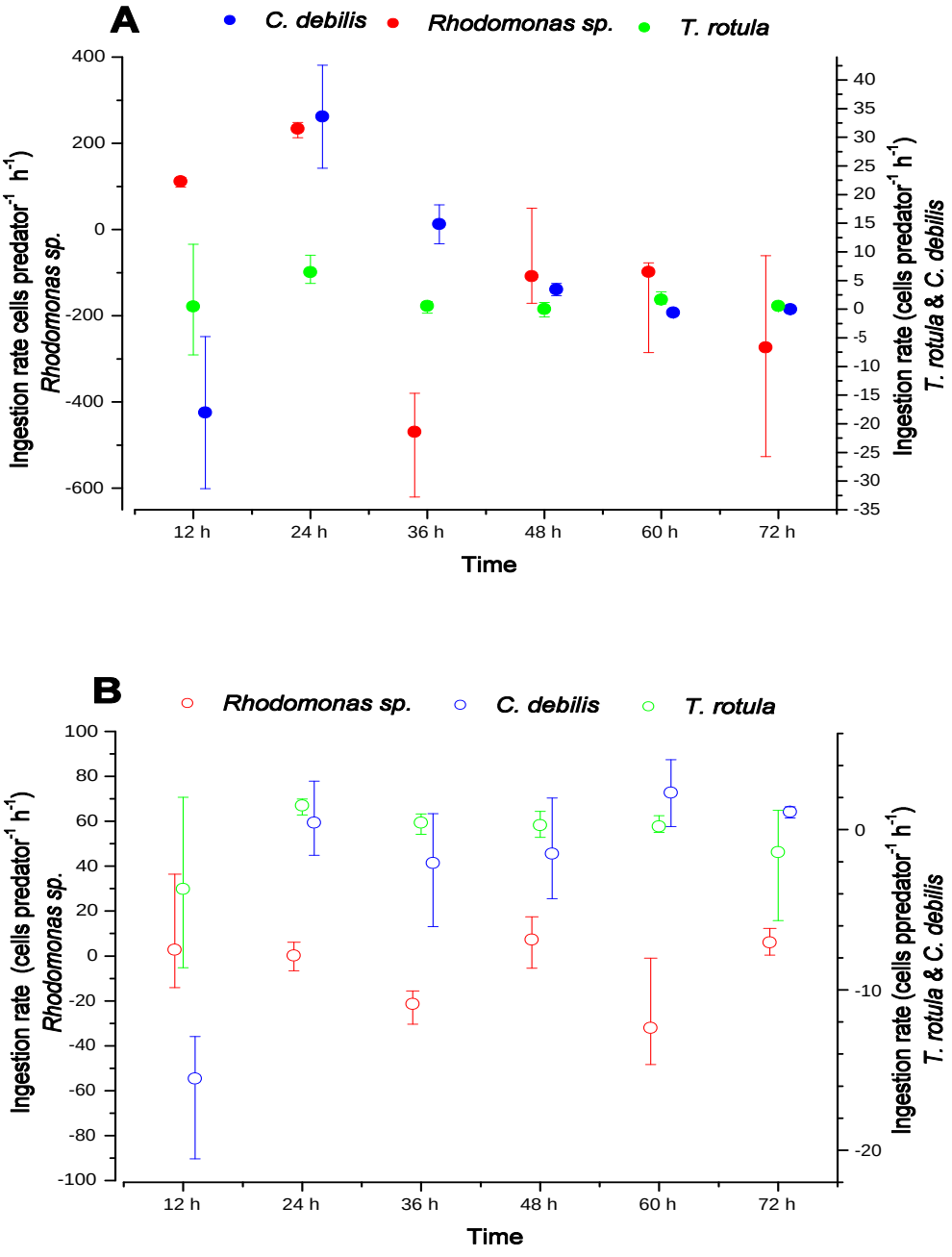

Figure 4.8: The grazing rates of *G. spirale* on monocultures (A) and mixed prey culture (B) with prey algae *Rhodomonas sp.*, *T. rotula*, *C. debilis*. Data points represent treatment means (n = 3) and bars indicate range

Selective predation

In selective feeding behaviour of *G. spirale* such a clear preference as for *P. cf. danica* was not detected. During the experiment the preferences between the prey species changed. In most cases which had a positive grazing rate for *Rhodomonas sp.* a discrimination of this species against the others was detected. In the first subsamples only *Rhodomonas sp.* was fed upon. Then the predator had preference for *T. rotula* until 36 h. In the subsample at 48 h *Rhodomonas sp.* was the most fed prey. In the end of the experiment a preference for *C. debilis* was detected.

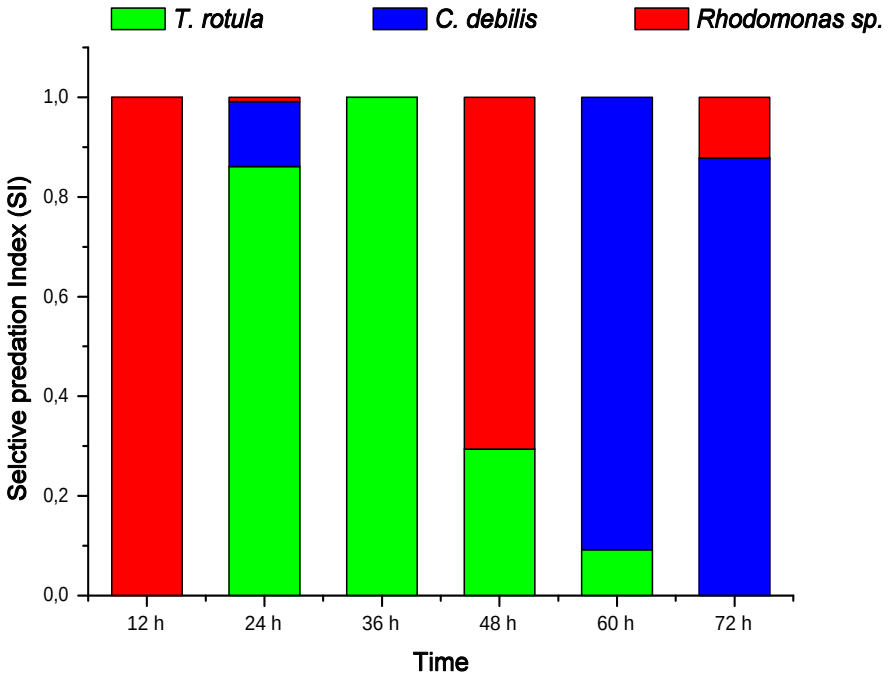

Figure 4.9: Selective predation of *G. spirale* feeding on a mixture *Rhodomonas sp.*, *T. rotula*, *C. debilis*. Bars represent treatment means (n = 3) of relative grazing rates.

4.3.3 Potential community grazing

To bring the determined data from the grazing experiments in context to the natural conditions (Jeong et al., 2005), the community grazing impact on the predator specific prey was calculated.

In situ

In the time from April to July the predator used in these experiments belonged to the abundant species on the Helgoland Roads (Helgoland Roads long-term series).

Figures 4.10 and 4.11 show the predator and prey abundances from these species on the Helgoland Roads from the beginning of April until the end of June 2005. To estimate the community grazing of *P. cf. danica* the data from the groups "thecate dinoflagellates" and with respect to the preferred prey species *Rhodomonas sp.* "flagellates 6:10 and 8:15 μm" were used. These groups were selected because we act on the assumption that they contain *P. cf. danica* and *Rhodomonas sp.* as main parts. As mentioned in the introduction the identification taxa to a species level needs much time and expertise. The group "thecate dinoflagellates" must include the species *Peridiniella danica*, because bigger species were identified to their species level and an another group include small *Gymnodinium spp.*. For the calculation of the community grazing impact of *G. spirale* the data of the prey species *T. rotula* and *Chaetoceros debilis* were used.

The groups of flagellates of the size 6:10 and 8:15 μm and "thecate dinoflagellates" for example were continually present on the Helgoland Roads at the considered months. On April 15 (thecate dinoflagellates: 890 cells l^{-1}, flagellates: 190,681 cells l^{-1}) and June 27 (thecate dinoflagellates: 31,003 cells l^{-1}, flagellates: 184,568 cells l^{-1}) peaks in the data series were detected for both groups, respectively to these the community grazing was calculated. For the group "Gyrodinium 50 and 75 μm" the data from April 28th and May 18th, 2005 were used for the calculations. In April the prey species *C. debilis* and *T. ro-*

tula had an abundance of 3,300 cells l^{-1} and Gyrodinium of 360 ind. l^{-1}. In May *T. rotula* had a concentration of 1220 cells l^{-1} while Gyrodinium had an abundance of 4000 ind. l^{-1}.

In vitro

Concerning the ingestion rate the predators showed a huge difference between monocultures and mixed prey. For these calculations the highest ingestion rates of monocultures and mixed prey were used, as an example. The grazing of the *P. cf. danica* community had max. ingestion rates of 6 *Rhodomonas sp.* ind. d^{-1} in monoculture and 2 *Rhodomonas sp.* ind. d^{-1} in mixed prey. For *G. spirale* feeding on *C. debilis* maximal ingestion rates of 69 cells ind. d^{-1} in monocultures and 2 cells ind. d^{-1} in mixed prey were calculated. The max. ingestion rates for this predator feeding on *T. rotula* were 13 cells ind. d^{-1} (monoculture) and 3 cells ind. d^{-1} (mixed prey). The prey densities in the experimental cultures were higher than in the natural environment.

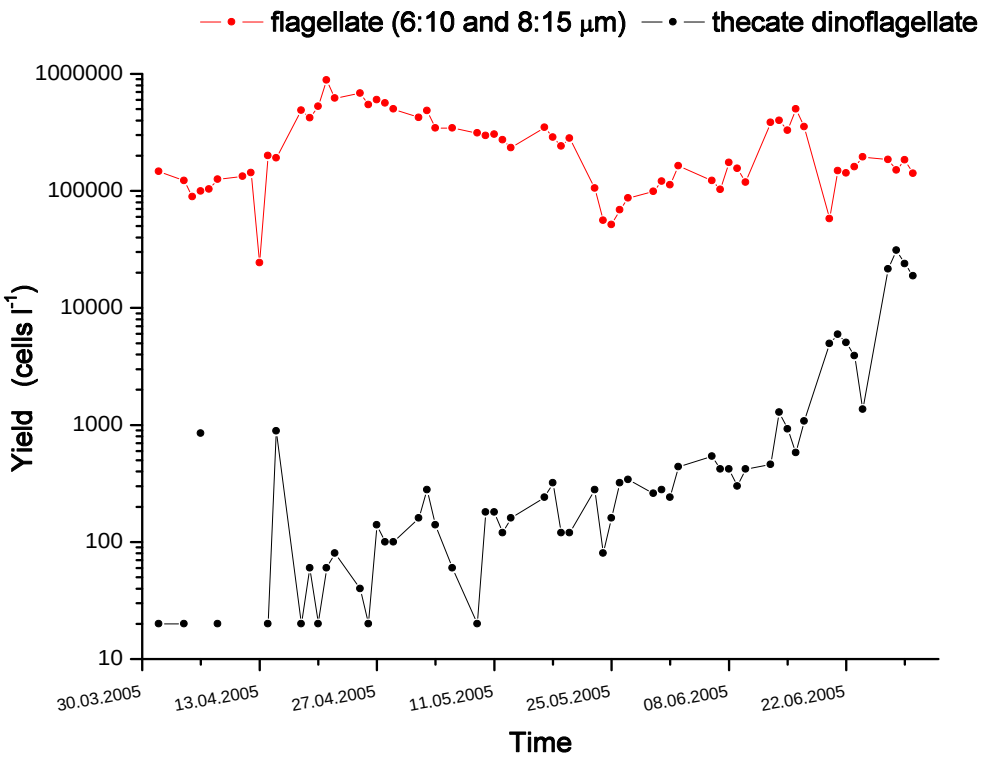

Figure 4.10: Cell abundances of the important prey of *P. cf. danica* on the Helgoland Roads from April- June 2005

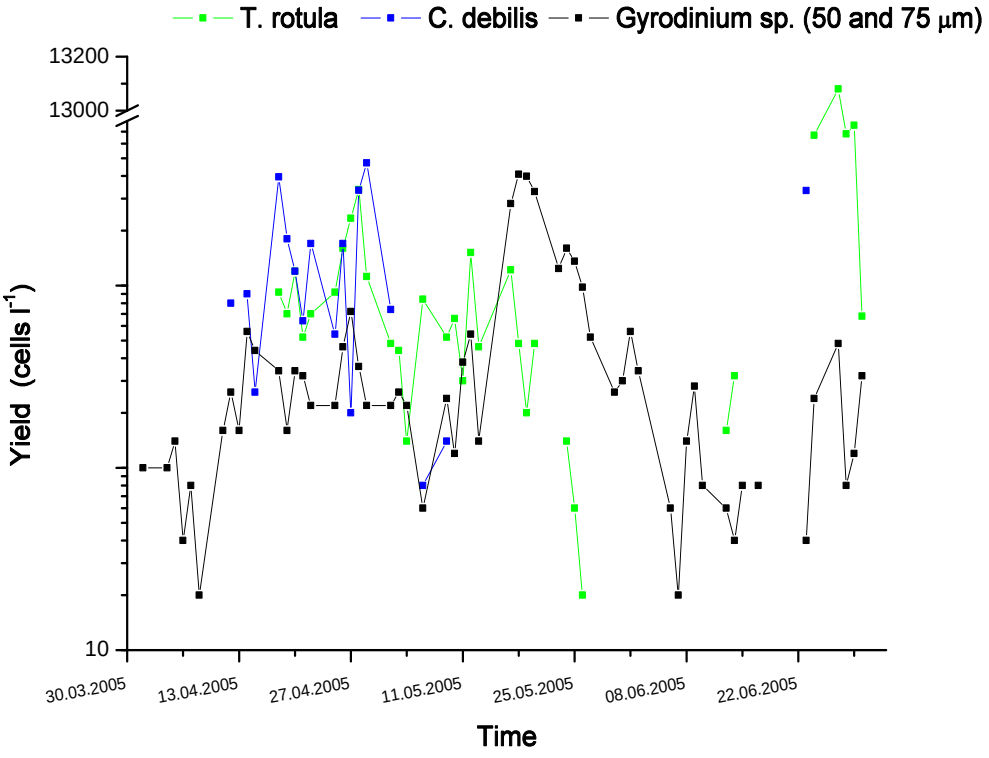

Figure 4.11: Cell abundances of the important prey of *G. spirale* on the Helgoland Roads from April- June 2005

5 DISCUSSION

This study was done to make a contribution to the important research field of food web interactions.

Mixotrophy: Effects of light and prey type on growth in *P. cf. danica*

In this study it was established that *Peridiniella cf. danica* belongs to the size range of the dinoflagellate species described in the introduction that are rarely identified and about which important information is therefore lost for microzooplankton compartments in marine food webs. For this species it was clearly demonstrated that it was able to ingest particular food and it seemed that the trophic mode of the species *P. cf. danica* which previously had been known as autotrophy was actually mixotrophy. In all experiments positive ingestion rates, although not throughout the whole experiment, could be detected and this was also supported by the observation of only slight growth in the treatment "light and no prey", which indicated that the species was not able to live with light as the only energy source. Otherwise it should have shown the same growth as with prey. Although, the actual feeding mode in *P. cf. danica* has not yet been described, personal observations during culturing the organisms supported the notion that *P. cf danica* feeds by using a peduncle. Under the microscope cells with a tube structure and attached prey cells were seen. But this needs further investigation. Despite the inability to grow completely autotrophically, light still

enhanced growth. This has also been shown in another study were light had a positive effect on the growth of the dinoflagellate *Gymnodinium sp.* which also has chloroplasts (Strom, 1991). This could also be an explanation for the difference in growth between the "light/ prey" and "dark" treatment. *P. cf. danica* showed slightly lower growth in the dark than in light but this was not significant. During the experiment the prey concentration in the treatment "light and prey" was saturated at all times. However, in the "dark and prey" treatment, the predator, might have become starved in the last intervals because of decreasing prey densities in the absence of light. And therefore *P. cf. danica* could not show the growth one would expect in the dark.

In addition, in the "light no prey" treatment a decrease in cell size had also been observed. This has been shown in previous studies. The naked species *G. spirale* for instance also forms smaller but also faster swimming cells under starvation (Hansen, 1992). Maybe this is a form of starvation capacity. It could also mean that the species is starting to encyst. Although this has not been described in either *P. cf. danica* or *G. spirale* before encystment has been shown in other species in response to starvation (Zhang et al., 2003).

However, in experiments from other authors (Menden-Deuer et al., 2005; Strom, 1991) it was shown that dinoflagellates can survive for long periods under starvation conditions without encystment. The thecate species *Protoperidinium depressum* for instance survived up to 71 days under starvation conditions (Menden-Deuer et al., 2005). The starvation capacity plays an important role in surviving a lag in prey distribution with respect to space and time. If dinoflagellates can survive for such a long time they are able to raise their chances to encounter prey at any time. Therefore, they might play a more important role in marine food webs compared to protists which only have a short survival time under starvation conditions (Joeng and Latz, 1994; Jackson and Berger, 1984; Fenchel, 1990). An alternative explanation for the growth under starvation could be their ability to feed on dissolved carbohydrates or bacteria. But

again this is a complex subject and needs further investigation.

Effects of prey density on growth and grazing in *P. cf. danica*

In this experiment no dependency on prey density was observed, because an error occurred during the experimental procedure.

Effects of prey morphology on growth and grazing

The main results of this experiment are firstly that the tested dinoflagellate species were able to feed on the species which were offered to them including non motile diatoms and a flagellate capable of escaping capture. However, although they could ingest all prey types they did not grow on some. Secondly in mixed prey there were clear trends in preference for prey species. *Peridiniella danica* preferred the small cryptophyte *Rhodomonas sp.*. *Gyrodinium spirale* showed a preference for the diatoms and a clear discrimination against *Rhodomonas sp.*. Lastly there was a difference in grazing rates between single and mixed diets and a change over time.

Ingestion vs. Growth and prey preference

In the present study it seemed that for *G. spirale* the prey size was the most important factor. As was shown in another study dinoflagellates have the ability to feed on a wide range of prey species (Naustvoll, 1998). Ingestion success varies with the predator:prey size ratio (Hansen et al., 1994), the feeding type and motility of the prey. In contrast to Hansen (1994) *G. spirale* fed on prey smaller than 15 μm in our study the small prey species failed to support growth,

possibly because the cryptophyte is too small and the energy which has to be spent for capture was too high, i.e. there still appears to be a lower prey size limit. This also supports the results of the preference studies in mixed prey diets. *G. spirale* is able to ingest 5 to 6 cells of *Thalassiosira rotula* at once (pers. obs.) which corresponds to a predator:prey ratio of 1:1.5 (or about a quarter of the predator size for a single prey cell), which is slightly higher than that found by (Hansen et al., 1994) where an optimal ratio of 1:3. *P. danica* showed the highest growth feeding on *Rhodomonas sp.* but did not grow with the diatoms as food source. *P. cf. danica* growth when feeding on *T. rotula* and *C. debilis* did not show a significant difference to growth under starvation. For *T. rotula* this might simply be the result of the low predator:prey ratio. On the other hand the negative interaction could be on the part of the diatom. If the assumption is right that *P. cf. danica* feeds by using a peduncle, the prey preference for the small flagellate could be that *Rhodomonas sp.* is a flagellate with thin cell walls which is easier to penetrate than a diatom with a hard frustule. Again this subject needs further investigations. In the treatment "fed with *C. debilis*" the prey concentration decreased.

Single vs. mixed diets and change over time

Both species *P. cf. danica* and *G. spirale* had shown very clear preferences for certain prey types, indicating an ability to distinguish between and select different prey species. However, both species showed lower ingestion rates concerning each prey species growing in mixed prey cultures than in monocultures, because neither of both species despite having preferences towards a particular species fed exclusivly on that species. In most subsamples two or more species were ingested in the mixed prey diets.

Over the time interval of the experiment for *P. cf. danica* fed with *T. rotula* a decrease in grazing was detected coupled with the consequent poor growth of the predator. As mentioned above a reason could be the low predator:prey

ratio. For *G. spirale* the same change in the treatments "fed with *C. debilis*" and "fed with *Rhodomonas sp.*" was observed. In case of the interaction with *C. debilis* the decreasing in grazing pressure can be explained by a decreasing prey concentration. As mentioned above *Rhodomonas sp.* could be ingested but did not support growth. If this is the case then one might expect, as seen here a decrease in the ability to graze on this clearly inadequate (with respect to the carbon content of a single cell), but highly motile food.

Potential community grazing impact and ecology importance

Regarding the prey situation in their natural environment it can be said that both predators are able to graze a considerable part of the phytoplankton (which belongs to their optimal size spectra) with the abundances attained at the Helgoland Roads. Below community grazing rates are estimated using the maximal grazing rates from the culture experiments and data from the Helgoland Roads long-term data series.
For instance, on April 15th thecate dinoflagellates (a category in the Helgoland Roads data that is likely to have contained P. danica reached a density of 890 cells l^{-1}. Based on the grazing rates in the single diet experiments this would have resulted in a removal of 3 % small flagellates. 31,003 predators l^{-1} will have removed the whole flagellate population (June 27th). The cell counts on April 15th might be a right cell abundance for *P. cf. danica*, but the counts on June 27th were probably not reached by this species alone. This subject of rarely identified small species needs further investigation in the Helgoland long-term data series. More realistic to the natural conditions seems to be the grazing rate in mixed prey, because within a natural plankton community they are unlikely to feed only one prey. According to this the predator might be able to feed 1 % (April 15th) and 34 % (June 27th) of the prey species.

The grazing rates of the group *Gyrodinium spirale* on the species *C. debilis* and *T. rotula* in the present study corresponds to the removal of the whole prey

populations by the group "*Gyrodinium spp.* 50 & 75 μm" on both dates (grazing rates from monocultures). In the data series it seemed that *Gyrodinium spp.* grew and the phytoplankton species were grazed down (see Figure 4.11). Using the mixed prey grazing rates *Gyrodinium spp.* should be able to graze the whole population in May. In April when the densities were lower the predator would still be able to remove 22 % of *C. debilis* and 33 % of *T. rotula*.

For the interpretation of these calculations it has to be taken into account that in the natural environment the total number and the quantity of species of the same size is lower than in the mixed prey cultures of the experiment. In these calculations also the growth of the prey and other predators which feed on the same prey were disregarded.

In a few studies the potential competition between marine copepods and dinoflagellates has been estimated. Dinoflagellates can have an order of magnitude higher ingestion rates than other microzooplankton (Jeong et al., 2004; Kim and Jeong, 2004). In comparison to the present study other studies showed that the microzooplankton was able to feed between 7 and 52 % of the daily primary production (Landry and Hassett, 1982; Klaas, 1997), although they did not determine grazing rates for individual species. However, together with other dinoflagellates the tested species might be able to remove a large proportion of a given phytoplankton population. As previous studies have shown the dinoflagellates serve as an important link between the classical food web photoplankton - copepods - fish and large fraction of the primary production is cycled through the protozooplankton fraction to higher trophic levels (Toennesson, 2005).

Conclusion & Outlook

To summarise feeding by both tested dinoflagellate species can cause a change in phytoplankton community structure that implies holding a population on the same level or a total remove it. *Peridiniella cf. danica* and *G. spirale* ingested all offered prey species but not all with successful growth. *P. cf. danica* seemed to have negative interactions with the diatoms but ingested both species *T. rotula* and *C. debilis*. *G. spirale* was able to ingest prey smaller than 15 μm, but did not grow. The difference between ingestion rates in single and mixed diets showed the importance of relevant experiments single vs. mixed prey. This has shown how little is still known about the grazing ecology but also of the physiology of heterotrophic/ mixotrophic dinoflagellates.

The small thecate dinoflagellate and the large naked dinoflagellate are potentially able to graze down considerable parts of the preferred prey populations. Our data have shown that species belonging to the heterotrophic/ mixotrophic dinoflagellates have to be considered more intensively within the microzooplankton compartment in future food web models.

Working on this study posed many questions with respect grazing and starvation behaviour. These lead into recommendations for further experiments.

To estimate the effect of saturated predators on the grazing behaviour over a time interval. There has to be an estimation for single cells of the length of the food uptake and digestion process as this will then allow an estimation of how often a dinoflagellate has to feed in a given time interval. In the literature there were only estimations of the duration of the feeding process in respect to ingested cells during a time interval (Jacobson and Anderson, 1993).

During starvation the thecate dinoflagellate *Peridiniella cf. danica* showed slight growth and a decrease in cell size. There have to be further investigations on the importance of starvation and low or inadequate prey triggering

the encystment of dinoflagellates.

Some modifications of the experiments of this study could lead to results that are related to encystment and excystment particularly with respect to temporary cysts. Temporary cyst are different to resting cysts and are able to react to changes in prey or nutrient supply. This might influence the forming of dinoflagellate blooms. Taking the same treatments of prey and extending the interval of the experiment could probably a link between low or inadequate prey and starting to encyst. Additionally the comparison of the growth of *Peridiniella danica* during starvation in the dark and in light and the measurement of decrease in nutrients could bring results about the question whether the species is able to ingest dissolved carbohydrates.

An interesting investigation might also be the feeding behaviour of *P. cf. danica* while feeding on diatoms with hard frustules. This could be done by microscope observations and making photographies.
Furthermore experiments like grazing experiments and the measurements of toxins could prove the interaction of diatoms and *P. cf. danica* in terms of a toxicity of this dinoflagellate. As shown here there was a negative interaction between the thecate dinoflagellate and the diatom *C. debilis*.

6 APPENDIX

6.1 Tables

Table 6.1: Significant differences SNK post hoc test growth rates of *P. cf. danica* with different prey types (prey type with subsample time in hours).

T. rotula 12, 72h	< C. debilis 72 = mixed72
T. rotula 12	< C. debilis 12 = Rhodo 12 = 48-72 = mixed 48
	< T. rotula 72 = starved 12
T. rotula 36	< C. debilis = mixed 36 = 72 = starved 36
T. rotula 48	> C. debilis 48
C. debilis 36	< mixed 36 = 72; Rhodo 36
C. debilis 60	> mixed 36- 72
	< Rhodo 60
C. debilis 72	> C. debilis 12 = 36 = 60
mixed 24	> starved 24
mixed 48	> starved 48 = C. debilis 48
mixed 72	> C. debilis 12 = mixed 24
	< starved 48

Table 6.2: Significant differences SNK post hoc test grazing rates of *P. cf. danica* with different prey types (prey type with subsample time in hours).

Rhodo 36	< Rhodo 12- 72 = C. debilis 12- 72 = T. rotula 12- 72
Rhodo 24	> Rhodo 48, 72 = C. debilis 12- 24, 48 = T. rotula 12- 72

Table 6.3: Significant differences SNK post hoc test growth rates of *G. spirale* with different prey types (prey type with subsample time in hours).

T. rotula 24	< T. rotula 60 -72 = C. debilis 24; Rhodo 24 = mixed 24
T. rotula 60	> C. debilis 60 = Rhodo 60 = mixed 48 = starved 12, 36
T. rotula 72	> C. debilis 12 = 72 = Rhodo 72 = mixed 48
	> starved 12- 24 = 72
C. debilis 24	> Rhodo 24 = starved 12 = 24
C. debilis 48	> mixed 48
C. debilis 60	< mixed 60
Rhodo 36	> T. rotula 36 = C. debilis 36
Rhodo 48	< T. rotula 48 - 72 = C. debilis 24 - 48, mixed 60
mixed 12 - 36	> starved 12 - 36

Table 6.4: Significant differences SNK post hoc test grazing rates of *G. spirale* with different prey types (prey type with subsample time in hours).

Rhodo 12	> Rhodo 72, C. debilis 12
Rhodo 24	> Rhodo 48 -72; C. debilis 12 - 24; T. rotula 24
Rhodo 36	> Rhodo 12 - 24, 48 - 72; C. debilis 12 - 24 = T. rotula 12 - 72
Rhodo 48	> C. debilis 48 = T. rotula 48
Rhodo 60	> C. debilis 60 = T. rotula 60
Rhodo 72	< C. debilis 24 - 72 = T. rotula 12 - 72
	> C. debilis 12

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Eidesstattliche Erklärung

Hiermit versichere ich, dass ich diese Arbeit selbstständig verfasst und keine anderen als die angebenen Quellen und Hilfsmittel benutzt habe.

Oldenburg, den 8. April 2006_____