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Feeding, growth and metabolism of the marine heterotrophic dinoflagellate *Gyrodinium dominans*

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ABSTRACT: Rates of grazing, growth, and respiration were studied in the heterotrophic dinoflagellate *Gyrodinium dominans* experiencing a single pulse of prey. Additionally, rates of grazing and growth were compared to those of *G. dominans* growing with constant concentrations of prey. The maximal specific growth rates of *G. dominans* with a single pulse of prey were similar to those observed when *G. dominans* was acclimated to constant levels of prey. Thus, our results support the hypothesis that the growth of *G. dominans* responds quickly to changes in the abundance of prey. Moreover, growth rates were negative when concentrations of prey were low; this would suggest that *G. dominans* is adapted to eutrophic conditions. Respiration rates were higher than growth rates when *G. dominans* was fed a single pulse of prey, and we hypothesize that the ability to respond numerically to a changing abundance of prey may inflict high metabolic costs. Gross growth efficiencies (GGEs), determined for *G. dominans* in both food availability conditions, were within the range of values reported for other heterotrophic protozoans, and while GGE decreased when concentrations of food were high in organisms fed a single pulse of food, the opposite was observed in organisms acclimatized to a constant level of food.

KEY WORDS: Heterotrophic dinoflagellate · Grazing · Growth · Respiration · GGE

INTRODUCTION

It is now well recognized that microzooplankton — ciliates and heterotrophic dinoflagellates — are major consumers of pelagic primary production (Calbet & Landry 2004). Moreover, the abundance and biomass of heterotrophic dinoflagellates are often comparable to, or in some cases exceed, that of ciliates in many planktonic ecosystems (Hansen 1991, Lessard 1991), and several studies emphasize the ecological importance of heterotrophic dinoflagellates (Lessard & Swift 1985, Bjørnsen & Kuparinen 1991, Hansen 1991, Strom 1991, Sherr & Sherr 2007). Due to their significant grazing pressure, heterotrophic dinoflagellates are important regulators of phytoplankton production (Putland 2000), as well as significant conveyors of remineralization in the euphotic zone (Sherr & Sherr 2000). Additionally, microscopic examination of the gut contents, feeding structures, and faecal material of invertebrates and fish larvae reveal that they consume microzooplankton, including heterotrophic dinoflagellates (Stoecker & Capuzzo 1990, Hansen et al. 2010). Thus, these organisms act as an important trophic link between nanoplankton and the larger mesozooplankton and macrozooplankton (Gifford 1988).

The strength of the trophic link is controlled entirely by the intrinsic energetics of the dinoflagellates. The ratio between growth and grazing, i.e. the gross growth efficiency (GGE), determines the efficiency by which these organisms convert ingested matter into biomass and thus convey energy to the next trophic level. Accordingly, the efficiency of the food chain is the product of GGE and predation pres-

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sure. However, matter is lost at varying rates from each trophic level as it is transported up through the food web. Part of the ingested and assimilated matter is used for energy production in respiration before it is transported to the next level. The result is a balance between GGE and respiration, which controls the transport of energy to the upper food web. While the importance of GGE is obvious, the significance of respiration may be more obscure. As in metazoan grazers such as copepods (Thor et al. 2002), respiration rates may vary with the food conditions encountered, and they may, as a result, account for considerably varying portions of the total energy budget.

Information about the ecological role of heterotrophic dinoflagellates is now increasing (e.g. Hansen 1991, 1992, Strom 1991, Nakamura et al. 1992, Jacobson & Anderson 1993, Strom & Buskey 1993, Verity et al. 1993), and some literature exists on their grazing and growth (e.g. Strom 1991, Hansen 1992, Jeong et al. 2005). However, knowledge about the underlying energetics of trophic transport by dinoflagellates is still sparse in comparison to our knowledge of ciliates (e.g. Verity 1985, Bernard & Rassoulzadegan 1990, Verity 1991). For instance, while Verity (1985) studied grazing, growth, excretion, and respiration in 2 tintinnid ciliate species, studies on *Gyrodinium* covered grazing and growth rates but unfortunately did not include respiration rates (Hansen 1992, Nakamura et al. 1992, 1995).

In the present study, we measured grazing, growth, and respiration rates in *Gyrodinium dominans*. Contrary to an earlier belief, the pelagic realm is not homogeneous (Andersen & Sørensen 1986, Owen 1989, Franks 1995); steady-state conditions are rarely found in nature and, if they ever occur, are found only during short intervals of time. We therefore measured these variables in *G. dominans* exposed to a single pulse of food. Furthermore, to examine to what extent pulsed food conditions influence the energetics of the dinoflagellate we compared the growth of *G. dominans* on a single pulse of food with growth under constant food conditions.

MATERIALS AND METHODS

Culture of the algal prey (*Rhodomonas salina*) and the heterotrophic dinoflagellate *Gyrodinium dominans*

Rhodomonas salina was maintained in exponential growth in non-axenic B1 algal growth medium (Hansen 1992) at 17°C in a light period of 24 h at ~150 µmol photons m^{-2} s^{-1} with gentle bubbling. A stock culture of exponentially growing *Gyrodinium dominans* was kept on a plankton wheel (75 cm diameter, rotation at 1 rpm) at high concentration levels (~3000 cells ml^{-1}) at 17ºC in a light period of 24 h (~10 µmol photons m^{-2} s^{-1}). *G. dominans* was fed every 24 h with excess *R. salina.*

Experiments with a single pulse of prey

Gyrodinium dominans was kept in 1 l bottles at 17°C in a light period of 24 h (~10 µmol photons m^{-2} s^{-1}) on the plankton wheel (1 rpm). For several days prior to the 3 experiments with a single pulse of prey, the organisms were fed excess *Rhodomonas salina* once every morning. Most *R. salina* were removed by grazing during the 24 h between feeding events, and so the cultures had experienced pulsed feeding for several generations prior to the experiments. The last acclimation feeding event took place 24 h prior to the onset of the experiments.

For each experiment, 4 bottles (each 500 ml) were prepared with known concentrations of *Rhodomonas salina*, and a specific quantity of *Gyrodinium dominans* cells from the acclimation culture was added to obtain specific prey:predator concentration ratios (Table 1). The initial prey:predator biomass ratio was set at 2.1:1 in Expt 1, 2.7:1 in Expt 2 and 6.8:1 in Expt 3. Initial concentrations of *G. dominans* were higher than those observed in the field (Nakamura et al. 1992, 1995) but concentrations were chosen to facilitate reliable measurements of respiration. Four control bottles (each 500 ml) containing only *R. salina* were similarly prepared in order to measure the growth of prey. All bottles were incubated on the plankton wheel for 48 h. Light and temperature conditions were similar to those for the *G. dominans* stock culture (see above). The light level was kept low (~10 µmol photons m^{-2} s^{-1}) to avoid excessive growth of the prey. To measure cell abundance, trip-

Table 1. Experiments with the heterotrophic dinoflagellate *Gyrodinium dominans* fed a single pulse of prey: average values (±SD) of the initial abundance and biomass of the prey (*Rhodomonas salina*) and of *G. dominans* in Expts 1 to 3

	Abundance (cells ml^{-1})		Biomass (µgC l^{-1})	
	R. salina	*G. dominans*	*R. salina*	*G. dominans*
Expt 1	33565 ± 3634	2775 ± 362	1309 ± 142	608 ± 41
Expt 2	41676 ± 281	2427 ± 527	1625 ± 11	599 ± 148
Expt 3	40354 ± 660	1367 ± 163	1574 ± 26	232 ± 20

licate 20 ml samples were pipetted from the bottles and measured in the particle counter (Coulter Multisizer M3). Measurements were taken every 2 h during the first 24 h and every 4 to 6 h for the remainder of the experiments.

Respiration rates of *Gyrodinium dominans* were measured at every sampling event in Expts 2 and 3. Oxygen consumption was monitored continually for 2 h in 1 bottle holding *G. dominans* and in a control bottle containing only *Rhodomonas salina*. This was accomplished using a Unisense Microrespiration System (Unisense A/S) submerged in a thermostatically controlled water bath at 17°C with the same light conditions as those used during the plankton wheel incubations (Jensen et al. 2006). The samples were pipetted from the incubation bottles and injected into 750 ml chambers, and an oxygen microelectrode (OX 25) was inserted for the measurements. Oxygen concentrations were monitored by a computer every 30 s for 2 h. The periods, each of 2 h, were sufficiently short to avoid significant population changes during measurements but long enough to obtain a significant reduction in the oxygen concentration signal. Due to methodological constraints, respiration measurements could only be performed in the experiments involving a single pulse of prey.

Experiments with a constant level of prey

For each concentration of prey, 8 bottles (each 500 ml) — 4 grazing bottles for *Gyrodinium dominans* and 4 controls — were prepared with known concentrations of *Rhodomonas salina*, and a specific quantity of *G. dominans* cells from the culture was added to each of the 4 grazing bottles. All bottles were then run for 24 h on the plankton wheel (light and temperature as described in the section above). Cell concentrations and volumes of *G. dominans* and *R. salina* were measured initially (at time 0) and after 24 and 48 h. The organisms were adapted to a constant level of food by exposing them to a high level of food during the 24 h before the start of the experiment. With this experimental design, the food concentration remained constant during the experiment. Thus, the first 24 h served as the acclimation period, and specific rates of *G. dominans* grazing and growth were calculated from the differences in cell concentrations between 24 and 48 h. During the incubations, average *R. salina* biomass was between 25 and 1263 µgC l^{-1} after 24 h of acclimation (see Table 2), and initial abundances of *G. dominans* were 470 ± 205 cells ml^{-1}.

Table 2. Experiments involving a constant level of prey: average values (±SD) of the initial and final abundance and biomass of the prey (*Rhodomonas salina*), after the acclimation period of *Gyrodinium dominans*. Six initial levels of prey were used, varying from 714 to 36 086 cells ml^{-1}

Abundance (cells ml^{-1})		Biomass (µgC l^{-1})	
After 24 h	After 48 h	After 24 h	After 48 h
714 ± 171	714 ± 171	25 ± 6	25 ± 6
7714 ± 1571	9114 ± 3228	270 ± 55	319 ± 113
8057 ± 2600	8600 ± 4657	282 ± 91	301 ± 163
7514 ± 1628	7371 ± 4000	263 ± 57	258 ± 140
13286 ± 6257	18971 ± 10628	465 ± 219	664 ± 372
36086 ± 2171	48343 ± 5628	1263 ± 76	1692 ± 197

Calculations

The abundance and cell size of both *Gyrodinium dominans* and *Rhodomonas salina* were measured using an electronic particle counter (Coulter Multisizer M3). *G. dominans* cell volumes were calculated from the equivalent spherical diameter (ESD) output from the particle counter, and carbon contents were calculated using the Menden-Deuer & Lessard (2000) carbon:volume relationship. The *R. salina* carbon content was assumed to be 39 pgC $cell^{-1}$ (Kiørboe et al. 1985).

Specific growth rates of *Gyrodinium dominans* (µ, h^{-1}) were calculated as:

$$\mu = \frac{\ln(M_2) - \ln(M_1)}{t} \quad (1)$$

where M_1 and M_2 are concentrations of *G. dominans* at the beginning and end of each incubation interval (µgC l^{-1}), respectively, and t is the sampling time interval (h). For comparison between the single pulse of prey and constant-prey experiments, specific growth rates from the single-pulse experiments were calculated as averages over 6 to 8 h.

Specific grazing rates (i, h^{-1}) were calculated as:

$$i = \frac{-k_{grz} + k_{cont}}{M} \quad (2)$$

where k_{grz} is the difference in concentration of *Rhodomonas salina* before and after incubations in bottles containing *Gyrodinium dominans* (µgC l^{-1}), k_{cont} is the average of differences in *R. salina* concentration in control bottles before and after incubations (µgC l^{-1}), M is the average of *G. dominans* concentration during incubations (µgC l^{-1}).

Specific growth rates were fitted to a modified Michaelis-Menten growth model allowing negative growth at low prey concentrations (Jeong et al. 2007):

$$\mu_{pred} = \frac{\mu_{max}(C_p - C')}{k + (C_p - C')} \quad (3)$$

where μ_{pred} is the predicted specific growth rate, μ_{max} is the maximum specific growth rate, C_p is the concentration of prey, C' is the concentration of prey when $\mu = 0$, and k is a constant.

Specific grazing rates were fitted to a Holling type II functional response model:

$$i_{pred} = \frac{i_{max}C_p}{K_m + C_p} \quad (4)$$

where i_{pred} is the predicted specific grazing rate, i_{max} is the maximum specific grazing rate, C_p is the concentration of prey, and K_m is the concentration of prey when $i_{pred} = i_{max}/2$.

Specific respiration rates (r, h^{-1}) were computed from the slope of the decrease in oxygen concentration in the 750 µl chamber during the incubation:

$$r = \frac{12(\alpha - \alpha_{control})}{V\bar{C}_G} \quad (5)$$

where α is the slope of the decrease in oxygen tension (µM O_2 h^{-1}) in chambers with *Gyrodinium dominans*, $\alpha_{control}$ is the slope of the decrease in oxygen tension in control chambers holding only *Rhodomonas salina*, V is the volume of the incubation chamber (l), and C_G is the average concentration of *Gyrodinium dominans* during the 2 h incubation period (µgC l^{-1}). We assumed equal bacterial concentrations in *G. dominans* and control bottles, so that subtraction of $\alpha_{control}$ removed interference from bacterial respiration as well as photosynthesis/respiration by *R. salina*. Furthermore, we assumed a respiratory quotient of 1 so that each µmol O_2 respired equaled 1 mol CO_2 generated. Thus, the factor 12 constitutes the conversion from µM CO_2 to µgC l^{-1}.

To calculate the parameters of the energy budget in the experiments with a single pulse of prey, data were grouped in relation to food concentration: low values (24 ± 11 µgC l^{-1}), medium values (650 ± 160 µgC l^{-1}) and high values (1146 ± 237 µgC l^{-1}) (see Table 3).

GGEs (%) were calculated as $\mu/i \times 100$, and assimilation efficiencies (AE, %) were calculated as $(\mu + r)/i \times 100$.

RESULTS

Constant concentration of prey

Specific grazing rates were significantly different among *Rhodomonas salina* concentrations (1-factor ANOVA: $F_{4,17} = 65.2$, $p < 0.001$) (Fig. 1A). Interestingly, grazing rates decreased from 0.22 h^{-1} at 804 µgC l^{-1} to 0.11 h^{-1} at 1409 µgC l^{-1}. We therefore applied the Holling type II functional response model only to the 4 lowest concentrations to extract meaningful values for i_{max} and K_m.

Specific growth rates were also significantly different among prey concentrations (1-factor ANOVA: $F_{4,17} = 5.75$, $p = 0.007$). The modified Holling type II functional response model fitted the relationship between growth and prey concentration with a μ_{max} of 0.05 ± 0.02 h^{-1}, whereas K_m was 715 ± 570 µgC l^{-1} (Fig. 1B). GGEs ranged from –0.13 to 0.28, with the highest values at the highest prey concentrations (1409 µgC l^{-1}) (Fig. 1C).

Experiments with a single pulse of prey

Abundance and biomass of the *Rhodomonas salina* prey decreased during the incubation period in all 3 experiments (Fig. 2A) so that *Gyrodinium dominans* experienced a pulse of prey with concentrations > 200 µgC l^{-1} for 16 h in Expt 2, 28 h in Expt 1, and 37 h in Expt 3.

After an initial decrease during the first 8 to 10 h, the abundance of *Gyrodinium dominans* increased significantly in all 3 experiments (linear regressions on *G. dominans* biomass vs. time — Expt 1: $r^2 = 0.818$,

Table 3. *Gyrodinium dominans*. Energy budget in the experiments with a single pulse of prey. C_p = biomass of the prey (*Rhodomonas salina*), i = specific grazing rate, μ = specific growth rate of *G. dominans*, r = specific respiration rate, GGE = gross growth efficiency, AE = assimilation efficiency. GGE was calculated as $\mu/i \times 100$, and AE as $(\mu + r)/i \times 100$

Concentration of *R. salina*	C_p (µgC l^{-1})	i (h^{-1})	μ (h^{-1})	r (h^{-1})	GGE (%)	AE (%)
High	1146 ± 237	0.420 ± 0.014	0.025 ± 0.021	0.080 ± 0.000	6 ± 6	25 ± 6
Medium	650 ± 160	0.122 ± 0.059	0.025 ± 0.033	0.058 ± 0.028	30 ± 13	76 ± 24
Low	24 ± 11	0.135 ± 0.024	0.005 ± 0.010	0.095 ± 0.031	17 ± 24	77 ± 27

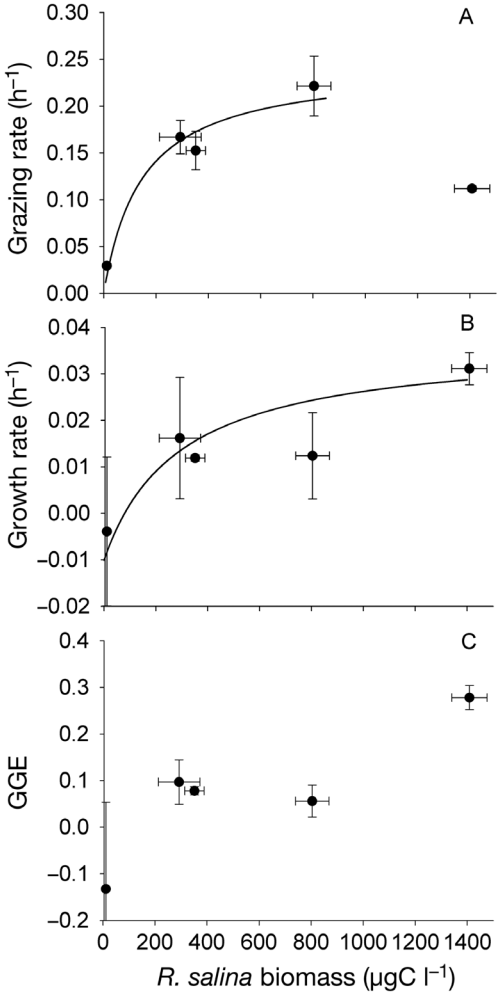

Fig. 1. Experiments with a constant concentration of prey. (A) Specific grazing rates of *Gyrodinium dominans* on the prey (*Rhodomonas salina*) (means ± SD). Parameters of the fitted model (Eq. 4) are i_{max} = 0.24 ± 0.03, K_m = 146 ± 65 (mean ± SD), r^2 = 0.96. The outlier was not considered in the regression line. (B) Specific growth rates of *G. dominans* (means ± SD). Parameters of the fitted model (Eq. 3) are μ_{max} = 0.036 ± 0.011, k = 370 ± 236, and C' = 79.8 ± 38.2, r^2 = 0.64. (C) Gross growth efficiency (GGE) calculated as specific growth rate/specific grazing rate (means ± SD)

$p < 0.001$; Expt 2: $r^2 = 0.772$, $p < 0.001$; Expt 3: $r^2 = 0.887$, $p < 0.001$) (Fig. 2B). The initial decline in *G. dominans* could be explained by factors such as stress, adaptation to the new incubation bottles, or death because of experimental manipulations.

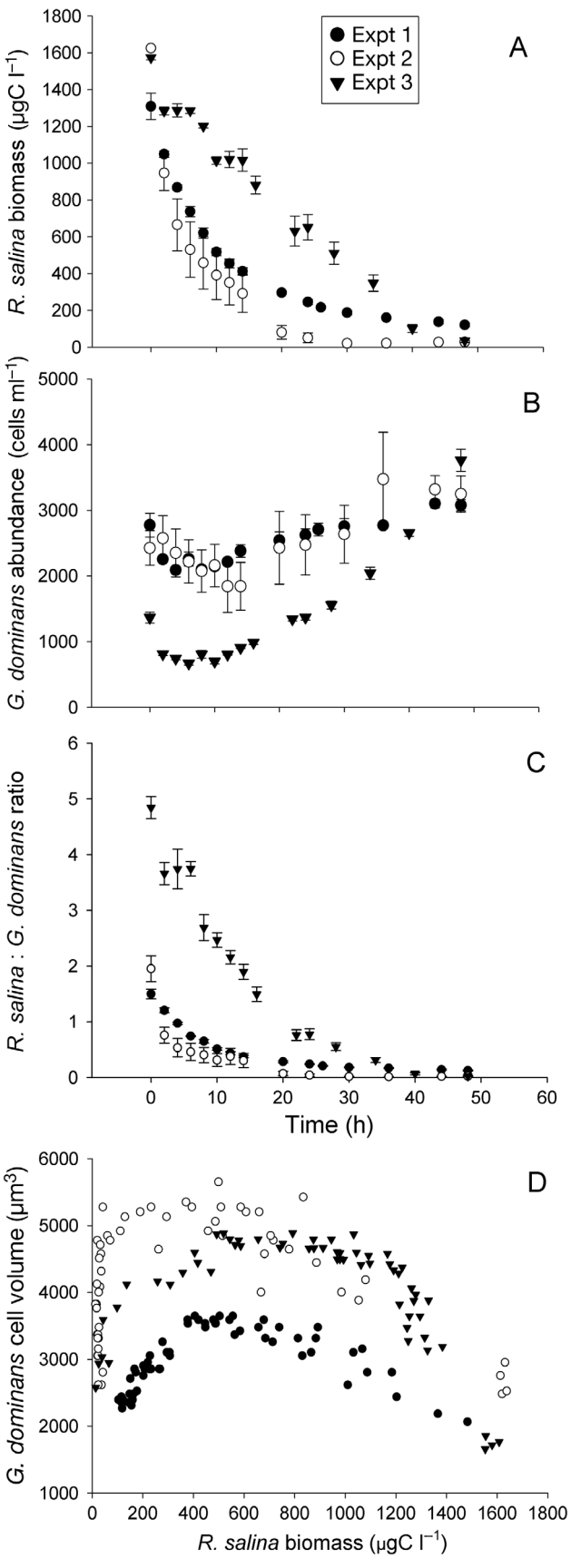

Fig. 2. Experiments with a single pulse of prey (Expts 1 to 3). Time series of average values (±SE) of (A) the biomass of *Rhodomonas salina*, (B) the abundance of *Gyrodinium dominans* and (C) the prey:predator biomass ratio. (D) Average values (±SE) of the biovolume of *G. dominans* as a function of the biomass of *R. salina*

Ratios of prey:predator biomass decreased directly from the beginning in Expts 1 and 2, whereas in Expt 3 it remained high during the first 8 h and then decreased towards the end of the incubation period (Fig. 2C). these differences gave rise to different and significant biomass increases among the 3 experiments (1-factor ANOVA among slopes from linear regressions on biomass vs. time: $F_{2,43} = 46.26$, $p < 0.001$).

The cell volume of *Gyrodinium dominans* increased during the first 8 to 10 h (increase: 197 ± 67%, mean ± SD) and returned to the initial volume towards the end when concentrations of *Rhodomonas salina* fell below 200 µgC l^{-1}. These differences in cell volume were significant (1-factor repeated measures ANOVA — Expt 1: $F_{14,59} = 38.2$, $p < 0.001$; Expt 2: $F_{13,55} = 18.8$, $p < 0.001$; Expt 3: $F_{14,59} = 13.2$, $p < 0.001$) (Fig. 2D). Cell volumes increased with specific grazing rates calculated from 8 h periods in Expts 1 and 2 and were correlated significantly in Expt 1 (linear regression: $r^2 = 0.382$, $p < 0.01$).

Specific growth rates varied from ca. −0.01 to 0.03 h^{-1} in Expt 1, ca. −0.04 to 0.06 h^{-1} in Expt 2, and ca. 0.01 to 0.06 h^{-1} in Expt 3 (Fig. 3). To test for differences in the relationships between growth rates and prey concentrations between the 2 treatments (single pulse of prey and constant prey concentrations), we compared their functional responses (Fig. 3). This test showed no significant differences in the shape of the functional response (1-factor ANOVA on R_0, R_{max} and K_m, $p > 0.85$). The initial concentrations of prey in both treatments were chosen to gain comparable growth rates between the 2 treatments (Fig. 3).

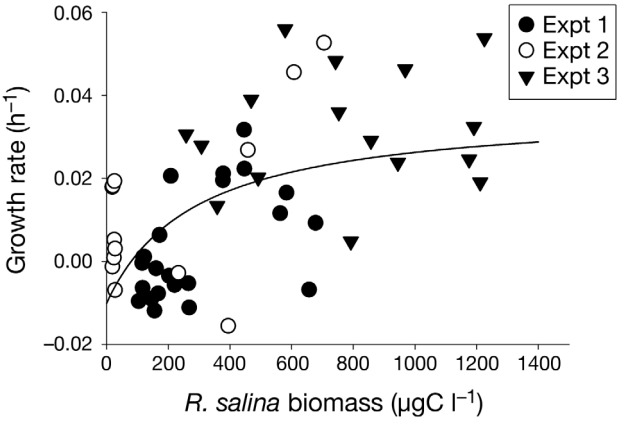

Fig. 3. Comparison of growth rates of *Gyrodinium dominans* between the 3 experiments involving a single pulse of prey and the experiment with a constant concentration of prey (continuous line). Growth rates with the single pulse of prey were calculated from distinct 8 h periods throughout the incubation period and plotted against the average concentration of *Rhodomonas salina* prey during those periods

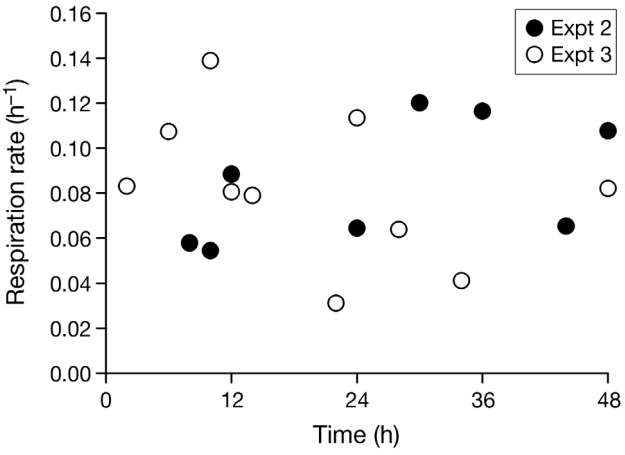

Fig. 4. *Gyrodinium dominans*. Non-steady-state experiments (Expts 2 and 3): specific respiration rate of *G. dominans* during the incubation period

Specific respiration rates showed no trend throughout the incubation periods but exhibited an average of 0.08 ± 0.01 h^{-1} for Expts 2 and 3 (Fig. 4; linear regressions, slopes: $p > 0.05$ not shown on the figure). In order to assess a preliminary energetic budget of *Gyrodinium dominans*, we grouped the data in relation to food concentration: low values (18 to 39 µgC l^{-1}), medium values (469 to 656 µgC l^{-1}) and high values (874 to 1314 µgC l^{-1}) (see Table 3). While growth and respiration rates were low and similar, ingestion rates increased more than 3-fold when levels of food were high. GGE was the highest at a medium level of food.

DISCUSSION

Specific growth rates at pulse feeding vs. constant food

We found no significant differences in the patterns of specific growth rates between the 2 treatments. This observation confirms the assertion that heterotrophic dinoflagellate growth rates respond quickly to changes in food abundance and that they are well adapted to an environment with fluctuating concentrations of prey. Hansen (1991) concluded that heterotrophic dinoflagellates successfully track increases in phytoplankton biomass during bloom situations and may be able to control phytoplankton biomass (during the spring bloom, for example) significantly better than mesozooplankton grazers. This ability is probably common in microzooplankton, as was shown for ciliates by Montagnes (1996) and Montagnes & Lessard (1999). These authors sug-

gested that many planktonic ciliates can exploit patches of food and that their survival is dependent on the occurrence of such patches.

The numerical response of *Gyrodinium dominans* acclimated to a constant algal concentration showed negative growth rates at prey concentrations <200 µgC l^{-1}. Thus, although *G. dominans* may be well adapted to fluctuations in food concentration, it is probably also adapted to relatively eutrophic conditions. At food concentrations between 200 and 400 µgC l^{-1}, we observed a major increase in the growth of *G. dominans*. μ_{max} = 0.05 h^{-1} is in accordance with data from the literature for this species or other heterotrophic dinoflagellates that feed on *Rhodomonas salina* (Strom 1991, Hansen 1992, Jakobsen & Hansen 1997).

Respiration

In metazoans, respiration is often coupled to the rate of growth through the specific dynamic action (SDA). The SDA is the result of an elevated energy demand for the integrated physical and physiological process of feeding (Jobling 1983, Kiørboe et al. 1985, Brown & Cameron 1991). Accordingly, the respiration rate is tightly coupled to both ingestion and growth rates in marine pelagic copepods (Thor 2000, 2002, Thor et al. 2002). However, in our study, respiration rates of non-steady-state *Gyrodinium dominans* were not significantly coupled to specific growth rates and remained fairly constant during the experiments. Moreover, specific respiration rates seemed to be higher than specific growth rates, which suggests an enhanced energy demand from acclimatization to the pulsed food concentration—suggesting, in turn, that pulsed prey conditions may be metabolically demanding. Thus, despite the apparent adaptation to fluctuating concentrations of food, there is a significant loss of energy during these fluctuating conditions.

Energy budget

A preliminary energy budget for a microzooplanktonic dinoflagellate was built using the physiological parameters obtained. A striking result of our study was the high assimilation efficiency at the lower levels of food (Table 3). With this behavior, the organisms can have a better assimilation efficiency at low vs. high concentrations of food, thereby optimizing their metabolism at low energy levels.

The GGE ratio is the fraction of prey carbon that is consumed and converted to body mass; it gives an estimate of the success of an organism in converting ration to biomass. In a review of the GGE of different taxonomic groups—from protozoans to metazoans—Straile (1997) concluded that mean and median values for all taxa scatter between 20 and 30%. Hansen et al. (1997), in their review on zooplankton (of 2 to 2000 µm body size), found values of 33 ± 3%. GGEs determined here for *Gyrodinium dominans*—under both conditions of food availability—are within the range of values reported for other heterotrophic protozoans (Caron et al. 1990). However, while GGE decreased with high concentrations of food in organisms exposed to a single pulse of food, the opposite was observed in organisms acclimatized to a constant level of food. In ciliates, GGEs generally decrease with increasing algal concentration (Verity 1985, Jonsson 1986, Strom 1991). This means that the success of an organism transferring phytoplankton carbon is higher when food is scarce, and this observation is in accordance with our energy budget. In contrast, the observation that GGE increases with food concentration when the organisms are exposed to a constant level of food is similar to the results for ciliates reported by Montagnes & Lessard (1999) for ciliates.

Evaluation of methodology

A source of variability in our experiments was related to the fact that both cultures of food and predator were not axenic. However, this is the procedure used in most studies on growth and grazing of dinoflagellates or ciliates (e.g. Hansen 1992, Nakamura et al. 1992, 1995, Strom & Buskey 1993, Jakobsen & Hansen 1997). This is because the optimal food source for small heterotrophic *Gyrodinium dominans* are organisms belonging to the nanoplankton (Hansen 1992). Nakamura et al. (1995) showed that growth rates of *G. dominans* feeding upon bacterial flocks showed the highest rates recorded for this dinoflagellate, but organisms fed with only free-living bacteria could not sustain growth. In our experiments, freely swimming bacteria may have been present but we argue that bacterial flocks did not form due to the short incubation periods.

Concluding remarks

In summary, our time-based experiments showed an increase in cell volume of *Gyrodinium dominans*

fed a single pulse of food. Cell volume decreased below a given concentration of prey concurrently with the increase in abundance of cells. Logically, this may be a result of cell division. It seems that the onset of cell division may relate to some specific concentration of prey because we observed decreased average cell volumes when concentrations of *Rhodomonas salina* decreased below 400 µgC l^{-1} in all 3 experiments. *Gyrodinium* spp. have the ability to adopt a swarmer strategy when they experience starvation; they produce small and fast swimming individuals when concentrations of food are low (Hansen 1992). Moreover, at the highest levels of food, the ingestion rate was the highest, while the mean growth rate was higher with medium levels of food. These results also support the suggestion that *G. dominans* responds quickly to changes in abundance of food. Finally, the energy budget of these organisms behaves similarly to the one found for other heterotrophs, suggesting that they should be normally adapted to poor feeding conditions, but can also efficiently exploit the occasional finding of concentrated patches of food.

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