Dominance and compensatory growth in phytoplankton communities under salinity stress

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ABSTRACT

Increasing levels of environmental stress due to global warming and eutrophication, and concerns about an unparalleled global diversity loss, have triggered new interest in the question whether the stability of ecosystem properties depends on population dynamics of dominant species or on compensatory growth of rare species. Recent meta-analyses suggest that compensatory dynamics are rare in natural systems. Experimental results, however, indicate that the interdependence of stressor regime, species traits, and species richness determines which mechanisms stabilise communities. Stability will depend on population dynamics of dominant species, if they remain the best performers regardless of disturbance. If dominant species become rare or lost, compensatory growth of rare species will insure natural communities against complete failure. Salinity is an important stressor governing growth and distribution of phytoplankton in brackish ecosystems, and its impact on coastal aquatic ecosystems is likely to change due to global warming. We performed two short-term experiments to investigate the effects of salinity stress on community structure and biomass production of natural phytoplankton communities collected in tidally influenced and polymictic Lake Waihola (New Zealand). The lake was brackish when the inoculum for the first experiment was collected. The inoculum for the second experiment originated from a fresh water situation. In both experiments, the phytoplankton assemblage was exposed to a salinity gradient ranging from 0 - 5. To assess the importance of dominance and compensatory growth, we determined biomass production, species richness, diversity, evenness and dominance indices, and species specific growth rates.

Biomass production in our experiments was determined by dominant species. *Anabaena flos-aquae* dominated in the first experiment, and *Asterionella formosa* in the second experiment. Despite the importance of these species, we found significant growth responses of rare and abundant species. Even if these species showed high growth rates, biomass production was carried by the dominant species as long as the salinity level allowed them to grow. When the

salinity level was detrimental to the growth of the dominant species, reduced dominance and increased diversity indices emphasised the importance of compensatory growth of rare species. The salinity stress applied in our experiments was strong enough to change the hierarchy of successful functional traits, which affected community structure and biomass production of the plankton communities. If the predicted sea water rise, increasing frequency of storm tides, rising water temperatures, and altered precipitation and run-off cause the salinity of coastal aquatic ecosystems to change, major changes in community composition, diversity and dominance structure of planktonic primary producers might be expected.

Keywords:

Stability

Disturbance

Dominance

Compensatory growth

Salinity

Global climate change

1. Introduction

Worldwide ecosystems are exposed to an unprecedented global diversity loss (Pimm et al., 1995) and an increasing level of environmental stress, due to global warming (Caldeira and Wickett, 2003) and eutrophication (Billen et al., 1991; Harashima et al., 2006). Potentially detrimental effects of increased stress levels and extinction rates on ecosystem functioning have renewed scientific interest in studying the relationship between biodiversity and stability. The question whether all species in an ecosystem are necessary to sustain important resource dynamics is central to the ongoing discussion (Díaz and Cabido, 2001). Reductions in species richness affect ecosystem processes such as efficiency of resource use and biomass production according to recent reviews (Hooper et al., 2005; Balvanera et al., 2006; Cardinale et al., 2006). Identity and dominance of high performing species, however, are important factors affecting the outcome of experimental biodiversity-ecosystem functioning studies (Balvanera et al., 2006; Cardinale et al., 2006). The importance of local dominance and species richness for natural systems is still under discussion.

A few dominant species contribute the majority of aggregate biomass within plant communities, however, rare species account for the majority of species richness (Whittaker, 1965; Grime, 1998).

The presence of rare species with different responses to disturbance or stress than dominant species could affect community stability in a positive way, if the system is affected by perturbation or environmental change (Grime 1998; Walker et al., 1999). This is the case if the contribution of rare species to an ecosystem process increases, while the contribution of dominant species decreases because they are negatively affected by the perturbation. Such compensation among species is thought to insure ecosystems against functional declines caused by environmental fluctuations (Yachi and Loreau, 1999).

According to recent meta-analyses compensatory dynamics are rare in natural communities. This suggests that insurance effects are not strong mechanisms stabilising community fluctuations (Houlahan et al., 2007; Valone and Barber, 2008). There is evidence, however, that the mechanisms that stabilise natural communities are determined by the interdependence of stressor regime, species traits, and species richness (Flöder and Hillebrand, *submitted*). Stability will depend on population dynamics of dominant species, if these species with successful functional traits remain the best performers regardless of disturbance (Wardle et al., 1997; Grime, 1998). In this case population dynamics are expected to be synchronised due to increased resource availability after disturbance (Houlahan et al., 2007; Valone and Barber, 2008). If, on the other hand, disturbance or environmental change reverses the hierarchy of successful functional traits and dominant species become rare or lost (Jablonski, 1994; Grime, 1998), compensatory growth of rare and abundant species will insure natural communities against complete failure.

Coastal aquatic ecosystems are excellent model systems to study community stability under the impact of environmental change and disturbance. Between the present and the end of the century, climate change is predicted to cause sea levels to rise e.g. by 35 cm on the east coast of New Zealand's South Island. Coastal areas will be affected by an increasing frequency of storm tides, rising water temperatures, and altered precipitation and run-off (IPCC 2007). Since changes in salinity (Schallenberg et al., 2003; Flöder and Burns, 2004) and temperature levels (Petchey et al., 1999; Burgmer et al., 2007) impose stress on aquatic communities, the functioning of coastal aquatic ecosystems is likely to be affected by the global climate change.

Salinity is an important factor affecting phytoplankton communities in coastal aquatic ecosystems (Hammer, 1986; Rijstenbil, 1987; Day et al., 1989). Freshwater as well as marine species suffer severe osmotic stresses at a salinity of approximately five on the Practical Salinity Scale. This salinity level forms a lethal barrier for most estuarine planktonic algae (Kies, 1997). Compared with freshwater and marine systems, therefore, diversity and species number are reduced in brackish systems (Hartog, 1967; Remane and Schlieper, 1971; Schallenberg et al.,

2003; Flöder and Burns, 2004). Salinity concentrations in coastal aquatic ecosystems are highly variable, both spatially and temporally, reflecting relative inputs from watersheds and tidal water intrusion, circulation patterns and vertical and horizontal mixing processes (Redden and Rukminasari, 2008). Comparative studies of the oligohaline water bodies at Dungeness (Chapman et al., 1998) and in the Salado River Basin (Izaguirre and Vinocur, 1994) showed that the salinity level strongly influenced phytoplankton communities. Where salinities fluctuate, interspecific differences in salinity tolerances of phytoplankton play a major role in structuring phytoplankton communities (Kirst, 1989).

The natural phytoplankton assemblages used in our study originated from tidally influenced, polymictic, Lake Waihola, east coast, South Island, New Zealand. Saline intrusions and periodic salinity changes have been shown to significantly affect diversity and composition of Lake Waihola's phytoplankton community (Flöder and Burns, 2004). We performed two short-term experiments, which differed in the origin of the inoculum. Lake Waihola was in a brackish state when the inoculum for the first experiment was collected, whereas the inoculum for the second experiment originated from a fresh water situation. To apply different levels of stress, natural phytoplankton assemblages were exposed to a salinity gradient (0 - 5). Biomass production, the biomass based diversity measures Shannon and Weaver index (HB'), evenness (EB), and dominance (domB), species richness, and initial growth rates of phytoplankton species were determined as response variables.

We aimed to answer the following questions with this study:

1. Do the initially dominant phytoplankton species maintain their importance under increasing levels of salinity stress?
2. How important is compensatory growth of rare or abundant species after saline intrusions?
3. Are community structure and functioning of coastal aquatic ecosystems likely to be affected by the predicted implications of global climate change?

2. Material and Methods

2.1. Study site

Eutrophic and phosphorus-limited Lake Waihola (maximum depth, 2 m) is a tidally influenced polymictic lake on the Taieri Plain, South Island, New Zealand. At high tide, water from the outflowing Taieri River backs up into the lake, creating a tidal range of 20–50cm (Schallenberg et al., 2003). The tidal hydrological input is usually fresh water, but when the river flows are low, saline water enters Lake Waihola, which leads to considerable fluctuations in salinity (Flöder and Burns, 2004). Large influxes of fresh water occur in winter when water from a hydroelectricity storage lake upstream is released (Hall and Burns, 2002).

2.2. Experimental setup

Lake Waihola was slightly brackish (salinity: 1.07, 12.2 °C, 2.05.2001), when the inoculum for the first experiment ('oligohaline experiment') was collected. At the time of the collection for the second experiment ('freshwater experiment') the lake was in fresh water condition (salinity: 0.05, 19 °C, 17.09.01). To collect an inoculum, lake water seston (experiment 1: 30 L; experiment 2: 50 L) was concentrated to approximately 0.5 L using a 20 µm mesh net. To increase the concentration of larger phytoplankton species, this inoculum was enriched with net phytoplankton taken with a net of 48 µm mesh. Zooplankton was removed by pouring the inoculum through a 100 µm mesh size net and by gently bubbling the phytoplankton suspension with nitrogen gas (2 h). After this treatment, 5 ml of the inoculum were used to inoculate 95 ml of a modified WC medium (Guillard, 1975). To simulate eutrophic conditions with a tendency towards phosphorus limitation, the concentrations of the most important nutrients for algal growth (50 µg P L^{-1}, 1000 µg N L^{-1} and 1500 µg Si L^{-1}) were reduced in this medium. The medium was buffered and had a pH of 7. Using artificial seawater (Guillard, 1975) of different concentrations (salinity: 0.0, 0.5, 1, 2, 3, 4 and 5), we created a salinity gradient ranging from freshwater to oligohaline conditions (Venice System, 1958). This salinity treatment corresponded to the natural salinity range of Lake

Waihola. Experimental communities were grown in batch cultures in Erlenmeyer flasks for five days. A shaking table (74 rpm for 15 minutes every hour) kept the cultures in suspension. Lamps with an emission spectrum similar to daylight (Philips TDL 36W/89, Philips, Eindhoven, The Netherlands) supplied the cultures with light energy (110 µmol m^{-2} s^{-1} photosynthetic photon flux density). A day:night cycle of 16:8 hours simulated early summer conditions. Experimental temperature was 15 °C in both experiments. To minimize the effect of a slightly uneven light field, the Erlenmeyer flasks were randomly arranged on the shaking table every day. Phytoplankton samples were taken at the beginning and at the end of the experiment. Cells were counted under an inverted (Zeiss Axiovert 25) microscope (Utermöhl, 1958) following the method described by Lund et al. (1958).

2.3. Data analyses and calculations

To evaluate the hypotheses that community recovery is most likely to be carried by dominant species, we analysed the whole data set of the oligohaline experiment (a total 27 species), and compared it to a subset of the 12 species that were most abundant (≥ 200 cells L^{-1}) when the experiment was started. Based on the results of the oligohaline experiment 11 species that displayed signs of growth in at least one of the experimental treatments, were included in the analysis of the freshwater experiment. To assess the average biovolume of phytoplankton species, the dimensions of 20 individuals of each species were measured. Cell volumes were calculated using the formulae published by Hillebrand et al. (1999). Total biovolume (TB, based on the entire phytoplankton community and on the most abundant species respectively), biovolume based diversity indices [Shannon and Weavers H', E' (Washington 1984)] and the dominance index (domB, the relative proportional contribution of a species to TB) were determined as aggregate parameters describing the phytoplankton communities. In the context of this study, we define those species as dominant that contributed more than 80% to TB (domB > 0.8). Co-dominating species score an individual domB of > 0.1 and contributed more than 80 % to TB as a

group. Species that occurred with a density of ≥ 200 cells L^{-1} are considered abundant, and species with a cell density of < 200 L^{-1} are considered rare. Initial growth rates of phytoplankton species were calculated according to:

$$\mu = \frac{\ln N_2 - \ln N_1}{t_2 - t_1}$$

where μ signifies the specific growth rate per day, t_1 and t_2 are the days 0 and 5 of the experiment, and N_1 and N_2 the number of individuals of a species at t_1 and t_2 respectively. The response of the aggregate parameters and growth rates to gradually increasing salinity may be positive, negative or hump-shaped. Species specific growth rates can also display a threshold level above or below which a species is not able to grow.

2.4. Statistical analyses

We performed second degree polynomial regression analyses with a stepwise variable selection (backwards procedure, F to remove = 4) to analyse the response of aggregate parameters and growth rates to the salinity gradient. Whenever the graphical representation of the growth rates regression result suggested the existence of a threshold level, one-way ANOVA and Tukey's HSD test were performed to analyse its significance.

3. Results

3.1. Oligohaline experiment

3.1.1. Biovolume production

In the oligohaline experiment, total biovolume displayed a hump-shaped response to the salinity gradient. According to graphical representation (Fig. 1) and stepwise regression analysis (Table 1) of the data the pattern of biomass accumulation was very similar, regardless of whether all species were included in the analysis or if it was restricted to abundant species. Total biovolume was 0.0204 mm^3 L^{-1} (*Ln* TB = 0.0202) at the start of the experiment. Total biovolume

increased in all salinity treatments. In the 0 and 0.5 treatments, however, biovolume production was low. The highest biomass production was observed in the treatment with a salinity of 3, where the average biovolume produced by the entire phytoplankton community was 0.154 $mm^3 L^{-1}$ and 0.147 $mm^3 L^{-1}$ for the 12 initially abundant species. According to the regression result, biomass production peaked with 0.121 $mm^3 L^{-1}$ at a salinity of 3.21 (entire community) and 0.116 $mm^3 L^{-1}$ at a salinity of 3.26 (abundant species) respectively.

3.1.2. Diversity and dominance:

Species number decreased with increasing salinity when analysing the entire community. Stepwise regression analysis revealed a significant negative linear relationship (Table 1). The coefficient of determination, however, is rather low ($R^2 = 0.23$), indicating a weak relationship between these parameters. Biovolume based diversity measures, in contrast, were strongly related to salinity. Diversity (HB') and evenness (EB) indices decreased with increasing salinity (Fig. 1), displaying a tendency towards a u-shaped response. These responses were significant according to stepwise polynomial regression analysis (Table 1), as the linear term was significantly negative and the quadratic term significantly positive for both variables. Minima of diversity indices were within the salinity range tested. For HB' salinities of 3.61 (entire community) and 3.50 (abundant species) were determined, and 3.59 (entire community) and 3.48 (abundant species) for EB.

The response of HB' and EB could be attributed to the population dynamics of the cyanobacterium *Anabaena flos-aquae*, which had co-dominated (DomB = 0.38) with *Cyclotella radiosa* (DomB = 0.40) and *Stephanodiscus* c.f. *rotula* (DomB = 0.22) at the start of the experiment. In the course of the experiment, *A. flos-aquae* became dominant (DomB > 0.8) in treatments with a salinity of 3 and 4 (Fig. 1). In the 0, 0.5 and 1 treatments *Eudorina elegans* scored values > 0.10 DomB. The species co-dominated with *A. flos-aquae*, *Aulacoseira granulata* and *Synedra ulna* in one replicate of the salinity level of 0.5. Polynomial regression analysis identified a highly significant hump-shaped response of *A. flos-aquae* dominance to salinity

(Table 1). The calculated maximum was at a salinity of 3.81 (entire community) and 3.62 (abundant species).

3.1.3. Initial growth rates

Although the response of diversity and evenness of the experimental phytoplankton communities could be attributed to the biovolume development of *A. flos-aquae*, this species had positive growth rates only in treatments with a salinity of 3 and 4 (Fig. 2). The hump-shaped response was significant according to polynomial regression analysis (Table 2). The calculated peak for *A. flos-aquae* growth rate (salinity: 3.33) roughly corresponded to the peak biovolume production determined for the entire community and the subset of initially abundant species.

Of the twelve species that initially were abundant, besides *A. flos-aquae,* growth rate of the pennate diatom *Synedra ulna* (Fig. 2) showed a significant (Table 2) hump-shaped response (peak salinity: 2.24). The growth rates of the diatom *Aulacoseira granulata* and the green algae *Monoraphidium arcuatum*, *M. tortile* and *Scenedesmus quadricauda* decreased with increasing salinity, whereas the ones of the diatoms *Cylindrotheca closterium* and initially co-dominant *Stephanodiscus* c.f. *rotula* increased with salinity (Fig. 2, Table 2). The population size of the diatom *Cyclotella radiosa* and the green algae *Scenedesmus acutus*, *S. bicaudatus* and *S. ovalternus* increased in none of the salinity treatments. Four initially rare species, however, had considerable growth responses to the salinity gradient (Fig. 2). The growth rate of the cyanobacterium *Merismopedia elegans* increased with increasing salinity, whereas the population growth of the diatom *Nitzschia* sp. decreased. The latter species grew only within the salinity range of 0 – 2; above a salinity of 2 population sizes declined (significant difference according to Tukey's HSD, one-way ANOVA, d.f.: 6, 14, F: 83.91, $p < 0.001$). The green algae *Ankistrodesmus fusiformis* and *Eudorina elegans* were able to grow within the entire range of salinities tested. *A. fusiformis* growth rates showed a significant humped response (Table 2). Highest growth rates were determined at a salinity of 2 (calculated peak: 2.17). Growth rates of

Eudorina elegans tended to decrease with increasing salinity. Due to one outlier in the treatment with a salinity of 1 (Fig. 2), however, all variables were removed from the stepwise regression analyses.

3.2. Freshwater experiment

3.2.1. Biovolume production

Eleven species displayed signs of growth in at least one of the salinity treatments of the freshwater experiment. Total biovolume production of these species decreased with increasing salinity (Fig. 1), tending to stabilise at low salinities (< 3) and to decrease at higher salinities (> 3). Since total biovolume was 4.23 mm^3 L^{-1} (*Ln* TB = 1.66) at the start of the experiment, biomass was produced throughout the range of salinities tested. In two replicates of the salinity level of 5, however, biomass production was low. According to stepwise polynomial regression analysis, the relationship between total biovolume and salinity was significant and could be described by a power function (Table 3).

3.2.2. Diversity and dominance

Biomass based diversity indices (HB' and EB) increased with increasing salinity in the freshwater experiment (Fig. 1). The relationship between both diversity measures and salinity level was significant according to the result of stepwise regression analysis, and is best described by power functions (Table 3). As in the oligohaline experiment, the population development of a dominant species is closely linked to the response of HB' and EB. In the freshwater experiment the diatom *Asterionella formosa* dominated the biovolume at the beginning of the experiment (DomB = 0.97). This species remained dominant (DomB > 0.8) in all salinity treatments except in the treatment with a salinity of 5, where the average DomB was 0.63.

3.2.3. Initial growth rates

Dominant *Asterionella formosa* was able to grow throughout the entire salinity gradient, except in two replicates of the salinity level of 5 (Fig. 3), which resulted in higher diversity indices and a

lower total biovolume. The initially rare chlorophyte *Actinastrum hantzschii* showed a similar pattern. High growth rates were determined within a salinity of 0 – 4. *Dictyosphaerium pulchellum* grew well within the salinity range of 0 – 3 but growth rates decreased at higher salinity (Table 4). The chrysophyte *Dinobryon divergens* was able to grow only in the freshwater treatment, whereas the small diatom *Cyclotella sp.* and the chlorophyte *Monoraphidium tortile* showed no preference regarding the salinity level and grew in each treatment. Growth rates of *M. komarkovae* increased with increasing salinity. The low coefficient of determination of the regression analysis, however, indicates a rather weak relationship (Table 4). Three diatom and one chlorophyte species displayed hump shaped responses to the salinity gradient (Fig. 3, Table 4). The calculated maximum growth rate was at a salinity of 3.32 for *Aulacoseira granulata*, 3.78 for *Cyclotella radiosa*, 2.34 for *Cylindrotheca closterium* and 2.11 for the initially rare chlorophyte *Treubaria* sp.

4. Discussion

4.1. Population dynamics and biomass production of dominant and rare species

Population dynamics of the dominant species determined the response of total biovolume and biovolume based diversity measures of the phytoplankton communities in both experiments. Biomass production was high and diversity was low in those salinity ranges that were associated with high growth rates of the dominant species. This indicates that, as it is the case for ecosystem processes in most systems (Grime, 1998; Smith and Knapp, 2003), biomass production in our experiments was determined by dominant species. Despite the importance of these species, however, we found compensatory growth responses of abundant and rare species in both experiments. Even if these species displayed high growth rates, the dominant species carried the biovolume production as long as the salinity level allowed them to grow. In the absence of nutrient limitation dominant fast growing species were able to produce a larger proportion of biomass than initially rare species, which was due to their high initial biovolume level. This is

consistent with results from experimental biodiversity stability studies that found increasing resilience to be related to the increasing dominance of fast growing species (Steiner et al., 2005; 2006). Whenever the salinity level was detrimental to the growth of the dominant species, reduced dominance and increased diversity measures indicated that the importance of compensatory growth by rare and abundant species increased in these situations. Our result supports the hypothesis that interdependence of stressor regime, species traits, and species richness determines which mechanisms stabilise natural communities. If dominant species remain the best performers regardless of disturbance, stability will depend on population dynamics of these dominant species. If disturbance or environmental change reverses the hierarchy of successful functional traits and dominant species become rare or lost, stability will depend on compensatory growth of rare species (Flöder and Hillebrand, *submitted*).

Salinity is an important stressor governing growth and distribution of phytoplankton in marine and brackish ecosystems (Hammer, 1986; Rijstenbil, 1987; Day et al., 1989). Salinity changes and fluctuations within the mesohaline to euhaline range of the salinity spectrum (Venice system, 1958) can result in osmotic shock, which usually affects phytoplankton growth rates (Kirst, 1989). Variable salinities affect phytoplankton community composition because recovery times after osmotic shock vary among species (Kies, 1997). The salinity levels that we used in our experiment ranged from fresh water to oligohaline according to the Venice system for the classification of marine waters (Venice system, 1958). Since a salinity of circa 5 forms a lethal barrier for many estuarine algae because freshwater and marine species suffer severe osmotic stresses at this salinity level (Kies, 1997), the salinity in our experiment treatment is likely to have acted as stress or disturbance (sensu Grime, 1979). Salinity changes within this range, therefore, are very likely to have the potential to change the hierarchy of successful functional traits and to change the dominance structure in phytoplankton communities.

4.2. Salinity affects specific growth rates: consequences for plankton community composition

We observed species specific growth rate differences in response to the salinity gradient in our experiments, regardless whether the phytoplankton communities originated from oligohaline or from fresh water conditions. Salinity optima and tolerances have previously been shown to be species specific (e.g. Braarud, 1951; Carpelan, 1964; Tanaka et al., 1983; Saros and Fritz, 2000; Thessen et al., 2005). Typical estuarine phytoplankton species generally tolerate low salinities better than oceanic species, while coastal phytoplankton species cover an intermediate range. Lower and upper limits of salinity tolerance, however, depend largely on the adaptation of the species (Kirst, 1989). Such differences in salinity adaptation are likely to be responsible for the inconsistency in growth responses that two species, *Aulacoseira granulata* and *Cylindrotheca closterium*, displayed in our study.

The dominant species in the oligohaline experiment was the filamentous cyanobacterium *Anabaena flos-aquae*, while the diatom *Asterionella formosa* dominated the freshwater experiment. *A. flos-aquae* and *A. formosa* have been characterised as freshwater species that are able to tolerate low levels of salinity, as do the majority of species in our experiments (Komarek and Fott, 1983; Pankow et al., 1990; Hällfors, 2004). Over the summer months, *A. flos-aquae* tends to form massive plankton blooms in Lake Waihola (Faithfull and Burns, 2006; Downs et al., 2008). *A. flos-aquae* displayed a clear preference for the salinity level of 3, probably due to adaptation to the oligohaline conditions that predominated at the time the inoculum was collected. Towards the fresh water end of the salinity gradient, when *A. flos-aquae* ceased to grow and dominance values were low, the initially abundant *Aulacoseira granulata* (diatom), *Monoraphidium arcuatum*, *Monoraphidium tortile*, *Scenedesmus quadricauda* (green algae), and the initially rare *Nitzschia* sp. (diatom) and *Eudorina elegans* (green algae) showed compensatory growth. Compensatory growth at higher salinities was observed in the initially abundant

Stephanodiscus c.f. *rotula* (diatom), the marine species (Hällfors, 2004; Pankow, 1990) *Cylindrotheca closterium* (diatom) and the initially rare *Merismopedia elegans* (cyanobacterium).

In the freshwater experiment, growth rates of *A. formosa* were in the same range, up to the salinity level of 5 that has been reported as representing a lethal barrier for most estuarine plankton algae (Kies, 1997). Compensatory growth at high salinity levels was observed for the initially abundant diatoms *Aulacoseira granulata*, *Cyclotella radiosa* and *Cyclotella* sp., and the green algae *Monoraphidium komarkovae*, *M. tortile* and initially rare *Treubaria* sp.

Based on the responses described above, even small changes in salinity primarily affect the composition of phytoplankton communities of oligohaline systems. Our results are in close agreement with those of Redden and Rukminasari (2008), who observed that raising the salinity from 1.5 to 5.5 resulted in significant alteration of phytoplankton community composition. Similarly, Pilkaitytë et al. (2004) found that shifting salinity from oligohaline (salinity: 3) to mesohaline (salinity:12) primarily influenced the taxonomic composition of the phytoplankton community.

Owing to the short duration of our experiments the response of species richness was weak in the oligohaline experiment. The strong relationships between salinity and the diversity measures HB', EB and domB, which are expected to react instantly to environmental stress (Hillebrand et al., 2008), emphasised the importance of salinity as a stressor in coastal aquatic ecosystems. We observed relevant changes in the dominance structure of the phytoplankton assemblages after only five days of salinity stress. These changes are likely to signify a transient process to a completely different community. As phytoplankton characteristics like productivity, size, nutritional quality or potential toxicity are crucial for the growth and reproduction of grazing zooplankton (e.g. Lampert, 1981; Richman and Dodson, 1983; Gliwicz, 1990; Urabe and Sterner, 1996; Sterner and Elser, 2002), changes in the phytoplankton community composition could affect not only

processes at the primary producer level, but also have the potential to influence ecosystem functions at higher trophic levels.

4.3. Conclusions

Phytoplankton communities in our experiments were governed by dominant species as long as these species were not affected by the environmental stress applied. Salinity, the stressor used in this study, was strong enough to change the hierarchy of successful functional traits. Compensatory growth of abundant and rare species occurred where the salinity level inhibited the growth of dominant species. Structure and biomass production of the phytoplankton communities were affected as a consequence. This leads to the conclusion that coastal aquatic ecosystems are likely to be affected by the global climate change. If the predicted sea level rise, increased frequency of storm tides, rise in water temperatures, and altered precipitation and run-off (IPCC 2007) cause the salinity level of coastal aquatic ecosystems to change, major changes might be expected in community composition, diversity, and dominance structure of planktonic primary producers, with possible consequences throughout the food web.

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Table 1: Polynomial regression results for experiment 1 (oligohaline experiment). Dependent variables: total biovolume (*Ln* TB, in $mm^3\ L^{-1}$), species richness (S), diversity- (HB'), evenness- (EB) indices and dominance (DomB) index of *Anabaena flos-aquae* based on biovolume density. Independent variable: salinity, entered in linear (sal) and squared (sal^2) form to account for possible hump shaped responses. TB and the indices were calculated based on the whole data set comprising 27 species (All Species) and on the data of the 12 most abundant species (initial abundance ≥ 200 cells L^{-1}).

Dependent Variable	sal		sal^2		Regression equation	R^2	*P*
	ß	*p*	ß	*p*			
All Species							
Ln TB	+	0.008	–	0.029	$= 0.0276 + 0.0540\ sal - 0.0084\ sal^2$	0.42	< 0.008
S	–	0.029			$= 18.405 - 0.3550\ sal$	0.23	< 0.030
HB'	–	0.000	+	0.005	$= 2.0312 - 0.6967\ sal + 0.0965\ sal^2$	0.70	< 0.001
EB	–	0.000	+	0.005	$= 0.6915 - 0.2323\ sal + 0.0324\ sal^2$	0.69	< 0.001
DomB	+	0.000	–	0.010	$= 0.4420 + 0.2178\ sal - 0.0286\ sal^2$	0.70	< 0.001
Abundant Species							
Ln TB	+	0.005	–	0.022	$= 0.0171 + 0.0568\ sal - 0.0087\ sal^2$	0.46	< 0.004
HB'	–	0.000	+	0.004	$= 1.6419 - 0.6162\ sal + 0.0880\ sal^2$	0.67	< 0.001
EB	–	0.000	+	0.005	$= 0.6993 - 0.2683\ sal + 0.0386\ sal^2$	0.66	< 0.001
DomB	+	0.001	–	0.014	$= 0.5527 + 0.1868\ sal - 0.0258\ sal^2$	0.62	< 0.001

Table 2: Polynomial regression results for experiment 1 (oligohaline experiment). Dependent variables: initial growths rates of *Anabaena flos-aquae* (*Ana flo*), *Aulacoseira granulata* (*Aul gra*), *Cyclotella radiosa* (*Cyc rad*), *Monoraphidium arcuatum* (*Mon arc*), *Monoraphidium tortile* (*Mon tor*), *Cylindrotheca closterium* (*Cyl clo*), *Scenedesmus acutus* (*Sce acu*), *Scenedesmus bicaudatus* (*Sce bic*), *Scenedesmus ovalternus* (*Sce ova*), *Scenedesmus quadricauda* (*Sce qua*), *Stephanodiscus* c.f. *rotula* (*Ste rot*), *Synedra ulna* (*Syn uln*), and the initially rare *Ankistrodesmus fusiformis* (*Ank fus*), *Eudorina elegans* (*Eud ele*), *Merismopedia elegans* (*Mer ele*), and *Nitzschia sp*. (*Nitz sp.*). Independent variable: salinity, entered in linear (sal) and squared (sal^2) form to account for possible hump shaped responses.

Species	sal		sal^2		Regression equation	R^2	P
	ß	p	ß	p			
Ana flo	+	0.000	–	0.001	$\mu = -0.326 + 0.2404\ sal - 0.0361\ sal^2$	0.71	< 0.001
Aul gra	–	0.000			$\mu = 0.1087 - 0.1035\ sal$	0.66	< 0.001
Cyc rad							
Mon arc			–	0.010	$\mu = 0.4008 - 0.0062\ sal^2$	0.30	< 0.010
Mon tor			–	0.003	$\mu = 0.7481 - 0.0094\ sal^2$	0.37	< 0.003
Cyl clo	+	0.000			$\mu = -0.3997 + 0.2097\ sal$	0.81	< 0.001
Sce acu	+	0.043			$\mu = -0.7694 + 0.0833\ sal$	0.20	< 0.043
Sce bic							
Sce ova							
Sce qua	–	0.022			$\mu = 0.0686 - 0.0418\ sal$	0.25	< 0.022
Ste rot	+	0.000			$\mu = -0.4339 + 0.2199\ sal$	0.76	< 0.001
Syn uln	+	0.020	–	0.010	$\mu = 0.3732 + 0.1583\ sal - 0.0353\ sal^2$	0.34	< 0.024
Initially rare species							
Ank fus	+	0.002	–	0.000	$\mu = 0.5393 + 0.4301\ sal - 0.0991\ sal^2$	0.56	< 0.001
Eud ele							
Mer ele	+	0.002			$\mu = -0.0194 + 0.0709\ sal$	0.41	< 0.002
Nitz sp.	–	0.000			$\mu = 0.8926 - 0.2739\ sal$	0.69	< 0.001

Table 3: Polynomial regression results for experiment 2 (freshwater experiment). Dependent variables: total biovolume (*Ln* TB, in $mm^3\ L^{-1}$), species richness (S), diversity- (HB'), evenness- (EB) indices and dominance (DomB) index of *Asterionella formosa* based on biovolume density. Independent variable: salinity, entered in linear (sal) and squared (sal^2) form to account for possible hump shaped responses.

Dependent Variable	sal		sal^2		Regression equation	R^2	*P*
	ß	*p*	ß	*p*			
Ln TB			–	0.000	$= 3.816 - 0.0556\ sal^2$	0.65	< 0.001
HB'			+	0.001	$= 0.4271 + 0.0185\ sal^2$	0.48	< 0.001
EB			+	0.000	$= 0.1801 + 0.0084\ sal^2$	0.51	< 0.001
DomB			–	0.001	$= 0.9096 - 0.0082\ sal^2$	0.44	< 0.002

Table 4: Polynomial regression results for experiment 2 (freshwater experiment). Dependent variables: initial growths rates of *Actinastrum hantzschii* (*Act han*), *Asterionella formosa* (*Ast for*), *Aulacoseira granulata* (*Aul gra*), *Cyclotella radiosa* (*Cyc rad*), *Cyclotella sp* (*Cyc* sp.), *Dictyosphaerim pulchellum* (*Dic pul*), *Dinobryon divergens* (*Din div*), *Monoraphidium komarkovae* (*Mon kom*), *Monoraphidium tortile* (*Mon tor*), *Cylindrotheca closterium* (*Cyl clo*) and initially rare *Treubaria sp.* (*Tre* sp.). Independent variable: salinity, entered in linear (sal) and squared (sal^2) form to account for possible hump shaped responses.

Species	sal		sal^2		Regression equation	R^2	P
	ß	p	ß	p			
Act han			–	0.011	$\mu = 0.9392 - 0.0136\ sal^2$	0.30	< 0.011
Ast for			–	0.000	$\mu = 0.4606 - 0.0143\ sal^2$	0.61	< 0.001
Aul gra	+	0.000	–	0.002	$\mu = 0.4716 + 0.2254\ sal - 0.0340\ sal^2$	0.67	< 0.001
Cyc rad	+	0.000	–	0.002	$\mu = 0.5141 + 0.1618\ sal - 0.0214\ sal^2$	0.79	< 0.001
Cyc sp.							
Dic pul			–	0.000	$\mu = 0.5082 - 0.0226\ sal^2$	0.77	< 0.001
Din div	–	0.000	+	0.008	$\mu = 0.0663 - 0.9444\ sal + 0.1204\ sal^2$	0.74	< 0.001
Mon kom	+	0.016			$\mu = 0.1756 + 0.0810\ sal$	0.27	< 0.016
Mon tor							
Cyl clo	+	0.003	–	0.002	$\mu = 0.0112 + 0.3172\ sal - 0.0679\ sal^2$	0.44	< 0.005
Tre sp.	+	0.032	–	0.012	$\mu = 1.2090 + 0.0983\ sal - 0.0233\ sal^2$	0.36	< 0.019

Figure legends

Figure 1: Aggregate parameters after five days – oligohaline and freshwater experiments. Total biovolume (*Ln* TB, in mm^3 L^{-1}), diversity- (HB'), evenness- (EB) indices and dominance (DomB) indices of *Anabaena flos-aquae* (oligohaline experiment) and *Asterionella formosa* (freshwater experiment), based on biovolume density, in response to the salinity gradient.

Figure 2: Initial growth rates (μ) of some phytoplankton species from Lake Waihola along a salinity gradient – oligohaline experiment. Growth rates of two species (*Nitzschia* sp. and *Stephanodiscus* c.f. *rotula*) display a salinity threshold with respect to the salinity gradient. Significant differences according to Tukey's HSD test are signified by a different letter.

Figure 3: Initial growth rates (μ) of some phytoplankton species from Lake Waihola along a salinity gradient – freshwater experiment.

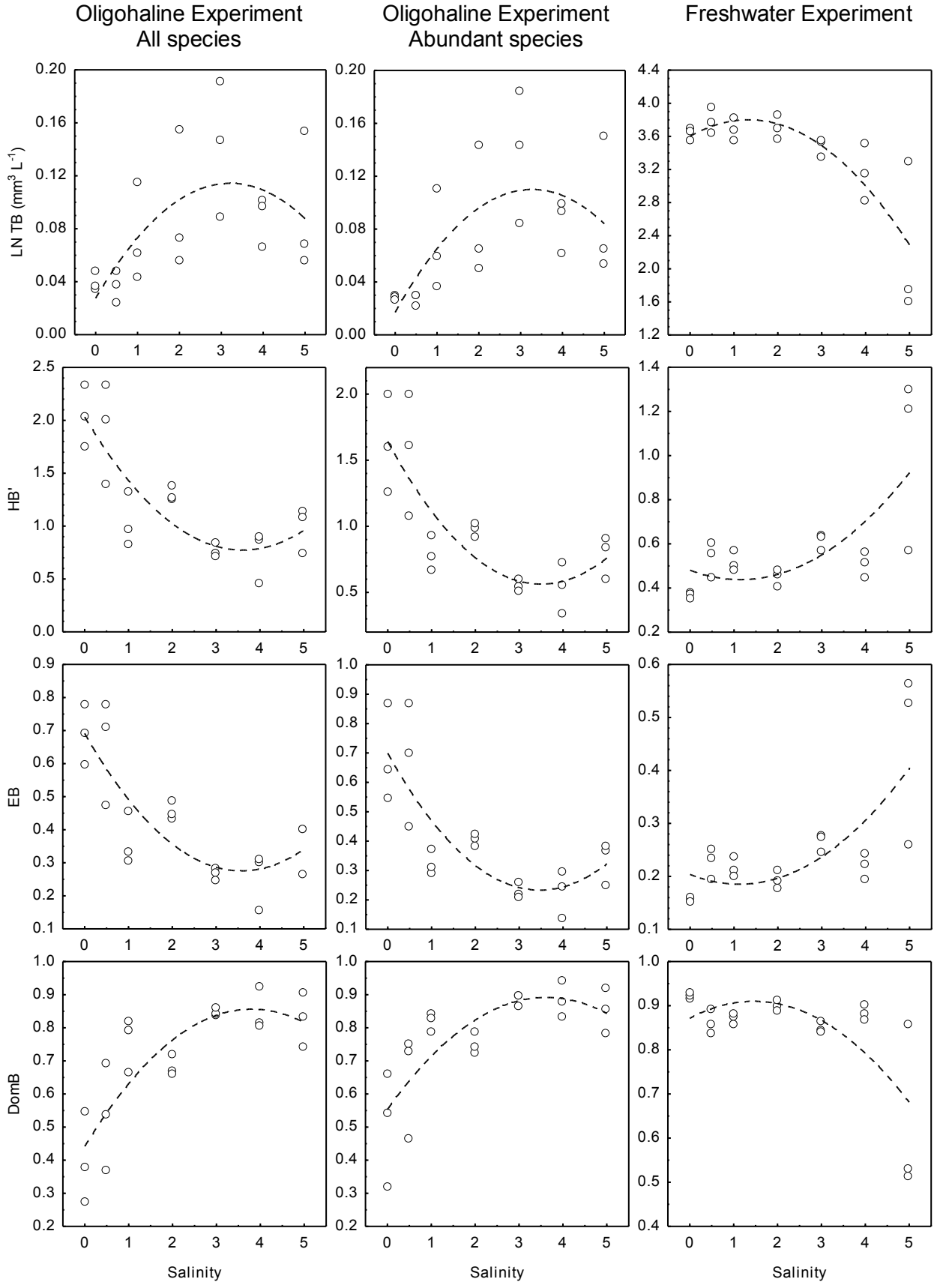
Oligohaline Experiment
All species
Oligohaline Experiment
Abundant species
Freshwater Experiment
LN TB (mm3 L-1)
HB'
EB
DomB
Salinity
Salinity
Salinity

Fig. 1

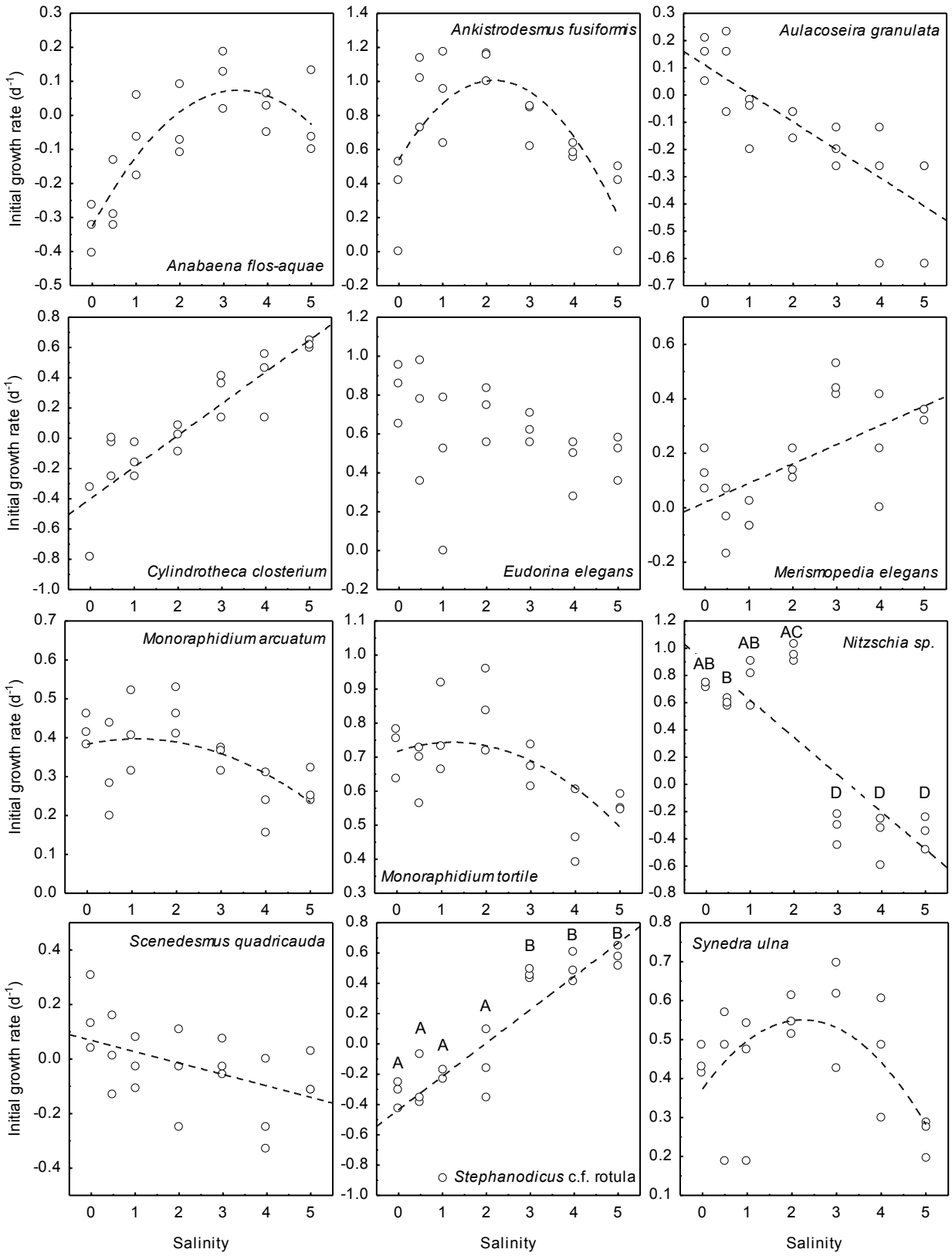
Anabaena flos-aquae
Ankistrodesmus fusiformis
Aulacoseira granulata
Cylindrotheca closterium
Eudorina elegans
Merismopedia elegans
Monoraphidium arcuatum
Monoraphidium tortile
Nitzschia sp.
Scenedesmus quadricauda
Stephanodicus c.f. rotula
Synedra ulna
Initial growth rate (d-1)
Salinity

Fig. 2

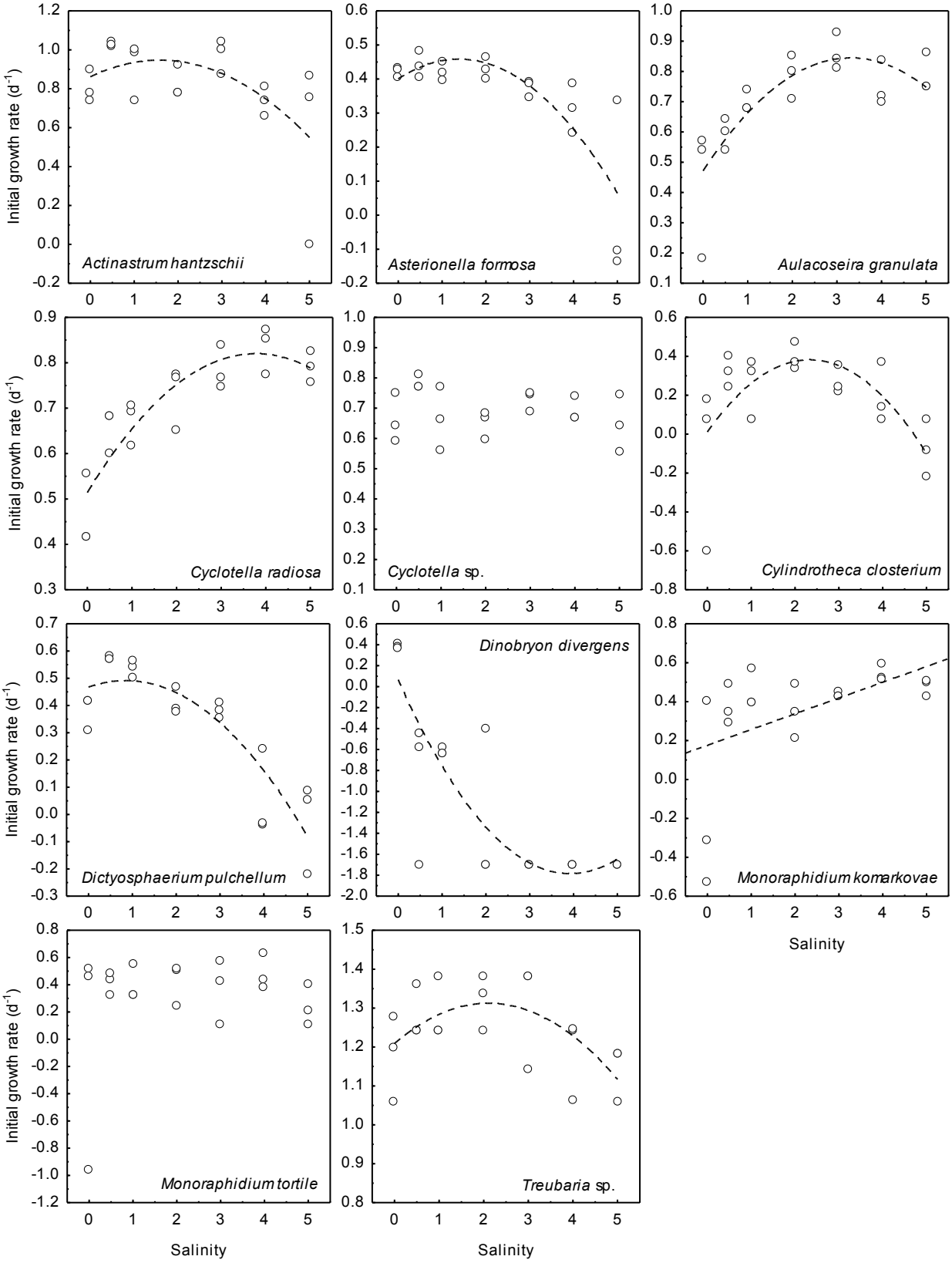
Initial growth rate (d-1)
Actinastrum hantzschii
Asterionella formosa
Aulacoseira granulata
Cyclotella radiosa
Cyclotella sp.
Cylindrotheca closterium
Dictyosphaerium pulchellum
Dinobryon divergens
Monoraphidium komarkovae
Monoraphidium tortile
Treubaria sp.
Salinity

Fig. 3