

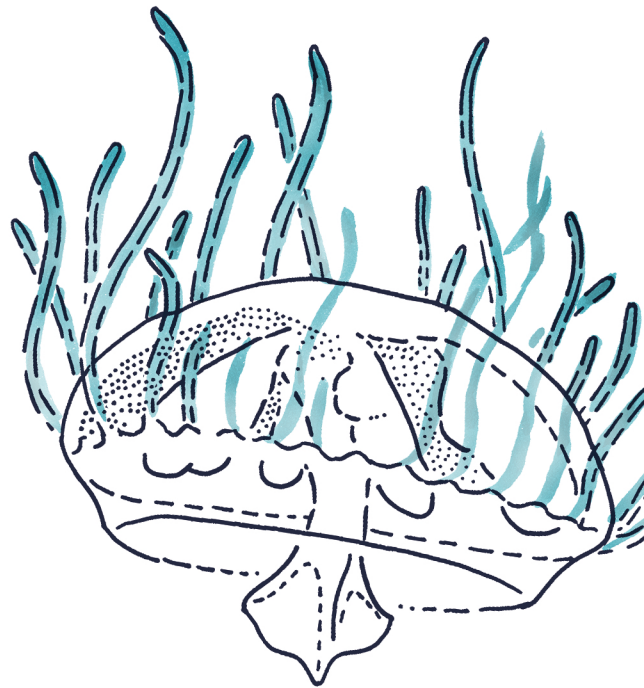
Genetic characterization and ecological effects of the invasive freshwater jellyfish *Craspedacusta sowerbii*

Dissertation

zur Erlangung des Doktorgrades der Naturwissenschaften
an der Fakultät für Biologie der
Ludwig-Maximilians-Universität München

vorgelegt von

Katrin Franziska Schachtl



München, den 25. Juni 2019

Eingereicht am: 25. Juni 2019

Termin der mündlichen Prüfung: 14. November 2019

Erstgutachten: Prof. Dr. Herwig Stibor

Zweitgutachten: Prof. Dr. Gerhard Haszprunar

Table of Contents

Summary	6
1 Introduction	9
1.1 Biological Invasions and Jellyfish	10
1.2 The Invasive Freshwater Jellyfish <i>Craspedacusta sowerbii</i>	11
1.2.1 Origin, Habitat and Distribution of <i>C. sowerbii</i>	11
1.2.2 Life Cycle of <i>C. sowerbii</i>	13
1.2.3 Taxonomy and Genetic Diversity of <i>Craspedacusta</i>	15
1.2.4 Limited Bisexual Reproduction of <i>C. sowerbii</i>	17
1.2.5 Feeding Ecology and Trophic Position of Polyps	18
1.2.6 Feeding Ecology and Trophic Position of Medusae	19
1.2.7 Top-down Influences by Jellyfish	21
1.2.8 Nutrient Redistribution by Jellyfish	22
1.3 Central Research Topics	24
2 Material and Methods	26
2.1 Genetic Analyses of <i>Craspedacusta</i>	27
2.1.1 Sampling Sites and Sampling Procedure	27
2.1.2 DNA Extraction	29
2.1.3 Mitochondrial COI and 16S rRNA Gene Sequence Analyses	29
2.1.4 Data Sets	30
2.1.5 Data Analyses	33
2.2 Functional and Numerical Response Analyses of Polyps	34
2.2.1 Experimental Design and Set-up	34
2.2.2 Data Analyses	36
2.3 Stable Isotope Analyses	37
2.3.1 Sampling Sites and Procedure	37
2.3.2 Sample Preparation and Isotopic Measurements	37
2.3.3 Data Analyses	38
2.4 Outdoor Mesocosm Experiments	40
2.4.1 Experimental Design and Set-up	40
2.4.2 Sampling and Measurements	41

Table of Contents

2.4.3 Data Analyses	42
2.5 Nutrient Distribution Experiments	44
2.5.1 Experimental Design and Set-up	44
2.5.2 Sampling and Measurements	45
2.5.3 Data Analyses	45
2.6 Field Survey of Lakes with and without Jellyfish	46
2.6.1 Sampling and Measurements	46
2.6.2 Data Analyses	46
3 Results	48
3.1 Genetic Analyses of <i>Craspedacusta</i>	49
3.1.1 Large-scale Data Set – Genetic Variation among Polyps and Medusae	49
3.1.2 Taxonomic Assignment – COI and Mitochondrial 16S rRNA Gene Phylogenies	52
3.1.3 Genetic Population Structure of Medusae	56
3.1.4 Small-scale Spatial Population Structure of Polyps	58
3.2 Feeding Ecology and Trophic Position of Polyps	60
3.2.1 Functional and Numerical Response Analyses of <i>Craspedacusta</i> and <i>Hydra</i>	60
3.2.2 Isotopic Niche Differentiation of <i>Craspedacusta</i> and <i>Hydra</i>	62
3.3 Trophic Cascades Mediated by Jellyfish	65
3.3.1 Initial Plankton Communities and Seston Stoichiometry	65
3.3.2 Mesozooplankton	66
3.3.3 Phytoplankton	73
3.4 Jellyfish and Phosphorus Distribution	81
3.4.1 Experiments with <i>C. sowerbii</i>	81
3.4.2 Experiments with Pelagic <i>Chaoborus spp.</i> Larvae	82
3.4.3 Experiment with a Crustacean Zooplankton Gradient	82
3.5 Evidence of Jellyfish Food Web Effects in the Field	83
4 Discussion	85
4.1 Genetic Diversity of <i>Craspedacusta</i>	86
4.1.1 Two <i>Craspedacusta</i> Species Invaded Europe	86
4.1.2 Haplotype Diversity	86
4.1.3 Association between Haplotype, Life Stage and Sex of Medusae	87

Table of Contents

4.1.4 Phylogenetic Analysis, Species Assignment and Species Names	87
4.1.5 Genetic and Sexual Structure of Medusae Populations	89
4.1.6 Sex Determination	90
4.1.7 Ecology and Genetic Diversity	91
4.1.8 Large-scale Dispersal and Multiple Introductions	93
4.1.9 Conclusion	94
4.2 Feeding Ecology and Trophic Position of Polyps	95
4.2.1 Functional and Numerical Response Analyses of <i>Craspedacusta</i> and <i>Hydra</i>	95
4.2.2 Isotopic Niche Differentiation of <i>Craspedacusta</i> and <i>Hydra</i>	97
4.2.3 Conclusion	99
4.3 Trophic Cascades Mediated by Jellyfish	100
4.3.1 Direct Jellyfish Effects on Mesozooplankton	100
4.3.2 Indirect Jellyfish Effects on Phytoplankton	102
4.3.3 Conclusion	106
4.4 Jellyfish and Phosphorus Dynamics	108
4.5 Evidence of Jellyfish Food Web Effects in the Field	110
5 Outlook	112
5.1 Tolerance Range and Dispersal Limitation of the Polyp Stage	113
5.2 Mechanisms Regulating Medusae Production and Sex Determination	113
5.3 Jellyfish and the Pelagic-Benthic Couplings of Fluxes of Energy and Matter	114
5.4 Migration Patterns of Jellyfish	114
5.5 Future Importance of Jellyfish as Members of Freshwater Food Webs	115
References	116
Index of Figures	132
Index of Tables	136
Supplementary Figures	138
Supplementary Tables	141
Curriculum Vitae	151
Publications and Presentations	153
Acknowledgements	155
Declarations	158

Summary

The freshwater jellyfish *Craspedacusta sowerbii* (Lankester 1880) is a globally recognized invasive species in freshwater ecosystems and presumably native to the Yangtze River System in China. This jellyfish species is characterized by specific life history traits, including several life history stages (e.g. benthic polyp, pelagic medusa) and reproductive strategies that allow high dispersal and the occurrence of high abundances within short times. Since the year 2000, numerous first-time records of *C. sowerbii* medusae from all over the world, often accompanied by conspicuous blooms, suggest a continued expansion of its range and trigger increasing public and scientific attention. Besides records of *C. sowerbii* presence outside its native range, little is known about its ecological impacts in invaded freshwater habitats. Information regarding the genetic properties relating to adaptive ability, invasive success and the ecological role of *Craspedacusta* polyps and medusae is also missing. In this thesis, the following topics were investigated: (i) the genetic variation among European polyps and medusae, (ii) the trophic ecology and niche of the polyp stage in comparison to a functionally similar resident polyp species (iii) the top-down influences by jellyfish predation on the pelagic food web of lakes, (iv) vertical nutrient redistribution induced by jellyfish migration and (v) the effects of the presence of jellyfish on plankton dynamics.

The genetic variation among 481 individuals (polyps and medusae) from 53 European lakes, which were presumed to represent *C. sowerbii*, was determined by screening for mitochondrial 16S rRNA and COI polymorphisms. Four mtDNA haplotypes were present at different frequencies and haplotype pairs were grouped in two major clades. Genetic divergence between clades at the species level was discovered which strongly supports the formerly described invasion of multiple genetic lineages to Europe. The phylogenetic analysis conducted in this thesis revealed a global distribution of only a few haplotypes that indicates an efficient spread of certain haplotypes originating from China. One haplotype was newly detected and seems to be restricted to Europe at the present stage. Surprisingly, sex of medusae was associated with haplotype in both species, suggesting that sex of medusae is rather genetically defined by the maternal polyp line and not by environmental factors. Medusae from almost all lakes were fixed for a single haplotype over space and time and female medusae dominated, but also evidence of the so far scarcely reported co-occurrence of both sexes of medusae was found in a single European lake. In addition, several haplotypes of both species coexisted within this lake, indicating that requirements for bisexual reproduction

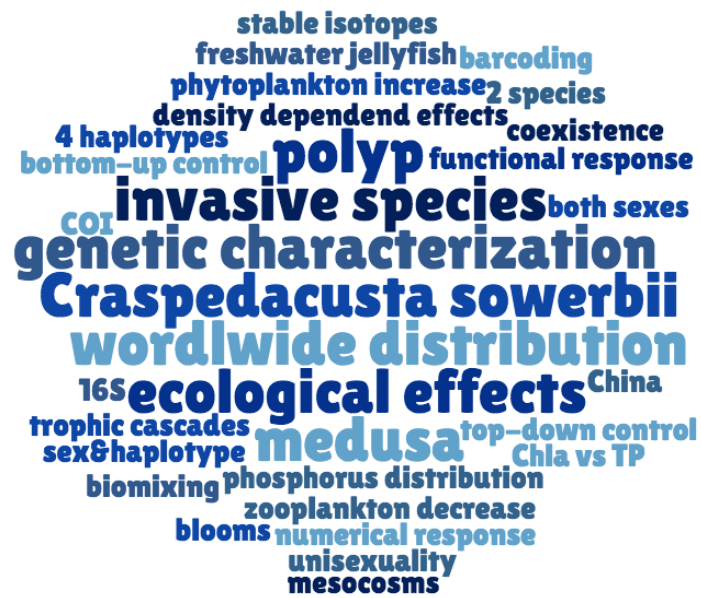
Summary

and even for hybridization of the two species are given. Evidence for high gene flow detected in medusae populations within and among regions and continents addresses the high dispersal power of respective benthic life stages and their invasiveness.

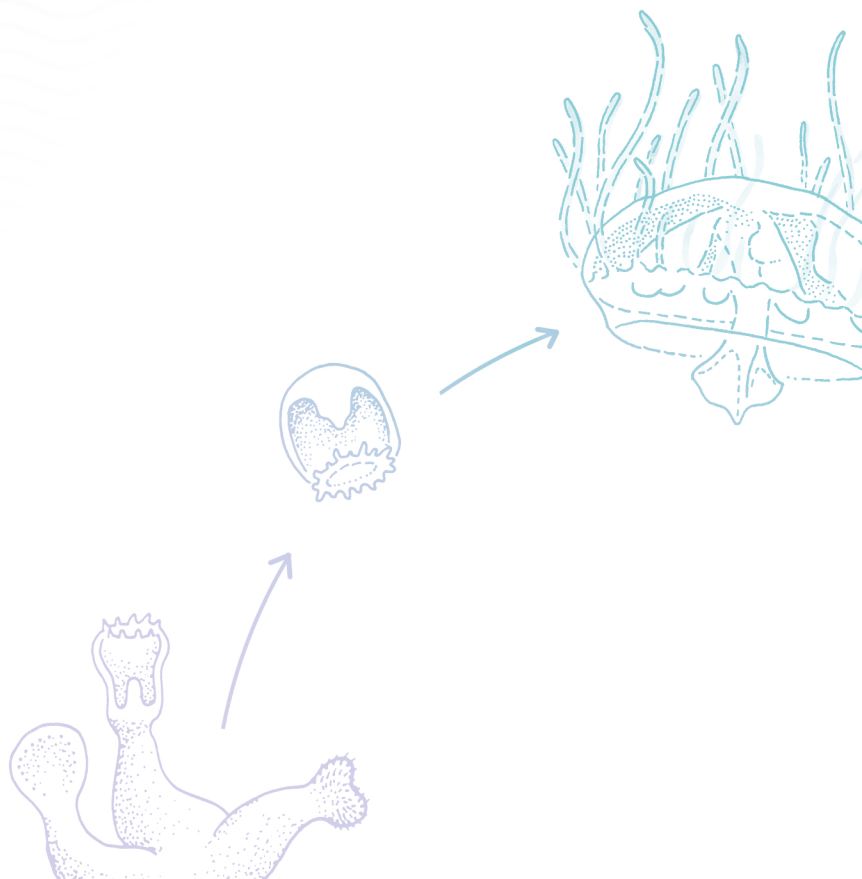
The main life stage for the establishment of *Craspedacusta* in a newly invaded habitat is the polyp stage, which might compete with the functionally similar resident *Hydra* polyps for space and food. Functional and numerical response analyses showed that *Craspedacusta* polyps have advantages compared to *Hydra* polyps due to a higher feeding efficiency and better numerical responses at low food densities. Stable isotope analyses from four different lakes revealed that *Craspedacusta* and *Hydra* polyps occupy separate dietary niches independently of season and lake type, which is most likely due to morphological differences (tentacles, body size). The niche analyses indicate that the establishment of newly invading *Craspedacusta* polyps should not be constrained by competition with *Hydra* and that coexistence of both - functionally very similar polyps - within the same benthic food web is possible in a long-term perspective.

Top-down influences of *C. sowerbii* medusae were analysed in outdoor mesocosm experiments with natural plankton communities from three oligotrophic lakes. *C. sowerbii* medusae triggered trophic cascades already at low abundances. The biomass of zooplankton decreased with increasing jellyfish abundance while algal biomass increased. A shift in zooplankton community composition had further effects on phytoplankton composition and growth. According to the results of these experiments, freshwater jellyfish have very similar food web effects as already described for marine jellyfish. Jellyfish have been present in European lakes for about 100 years, and abundances of jellyfish tend to increase rapidly within the last twenty years. It is therefore important to take trophic cascades mediated by jellyfish into account when predicting future food web dynamics in lakes.

Evidence for the vertical transport of nutrients (phosphorus) by the swimming behavior of the freshwater jellyfish *C. sowerbii* was found in experimental laboratory setups. The magnitude of the effect was positively correlated with jellyfish density. The degree of upward nutrient transport by jellyfish migration was detected to be much larger than that of similar large-sized native migrating zooplankton such as *Chaoborus spp.* larvae. On average, one jellyfish was able to transport ten times more phosphorous from the bottom to the top of an experimental column than a native lake crustacean zooplankton community at natural density. These results indicate that nutrient fluxes within lakes can be significantly modified after a jellyfish invasion.



1 Introduction



1.1 Biological Invasions and Jellyfish

Increasing human mobility and globalization of trade and travel has facilitated the intentional and unintentional transfer of organisms among ecosystems that were previously separate (Perrings et al. 2005, Meyerson and Mooney 2007). These organisms introduced into a region outside of their native range are then called exotic or non-indigenous. Subsequent to the initial introduction, a non-indigenous species has to overcome biotic and abiotic barriers and has to pass several steps to become a successful invader (Lodge 1993, Sakai et al. 2001, Lockwood et al. 2005). An introduced species is then called “invasive” when it is established, widespread, and abundant and often causes some sort of ecological or economic harm (Richardson et al. 2000, Colautti and MacIsaac 2004, Lockwood et al. 2005, Ricciardi and Cohen 2007). According to the “tens rule”, approximately 10% of the introduced species become established and only 10 % of those species become invasive (Williamson 1996). Although most introduced species fail to establish and spread (Williamson 1996), the number of new records of invasive species, ranging from viruses and bacteria to fungi, plants, and animals, in terrestrial and aquatic systems are not declining worldwide.

Jellyfish (including Cnidaria and Ctenophora) are a well-known example of aquatic invasive species that are causing global concern because large blooms of them occur at an alarming rate outside their native ranges (Purcell et al. 2007, Bayha and Graham 2014). These blooms have often negatively affected local and regional biodiversity, public health and coastal tourism in the invaded region (Purcell 2012, Brotz et al. 2012, Duarte et al. 2013, Graham et al. 2014). The most cited example of a jellyfish invasion is the one of *Mnemiopsis leidyi*, an Atlantic ctenophore, to the Black Sea (GESAMP 1997, Purcell et al. 2007, Costello et al. 2012). Presumably introduced accidentally by ballast waters (Reusch et al. 2010, Ghabooli et al. 2011), this species exploded in number in the 1980s in the Black Sea and reached averages up to 310 ctenophores per m² (average biomass of up to 1 kg wet weight per m²; Vinogradov et al. 1989). Its massive occurrence was considered to be responsible for the collapse of fisheries in the whole basin with attributed dramatic economic losses (GESAMP 1997, Knowler 2005). From the Black Sea, *M. leidyi* has spread to several other marine environments. Since 2006 it also occurs in the North Sea and the Baltic Sea (reviewed in Bayha and Graham 2014).

Introduction

The high invasive success of *M. leidy* is favored by jellyfish-specific traits regarding reproductive and life history strategies, environmental tolerance and trophic plasticity (Bayha and Graham 2014). For example, high fecundity, rapid maturation and the combination of both sexual and asexual reproduction are common among jellyfish and were found to be advantageous in establishing populations in new habitats (Lodge 1993, Kolar and Lodge 2001, Sakai et al. 2001, Funk and Vitousek 2007). Additionally, many species of jellyfish are generalist feeders, allowing them to benefit from a wide range of novel prey items in a new environment (Lodge 1993). These traits facilitate a fast increase in population size of introduced jellyfish, which has substantial ecological impacts on local communities, such as predatory pressure on zooplankton or juvenile fish or successful competition with fish populations for prey (Sommer et al. 2002, Bayha and Graham 2014, Graham et al. 2014). In marine ecosystems, eutrophication coupled with ocean warming, overfishing, and habitat modification has been associated with an increase in the bloom frequency of these invasive gelatinous organisms and some authors already speak of a “rise of slime” (Jackson 2008, Richardson et al. 2009, Purcell 2012, Brotz et al. 2012, Pitt and Lucas 2014).

1.2 The Invasive Freshwater Jellyfish *Craspedacusta sowerbii*

1.2.1 Origin, Habitat and Distribution of *C. sowerbii*

Besides several examples of jellyfish invasions in marine habitats, the worldwide invasion of the freshwater jellyfish *Craspedacusta sowerbii* is the most prominent case of jellyfish invasions in freshwater. *C. sowerbii* was first detected in a water-lily tank in the gardens of the Botanical Society in London in 1880 (Lankester 1880) and is presumably originating from China (Kramp 1950). Even though deliberate introductions have not been described, this freshwater invertebrate (phylum Cnidaria, class Hydrozoa, order Limnomedusa, family Olindiidae) managed to invade all the continents apart from Antarctica (Figure 1; Dumont 1994, Jankowski 2001, Jankowski et al. 2008). Its colonization was more efficient than that of any other limnic medusa species and it is considered to be one of the most widespread freshwater invaders globally (Duggan and Eastwood 2012). In comparison, *Limnocnida*, the closest related limnomedusan genus, is so far restricted to Africa, the Himalayan Mountains and to Southern and Southeastern Asia (Figure 1; Rayner 1989, Dumont 1994, Jankowski et al. 2008, Jankowski and Anokhin 2019).

Introduction

The occurrence of *C. sowerbii* is reported from virtually all types of freshwater ecosystems, such as lakes, slow-flowing parts of streams and rivers, backwaters, reservoirs, quarry or garden ponds, aquaria and even wastewater treatment facilities (Dejdar 1934, Dexter et al. 1949, Davis 1955, Matthews 1963, Beckett and Turanchik 1980, Augustin et al. 1987, Rayner and Appleton 1992, Jankowski 2000, Oscoz et al. 2010, Fuentes et al. 2019). This variety of invaded ecosystems is indicating that *C. sowerbii* is characterized by a broad ecological niche (Karaouzas et al. 2015) and that it is able to enlarge its geographical extension.

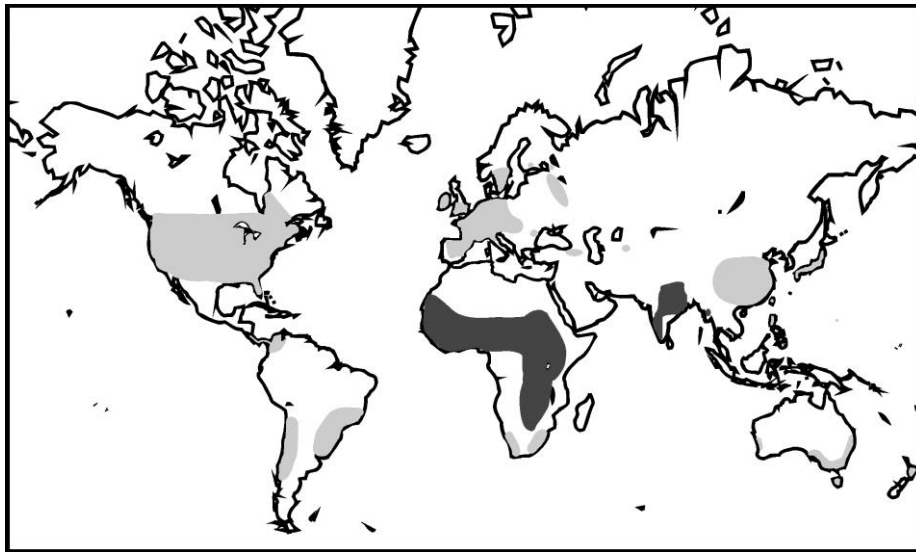


Figure 1: Worldwide distribution of *Craspedacusta sowerbii* (light gray) and of *Limnocyclus tanganicae* (dark grey; with permission from Jankowski et al. 2008).

Records of *C. sowerbii* are mostly due to random observations of large pelagic medusae (Figure 2), which are rather visible by their swimming behavior, size (1-2 cm) and occurrence in high densities (blooms). However, similar to marine jellyfish, *C. sowerbii* has a life cycle with diverse benthic life stages such as polyps, frustules or podocysts (Dejdar 1934). While specimens in the medusa stage are short-lived, the benthic life stages form long-term persisting local populations and some can for example survive without or limited food supply (Acker and Muscat 1976). Mechanisms like hitchhiking on migrating organisms such as waterbirds, crayfish or mussels, and especially human-mediated dispersal can explain the wide distribution of those robust benthic stages (Lundberg et al. 2005, Stanković and Ternjej 2010). So far, only little evidence for the distribution of *C. sowerbii* in form of these benthic life stages is given (Payne 1924, Dejdar 1934, Pennak 1956, Bushnell and Porter 1967, Hubschman and Kishler 1972, Stanković and Ternjej 2010, Siquier et al. 2017). However, the

presence of local *C. sowerbii* populations in lakes without medusa sightings is supported by a monitoring study in New Zealand (Duggan and Eastwood 2012). Herein, in 61 % of the investigated lakes specimens in the benthic polyp stage were found, but no medusa (Duggan and Eastwood 2012). Consequently, *C. sowerbii* is probably even more widespread than currently noted and many first-time records from countries worldwide since the year 2000 (Väinölä 2002, Arbačiauskas and Lesutienė 2005, Pérez-Bote et al. 2006, Saadalla 2006, Stefani et al. 2010, Gasith et al. 2011, Raposeiro et al. 2011, Galarce et al. 2013, Gomes-Pereira and Dionísio 2013, Karaouzas et al. 2015) suggest a continued expansion of its range.

1.2.2 Life Cycle of *C. sowerbii*

A prerequisite for the wide distribution of *C. sowerbii* is its highly complex life cycle that allows adaption to challenging environmental conditions (Figure 2). In addition to the obvious pelagic medusa, inconspicuous benthic life stages (polyps, frustules, podocysts) and a tiny pelagic larval stage (planula larva) exist. These life forms are only a few millimeters or even less than one millimeter in size (Figure 2). The polyp is considered to be the dominant stage in the life history because it usually persists throughout the whole year and all other forms (frustula, podocyst, medusa, planula larvae) occur in response to specific conditions (Acker and Muscat 1976).

The **polyp** is tubular in shape with a reduced perisarc localized at the basal part of the polyp for attachment to living and non-living substrates like small pebbles, rocks, plant material, mussels or even tin cans (Acker and Muscat 1976, Park 1998, Stanković and Ternjej 2010, Folino-Rorem 2015). The head region, called capitulum, has a mouth surrounded by small papillae that are containing nematocysts to capture prey. The sessile polyp lives solitary or can form colonies of up to seven physically attached clones (Figure 2; Payne 1924, McClary 1959). Polyps were found from surface areas down to a depth of 9 m, but data about their distribution and depth of occurrence is scarce (Stanković and Ternjej 2010).

The polyp is not able to detach from the substrate, but it can produce or transform into **frustules**, which are mobile (Figure 2; Dejdar 1934). Frustules are non-ciliated and rod-shaped; they can crawl slowly on the substrate, attach to it and form a polyp (Hyman 1940, Folino-Rorem 2015). It is proposed that this stage is unable to feed, thus the stored energy (e.g. in form of lipids) would be the limiting factor for the dispersal of the frustules (Dejdar 1934).

Introduction

Additionally, polyps or frustules both can transform into resting bodies called **podocysts**, which have a polygonal, lentil-like shape and a chitinous coat (Figure 2; Reisinger 1957, Folino-Rorem 2015). These podocysts ensure long-term survival under stressful environmental conditions like heat, aridity and cold temperatures (Payne 1924, Reisinger 1957, Acker and Muscat 1976). Podocysts kept at 4°C were able to transform into polyps after a temperature raise to 20°C (Dunham 1941). Moreover, it was reported that a podocyst survived 40 years of complete desiccation (Bouillon and Boero 2000).

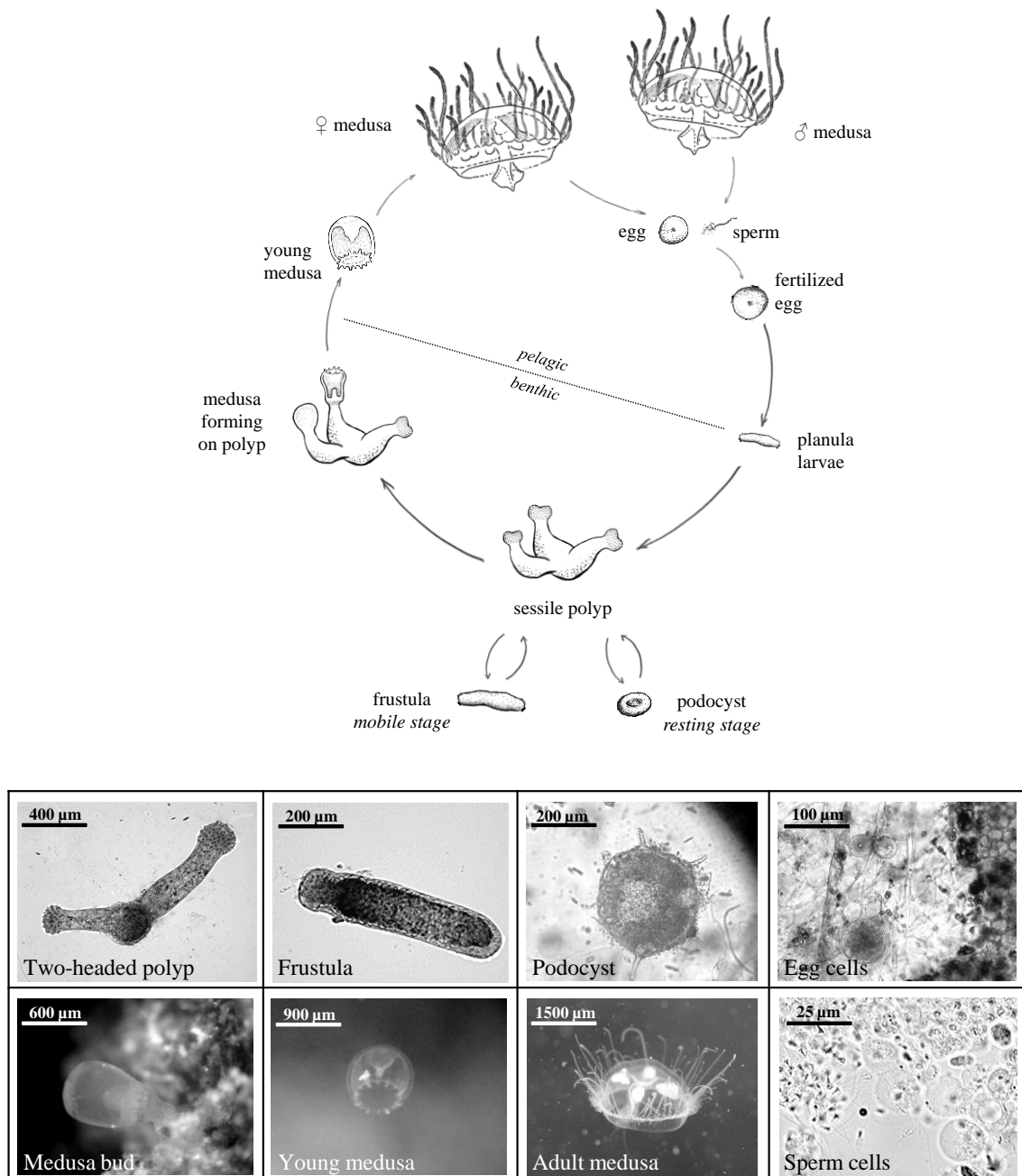


Figure 2: Schematic life cycle of *Craspedacusta sowerbii* (modified after Lundberg et al. 2005) with pictures of the different life stages and of gonadal tissue of adult male and female medusae.

Introduction

Alternatively, polyps can also produce free-swimming **medusae** by budding (Figure 2). The buds take from four to thirteen days to grow on the polyp and are then released as small medusae with a bell diameter of approximately 1 mm (Payne 1924). In this stage, about eight stinging tentacles serve to capture prey like tiny zooplankton stages (Dejdar 1934). The medusae are seldom observed in the field at that size (Acker and Muscat 1976). Five to six weeks after release medusae become **sexually mature males or females**, respectively (Figure 2; Dunham 1941, Acker and Muscat 1976). They have an umbrella of up to 20 mm or more in diameter (Acker and Muscat 1976) and about 200 to 400 stinging tentacles (Pennak 1956). Depending on their sex, medusae produce eggs or sperms in four bag-shaped gonads, which are attached to four radial canals hanging in the subumbrella. The sperms and eggs (Figure 2) are released into the water for external fertilization. From fertilized eggs, ciliated planktonic **planula** larvae hatch and develop into primary polyps (Payne 1926, Dejdar 1934).

Several factors such as temperature, food supply, light, current, CO₂ and chemical parameters influence the life cycle stages of *C. sowerbii* (Payne 1924, Acker and Muscat 1976). The medusa stage is the most noticeable one and its occurrence is seasonally, usually from summer to autumn, lasting only a few weeks or months (Dejdar 1934, Pennak 1956, Acker and Muscat 1976). Especially temperature is an important contributor for medusae bud production (Acker and Muscat 1976, Folino-Rorem et al. 2015), and it is known to be a trigger also in many marine jellyfish species (reviewed in Purcell 2005). Moreover, in some studies, it was reported that the abundance of medusae was greater in years with over-average temperatures (Pennak 1956). However, different temperatures were documented as being ideal for medusa budding and it was suggested that optimum temperatures might depend on the population of *Craspedacusta* being studied, in temperate or tropical populations (McClary 1959, Lytle 1961, Acker and Muscat 1976). Moreover, the artificial induction of medusa bud production within laboratory experiments was unsuccessful in some studies. It was suggested that there might be polyp strains, which have secondarily lost the ability to produce medusae (Acker and Muscat 1976), similar as it has been proposed for freshwater polyps of the genus *Hydra* (Siebert and Juliano 2017).

1.2.3 Taxonomy and Genetic Diversity of *Craspedacusta*

Crucial for the assumption that China is the origin of *C. sowerbii* was the description and distribution of several species, subspecies, and variations of freshwater jellyfish of the genus *Craspedacusta* especially in the Yangtze River System (Kramp 1950). Temporarily up

Introduction

to eleven different Chinese *Craspedacusta* “species” had been described, using the number of tentacles and tentacle orders, the number and shape of statocysts, the shape and the color of gonads and patterns of nematocyst warts as species-diagnostic traits (reviewed in Jankowski 2001, Jankowski and Anokhin 2019). However, the taxonomic assignment based on these characters proved to be ambiguous (Bouillon and Boero 2000, Jankowski 2001, He 2003, Jankowski et al. 2008), suggesting that the morphology-based traditional taxonomy of the genus *Craspedacusta* needs a revision (Jankowski and Anokhin 2019).

To overcome the problem with morphology-based species assignment, molecular markers were used to disentangle genetic relationships among the Cnidaria at genera, species and population levels (e.g. Jankowski 2001, France and Hoover 2002, Collins et al. 2006, Jankowski et al. 2008, Van Walraven et al. 2016). Based on molecular studies and phylogenetic analyses (Collins et al. 2008, Fritz et al. 2009, Zhang et al. 2009, Schifani et al. 2019), only three different lineages of species rank are supported within the genus *Craspedacusta* at the present stage. These correspond to the morphologically-defined species *C. sowerbii* (Lankester 1880), *C. sowerbii* var. *kiatingi* (Gaw and Kung 1939), and *C. sinensis* (Gaw and Kung 1939). The taxonomic status of another morphologically-defined species, *C. ziguiensis* (He and Xu 1985), is still uncertain despite phylogenetic analyses (Zhang et al. 2009).

Based on morphological taxonomy, it was long-time assumed that only one species, *C. sowerbii*, was able to spread worldwide. However, some recent molecular studies based on mitochondrial and nuclear markers revealed that two species of *Craspedacusta* invaded at least Central Europe (Karaouzas et al. 2015, Schifani et al. 2019). Phylogenetic comparisons with previous GenBank entries from Chinese specimens identified one Greece and one Italian individual as *C. sowerbii* by sequence similarities and German and Austrian sequences from individuals from eight different lakes were genetically defined as *C. kiatingi* (Fritz et al. 2009, Karaouzas et al. 2015, Schifani et al. 2019). Before molecular evidence, individuals of both species were presumed to be *C. sowerbii*, as they were not distinguishable by morphological features. The actual identity of European *Craspedacusta* populations, for which no molecular data are available, is therefore questionable. This also refers to the finding that the morphology of genetically-defined *C. kiatingi* specimens from Europe did not correspond to the previously published species-diagnostic morphological traits (Fritz et al. 2009).

Important to mention is that the genetic diversity among medusae populations may not correspond to the genetic diversity among polyp populations. This is because the production

of medusae of all *Craspedacusta* species depends on the reproductive success of individuals at the polyp stage and polyps from the different species may need different triggers for medusa budding (Jankowski 2001). Lakes where medusae from specific genotypes only or where no medusae have been found so far can nevertheless be inhabited by genotypically diverse polyps and even higher species diversity among *Craspedacusta* polyps compared to medusae cannot be excluded. For example, variation in the cytochrome *c* oxidase I (COI) proved to be higher among polyps than among medusae of the scyphozoan jellyfish *Aurelia aurita* (Dawson et al. 2015, Van Walraven et al. 2016). Similar patterns may apply for *Craspedacusta* species, in semi-enclosed freshwater systems, but at the present stage molecular data of the polyp stage is missing to corroborate different scenarios.

1.2.4 Limited Bisexual Reproduction of *C. sowerbii*

Since the first description of *C. sowerbii*, in many field collections of sexually mature medusae either only male or female individuals were found (reviewed in Stadel 1961). Male-only populations were reported from New Zealand (Fish 1971, Boothroyd et al. 2002) and female-only populations from Mexico (Moreno-Leon and Ortega-Rubio 2009). Also in Europe, purely female or male populations have been found e.g. in Sweden (Lundberg et al. 2005), Spain (Pérez-Bote et al. 2006), France (Germain 1934) and Germany (Boecker 1905). Interestingly, the sex of medusae populations can also vary between years, at least within some lakes (Rice 1958). Only in few cases, medusae of both sexes have been observed together and so far, only in USA, China and France (Payne 1924, Kramp 1950, Reisinger 1957, Rice 1958, Deacon and Haskell 1967, Zhang et al. 2016). This rare coexistence of both sexes in the medusa stage of *C. sowerbii* suggests that sexual reproduction is limited.

Reasons for this phenomenon of predominantly unisexual medusae populations have been largely disputed, but no sound consensus has been reached to date. On the one hand, it was suggested that the sex is determined genetically and that polyps are either male or female that can produce medusae of one sex only (Payne 1924, Acker and Muscat 1976, Lundberg et al. 2005). On the other hand, it was suggested, that slightly different environmental conditions could control the formation of male and female medusae (Payne 1924). From other cnidarian taxa it is well known that genetic as well as environmental factors can play important roles in the development of germ cells, sex determination and even in sex inversion (Ayre and Willis 1988, Littlefield et al. 1991, Littlefield 1994, Carré and Carré 2000, Schlesinger et al. 2010, Nishimiya-Fujisawa and Kobayashi 2012, Liu et al. 2018).

1.2.5 Feeding Ecology and Trophic Position of Polyps

Besides genetic determinants, the invasion success of the asexually reproducing polyps and their long-term establishment depends on a suite of ecological factors in the new environment. In addition to abiotic factors such as water chemistry, temperature or oxygen concentrations the polyp might also have to compete with functionally similar resident species for resources such as food or space. Examples for mechanisms that potentially enable competing species to coexist are dietary segregation associated with differences in feeding behavior (Page et al. 2005), resource partitioning based on morphology (Leyequién et al. 2007) or temporal segregation in periods of high resource use (Kotler et al. 1993). A recent study, for example, showed that successful invasive crustaceans had higher attack rates, lower prey handling times and higher maximum feeding rates than those of trophically or taxonomically similar native species (Dick et al. 2013). Such functional response analyses are important key tools to investigate different resource use patterns of invasive compared to native species (Dodd et al. 2014, Jackson et al. 2017). They describe the relationship between predation rate (i.e. the number of prey eaten per time) and prey density (Solomon 1949), which is specific for each predator-prey system. Moreover, the response of consumers to resource densities through population growth and aggregation or dispersal (the so-called numerical response; Holling 1966) might also be higher for invasive predators compared to native ones, resulting in higher population densities accompanied by enlarged competitive pressure.

Resident species that are similar to polyps of *Craspedacusta* are polyps of the genus *Hydra* (subclass Hydroidolina, family Hydridae), which are common members of benthic freshwater communities (Jankowski et al. 2008, Quinn et al. 2012, Folino-Rorem 2015). The genus *Hydra* comprises high species diversity of 12-15 species (Martinez et al. 2010, Schuchert 2010, Folino-Rorem 2015) with some of them having a cosmopolitan distribution (Jankowski et al. 2008). *Hydra* polyps range in a height from 2 to 15 mm, have five to seven tentacles and attach to the substrate via an adhesive disk (Hyman 1940). Notably and in contrast to *Craspedacusta*, the life cycle of *Hydra* lacks a medusa stage. Both *Craspedacusta* and *Hydra* polyps, have a very similar carnivore feeding strategy. They are passive predators waiting for potential prey touching cnidocytes on tentacles (*Hydra*) or on the head of the polyp (*Craspedacusta*, Figure 2). Both polyps feed on several crustacean zooplankton species, rotifers, oligochaete worms, nematodes, chironomid and other insect larvae (Dunham 1941, Bouillon et al. 1957, McClary 1959, Walsh et al. 2006, Massaro et al. 2013, Rivera-De La Parra et al. 2016).

Similar predation strategies, food resources and worldwide distribution of *Hydra* and *Craspedacusta* polyps suggest very similar properties of their ecological niches (Folino-Rorem 2015). In consequence, competition between polyps of the two genera seems to be high. Because two functionally similar taxa occupying the same niche are not expected to occur at the same place at the same time (competitive exclusion principle after Gause 1934) the long-term outcome seems undecided. So far, scarce data exists documenting co-occurrence of polyps from the two genera, even on the same substrate such as dreissenid mussels (Dodds and Hall 1984, Koetsier and Bryan 1989, Stanković and Ternjej 2010, Folino-Rorem 2015) which raises questions about the significance of niches partitioning at small scales.

1.2.6 Feeding Ecology and Trophic Position of Medusae

For marine pelagic food webs, two separate pathways are described. In the “muscular food chain” fish have the position of primary consumers, which prey on herbivorous zooplankton (mainly copepods), which further graze on primary producers (Figure 3 a, left pathway; Sommer et al. 2002). In the “gelatinous food chain” the position of primary carnivores is replaced by jellyfish (Cnidaria and Ctenophora) and pelagic tunicates are additionally on the position of herbivores (Figure 3 a, right pathway; Sommer et al. 2002). Besides preying upon tunicates, jellyfish are mostly zooplankton predators, but they can also feed on fish larvae. They can, therefore, affect fish stocks strongly by competition for food and predation of the next generation (Alldredge et al. 1984, Behrends and Schneider 1995, Nicholas and Frid 1999). Traditionally jellyfish are considered as “dead-ends”, because their high water and gelatinous mass content indicate that their food quality is low and they have few predators compared to other zooplankton groups (Verity and Smetacek 1996, Sommer et al. 2002). New methods such as stable isotope analyses or DNA analysis of fecal and gut samples are, however, indicating that much more taxa routinely consume jellyfish and that the contribution of jellyfish to the energy budgets of predators might be higher than assumed (Hays et al. 2018).

The introduction of freshwater jellyfish created a new functional guild in invaded freshwater plankton communities outside its native range, as jellyfish (gelatinous planktonic predator) were not represented in these lake systems before. Therefore, jellyfish are usually not included in lake food chain concepts. Traditionally, the trophic level of zooplankton predators is mostly composed of planktivorous fish or insect larvae and both groups are well edible prey

Introduction

for higher food web levels, such as planktivorous and piscivorous fish (Carpenter et al. 1985; Figure 3 b, left pathway). Consequently, a very efficient food web flow from phytoplankton to zooplankton along to fish is observed in freshwater ecosystems (Stibor et al. 2004). Similar to marine jellyfish, freshwater jellyfish are predators of a variety of prey types. By preying upon crustacean zooplankton, they have similar prey spectra as planktivorous fish, insect larvae and piscivores, but *C. sowerbii* medusae can also prey upon young stages of these consumers (Dexter 1949, Kramp 1950, Dodson and Cooper 1983, DeVries 1992, Jankowski et al. 2005; Figure 3 b, right pathway). As the water content of *C. sowerbii* medusa is between 96 and 99 % (Jankowski 2000) the nutritional quality is definitely low and assimilation efficiencies of predators eating this jellyfish would be most probably also very low. So far, no important pelagic predator of *C. sowerbii* is known.

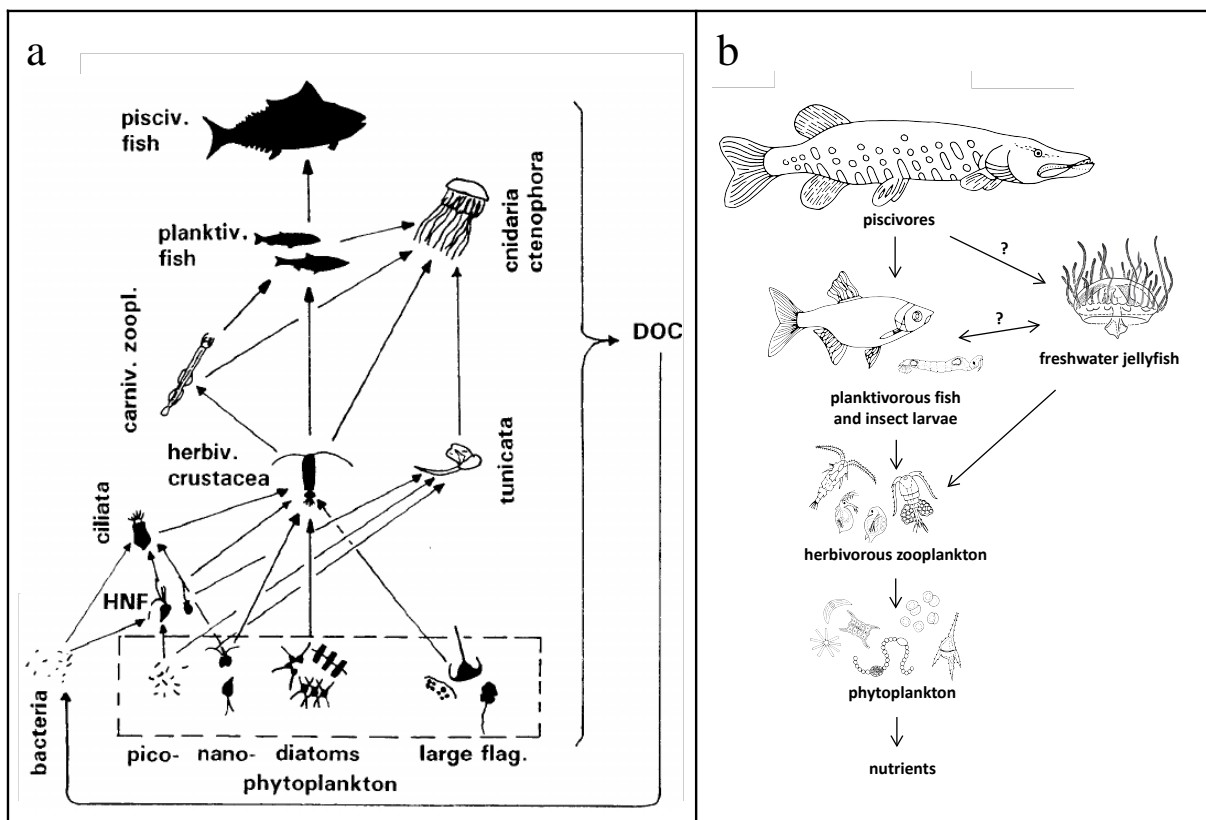


Figure 3: Simplified (a) marine (adapted with permission from Sommer et al. 2002) and (b) freshwater pelagic food web with fish and jellyfish as top-predator. Please note that the arrows indicate a bottom-up perspective for the marine food web in opposite to a top-down perspective for the freshwater food web. Organisms are not to scale.

1.2.7 Top-down Influences by Jellyfish

Marine jellyfish are considered to be important members of pelagic food webs and have been shown to induce strong trophic cascades on lower trophic levels and can alter food webs from a “top-down” perspective (Stibor et al. 2004, Pitt et al. 2007, West et al. 2009). Trophic cascades are generally manifested as inverse changes in abundance and biomass between adjacent pairs of trophic levels (Carpenter et al. 1985, Pace et al. 1999, Polis et al. 2000). For example, if the abundance of large piscivorous fish is increased, the abundance of their prey, smaller fish that eat zooplankton, should decrease. The resulting increase in zooplankton, in turn, causes the biomass of its prey, phytoplankton, to decrease.

The high degree of marine food web complexity and the numerous pathways for the flow of energy and matter, however, makes it hard to draw general conclusions about jellyfish-to-phytoplankton cascades (Stibor et al. 2004, Purcell and Decker 2005). In mesocosm studies by Stibor et al. (2004) the potential dual role of jellyfish via their predation on copepods, the dominant group of marine crustacean zooplankton, was highlighted. Jellyfish reduced copepods but produced two distinct, opposite responses of algal biomass. The net effect of jellyfish on total algal biomass was positive when large algae were initially abundant, negative when small algae were dominant and zero in joint analyses independent on algae size. These alternative trophic cascades in marine pelagic food webs are due to the dual role of copepods, which are both grazers on phytoplankton and predators on microzooplankton, which themselves graze on phytoplankton (Figure 3 a; Stibor et al. 2004).

Cascading effects strongly depend on community composition and connectivity of the food web (Shurin et al. 2002, Stibor et al. 2004) and the question arises whether freshwater jellyfish are functionally similar to marine jellyfish in the context of top-down control. Pelagic freshwater food webs are considered to be less reticulated in comparison to marine ones and changes at the top often result in clearer trophic cascades (reviewed in Hessen and Kaartvedt 2014). First investigations have already tried to determine the role of freshwater jellyfish in the plankton food web of a shallow hypertrophic pond (Jankowski et al. 2005). Results of a mesocosm experiment revealed that in treatments with very high jellyfish densities (about 450 jellyfish m⁻³) the abundance of herbivorous crustacean zooplankton was significantly reduced in comparison to jellyfish-free treatments (Jankowski et al. 2005). This reduction of zooplankton resulted in an increase of phytoplankton biomass (measured by chlorophyll *a* concentration), albeit the effect was at the limit of significance. These observed

effects support the hypothesis that *C. sowerbii* jellyfish might trigger trophic cascades, but the effects might be lake specific and related to a specific composition of the food web community. Hence, further investigations of cascading effects triggered by freshwater jellyfish are therefore needed to describe its general food web impacts.

1.2.8 Nutrient Redistribution by Jellyfish

In addition to the above described “top-down” effects, marine jellyfish gained increasing attention regarding biologically generated (or biogenic) fluid disturbances that affect the mixing of waters. Jellyfish can redistribute nutrients by such biogenic mixing and thereby potentially affect food web dynamics also from a “bottom-up” perspective (Katija and Dabiri 2009, Katija et al. 2012). In situ measurements were conducted in a marine lake in Palau to visualize fluid disturbances by swimming jellyfish (*Mastigias sp.*) during migration (Katija and Dabiri 2009). Video recordings of dye injected upstream of individual jellyfish showed that dye was carried along behind the jellyfish for several swimming cycles. Furthermore, it was shown that the animal’s shape and orientation during migration affected drift processes in the water column (Katija and Dabiri 2009).

Besides jellyfish, also smaller animals are considered to generate mixing by their swimming behavior (Simoncelli et al. 2017). For example, most of the crustacean zooplankton performs synchronized diel vertical migrations to escape predation by visible orientated predators. Zooplankton moves towards deeper waters during the day and back to the surface during the night for feeding purposes (Stich and Lampert 1981). By such vertical movements, zooplankton is considered to generate mixing (Simoncelli et al. 2017). That such movements can further result in a redistribution of nutrients has been shown for example for the water flea *Daphnia*. By indoor mesocosm experiments, Haupt et al. (2010) have shown that the migration behavior of *Daphnia* can transport and release small amounts of phosphorus from the bottom to the top of a defined water column.

Such nutrient distribution processes can especially be important in freshwater lakes during summer, a time when many freshwater lakes are stratified because of high surface water temperatures. During that stratification period, the unidirectional gravity-driven downward flow of matter results in decreasing nutrient concentrations in the epilimnion and limits primary production despite sufficient light conditions. External factors like wind create shear forces and waves in the surface layer, but can only generate weak boundary mixing with low

Introduction

nutrient redistribution between epi- and hypolimnion (Spigel and Imberger 1987).

Medusae of *C. sowerbii* can occur in big blooms during summer and it has often been observed that the medusae actively swim up in the water column and passively sink downwards, with their tentacles extended to capture prey (Boulenger and Flower 1928, Milne 1938, Acker and Muscat 1976). Especially during the active upward swimming behavior, a certain volume of water is entrained behind the bell during both contraction and expansion phases (Figure 4; Colin et al. 2006, Lucas et al. 2013). The question arises, if within this water measurable amounts of nutrients are transported, similar as it was observed for *Daphnia*. This potential biogenic nutrient transport by jellyfish swimming dynamics could then be an important process for an internal nutrient supply from nutrient-rich deep-water layers to the nutrient-poor epilimnion. Nutrient dynamics in lakes with jellyfish presence could, therefore, be different to jellyfish-free lakes during summer.

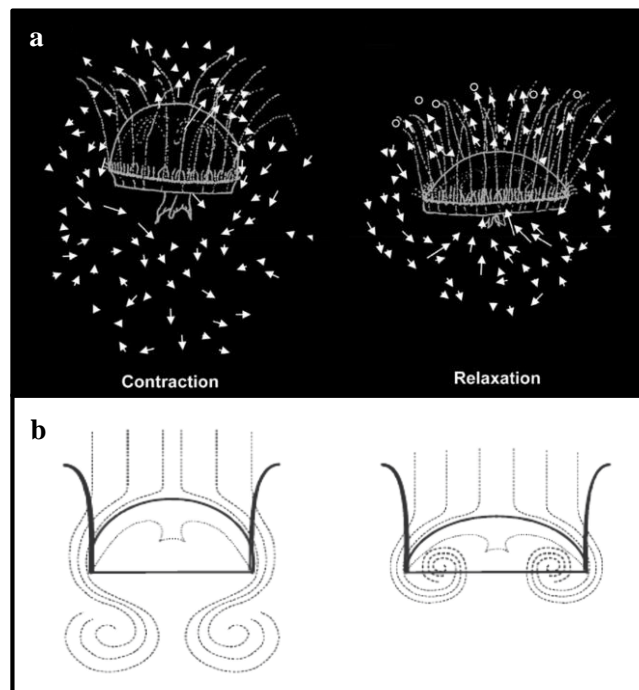


Figure 4: (a) Particle tracks and in the flow (arrows indicate the distance that particles travelled over 0.1 s) and (b) schematic flow (dotted lines) surrounding *C. sowerbii* during contraction and relaxation phases of the swimming cycle (adapted with permission from Colin et al. 2006).

1.3 Central Research Topics

This thesis includes five topics addressing genetic and ecological aspects of the invasive freshwater jellyfish *Craspedacusta sowerbii*. Several field samplings, laboratory and outdoor experiments were conducted.

Topic 1: Genetic diversity among invaded *Craspedacusta*

The genetic diversity, especially in the polyp stage, is important for the establishment and the invasion success of *C. sowerbii* in a newly invaded habitat. Despite low sample sizes, a recent molecular study revealed the presence of two species of *Craspedacusta* among European medusae, which were presumed to be *C. sowerbii* by morphological traits. This indicates that genetic variation of the freshwater jellyfish is higher than so far assumed. Moreover, molecular data about the polyp stage are completely missing and a high genetic diversity of *Craspedacusta* polyps might have been overlooked. For these reasons, genetic variation among polyps and medusae and the spatial and temporal variation of their genetic population structure were investigated by analyses of mitochondrial DNA genes. Regarding potential sexual reproduction of *Craspedacusta*, the sex of medusa individuals in local populations was also examined.

Topic 2: Feeding ecology and trophic position of polyps

In contrast to the medusa stage of *Craspedacusta*, polyps have potential native cnidarian competitors, *Hydra* polyps, with similar resource demands. Hence, functional and numerical response analyses were conducted to identify potential differences in the feeding ecology of both polyps. Additionally, stable isotope signatures of *Craspedacusta* and *Hydra* polyps from several lakes at different seasons were analysed to figure out potential differences in their dietary niche, which could enable their coexistence at small scales.

Topic 3: Trophic cascades mediated by jellyfish

Three outdoor mesocosm experiments were carried out to examine potential predatory effects of *C. sowerbii* on natural plankton communities of three lakes. The aim was to get more insight into trophic dynamics entailing direct and indirect effects of jellyfish presence on

Introduction

mesozooplankton and phytoplankton communities and on nutrient dynamics. It was further tested if these potential effects depend on jellyfish density.

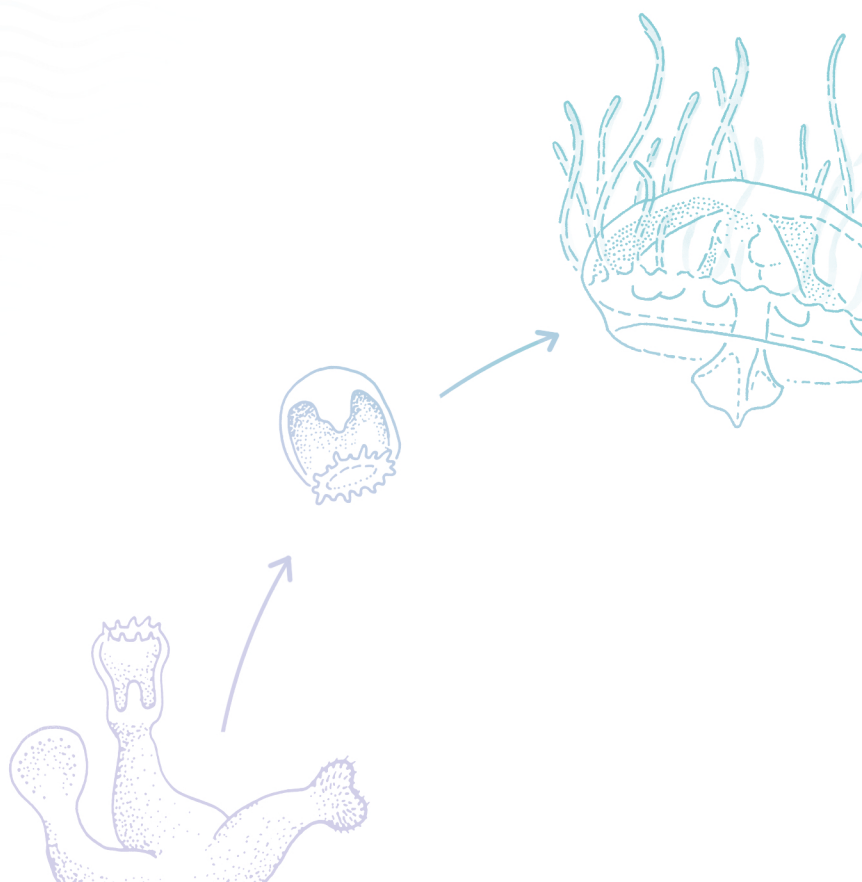
Topic 4: Jellyfish and phosphorus dynamics

The potential modification of phosphorus fluxes by migrating medusae of *C. sowerbii* compared to other native migrating zooplankton were investigated within controlled laboratory experiments. This is of special concern, as high densities of medusae mainly occur during summer, at a time when lakes are stratified and primary production in upper water layers is mainly limited by phosphorus, despite sufficient light conditions.

Topic 5: Evidence of jellyfish food web effects in the field

Cascading effects by jellyfish predation and also the modification of phosphorus fluxes by jellyfish migration could alter lake productivity during summer. Especially in stratified lakes, phytoplankton abundances might increase by the combination of both effects. The aim within topic 5 was to investigate these jellyfish effects in the field. Therefore, a lake survey was conducted to investigate, if pelagic food webs in lakes with medusae show different dynamics compared to similar lakes without medusae. In detail, jellyfish-lakes could enclose more phytoplankton (measured as chlorophyll *a*) per unit growth-limiting nutrient (phosphorus) compared to jellyfish-free lakes.

2 Material & Methods



2.1 Genetic Analyses of *Craspedacusta*

2.1.1 Sampling Sites and Sampling Procedure

Sampling of polyps

Polyps of *Craspedacusta* were sampled from stone substrates in altogether 34 freshwater lakes in Africa, Austria, Germany and Greece at different seasons between 2014 and 2017 (Figure 5, Suppl. Table 1). Stones were collected from a water depth of about 50 cm along the shoreline of a lake. Over a distance of 20 m (parallel to the shoreline) one stone (1 - 5 cm in diameter) per meter was collected by hand at each site. The stones were transported to the laboratory in lake water and stored at 18°C for further analyses and experiments. Stones were screened for the presence of polyps using a binocular microscope with a maximum magnification of 25x. For genetic analyses, polyps were gently removed from the stone surface with a needle and, after removing detritus, transferred alive with pipettes or forceps to reaction tubes for DNA extraction. Polyp samples from two additional lakes in Switzerland were provided as DNA eluates by P. Schuchert (DOI: 10.5281/zenodo.57119, DOI: 10.5281/zenodo.57120).

Sampling of medusae and sex determination

Altogether 50 lakes in Austria, Czech Republic and Germany were screened for the presence of medusae. In 25 lakes, medusae of *Craspedacusta* were detected at the time of sampling over the duration of four years (2014 to 2017) and during different seasons (Figure 5, Suppl. Table 1). Multiple lakes were screened more than once. Free-swimming medusae were caught manually using a plastic bag during snorkeling which was closed by hand to avoid the escape of individuals and were transported in lake water to the laboratory. The sex of medusae was determined by examining gonad tissues of living animals with appropriate magnification (up to 400x) to identify egg or sperm cells, respectively (Dejdar 1934, Reisinger 1957). After sex determination, medusae were stored individually in 96 % ethanol at room temperature for later analyses. One medusa of *Limnocoidea* was sampled at Lake Tanganyika (-8.7124, 31.1281; 24.08.2015; Africa) and provided by F. Schedel in 96% ethanol.

Material and Methods

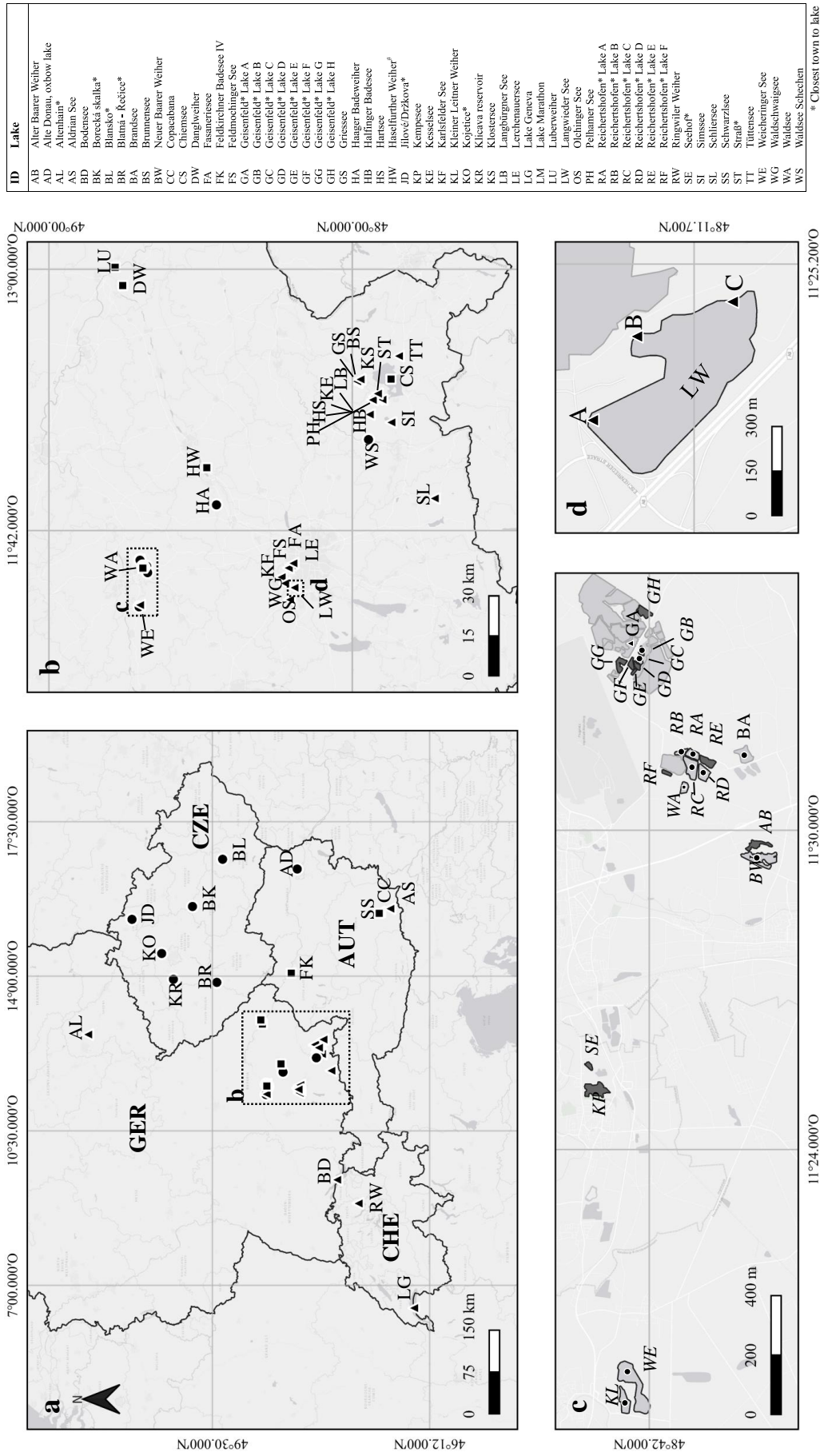


Figure 5: Sampling sites of *Craspedacusta* ▲ polyps, ● medusae and of ■ both life stages for genetic analyses (topic 1). (a) Overview of the sampling area (without sampling site Lake Marathon (Greece)). (b) Detailed view of Bavarian sampling sites. Lakes HW, HS, LW and WE are part of topic 2. Lakes HA, HW and WA are included in topic 3. BS, KS and HW are included in topic 4. (c) Detailed view of Ingolstadt area. Lakes with IDs in italics are included in topic 5 (jellyfish-free lakes = dark grey). (d) Sampling sites (A, B and C) of polyps at Lake Langwieder See (topic 1, data set 4).

2.1.2 DNA Extraction

Lysis and total genomic DNA extraction from single individuals were performed using DNeasy Blood and Tissue Kit (Qiagen Inc.) according to the manufacturer's protocol. The entire polyp, polyp colony or one medusa gonad were individually processed. DNA eluates from altogether 284 medusae and 197 polyps of *Craspedacusta* as well as from one medusa of *Limnognida tanganyicae* were stored at -20°C and used in further analyses (Suppl. Table 1).

2.1.3 Mitochondrial COI and 16S rRNA Gene Sequence Analyses

From each individual, two mitochondrial DNA (mtDNA) gene regions, the cytochrome *c* oxidase I protein-coding gene (COI) and the large subunit ribosomal RNA gene (16S), were amplified by polymerase chain reaction (PCR). Each PCR was carried out using 0.625 U DNA Polymerase (bioline MangoTaq™), 4.5 mM MgCl₂, 0.1 mM dNTPs, 5 µl (5 x) reaction buffer, 2-10 µl genomic DNA template, 0.2 µM of forward and reverse primers and sterile ddH₂O in a total volume of 25 µl. A Bio-Rad MyCycler™ was used for thermocycling. Amplification of COI was performed testing several newly designed primers (S. Gießler, pers. comm.; Suppl. Table 2 a) due to amplification difficulties. A PCR profile with an initial hot start followed by 94 °C for 5 min, 30 cycles each with 94 °C for 50 s, 58 °C for 50 s, 72 °C for 60 s finishing with a final step at 72 °C for 5 min was applied for the amplification of COI. The 16S region was amplified using the primers F2/R2 (Cunningham and Buss 1993, Collins et al. 2008, Suppl. Table 2 b). PCR amplification of 16S was conducted with a modified protocol: 94 °C for 5 min, 5 cycles each with 94 °C for 50 s, 45 °C for 50 s, 72 °C for 60 s, followed in turn by 30 cycles of 94 °C for 50 s, 50 °C for 50 s, 72 °C for 60 s, finishing with a final step at 72°C for 5 min. Amplification products were verified on 1.2 % agarose gels, purified using ethanol precipitation (1st step with sodium acetate (3M, pH 5.5) and 100% ethanol, 2nd step with 70% ethanol) and stored in ddH₂O at 8 °C until further processing. Cleaned PCR products were sequenced using the BigDye Terminator v3.1 Cycle Sequencing Kit in both, the forward and reverse directions with the same primers as in the initial PCRs. Sequence data were obtained from an ABI 3730 48 capillary sequencer (Applied Biosystems, Inc.) at the university's sequencing service (LMU Biocenter, Germany).

2.1.4 Data Sets

In order to investigate different questions, four sequence data sets were established.

Data set 1 “Large-scale data set – genetic variation among European polyps and medusae”

Based on the “data set 1”, genetic variation among *Craspedacusta* polyps and medusae from European lakes was investigated (Figure 5, Suppl. Table 1). The experimental design aimed to take a few individuals from as many sites as possible since the likelihood of finding genetic variation among invaders is greater between lakes rather than within individual lakes. The reason for this is that a successful establishment of different genetic lines, or even species, will depend on the composition of resident local communities and lake ecology. Altogether 53 lakes were successfully sampled with a maximum distance between lakes of 1700 km and a minimum distance of 35 m. Due to low polyp abundance on stone samples in contrast to a higher abundance of medusae in the pelagial, on average three polyps and/or five medusae individuals were analyzed for each site and sampling date. For the very remote location Lake Marathon (Greece), all 13 available polyp samples were analyzed. In total, COI and 16S sequences of 243 individuals (101 polyps and 142 medusae) were included in data set 1 (Suppl. Table 1). The number and frequencies of haplotypes were determined in the two *Craspedacusta* life stages (polyp and medusa) individually. In addition, the association between the sex of medusae and the haplotype was investigated.

To also cover temporal variation within specific lakes, *Craspedacusta* medusae that were sampled in two or three consecutive years at four lakes (Lake near Blatná - Řečice, Lake Haselfurther Weiher, Reichertshofen Lake A, Lake Waldsee) were included in data set 1 (Suppl. Table 1).

Data set 2 “Species assignment – 16S and COI phylogenies”

To identify the species membership of sampled *Craspedacusta* individuals, a second data set was created to compare haplotypes detected among *Craspedacusta* polyps and medusae from data set 1 with available COI and 16S sequences from species from the genus *Craspedacusta* published in GenBank (Table 1, Suppl. Table 1). Identical sequences of a specific study are represented by a single sequence in phylogenetic analyses. Additionally, newly generated 16S sequences of two African *Craspedacusta* polyps were included (LTP1, LTP2; Suppl. Table 1). Phylogenetic relationships were analyzed for each locus individually.

Data set 3 "Genetic population structure of medusae"

A third data set was generated to examine the genetic population structure of medusae within and among lakes (Figure 5, Suppl. Table 1). To investigate spatial structure, three remote and presumed ecologically similar lakes were chosen: a drinking water reservoir near Jílové/Držkova (Czech-Republic), as well as Lake Schwarzlsee (Austria), and Lake Waldsee (Germany), which are clear quarry lakes with high transparency (pairwise geographic distance between 350 and 410 km). Forty medusae from each lake were analyzed (N = 120 individuals). In addition, a fourth population was analyzed namely from Lake Neuer Baarer Weiher (Germany) to cover variation in ecologically different lakes. This is a small gravel pit that is two kilometers apart from Lake Waldsee and that showed ecological differences to other lakes containing medusae in analyses conducted for topic 5 (Figure 30). Since medusae abundance was low in Lake Neuer Baarer Weiher, all available individuals from population samples in 2016 (N = 13) and 2017 (N = 29) were pooled. Concatenated COI and 16S sequences of in total 162 medusae individuals were used in later analyses.

Data set 4 "Small-scale spatial population structure of polyps"

A fourth dataset was established to investigate the genetic population structure in the polyp life stage within a specific lake, Lake Langwieder See (Germany), where polyp abundance was high (Figure 5 d, Suppl. Table 1). Polyp samples from two different samplings were used. In 2015, three transects (site A, B, C) were sampled once (19 November 2015) and five polyps (each from a different stone) were analyzed in each transect (N = 15). Distances between sites A and B were ~ 400 m, between site B and C ~ 300 m, and between A and C ~ 700 m, respectively (Figure 5 d). In 2016, a more detailed sampling was conducted at site B (8 December 2016) and as many polyps as possible were picked from individual stones and genotyped, resulting in a sample of 82 polyps from seven different stones. A concatenated dataset of COI and 16S sequences based on all available 97 polyps was used for the analyses of haplotype frequencies at a small-scale level.

Material and Methods

Table 1: All available COI and mitochondrial 16S rRNA gene sequences of medusae of *Craspedacusta* and *Limnocnida* published in GenBank, listed with accession numbers (na: information is missing).

Species	Sampling site	Latitude	Longitude	Country	Sample from	Reference	COI accession number	16S accession number
<i>C. sowerbyi</i>	Lake in Wuhan	30.4937	114.7278	CHN	na	Zou et al. 2012	JN593332	JN593332
<i>C. sowerbyi</i>	Lake Hauto	40.8414	-75.9117	USA	1999	Collins et al. 2008		EU293971
<i>C. sowerbyi</i>	Alsodfer Weiher	50.8627	6.1536	GER	2002	Grange et al. 2017		KY077294
<i>C. sowerbyi</i>	Schoenbach	na	na	GER	2006	Fritz et al. 2009	FJ423613	
<i>C. sowerbyi</i>	Flueckiger See	48.0101	7.8183	GER	2006	Fritz et al. 2009	FJ423614	
<i>C. sowerbyi</i>	Matschelsee	48.4059	7.8161	GER	2006	Fritz et al. 2009	FJ423615	
<i>C. sowerbyi</i>	Loebejuen	na	na	GER	2006	Fritz et al. 2009	FJ423616	
<i>C. sowerbyi</i>	Klingenberg	na	na	GER	2006	Fritz et al. 2009	FJ423617	
<i>C. sowerbyi</i>	Sueplinger Canyon	52.2821	11.3129	GER	2006	Fritz et al. 2009	FJ423618	
<i>C. sowerbyi</i>	Hohwiesensee	49.3595	8.5130	GER	2006	Fritz et al. 2009	FJ423619	
<i>C. sowerbyi</i>	Baggersee Dietz	50.3704	7.9916	GER	2006	Fritz et al. 2009	FJ423620	
<i>C. sowerbyi</i>	Lake in Sichuan	29.0500	104.2300	CHN	2010	Cai et al. unpubl.	KF510026	KX267739
<i>C. sowerbyi</i>	Del Medio Lagoon	-34.0962	-56.2031	URY	2010	Martinez unpubl.		
<i>C. sowerbyi</i>	Lake Marathon	38.1686	23.9000	GRC	2014	Karaouzas et al. 2015	KP231217	
<i>C. sowerbyi</i>	Lake Lleu Lleu	-38.1651	-73.3288	CHL	2015	Fuentes et al. 2019	MF177101 to MF177110	
<i>C. sowerbyi</i>	Lake Illahuapi	-40.2712	-72.2997	CHL	2015	Fuentes et al. 2019	MF177111 to MF177120	
<i>C. sowerbyi</i>	Lake Espejo	-40.6361	71.7496	CHL	2015	Fuentes et al. 2019	MF177121 to MF177130	
<i>C. sowerbyi</i>	Lake Ancapulli	-39.334	-71.715	CHL	2015	Fuentes et al. 2019	MF177131 to MF177133	
<i>C. sowerbii</i>	Concrete reservoir	38.107	13.35085	ITA	2017	Schifani et al. 2019	MH230079	
<i>C. sinensis</i>	na	na	na	CHN	na	Collins et al. 2005		AY512507
<i>C. ziguensis</i>	na	na	na	CHN	1985	Collins et al. 2008		EU293974
<i>L. tanganyicae</i>	Lake Tanganyika	-4.8542	29.5922	Africa	2003	Collins et al. 2008		EU293972

2.1.5 Data Analyses

Multiple sequence alignments were obtained based on consensus sequences of forward and reverse reads of individual amplification products, using Clustal W with default settings as implemented in BioEdit (version 7.2.5; Hall 1999). Quality of sequence reads was examined in associated electropherograms and sequencing was repeated in case of uncertain base callings. Final alignments were trimmed to the highest coverage regarding sequence length for each locus, mitochondrial 16S rRNA and COI, respectively.

Mitochondrial 16S rRNA and COI gene sequences from *Craspedacusta* individuals were combined using BioEdit and statistical parsimony networks were generated from the concatenated data set by using TCS 1.21 (Clement et al. 2000). Gaps were treated as missing data and a 90% cut-off level was used. The layout of the TCS network output was optimized using the browser-based javascript program tcsBU (Múrias Dos Santos et al. 2015) resulting in a pie-chart display.

Representative sequences for COI and 16S haplotypes were obtained from TCS analysis of data set 1 and were used to investigate the phylogenetic relationships in joint data sets with already published *Craspedacusta* sequences for each locus individually (data set 2).

Phylogenetic trees were constructed individually using the Maximum Composite Likelihood method and Kimura 2-parameter (K2P) model as implemented in MEGA7.0 (Kumar et al. 2016). The K2P-model was selected among different nucleotide substitution models based on the Maximum Likelihood fits (MEGA7.0). The stability of internal nodes was estimated by 100 bootstrap replications. Respective sequences of *Limnocoñida* were used as an outgroup in tree reconstructions, including newly obtained COI and 16S sequences and a single published 16S sequence of *L. tanganyicae* from GenBank (Table 1, Suppl. Table 1).

To compare genetic distances within and between groups of sequences, the number of base pair differences, K2P-distances and p-distances were computed as implemented in MEGA7.0.

2.2 Functional and Numerical Response Analyses of Polyps

To investigate the competitiveness among polyps of *Craspedacusta* and of brown *Hydra* for food, functional and numerical response analyses were conducted.

2.2.1 Experimental Design and Set-up

For functional response analyses, the prey species *Brachionus calyciflorus* (Rotifera) was offered to single polyps in density treatments of 5, 10, 20, 30 and 50 individuals per 10 ml. Each prey density treatment was replicated 15 times for each predator. In total 150 experimental units were examined, 75 units with *Craspedacusta* polyps as predators and 75 units with *Hydra* polyps as predators. To check for rotifer reproduction during experimental runs, control treatments without predators were run in parallel to predation treatments and each density treatment of 5, 10, 20, 30 and 50 *Brachionus* per 10 ml was replicated 11 times.

Polyps of *Craspedacusta* and of *Hydra* were sampled in Lake Langwieder See (48.1942, 11.4163; Germany) as described in section 2.1.1. While *Hydra* polyps can be easily cultured under standardized conditions for later use in experiments, polyps from *Craspedacusta* field samples needed more attention. This is due to the initial transformation of the polyps into a frustule stage (Figure 2) after removal from their substrate. *Hydra* polyps do not undergo such a transformation. The time for the transition from frustules to polyps can vary under standardized laboratory conditions (McClary 1960). At 18°C, with a light intensity of 12.31 $\mu\text{mol photons m}^{-2} \text{ s}^{-2}$ (LI-250A-Light Meter, LI-COR Biosciences, USA) and a light/dark cycle of 16/8 hour this process lasted about 14 days (pers. obs.). For this reason, polyps were sampled three weeks before the start of the experiment to establish experimental polyps in time. Polyps from field samples were picked from their substrate and transferred to 6-well plates (polystyrene; Greiner Bio-One, Kremsmünster, Austria) filled with 5 ml of Hydra Medium (HM) solution (pH: 7.6) per well. The HM was prepared by adding 1 ml each from stock solutions: $\text{CaCl}_2 \cdot \text{H}_2\text{O}$ (1.0 M), $\text{MgCl}_2 \cdot 6 \text{H}_2\text{O}$ (0.1 M), KNO_3 (0.03 M), MgSO_4 (0.08 M) and 3 ml of NaHCO_3 (0.5 M), to one liter of Millipore water (receipt by T. Peard, pers. comm.).

As soon as all *Craspedacusta* individuals recovered from the resting stage and transformed back to polyps (Figure 2), they were fed each individually by hand with larvae of *Artemia*

Material and Methods

salina (cultured from resting eggs, Sanders, USA). After this initial feeding, the medium was changed completely to prevent bacterial or fungal growth and animals were raised in 5 ml HM per well. One week of no feeding followed and then the density treatment experiments with polyps of *Craspedacusta* started by adding 5 ml HM and the defined amounts of *Brachionus*. To maintain similar conditions for polyps from both genera, individuals of *Hydra* were also sampled three weeks before the start of the experiment and were transferred into 10 ml HM. However, as *Hydra* polyps lack a frustule stage, they were fed with larvae of *A. salina* every second day for two weeks to keep them alive. Before the start of experiments, the same standardization procedure was applied, with a one-week starvation period in completely exchanged HM. Only two-headed *Craspedacusta* polyps (Figure 2) and one-headed *Hydra* polyps were used in the experiments, as these types represented the most common polyp types of each species in the field.

The experimental prey species, *Brachionus calyciflorus*, was cultured from resting eggs (Florida Aqua Farms Inc., USA). Since the generation time of *B. calyciflorus* is very short, it was necessary to control for consistent numbers of prey individuals in the different treatments. Therefore, only juvenile specimens (without eggs) were used as prey to avoid offspring production during the experiment.

After adding *Brachionus* in the defined densities (see above) to *Hydra* and *Craspedacusta* the plates were placed next to each other in a climate chamber (18°C, 16 h light/8h dark, light intensity of 12.31 $\mu\text{mol photons m}^{-2} \text{s}^{-2}$). After 24 hours, the complete medium with the surviving prey organisms was removed and preserved with a 40% sugar-formaldehyde solution (1:10 diluted). The formol-preserved prey individuals were counted under a stereomicroscope with a maximum magnification of 16x.

The conversion of food into asexual reproduction was observed after the functional response experiments for the duration of 16 days. For this purpose, 10 ml of HM was added to the experimental units immediately after removing the medium with the remaining prey organisms. After 3, 6, 9, 14 and 16 days, the number of offsprings was counted for each polyp. Numerical response analyses had five replicates per prey density treatment, resulting in a total of 50 experimental units. Polyp individuals were not fed or treated in any way during the period of observation. For polyps of *Craspedacusta* a two-headed polyp was defined as one specimen corresponding to functional response experiments and an increase in body structure, in the form of another head or a frustule, was counted as one additional individual. For polyps of *Hydra*, new buds were counted as additional individuals.

Material and Methods

For calculations of carbon transfer of ingested prey to predator, dry weight and carbon content of prey and predator types were determined. Four replicates, each with 100 specimens of *B. calyciflorus* in the same size group as the experimental animals, were used to determine the carbon content by combustion in an elemental analyzer (vario MicroCube, Elementar, Germany). Because of the small size and the high water content of polyps, it was not possible to measure the individual weights of polyps. Therefore, pooled samples were used to determine the dry weight of polyps from the two genera: 10 one-headed polyps of *Hydra* and 20 two-headed polyps of *Craspedacusta* were pooled and the dry weight was determined by a Sartorius microbalance. Mean carbon contents of polyps from the two genera were calculated as being approximately 30% of their dry weight (Jankowski 2000).

2.2.2 Data Analyses

For functional response analyses, the relationship of the ingestion rate ($\mu\text{g C d}^{-1}$) as a function of the initial prey density ($\mu\text{g C ml}^{-1}$) was described by regression analyses. Ingestion rates were calculated from the initial number and the remaining number of prey items after 24 hours. The handling time (T_h) was calculated as $T_h = 24 \text{ h} / I_{max}$, where I_{max} is the maximum amount of carbon which the organism can ingest within 24 h (I_{max}). The relationship of the number of offspring at a certain observation day as a function of the initial prey density (in $\mu\text{g C ml}^{-1}$) was also described by regression analyses. All analyses were conducted in Sigma Plot 11.0 (Systat Software 2008).

2.3 Stable Isotope Analyses

The food web position of polyps of *Craspedacusta* and of *Hydra* was examined with stable isotope analyses of carbon and nitrogen. In total six samplings were conducted to figure out potential spatial and temporal differences in their food web positions.

2.3.1 Sampling Sites and Procedure

Samples of polyps from the two genera and of other invertebrate organisms (found near the polyps) were collected from four different lakes (Lake Hartsee, Lake Haselfurther Weiher, Lake Langwieder See, Lake Weicheringer See; Germany; Table 2, Figure 5 b). In total six samplings were conducted; each lake was sampled once between 2015 and 2016, only for Lake Langwieder See two additional samplings were conducted to figure out seasonal changes within one lake. Table 2 describes the study sites, years and months of sampling and the sampled invertebrate taxa with main habitat type and trophic group affiliation.

The sampling of polyps was conducted as described in section 2.1.1. All other invertebrates (Table 2) were collected from stones or from the lake water in which the stones were stored. Species identification of associated zooplankton was done morphologically, and if necessary, confirmed by species assignment based on COI barcodes (using the standard invertebrate primer LCO1490 and HCO2198; Folmer et al. 1994; Suppl. Table 2) compared to GenBank entries.

2.3.2 Sample Preparation and Isotopic Measurements

For stable isotopes analyses, whole organisms were transferred alive to tin cups (cylindrical, 5 x 9 mm, HEKAtech GmbH, Wegberg, Germany) immediately after returning from sampling to avoid potential excretion losses. As a dry weight of about 0.2 mg is required for measurement accuracy (T. Hansen, pers. comm.), a corresponding number of individuals needed to be pooled for each taxon of interest (20 two-headed polyps from *Craspedacusta* and about five one-headed polyps from *Hydra*). For each taxon, at least three replicates were prepared for each sampling site and day and dried at 65°C until weight remained constant. The dried samples were measured at GEOMAR (Helmholtz-Zentrum für Ozeanforschung Kiel, Germany; Hansen and Sommer 2007). The values of the stable carbon and nitrogen

Material and Methods

isotopes are presented as δ -values (‰) relative to international reference standards for carbon and nitrogen according to the equation: δ (‰) = $1000 \times [(R_{\text{sample}}/R_{\text{standard}})-1]$.

2.3.3 Data Analyses

For each of the six samplings, mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (\pm standard errors) of polyps and of other invertebrates are shown. Statistical comparisons of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of polyps of *Hydra* and of *Craspedacusta* were made using Student *T*-test or Mann Whitney *U* test, as appropriate. The 95% confidence interval of the bivariate means of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was determined for polyps of *Hydra* and of *Craspedacusta* and compared using analyses of Stable Isotope Bayesian Ellipses in R (R Development Core Team 2013; SIBER package, Version 2.1.3, Jackson et al. 2011). No overlap of ellipses indicates significant differences of the isotopic niches of the analyzed organisms.

Table 2: Samplings of *Craspedacusta* polyyps, *Hydra* polyyps and of other invertebrates for stable isotope analyses. Superscript numbers refer to three different sampling dates at Langwieder See. Main habitat and trophic group affiliations of invertebrates (according to Dejdar 1934, Reavell 1980, Barnett et al. 2007, Reynoldson and Association 1978, Casper 2012) are shown in parentheses.

	Hartsee	Haselfurther Weiher	Langwieder See	Weicheringer See
Latitude	47.9268	48.4820	48.1969	48.7036
Longitude	12.3671	12.0130	11.4166	11.3296
Max. depth (m)	39.1	5.2	8.7	5.0
Area (m ²)	860 000	70 500	184 000	180 000
TP (µg L ⁻¹)	13.58	8.48	8.20	11.88
Lake type	kettle lake	quarry pond	quarry pond (since 1930)	quarry pond (since 1965)
Sampling date	01 June 2016	28 July 2016	(1) 15 October 2015 (2) 10 May 2016 (3) 11 July 2016	20 October 2015
Sampled invertebrate taxa	<p>Polyyps of <i>Craspedacusta</i></p> <p>Polyyps of <i>Hydra</i></p> <p><i>Pleuroxus truncatus</i> (littoral herbivore)</p> <p><i>Dreissena polymorpha</i> (benthic filter-feeder)</p>	<p>Polyyps of <i>Craspedacusta</i></p> <p>Polyyps of <i>Hydra</i></p> <p><i>Bosmina</i> sp. (pelagic filter-feeder, herbivore)</p> <p><i>Daphnia longispina</i> (pelagic filter-feeder, herbivore)</p> <p>Calanoid copepods (pelagic herbivore/omnivore)</p> <p>Cyclopoid copepods (pelagic carnivore/omnivore)</p> <p><i>Lymnea stagnalis</i> (littoral/pelagic filter-feeder, omnivore)</p> <p>Medusa of <i>Craspedacusta</i> (pelagic carnivore)</p>	<p>Polyyps of <i>Craspedacusta</i>^{1,2,3}</p> <p>Polyyps of <i>Hydra</i>^{1,2,3}</p> <p><i>Alona</i> sp.² (littoral filter-feeder, herbivore)</p> <p><i>Polyphemus pediculus</i>^{1,2,3} (pelagic carnivore)</p> <p><i>Sida crystallina</i>^{1,2,3} (littoral filter-feeder, herbivore)</p> <p><i>Dugesia</i> sp.^{1,3} (benthic carnivore)</p>	<p>Polyyps of <i>Craspedacusta</i></p> <p>Polyyps of <i>Hydra</i></p> <p><i>Bosmina</i> sp. (pelagic filter-feeder, herbivore)</p> <p>Calanoid and cyclopoid copepods (pelagic omnivore)</p> <p><i>Dugesia</i> sp. (benthic carnivore)</p>

2.4 Outdoor Mesocosm Experiments

2.4.1 Experimental Design and Set-up

To investigate the impact of the freshwater jellyfish *C. sowerbii* on the pelagic plankton communities of lakes, outdoor mesocosm experiments were conducted. Jellyfish impacts on summer communities of the three German pre-alpine lakes, Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher were tested within three separate experiments (Figure 5 b). The lakes differed in several parameters, such as their amount of resources and stratification (Table 3).

Table 3: Sampling sites for investigation of trophic cascade effects mediated by *C. sowerbii* medusae in three separate outdoor mesocosm experiments.

	Haselfurther Weiher	Waldsee	Haager Weiher
Experimental time	20.07.-02.08.2016	09.08.-22.08.2016	08.08.-21.08.2017
Latitude	48.4820	48.6925	48.4503
Longitude	12.0130	11.5133	11.8283
Max. depth (m)	5.2	10.1	6.9
Area (m ²)	57000	36 772	47 000
Summer stratification	no	yes	no
Total phosphorus ($\mu\text{g L}^{-1}$)	8.48	11.58	18.42

Each experiment lasted for 13 days. An experimental gradient of jellyfish densities (0, 2, 4, 8, 16 jellyfish per enclosure) was designed to examine the potential predation pressure on the natural phyto- and zooplankton community. Each density treatment was replicated three times. For each experiment, 15 enclosures (cylindrical bags made of plastic foil (LDPE foil, EDDI-Plastik GmbH, Germany); dimensions: 0.7 m in length, 0.5 m in diameter) were fixed to plastic foam rings and open to the atmosphere to ensure the establishment of natural lake conditions. The mesocosms were placed in four outdoor tanks, which were open at the top and filled with tap water. Each enclosure was filled with 140 L of 250 μm filtered lake water containing the natural phytoplankton community of the regarding lake. A water sample was taken from the filtered lake water for analyses of chlorophyll *a* (chl *a*) and other chemical parameters as described in the next section (2.3.2). Zooplankton was collected by 100 μm net

hauls from a depth of 5 m and 1.5 times the natural density of the respective lake was added to each enclosure. Two or three samples of the initial zooplankton community were preserved in 4% sugar-formaldehyde for later analyses. Specimens of *C. sowerbii* were collected manually during snorkeling and placed randomly into the enclosures according to the gradient design. The medusae used in each experiment were similar in bell diameter and fresh weight (Haselfurther Weiher: 1.96 cm and 0.48 g, Waldsee: 2.01 cm and 0.48 g, Haager Weiher: 1.51 cm and 0.26 g). With respect to the two species of *Craspedacusta* among European medusae (see topic 1), COI sequences of 40 medusae of each experiment/sampling site were generated for species assignment.

2.4.2 Sampling and Measurements

Daily sampling of phytoplankton

Chlorophyll *a* concentrations were used as an index of the abundance of primary producers. For this purpose, a 25 ml water sample was taken with a jar from each enclosure 0.5 m below the water surface at the same time every day. The sample was immediately filtered (250 µm) to exclude mesozooplankton and the remaining phytoplankton was adapted to dark conditions (15 min). Chl *a* concentration of each sample, based on multispectral fluorescence analyses, was measured in vivo with an AlgaeLabAnalyser (bbe Moldaenke GmbH, Schwentinental). By using six different excitation-wavelengths, chl *a* concentrations of four optical functional groups which were called green algae, blue-green algae, diatoms/dinoflagellates and cryptophytes were differentiated. Functional optical groups have similar pigmentation and thereby absorbance characteristics typical of for example chlorophyta, cyanobacteria, bacillariophyta or cryptophyta, but they do not necessarily match taxonomic groups.

Endpoint sampling

On day 13, a water sample was taken with a jar from each enclosure 0.5 m below the water surface for laboratory analyses. The water was pre-filtered through 250-µm gauze to exclude mesozooplankton. Total phosphorus (TP) was measured spectrophotometrically (880 nm) using the molybdenum blue method (Wetzel and Likens 1991). For measurements of soluble reactive phosphorus (SRP), 100-200 ml of the pre-filtered water were further filtered with a pre-combusted and acid-washed glass fiber filter (0.7 µm). The SRP content of the filtrate was measured spectrophotometrically (880 nm) after a molybdate reaction (Wetzel and Likens

1991). The filter was used for the determination of particulate phosphorus (PP), which was measured spectrofluorometrically (880 nm) after molybdate reaction following sulphuric acid digestion (Wetzel and Likens 1991). For measurements of particulate organic carbon (POC) and nitrogen (PN), water was filtered with a pre-combusted glass fiber filter (0.7 µm) and filters were frozen at -20°C for later analyses. POC and PN were measured in an elemental analyzer (vario MicroCube, Elementar, Hanau). Seston stoichiometric ratios of C : N : P were calculated accordingly.

Finally, the enclosures were completely emptied; the zooplankton assemblage of each enclosure was collected separately by filtering over gauze (100 µm) and preserved in 4% sugar-formaldehyde. Cladocerans were identified to the genus level, copepods were identified as calanoid or cyclopoid forms. Individuals were enumerated for each enclosure using a Bogorov tray and a stereomicroscope. For each treatment, at least 30 individuals per taxon were photographed and measured with ImageJ (Schneider et al. 2012) for body length calculations.

2.4.3 Data Analyses

The conversion of zooplankton abundance into dry weight was calculated using the length-weight regression ($\ln W = \ln a + b \cdot \ln L$), where W is the dry weight (µg), parameters a and b are the regression parameters specific for the respective taxon and L is the average length of individuals per taxon (McCauley 1984). Regression parameters were chosen according to the report of Landesanstalt für Umwelt und Naturschutz Baden-Württemberg (LUBW 2012).

Growth rates of the taxa were calculated with the following equation:

$$\text{Growth rate} = \frac{\ln(\text{abundance}_{\text{start}}) - \ln(\text{abundance}_{\text{end}})}{t}$$

where t represents the number of days.

The zooplankton species diversity was calculated as Shannon and Weaver's H' index, implying species richness (S) and Pielou's evenness J' (Pielou 1966, Krebs 1985):

$$H' = - \sum_{i=1}^s p_i \cdot \ln p_i$$

with $H'_{\text{max}} = \ln S$, where p_i is the proportion of individuals found in species i .

Pielou's evenness J' is derived from the Shannon's diversity H' as $J' = \frac{H'}{H'_{\text{max}}}$.

Material and Methods

Differences in assemblages of crustacean mesozooplankton were displayed graphically using non-metric multidimensional scaling (nMDS) plots based on Bray-Curtis similarity measures (Bray and Curtis 1957). Data were routinely square-root-transformed prior to the calculation of Bray–Curtis similarity indices to account for the contribution of rarer species to similarity. One-way analyses of similarities (ANOSIMs; Clarke and Green 1988) were used to test for differences in mesozooplankton assemblages among experimental treatments. Analyses were done separately for each experiment and 999 permutations were done for each analysis. When differences were detected, similarities of percentages (SIMPER) tests were used to identify the species that contributed the most to the dissimilarity between treatments (Clarke 1993).

Effect sizes (ES) of jellyfish treatments on zooplankton and phytoplankton were calculated as

$$ES = \ln \frac{N_x}{N_c}$$

(Osenberg et al. 1997, Hedges et al. 1999).

For ES calculation of zooplankton, N_x represents the dry weight of the regarding zooplankton taxon of treatments with jellyfish and N_c represents the dry weight of the regarding zooplankton taxon of treatments without jellyfish. For ES calculation of phytoplankton, N_E represents the chl *a* concentration of the regarding optical functional group in treatments with jellyfish and N_c represents the chl *a* content of the regarding optical functional group in treatments without jellyfish. Error bars in the effect size plot indicate 95% confidence intervals (CI). The effects are statistically significant if the 95% CI does not overlap zero.

Multivariate analyses were done using PRIMER v6 statistical software, for all other statistical analyses Sigma Plot 11.0 (Systat Software 2008) was used. In all regression plots, significant regression fits ($p < 0.05$) are displayed by solid lines, insignificant trends are indicated by dashed lines.

2.5 Nutrient Distribution Experiments

2.5.1 Experimental Design and Set-up

To investigate the impact of the freshwater jellyfish *C. sowerbii* on the phosphorus distribution in a defined water column, indoor mesocosm experiments were conducted. To compare the effect of jellyfish on nutrient transport with the effect of other vertically migrating organisms, the single effects of natural crustacean zooplankton and the pelagic insect larvae *Chaoborus spp.* was measured in the same experimental set-up.

The experiments were conducted in a temperature-controlled climate chamber at 23.5°C. The experimental set-up consisted of cylinders of translucent acrylic glass (length of 170 cm, inner diameter 7.4 cm), which were sealed at the bottom. Each column was filled with 7 L of lake water (Brunnensee, Germany), which was 0.2 µm-filtered for bacteria and phytoplankton removal. Every 10 cm, a 20 ml-syringe (Injekt ®, B. Braun Melsungen AG) was attached to a hole in the column via a port opening (cannula Sterican ®, B. Braun Melsungen AG). In total, 17 syringes were installed at each column for sample collection. The system was illuminated from above with a fluorescent lamp (Philips, Master TL5 HO, 39W/840) simulating 12 h of day-light and 12 h of darkness. The light intensity ranged from 36 µmol photons m⁻² s⁻² at the top of the tubes to 1.77 µmol photons m⁻² s⁻² at the bottom (LI-250A-Light Meter, LI-COR Biosciences, USA).

Experiments with C. sowerbii

For the *C. sowerbii* experiments, columns containing medusae (average bell diameter of 2.1 cm ± 0.07 cm; Haselfurther Weiher, Germany; Figure 5 b) were compared to columns without medusae. To ensure fitness of medusae, natural crustacean zooplankton (>100 µm; 10 ind L⁻¹) was added as a food source. It was also added in the same amount to control columns. In total ten columns with medusae were investigated, of which seven columns contained three jellyfish each, the other three columns contained two, four and eight jellyfish respectively.

Experiments with pelagic Chaoborus spp. larvae

To measure the effect of the pelagic insect larvae *Chaoborus spp.* on nutrient transport, columns containing larvae were compared to control columns without larvae. In total four

columns with 13 *Chaoborus spp.* larvae each (average length of 0.7 cm; Brunnensee, Germany; Figure 5 b) were set up. Natural crustacean zooplankton ($>100\ \mu\text{m}$, $10\ \text{ind L}^{-1}$) was added as a food source and was also added in the same amount to control columns.

Experiment with a crustacean zooplankton gradient

A potential density dependence of natural zooplankton P-transport was analyzed. Therefore, columns were assembled with a zooplankton gradient, with $8\ \text{ind L}^{-1}$, $16\ \text{ind L}^{-1}$, $32\ \text{ind L}^{-1}$ and $64\ \text{ind L}^{-1}$ ($> 100\ \mu\text{m}$; Klostersee, Germany; Figure 5 b).

After adding the organisms to the columns, the experiment started with the injection of 20 ml of a fridge-cooled (6°C) solution with 0.1 mmol phosphorus into the bottom hole of each cylinder.

2.5.2 Sampling and Measurements

To estimate the phosphorus transport after 6, 12, 18 and 24 hours, water samples (15 ml) were collected via syringes. The total phosphorus concentration ($\mu\text{g L}^{-1}$) of each sample was measured spectrophotometrically (880 nm) using the molybdenum blue method (Wetzel and Likens 1991).

2.5.3 Data Analyses

Statistical analyses were performed using Sigma Plot 11.0 (Systat Software 2008). The effect sizes (ES) of jellyfish and *Chaoborus* larvae on total phosphorus concentration were calculated as $\ln(\text{TP}_X/\text{TP}_C)$, where TP_X and TP_C are the concentrations of total phosphorus in the columns with or without jellyfish/*Chaoborus spp.* larvae, respectively (Osenberg et al. 1997, Hedges et al. 1999). Error bars in the effect size plot indicate 95% confidence intervals. The effects are statistically significant if the 95% CI does not overlap zero. For zooplankton and jellyfish gradient plots, mean total phosphorus concentrations of the top two syringe positions were averaged. The relationships of transported phosphorus with different densities of jellyfish or of zooplankton were described by linear functions and the 95% CI. To calculate the ratio of the transported to the injected amount of phosphorus, a concentration of $1128\ \mu\text{g P L}^{-1}$ was set as the 100% value. This is the mean value of the lowest sample of all control columns in jellyfish experiments taken after six hours.

2.6 Field Survey of Lakes with and without Jellyfish

To find field evidence of cascading effects and the upward phosphorus distribution mediated by the freshwater jellyfish *C. sowerbii*, a field survey was conducted in summer 2017. For that purpose, environmental parameters of ten lakes with and of ten lakes without jellyfish in close vicinity (max. distance of 18 km) were compared (Table 4, Figure 5 c).

2.6.1 Sampling and Measurements

Physical parameters such as temperature, pH, conductivity and dissolved oxygen were recorded as a function of depth with a multiparameter water probe (Exo 1© YSI Inc., WTW GmbH, Xylem Inc.).

Integrated water samples were taken once per lake using an integrated tubular water sampler with a volume of 2 L (KC Denmark A/S Research Equipment, Silkeborg). Samples were taken from a depth of 1 to 3 m at the position of the maximum depth of each lake. The water was pre-filtered through 250- μm gauze to exclude mesozooplankton. Water samples were further processed for determination of TP, SRP and seston stoichiometry as described in section 2.4.2. For chl *a* measurements, water samples were filtered on pre-combusted glass fiber filters (0.7 μm) and filters were extracted overnight in 90 % acetone (HPLC grade) at 8°C. The chl *a* concentration was quantified by fluorometry (TD 700 Laboratory fluorometer, Turner Designs, USA.) according to Jeffrey and Humphrey (1975).

2.6.2 Data Analyses

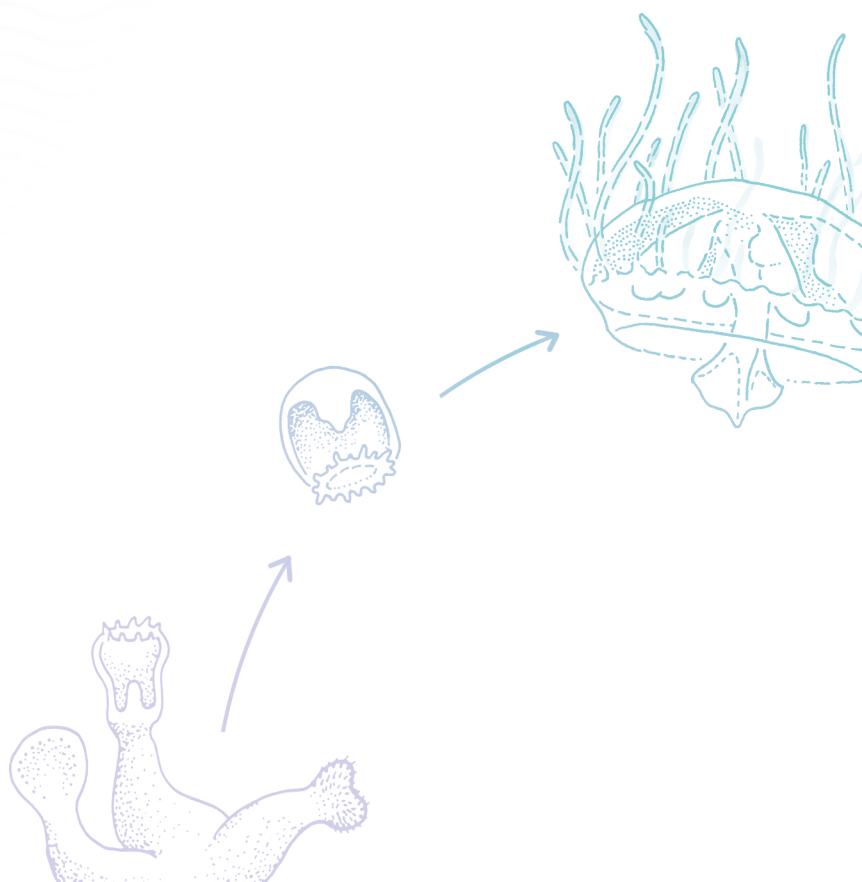
Principal-Component Analysis (PCA) was carried out in Primer (version 6.1.16) to identify differences among lakes with and without jellyfish with respect to the correlation of environmental parameters. To compare specific parameters of lakes with and without jellyfish, regression analyses, t-tests and Mann-Whitney rank sum tests were performed using Sigma Plot 11.0 (Systat Software 2008). Solid lines represent significant regression fits ($p < 0.05$), dashed lines indicate insignificant trends.

Material and Methods

Table 4: Sampling sites (*indicate closest town to lake) for investigations of jellyfish effects in the field survey. Samples were taken of ten lakes with and of ten lakes without jellyfish observations during sampling in summer 2017.

ID	Lake	Latitude	Longitude	Sampling date	Jellyfish
AB	Alter Baarer Weiher	48.6779	11.4956	14.08.17	no
BW	Neuer Baarer Weiher	48.6770	11.4911	14.08.17	yes
GB	Geisenfeld* Lake B	48.7017	11.5566	01.08.17	yes
GC	Geisenfeld* Lake C	48.7019	11.5530	22.08.17	yes
GD	Geisenfeld* Lake D	48.7025	11.5515	03.08.17	no
GE	Geisenfeld* Lake E	48.7030	11.5499	03.08.17	no
GF	Geisenfeld* Lake F	48.7038	11.5520	01.08.17	no
GG	Geisenfeld* Lake G	48.7055	11.5529	23.08.17	no
GH	Geisenfeld* Lake H	48.7013	11.5684	22.08.17	no
KL	Kleiner Leitner Weiher	48.7051	11.3211	18.07.17	yes
KP	Kempesee	48.7110	11.4189	14.08.17	no
RA	Reichertshofen* Lake A	48.6911	11.5237	12.07.17	yes
RB	Reichertshofen* Lake B	48.6931	11.5244	25.07.17	yes
RC	Reichertshofen* Lake C	48.6911	11.5193	23.08.17	yes
RD	Reichertshofen* Lake D	48.6887	11.5176	28.08.17	yes
RE	Reichertshofen* Lake E	48.6880	11.5215	01.08.17	no
RF	Reichertshofen* Lake F	48.6962	11.5179	25.07.17	no
SE	Seehof*	48.7124	11.4260	22.08.17	no
WA	Waldsee	48.6925	11.5133	12.07.17	yes
WE	Weicheringer See	48.7036	11.3296	18.07.17	yes

3 Results



3.1 Genetic Analyses of *Craspedacusta*

3.1.1 Large-scale Data Set – Genetic Variation among Polyps and Medusae

For the large-scale dataset (data set 1), both COI and mitochondrial 16S rRNA gene sequences of *Craspedacusta* were obtained for 101 polyps and 142 medusae from 53 European lakes (Suppl. Table 1). Concatenation resulted in an alignment of 243 haplotypes with a total sequence length of 1204 bp (COI: 600 bp, 16S: 604 bp). By TCS parsimony network analysis of this data set, haplotypes were arranged in two networks separated by a 90% cut-off (Figure 6; calculated maximum connection steps at 90% = 21). Individuals were unequally assigned to the two networks by haplotype, 213 individuals were assigned to network 1 and 30 to network 2. Each network was split into two subnetworks. Within subnetworks, the sequences were all fixed for the same type. Thus, four main haplotypes emerged, from now on called type 1.1, 1.2, 2.1 and 2.2 (Figure 6, for sample size see Table 5). Main networks from type 1 and type 2 were separated by 110 mutations. Subnetworks' type 1.1 and type 1.2 were four mutations apart, type 2.1 and 2.2 were even nine mutations apart. In only two cases, sequence variants from those four haplotypes were found. The two singleton sequences were one mutation apart from type 1.2 (subtype 1.2.1; polyp LB3) and type 2.1 (subtype 2.1.1; medusa KR743), respectively.

Association between haplotype, life stage and sex of medusae

Regarding network 1 most of the medusae were assigned to type 1.1 (92 %; $N_{M, 1.1} = 108$) and only a few to type 1.2 ($N_{M, 1.2} = 9$). In contrast, most of the polyps belonged to type 1.2 (78 %; $N_{P, 1.2} = 75$) and much less to type 1.1 ($N_{P, 1.1} = 21$). With respect to network 2, most medusae were assigned to type 2.2 (60%; $N_{M, 2.2} = 15$) and less to type 2.1 ($N_{M, 2.1} = 10$). Although only a few polyps were assigned to network 2, the frequencies of haplotypes among polyps were almost the same for both types 2.1 and 2.2 ($N_{P, 2.1} = 3$, $N_{P, 2.2} = 2$).

Female and male medusae were observed in both main networks and sex was always linked to one of the two subnetworks. Male medusae were from types 1.2 or 2.1 and female medusae were found with type 1.1 or 2.2 (Figure 6, Suppl. Table 1).

Results

Comparison of the variation in different life stages

Individuals from both polyp and medusa stages could be genotyped in seven lakes, with the consistent type 1.1 found for both life stages in four of the seven lakes. In three lakes (Haselfurther Weiher, Chiemsee, and Schwarzlsee) however, the polyps and medusae analyzed had different haplotypes (polyps: type 1.2 and medusae: type 1.1). Notably, the haplotype diversity among polyps within lakes was greater compared to that of medusae although in the case of polyps only three individuals had been analyzed from each lake compared to five randomly selected medusae individuals. This is because in six of 36 lakes two haplotypes were detected among polyps in contrast to medusae samples, which were always fixed for one haplotype within lakes (Table 5). Notably, medusae that were sampled in the same lake across years also had an identical haplotype (Table 5).

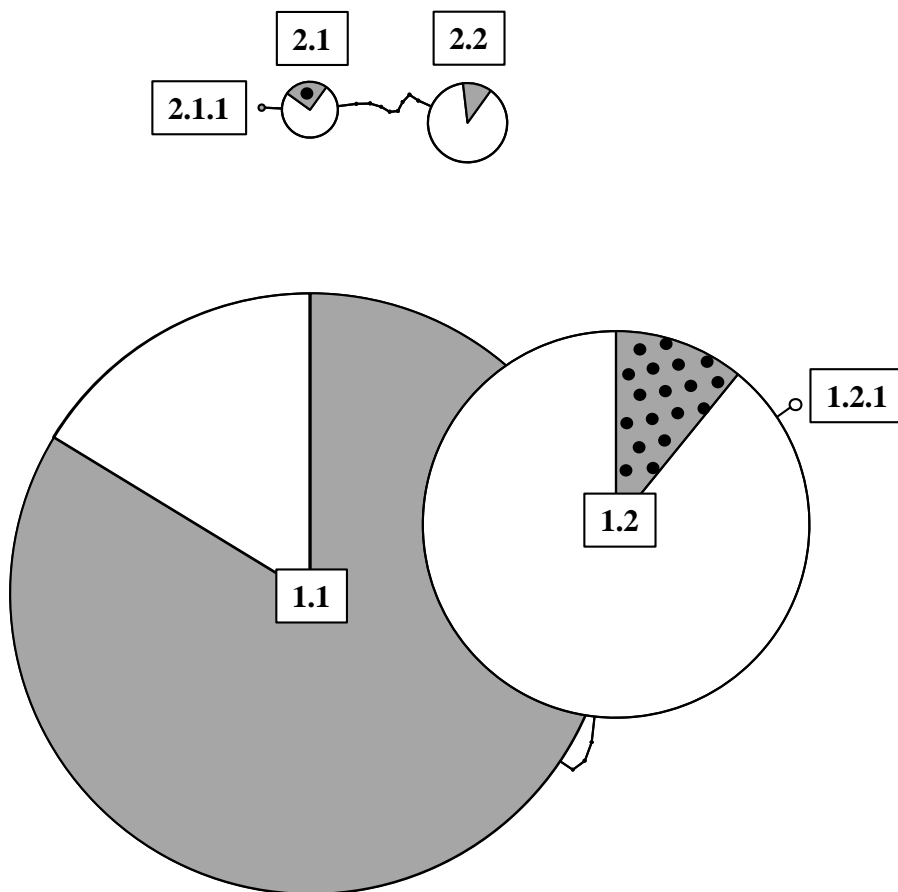


Figure 6: TCS-parsimony network based on concatenated COI and mitochondrial 16S rRNA gene regions from *Craspedacusta* individuals from 53 lakes in Europe. Six mtDNA haplotypes (types 1.1, 1.2, 1.2.1, 2.1, 2.1.1 and 2.2) are arranged in two separated networks (90% cut-off). Circle-size relates to the number of individuals with a specific haplotype. White color specifies polyps, grey color refers to female medusae and grey color with black dots refers to male medusae. For sample size see Table 5.

Results

Table 5: Assignment of *Craspedacusta* polyp (P) and medusa (M) haplotypes from 53 lakes to four types based on parsimony network analysis of concatenated COI and 16S sequences (*: closest town to lake, #: two sampling dates of medusae, †: three sampling dates of medusae, f: female medusae, m: male medusae). Type 1.2 includes subtype 1.2.1 (LB3) and type 2.1 includes subtype 2.1.1 (KR743), see Figure 6.

ID	Lake	Latitude	Longitude	Cnty	sample size		type 1.1		type 1.2		type 2.1		type 2.2	
					P	M	P	M _f	P	M _m	P	M _m	P	M _f
AD	Alte Donau, oxbow lake [#]	48.2359	16.4281	AUT		7		7						
AL	Altenhain*	51.3013	12.6797	GER	3				3					
AS	Aldrian See	46.8198	15.5299	AUT	3				3					
BD	Bodensee	47.6381	9.3899	GER	3		2		1					
BK	Borecká skalka*	49.7922	15.5800	CZE		5		5						
BL	Blansko*	49.3496	16.6499	CZE		1				1				
BR	Blatná - Řečice [#]	49.4349	13.8619	CZE		10		10						
BA	Brandsee	48.6802	11.5235	GER		5		5						
BS	Brunnensee	47.9842	12.4362	GER	3				3					
BW	Neuer Baarer Weiher	48.6770	11.4911	GER		5				5				
CC	Copacabana	46.9776	15.4573	AUT	3				2				1	
CS	Chiemsee	47.8712	12.4538	GER	3	1		1	3					
DW	Danglweiher	48.7587	12.9190	GER	3	5	3	5						
FA	Fasaneriesee	48.2042	11.5291	GER	2				2					
FK	Feldkirchner Badesees IV	48.3260	14.0689	AUT	3	5	3	5						
FS	Feldmochinger See	48.2134	11.5143	GER	3		2		1					
GA	Geisenfeld* Lake A	48.7047	11.5551	GER	3		3							
GB	Geisenfeld* Lake B	48.7017	11.5566	GER		5		5						
GC	Geisenfeld* Lake C	48.7019	11.5530	GER		5		5						
GS	Griessee	47.9858	12.4423	GER	3				3					
HA	Haager Badeweiher	48.4503	11.8283	GER		5		5						
HB	Halfinger Badesees	47.9434	12.2775	GER	3				3					
HS	Hartsee	47.9268	12.3671	GER	2				2					
HW	Haselfurther Weiher [#]	48.4820	12.0130	GER	2	10		10	2					
JD	Jílové/Držkova*	50.6691	15.2893	CZE		5						5		
KE	Kesselsee	47.9161	12.3528	GER	1				1					
KF	Karlsfelder See	48.2368	11.4682	GER	3				3					
KL	Kleiner Leitner Weiher	48.7051	11.3211	GER		5		5						
KO	Kojetice*	50.2407	14.5157	CZE		5		5						
KR	Klicava reservoir	50.0706	13.9311	CZE		5						5		
KS	Klostersee	47.9746	12.4523	GER	1				1					
LB	Langbürgner See	47.9015	12.3517	GER	3				3					
LE	Lerchenauersee	48.1974	11.5374	GER	2				1				1	
LG	Lake Geneva	46.4500	6.4858	CHE	1				1					
LM	Lake Marathon	38.1655	23.8975	GRC	13				10		3			
LU	Luberweiher	48.7838	13.0103	GER	3	5	3	5						
LW	Langwieder See	48.1942	11.4163	GER	3				3					
OS	Olchinger See	48.2090	11.3565	GER	3				3					

Results

Table 5 continued:

ID	Lake	Latitude	Longitude	Cnty	sample size		type 1.1		type 1.2		type 2.1		type 2.2	
					P	M	P	Mr	P	M _m	P	M _m	P	Mr
PH	Pelhamer See	47.9337	12.3502	GER	3				3					
RA	Reichertshofen* Lake A [#]	48.6911	11.5237	GER		10								10
RB	Reichertshofen* Lake B	48.6931	11.5244	GER		5		5						
RC	Reichertshofen* Lake C	48.6911	11.5193	GER		5		5						
RD	Reichertshofen* Lake D	48.6887	11.5176	GER		5								5
RW	Ringwiler Weiher	47.3116	8.8538	CHE	1				1					
SI	Simssee	47.8718	12.2385	GER	3				3					
SL	Schliersee	47.7267	11.8603	GER	3				3					
SS	Schwarzlsee	46.9830	15.4254	AUT	3	5		5	3					
ST	Straß*	47.9168	12.3812	GER	3				3					
TT	Tüttensee	47.8463	12.5683	GER	3				3					
WE	Weicheringer See	48.7036	11.3296	GER	3		2		1					
WG	Waldschwaigsee	48.2251	11.4375	GER	1				1					
WA	Waldsee [§]	48.6925	11.5133	GER	3	15	3	15						
WS	Waldsee Schechen	47.9460	12.1530	GER		3				3				
sample size					101	142	21	108	75	9	3	10	2	15
number of lakes					35	25	8	18	30	3	1	2	2	2

3.1.2 Taxonomic Assignment – COI and Mitochondrial 16S rRNA Gene Phylogenies

In order to estimate the taxonomic affiliation of all six haplotypes (1.1, 1.2, 1.2.1, 2.1, 2.1.1, 2.2) COI and mitochondrial 16S rRNA genes were subjected to separate phylogenetic analyses with all published *Craspedacusta* sequences from GenBank (Table 1), using *Limnocyclus* as outgroup. Because the singleton haplotypes 1.2.1 and 2.1.1 were 16S specific they are only present in the 16S tree. 16S sequences retrieved from African polyps (LTP1, LTP2) were also included (Suppl. Table 1).

Published COI sequences from a previous study (N = 6; Table 1) had been formerly assigned to “*C. sowerbii/sowerbyi*” and are publicly available in GenBank. Combined with the six haplotypes among the newly obtained *Craspedacusta* sequences two clades were observable in the COI ML-tree (Figure 7; 100 % bootstrap support). In the first main clade (*C. sowerbii* type 1), type 1.1 clustered together with previous *Craspedacusta* samples from Germany (FJ423613 to FJ423620, 74 % bootstrap support). In the second main clade (*C. sowerbii* type 2), there were two subclades. Type 2.1 was grouped together with two “*C.*

Results

sowerbii/sowerbyi” sequences, one from China (JN93332) and one from Greece (KP231217; 61 % bootstrap support). A Chinese “*C. sowerbii/sowerbyi*” sequence (KF510026) did not branch within either the type 1.1 or 1.2. Type 2.2 clade was in the same larger subclade as 33 identical sequences from Chile (MF177101-MF177133) and as one sequence from Italy (MH230079; bootstrap = 99 %). Genetic distance between *C. sowerbii type 1* and *C. sowerbii type 2* was 0.183 ± 0.029 (mean K2P distance \pm SE; Table 6). COI type 1.1 differed at 3.0 ± 1.8 sites from type 1.2 (0.5 %), while type 2.1 differed at 7.0 ± 2.6 sites from type 2.2 (1.4 %).

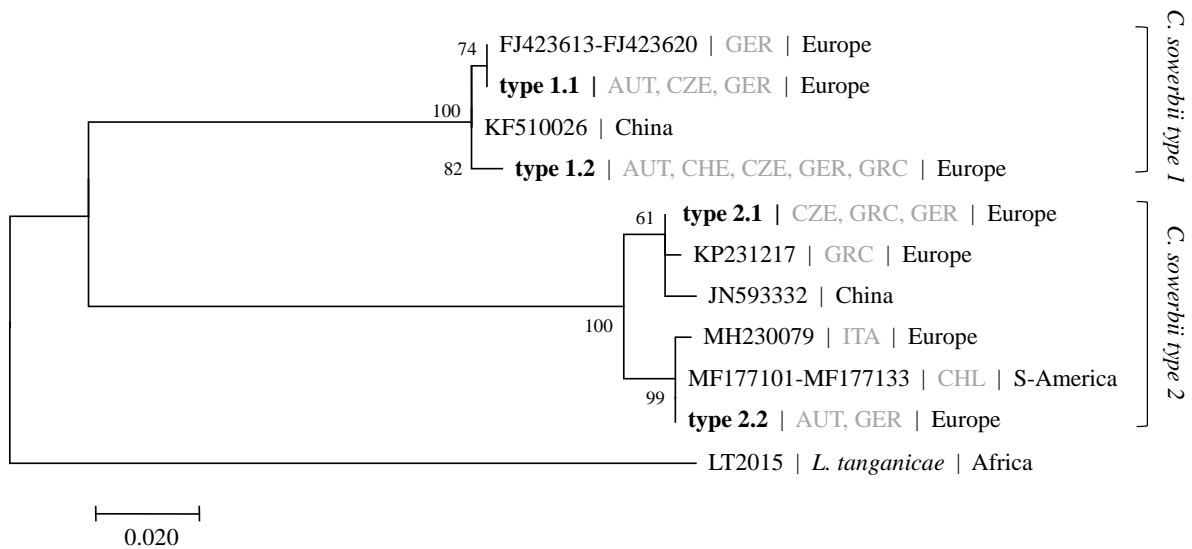


Figure 7: Maximum likelihood phylogenies including all available unique COI sequences of *Craspedacusta* and *Limnocnida*. Representative sequences for the six mtDNA haplotypes of newly generated *Craspedacusta* sequences (data set 1) are indicated by type 1.1, 1.2, 1.2.1, 2.1, 2.1.1 and 2.2; other sequences were obtained from GenBank (Table 1). Percent bootstrap support is shown at nodes. Scale bars indicate Kimura 2-parameter distances.

Table 6: Genetic distances among COI sequences (600 bp) of *C. sowerbii type 1* (n=5) and *type 2* (n=7) and *L. tanganycaae* (n=1) included in the ML tree in Figure 7. Kimura 2-Parameter (K2P) distances (below diagonal) and the uncorrected p-distances (shown in bold, above the diagonal) are displayed as mean value \pm standard error. Distances within *C. sowerbii type 1* and within *C. sowerbii type 2* were the same for both distance estimators (shown in italics).

	<i>C. sowerbii type 1</i>	<i>C. sowerbii type 2</i>	<i>L. tanganycaae</i>
<i>C. sowerbii type 1</i>	<i>0.005 \pm 0.003</i>	0.160 \pm 0.020	0.183 \pm 0.018
<i>C. sowerbii type 2</i>	0.183 \pm 0.029	<i>0.014 \pm 0.004</i>	0.211 \pm 0.022
<i>L. tanganycaae</i>	0.212 \pm 0.026	0.254 \pm 0.030	

Results

In the mitochondrial 16S rRNA gene phylogeny there were three main clades resolved with 100% bootstrap support (Figure 8). Clade 1 and 2 contained all six haplotypes from the present study and all formerly published "*C. sowerbii/sowerbyi*" sequences (N = 4; Table 1). Clade 3 contained two more Chinese *Craspedacusta* sequences from *C. sinensis* (AY512507) and *C. ziguiensis* (EU293974). Genetic distances between *C. sowerbii* clades (*type 1* and *type 2*) and *C. sinensis* and *C. ziguiensis* ranged between 0.074 ± 0.016 and 0.094 ± 0.017 , respectively (mean Kimura 2-Parameter distance \pm SE; Table 7). The genetic distance between *C. sowerbii type 1* and *C. sowerbii type 2* was smaller with a mean K2P distance of 0.049 ± 0.012 (Table 7). Within *C. sowerbii type 1*, sequences of type 1.1 were identical with one already published "*C. sowerbii/sowerbyi*" sequence from Germany (KY077294, bootstrap = 95%) and with one sequence of an African polyp (LTP2), whereby type 1.2 was combined with type 1.2.1 (bootstrap = 73 %). Within *C. sowerbii type 2* two subclades emerged. Type 2.1 was grouped together with the singleton Czech sequence of type 2.1.1 and with a Chinese "*C. sowerbii/sowerbyi*" sequence (JN593332, bootstrap = 86 %). Furthermore, type 2.2 was placed in the same subclade as one polyp sequence from Africa (LTP1), as one from Uruguay (KX267739) and as one from the USA (EU293971). Genetic distance between *C. sowerbii type 1* and *C. sowerbii type 2* mitochondrial 16S rRNA genes was 0.049 ± 0.012 (mean K2P distance \pm SE; Table 7), which was almost five times lower compared to that observed with COI genes (Table 6). The mitochondrial 16S rRNA gene types 1.1 and 1.2 showed differences at 1.0 ± 0.9 sites (0.2 %), while type 2.1 and 2.2 differed at 2.1 ± 1.3 sites (0.3 %).

All newly obtained and all formerly published *Craspedacusta* sequences were clearly different from the outgroup *Limnognida*, supported by high bootstrap values and genetic distances (Figures 7, 8; Tables 6, 7). The published *L. tanganicae* mitochondrial 16S rRNA gene sequence (EU293972) and the newly obtained one (LT2015) were identical (Table 7). For this reason, the newly obtained COI sequence from the same *Limnognida* individual LT2015 was assigned to the species *L. tanganicae* (Figure 7).

Results

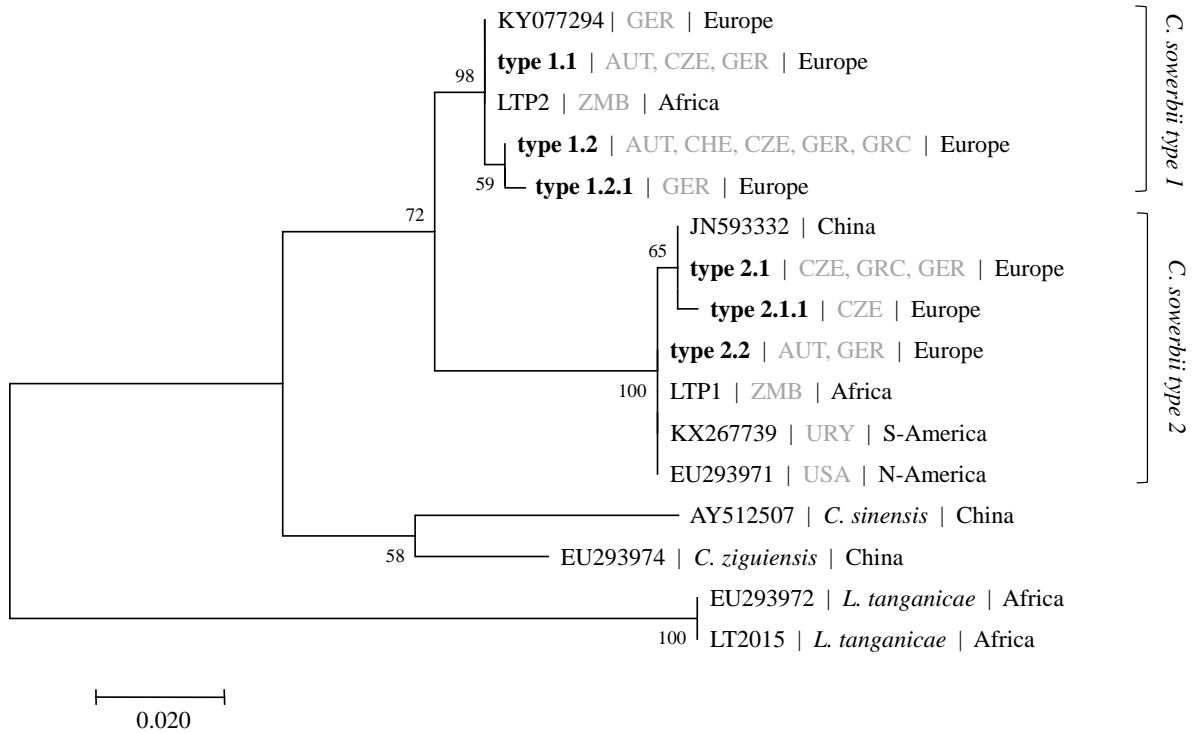


Figure 8: Maximum likelihood phylogenies including all available unique mitochondrial 16S rRNA gene sequences of *Craspedacusta* and *Limnocnida*. Representative sequences for the six mtDNA haplotypes of newly generated *Craspedacusta* sequences (data set 1) are indicated by type 1.1, 1.2, 1.2.1, 2.1, 2.1.1 and 2.2; all other sequences besides the two African *C. sowerbii* sequences were obtained from GenBank (see Table 1). Percent bootstrap support is shown at nodes. Scale bars indicate Kimura 2-parameter distances.

Table 7: Genetic distances among mitochondrial 16S rRNA gene sequences (604 bp) of *C. sowerbii type 1* (n=5), *C. sowerbii type 2* (n=7), *C. sinensis* (n=1), *C. ziguiensis* (n=1) and *L. tanganyicae* (n=2) shown in the ML tree in Figure 8. Kimura 2-Parameter (K2P) distances (below diagonal) and the uncorrected p-distances (shown in bold, above the diagonal) are displayed as mean value \pm standard error. Distances within *C. sowerbii type 1* and within *C. sowerbii type 2* were the same for both parameters (shown in italics).

	<i>C. sowerbii type 1</i>	<i>C. sowerbii type 2</i>	<i>C. sinensis</i>	<i>C. ziguiensis</i>	<i>L. tanganyicae</i>
<i>C. sowerbii type 1</i>	<i>0.002 \pm 0.002</i>	0.047 \pm 0.010	0.079 \pm 0.015	0.069 \pm 0.013	0.148 \pm 0.019
<i>C. sowerbii type 2</i>	0.049 \pm 0.012	<i>0.005 \pm 0.003</i>	0.087 \pm 0.015	0.084 \pm 0.015	0.173 \pm 0.021
<i>C. sinensis</i>	0.085 \pm 0.017	0.094 \pm 0.017		0.059 \pm 0.012	0.157 \pm 0.020
<i>C. ziguiensis</i>	0.074 \pm 0.016	0.090 \pm 0.019	0.062 \pm 0.014		0.154 \pm 0.020
<i>L. tanganyicae</i>	0.168 \pm 0.026	0.202 \pm 0.029	0.179 \pm 0.027	0.175 \pm 0.025	0

3.1.3 Genetic Population Structure of Medusae

For analysis of population structure of medusae, COI and mitochondrial 16S rRNA gene sequences of 162 medusae were obtained from the three lakes: Lake Neuer Baarer Weiher (GER), Lake Schwarzlsee (AUT), Lake Waldsee (GER) and from a lake near Jílové/Držkova (CZE; COI: 600 bp, 16S: 568 bp in the trimmed data set). TCS parsimony network analysis of the concatenated sequences (1168 bp, calculated maximum connection steps at 90% = 21; Figure 9) revealed no more than the previously identified two main networks with two subnetworks each, corresponding to the types 1.1, 1.2, 2.1 and 2.2 found in the large-scale dataset (Figure 6). Notably, only a single haplotype was detected among medusae. Medusae from Lake Schwarzlsee belonged to type 1.1 and medusae from the lake near Jílové/Držkova belonged to type 2.2. But in Lake Waldsee, which was mainly composed of medusae from type 1.1, a variant was found in low frequency. This variant consisted of a subset of four sequences one mutation apart from type 1.1 (WS054, WS062, WS079, WS081; type 1.1.1 in Figure 9), which is an additional type not included in the phylogenies (Figures 7 and 8). The effect of increased sampling intensity was most pronounced in Lake Neuer Baarer Weiher: while only one type (1.2) had been detected among five randomly selected medusae in data set 1, now altogether three types 1.2, 2.1 and 2.2 were detected (Figure 9). All three haplotypes were found among medusae from 2017 (n = 29), and two types (type 1.2, type 2.1) in the 2016 sample (n = 13; Suppl. Table 1).

Results

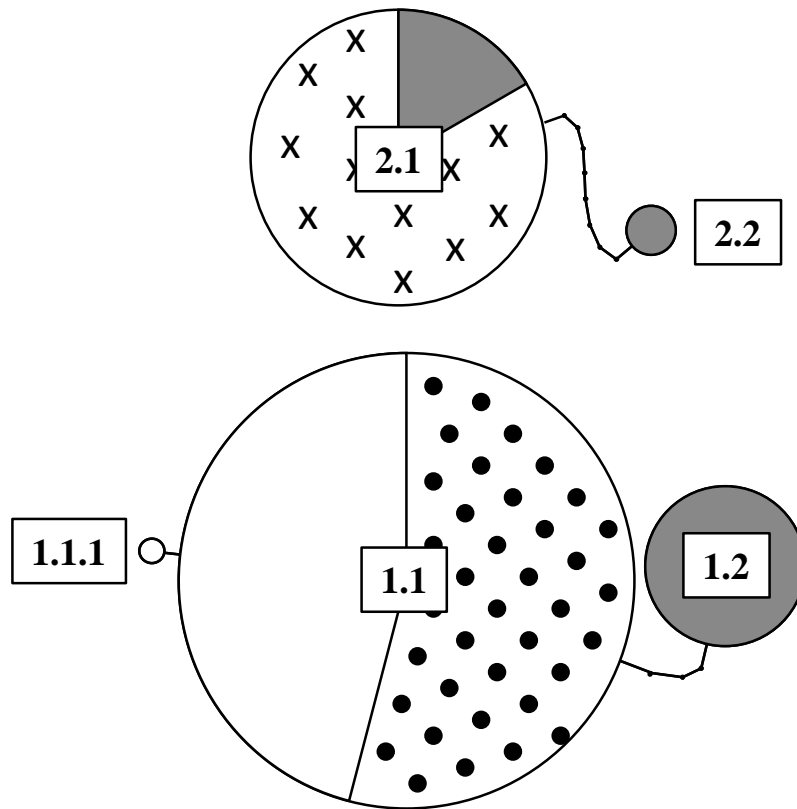


Figure 9: TCS parsimony network based on concatenated COI and mitochondrial 16S rRNA gene regions from *Craspedacusta* medusa samples from four different lakes. Five mtDNA haplotypes (type 1.1, 1.1.1, 1.2, 2.1 and 2.2) are arranged in two separated networks (90% cut-off). Circle-size relates to the number of individuals with a certain haplotype. Shades and colors refer to medusae from different lakes. Grey color = Lake Neuer Baarer Weiher (N = 42, samples in 2016 and 2017), crosses = lake near Jílové/Držkova (N = 40), dots = Lake Schwarzlsee (N = 40), white = Lake Waldsee (N = 40).

3.1.4 Small-scale Spatial Population Structure of Polyps

An intensively screened lake was chosen to study the genetic population structure of polyps within lakes. In Lake Langwieder See (Germany; Suppl. Table 1), at any time polyps have been found, although medusae were never observed across years (pers. obs.). Altogether 47 stones were screened from one site (site B, Figure 5 d) in 2016 and polyps were found on about half of the stones ($n = 25$) while the number of polyps on individual stones ranged between three and 30. Only polyps from stones colonized by more than one polyp ($N = 7$ stones) were used for genetic analysis. Additionally, five polyps each from three sites (A, B, C; Suppl. Table 1) sampled in 2015 were used for the analysis of the spatial population structure of polyps in Lake Langwieder See.

COI (822 bp) and mitochondrial 16S rRNA gene (604 bp) sequences from 97 polyps were obtained and concatenated (1426 bp). TCS analysis of this data set again confirmed two separate networks (calculated maximum connection steps at 90% = 23; Figure 10), whereby only network 1 contained two subnetworks. These three haplotypes were identical to the three types 1.1, 1.2 and 2.1 identified in data set 1 (Figure 6). Notably, among polyps, more than one haplotype colonized individual stones: all three types (stone LWS2) or at least two types (stone LWS1, LWS5) co-occurred on the same stone, sitting only a few millimeters apart (Suppl. Table 1). Haplotype frequencies were unequal and type 1.2 was again the most common type among polyps (68%, $N_{P, 1.2} = 56$); polyps of type 1.2 were detected at all three sites (A, B, C) and on all seven stones from the small-scale sampling at site B. In comparison, less polyps were found from type 2.2 ($N_{P, 2.2} = 18$) and from type 1.1 ($N_{P, 1.1} = 8$). Site A was inhabited by polyps of type 1.1 and 1.2, at site C polyps of type 1.2 and 2.2 (Figure 10) were detected.

Results

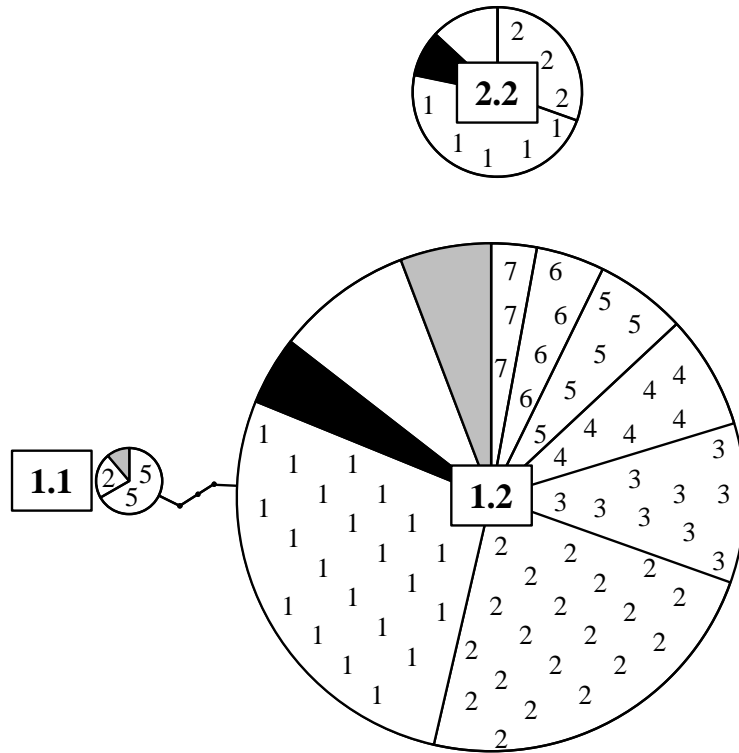


Figure 10: TCS-parsimony network based on concatenated COI and mitochondrial 16S rRNA gene regions from *Craspedacusta* polyp samples from Lake Langwieder See (Germany). Three mtDNA haplotypes (type 1.1, 1.2, 2.1 and 2.2) are arranged in two separated networks (90% cut-off). Circle-size relates to the number of individuals with a specific haplotype. Colors indicate polyps from three different sites, which were sampled in 2015: Grey = site A, white = site B, black = site C. Numbers from 1 to 7 refer to polyps from seven different stones at site B, which were sampled in 2016.

3.2 Feeding Ecology and Trophic Position of Polyps

3.2.1 Functional and Numerical Response Analyses of *Craspedacusta* and *Hydra*

The average dry weight of *Craspedacusta* polyps was $0.7 \pm 0.2 \mu\text{g}$ (\pm standard deviation), and the carbon content was $0.21 \pm 0.06 \mu\text{g}$. *Hydra* polyps averaged a dry weight of $7.0 \pm 5.1 \mu\text{g}$ with a carbon content of $2.10 \pm 1.53 \mu\text{g}$. The average carbon content of the prey species *Brachionus calyciflorus* was $0.23 \pm 0.03 \mu\text{g}$.

Both separate functional response experiments with polyps of the two genera *Craspedacusta* and *Hydra* revealed increasing prey ingestion with increasing prey densities (Figure 11).

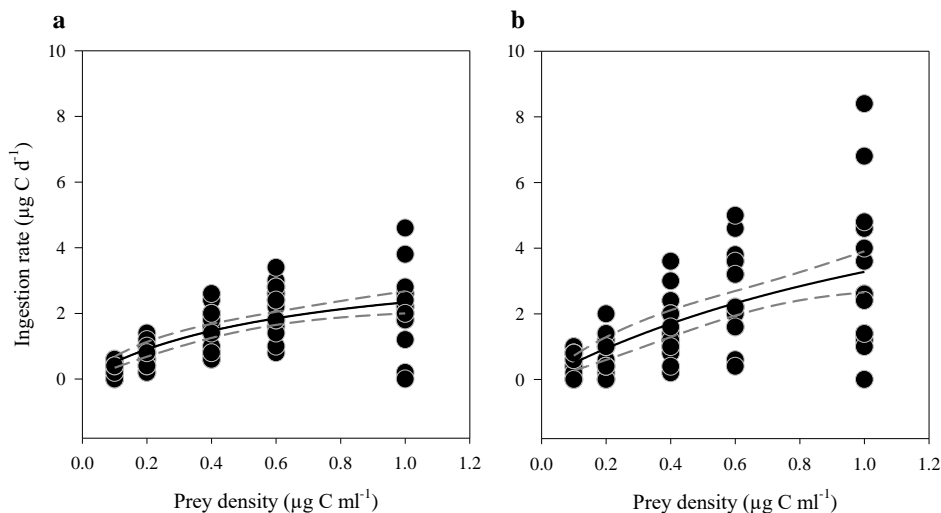


Figure 11: Functional response of the (a) polyp of *Craspedacusta* and of the (b) polyp of *Hydra*. The relationship between prey density (*Brachionus calyciflorus*) and ingestion rate is described by the function: (a) $y = (3.86 \pm 0.87) x / (0.65 \pm 0.28) + x$, $R^2 = 0.49$, $p = <0.0001$; (b) $y = (8.61 \pm 5.10) x / (1.62 \pm 1.38) + x$, $R^2 = 0.39$, $p = <0.0001$. Dashed lines represent 95% confidence intervals.

For *Craspedacusta* the carbon ingestion started from about $0.35 \pm 0.06 \mu\text{g C d}^{-1}$ (mean \pm standard error) at low *Brachionus* densities ($0.1 \mu\text{g C ml}^{-1}$) up to around $2.15 \pm 0.30 \mu\text{g C d}^{-1}$ at the highest *Brachionus* densities in the experiment ($1.0 \mu\text{g C ml}^{-1}$, Figure 11 a). Based on the regression between prey density and ingestion rate, the handling time of polyps of *Craspedacusta* was calculated as 6.2 hours per $\mu\text{g C}$ (corresponding to a dry weight of five *Brachionus* individuals). In addition, from this relationship, it can be concluded that a maximum amount of carbon ingested per day (I_{max}) was $3.86 \pm 0.87 \mu\text{g}$. The increase in the ingestion rate started to slow down at food concentrations $> 0.6 \mu\text{g C ml}^{-1}$. However, the

Results

saturation part of the functional response curve was not completely reached within the experiments with *Craspedacusta*.

For polyps of *Hydra* the carbon ingestion started from about $0.52 \pm 0.09 \mu\text{g C d}^{-1}$ at low *Brachionus* densities ($0.1 \mu\text{g C ml}^{-1}$) up to around $3.16 \pm 0.59 \mu\text{g C d}^{-1}$ at the highest *Brachionus* densities in the experiment ($1 \mu\text{g C ml}^{-1}$, Figure 11 b). Based on the regression between prey density and ingestion rate, the handling time of polyps of *Hydra* was calculated as 2.8 hours per $\mu\text{g C}$ (corresponding to a dry weight of five *Brachionus* individuals) and I_{max} was $8.60 \pm 5.10 \mu\text{g C d}^{-1}$. The saturation part of the functional response was not fully reached within the experiments with *Hydra*.

The reproductive output of both species was analyzed for additional 16 days after the end of these functional response experiments. On the third day, the mean abundance of polyps of *Craspedacusta* in each experimental replicate was 1.4 ± 0.2 individuals. No significant relationship between initial prey density and reproduction was visible ($p = 0.9336$). On day six, polyps of *Craspedacusta* showed a reproductive output from on average 1.2 ± 0.2 offspring at low *Brachionus* densities ($0.1 \mu\text{g C ml}^{-1}$) to about 3.0 ± 0.3 offspring at the highest *Brachionus* densities in the experiment ($1.0 \mu\text{g C ml}^{-1}$; Figure 12 a). Regression analyses revealed a significant relationship between initial prey density and reproduction at day six and at day nine ($p < 0.0001$; Figure 12). After day nine, no further reproduction by *Craspedacusta* polyps was visible. No significant relationship between initial prey density and reproduction was observed for *Hydra* during the 16 days of observation.

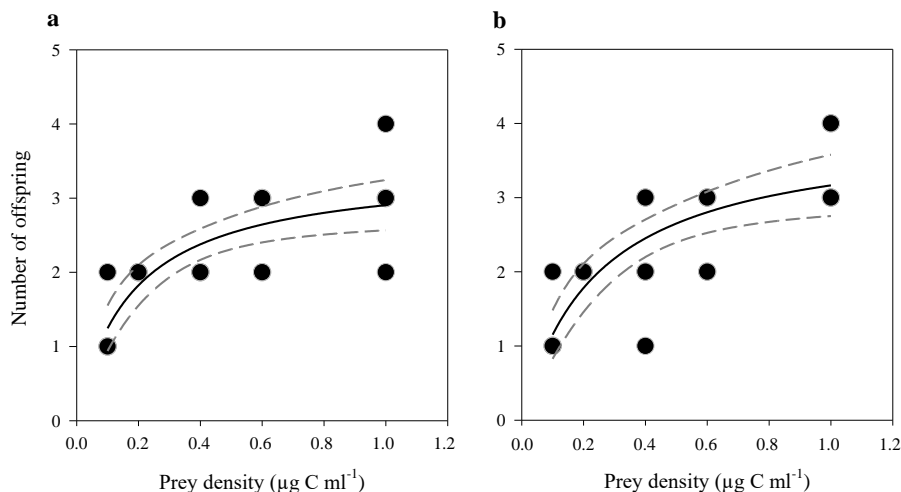


Figure 12: Numerical response of polyps of *Craspedacusta* observed at (a) day 6 and (b) day 9 after the end of functional response experiments. The relationship between prey density and offspring production is described by the function: (a) $y = (3.41 \pm 0.32) x / (0.87 \pm 0.27) + x$, $R^2 = 0.63$, $p < 0.0001$; and (b) $y = (3.93 \pm 0.46) x / (1.20 \pm 0.40) + x$, $R^2 = 0.63$, $p < 0.0001$. Dashed lines indicate 95% confidence intervals.

3.2.2 Isotopic Niche Differentiation of *Craspedacusta* and *Hydra*

In all four investigated lakes and at all sampling dates, polyps of *Craspedacusta* showed significant differences in $\delta^{13}\text{C}$ signatures compared to polyps of *Hydra* (Table 8). Mean $\delta^{13}\text{C}$ values of polyps of *Craspedacusta* were similar to $\delta^{13}\text{C}$ values of the littoral herbivore *Pleuroxus truncatus* and *Lymnea stagnalis* (Figure 13). The $\delta^{13}\text{C}$ values of *Hydra* were similar to the $\delta^{13}\text{C}$ values of the pelagic herbivores *Polyphemus pediculus*, *Sida crystallina*, *Alona sp.*, *Daphnia sp.* and of the zebra mussel *Dreissena polymorpha* (Figure 13). Also, $\delta^{13}\text{C}$ values of the pelagic carnivore free-swimming medusae of *Craspedacusta* were more similar to the $\delta^{13}\text{C}$ values of *Hydra* compared to the values of the polyps of *Craspedacusta*. The $\delta^{13}\text{C}$ values of the benthic carnivore *Dugesia sp.* (Plathelmintha) and of copepods (pelagic omnivore) were within or in between the range of both polyp genera (Figure 13). At four of the sampling dates no significant differences in the $\delta^{15}\text{N}$ signatures among polyps of *Craspedacusta* and of *Hydra* were observed (Table 8). $\delta^{15}\text{N}$ values of the two polyp genera were only significantly different in two of the samplings (Table 8).

Similar results emerged from SIBER analyses using data from all six sampling dates (Figure 14). Ellipses displaying the 95 % confidence interval based on bivariate means of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures did not overlap among polyps of *Craspedacusta* and *Hydra* (Figure 14). A temporal relationship with niche space is suggested by the data of Lake Langwieder See, since the ellipses nearly overlapped in May but became increasingly separate from July to October (Figure 14 a, c, e).

Table 8: Summary of statistical comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among polyps of *Craspedacusta* and of *Hydra*. Shown are mean values \pm standard errors (SE), significant p-values are indicated by bold numbers.

sampling site	sampling date	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
		<i>Craspedacusta</i>	<i>Hydra</i>	p-value	<i>Craspedacusta</i>	<i>Hydra</i>	p-value
Langwieder See	10 May 2016	-31.3 \pm 0.3	-36.0 \pm 0.9	0.024	10.1 \pm 0.3	8.7 \pm 0.4	0.069
	11 July 2016	-28.8 \pm 0.4	-36.2 \pm 0.6	< 0.001	8.6 \pm 0.2	6.9 \pm 0.1	0.002
	15 October 2015	-27.3 \pm 0.3	-38.3 \pm 0.5	< 0.001	9.4 \pm 0.2	8.0 \pm 0.2	0.002
Hartsee	01 June 2016	-31.3 \pm 0.1	-33.6 \pm 0.1	< 0.001	12.5 \pm 0.2	12.5 \pm 0.2	0.825
Haselfurther Weiher	28 July 2016	-29.5 \pm 0.1	-34.6 \pm 0.2	< 0.001	13.1 \pm 0.4	13.9 \pm 0.1	0.100
Weicheringer See	20 October 2015	-20.8 \pm 0.1	-25.2 \pm 0.5	< 0.001	4.4 \pm 0.2	4.2 \pm 0.4	0.636

Results

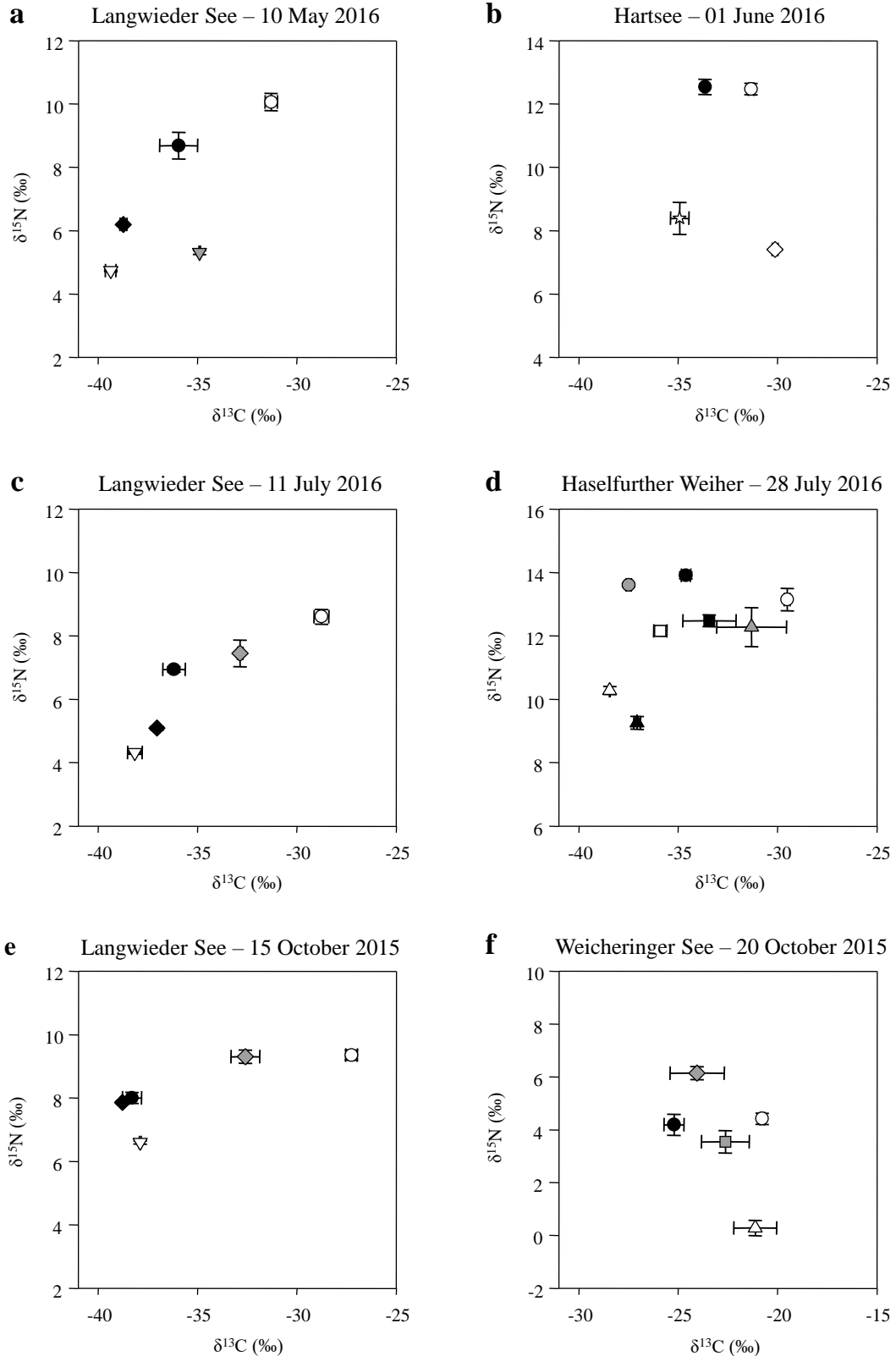


Figure 13: Mean \pm standard error (SE) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of (\circ) polyps of *Craspedacusta* and of (\bullet) *Hydra* from (a) Langwieder See 2, (b) Hartsee, (c) Langwieder See 3, (d) Haselfurther Weiher, (e) Langwieder See 1 and (f) Weicheringer See. Isotopic values of (∇) *Alona* sp., (Δ) *Bosmina* sp., (\blacktriangle) *Daphnia longispina*, (\star) *Dreissena polymorpha*, (\blacktriangle) *Lymnea stagnalis*, (\diamond) *Pleuroxus truncatus*, (\blacklozenge) *Polyphemus pediculus*, (∇) *Sida crystallina*, (\square) Calanoida, (\blacksquare) Cyclopoida, (\blacksquare) Copepoda, (\blacklozenge) *Dugesia* sp. and of (\bullet) medusae of *Craspedacusta*.

Results

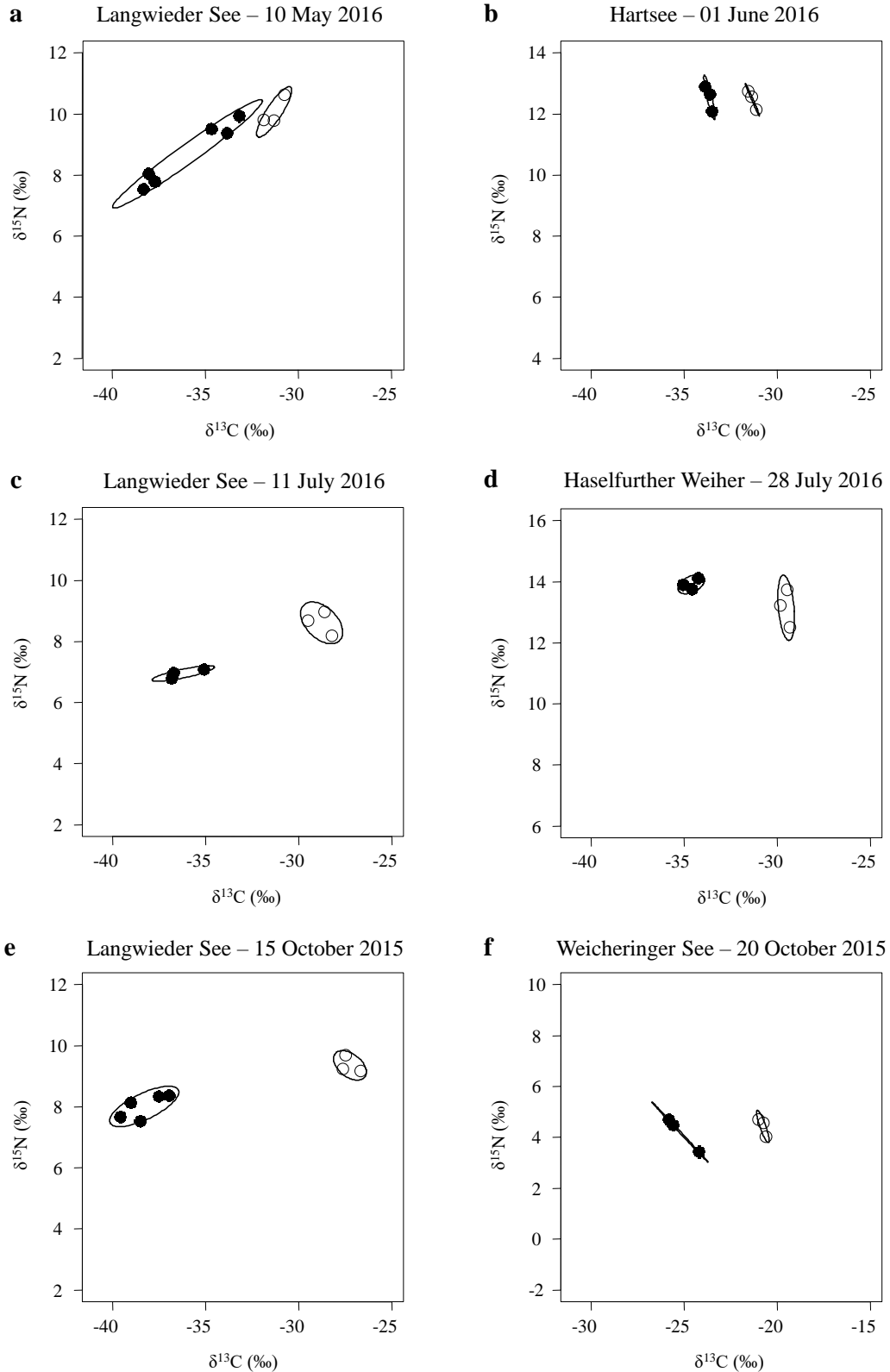


Figure 14: Stable isotope bi-plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of (○) polyps of *Craspedacusta* and of (●) *Hydra* from (a) Langwieder See 2, (b) Hartsee, (c) Langwieder See 3, (d) Haselfurther Weiher, (e) Langwieder See 1 and (f) Weicheringer See. Ellipses depict the 95% confidence intervals (SIBER). No overlap of ellipses indicates significant differences of the isotopic niches between *Craspedacusta* and *Hydra* polyps.

3.3 Trophic Cascades Mediated by Jellyfish

Three separate outdoor mesocosm experiments were conducted to investigate the impact of the freshwater jellyfish *C. sowerbii* on the pelagic plankton communities of three German pre-alpine lakes, Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher. The impact of 0, 2, 4, 8 and 16 jellyfish per enclosure (140 L) on the plankton community of each lake was tested. Molecular analyses revealed that all three experiments were conducted with medusae of *C. sowerbii* type 1 (mtDNA haplotype 1.1), which represents the dominant *Craspedacusta* species in European lakes at the present stage (topic 1).

3.3.1 Initial Plankton Communities and Seston Stoichiometry

The initial mesozooplankton community composition included mainly copepods and cladocerans in all three experiments. In the mesocosm experiments of Lake Haselfurther Weiher and of Lake Waldsee, the cladocerans were dominant with about 70%. In Lake Haager Weiher, the community was dominated by copepods with 65% (Table 9).

The initial phytoplankton community in the mesocosm experiments of Lake Haselfurther Weiher and of Lake Waldsee, was dominated by green algae with about 58 %. Diatoms/dinoflagellates were dominant in the enclosures of Lake Haager Weiher with 57 % (Table 9).

Table 9: Initial composition of the plankton communities and related seston stoichiometry in mesocosm experiments of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher.

	Haselfurther Weiher	Waldsee	Haager Weiher
Total dry weight mesozooplankton ($\mu\text{g L}^{-1}$)	127	109	143
Cladocera	69 %	70 %	35 %
<i>Bosmina</i> sp.	47 %	39 %	15 %
<i>Ceriodaphnia</i> sp.	20 %	8 %	20 %
<i>Daphnia</i> sp.	2 %	23 %	-
<i>Diaphanosoma</i> sp.	-	<1 %	<1 %
Copepoda	31 %	30 %	65 %
calanoid	6 %	4 %	-
cyclopoid	25 %	26 %	65 %

Results

Table 9 continued:

	Haselfurther Weiher	Waldsee	Haager Weiher
Total chlorophyll a ($\mu\text{g L}^{-1}$)	4.43	2.00	2.95
<i>Green algae</i>	57 %	58 %	28 %
<i>Blue-green algae</i>	-	16 %	14 %
<i>Diatoms/dinoflagellates</i>	43 %	2 %	57 %
<i>Cryptophytes</i>	-	24 %	1 %
Seston C:N	5.6	4.3	6.2
Seston C:P	189	304	220
Seston N:P	34.4	75.4	36.0

3.3.2 Mesozooplankton

Impact on mesozooplankton quantity

As a common trend in all three experiments, total crustacean mesozooplankton biomass (measured as dry weight) decreased with increasing jellyfish density, despite different zooplankton parameters differing between the lakes. For example, in Lake Haselfurther Weiher the mesozooplankton biomass exponentially decreased with the increasing jellyfish density (Figure 15, Table 10). The average total biomass declined from $239.94 \pm 29.84 \mu\text{g L}^{-1}$ (mean \pm standard error) in jellyfish-free treatments to $9.34 \pm 1.28 \mu\text{g L}^{-1}$ in treatments with 16 jellyfish per enclosure. In Lake Waldsee and in Lake Haager Weiher, the total biomass of the mesozooplankton community decreased linearly with increasing jellyfish density (Figure 15, Table 10). In Lake Waldsee, the average total biomass declined from $46.37 \pm 2.79 \mu\text{g L}^{-1}$ in jellyfish-free treatments to $27.84 \pm 1.82 \mu\text{g L}^{-1}$ in treatments with 16 jellyfish per enclosure. In Lake Haager Weiher, the average total biomass declined from $152.69 \pm 13.44 \mu\text{g L}^{-1}$ in controls to $95.91 \pm 8.39 \mu\text{g L}^{-1}$ in treatments with 16 jellyfish per enclosure.

In Lake Haselfurther Weiher, higher jellyfish densities significantly correlated with the total dry weight of all crustacean mesozooplankton species observed. An exponential decay of biomass with increasing jellyfish density was observed for *Ceriodaphnia sp.* and for cyclopoid copepods. The biomass of *Bosmina sp.*, *Daphnia sp.* and of calanoid copepods showed a linear decay with increasing jellyfish concentrations (Figure 16 a, b; Table 10).

Results

In Lake Waldsee, the biomass made up by *Daphnia sp.* was exponentially reduced in the presence of higher jellyfish densities (Figure 16 c; Table 10). Linear regressions were significant for biomass changes of calanoid and of cyclopoid copepods (Figure 16 d; Table 10). In contrast, the biomass of *Ceriodaphnia sp.* and of *Bosmina sp.* increased with higher jellyfish densities, although these trends were not significant (Figure 16 c; Table 10).

In Lake Haager Weiher, the biomass of *Ceriodaphnia sp.* showed a significant negative trend with increasing jellyfish density (Figure 16 e; Table 10). Similar but insignificant trends were observed for *Daphnia sp.*, *Diaphanosoma sp.*, and for cyclopoid and calanoid copepods (Figure 16 e, f; Table 10). However, *Bosmina sp.* biomass correlated positively with higher densities of jellyfish, albeit not significantly (Figure 16 e; Table 10).

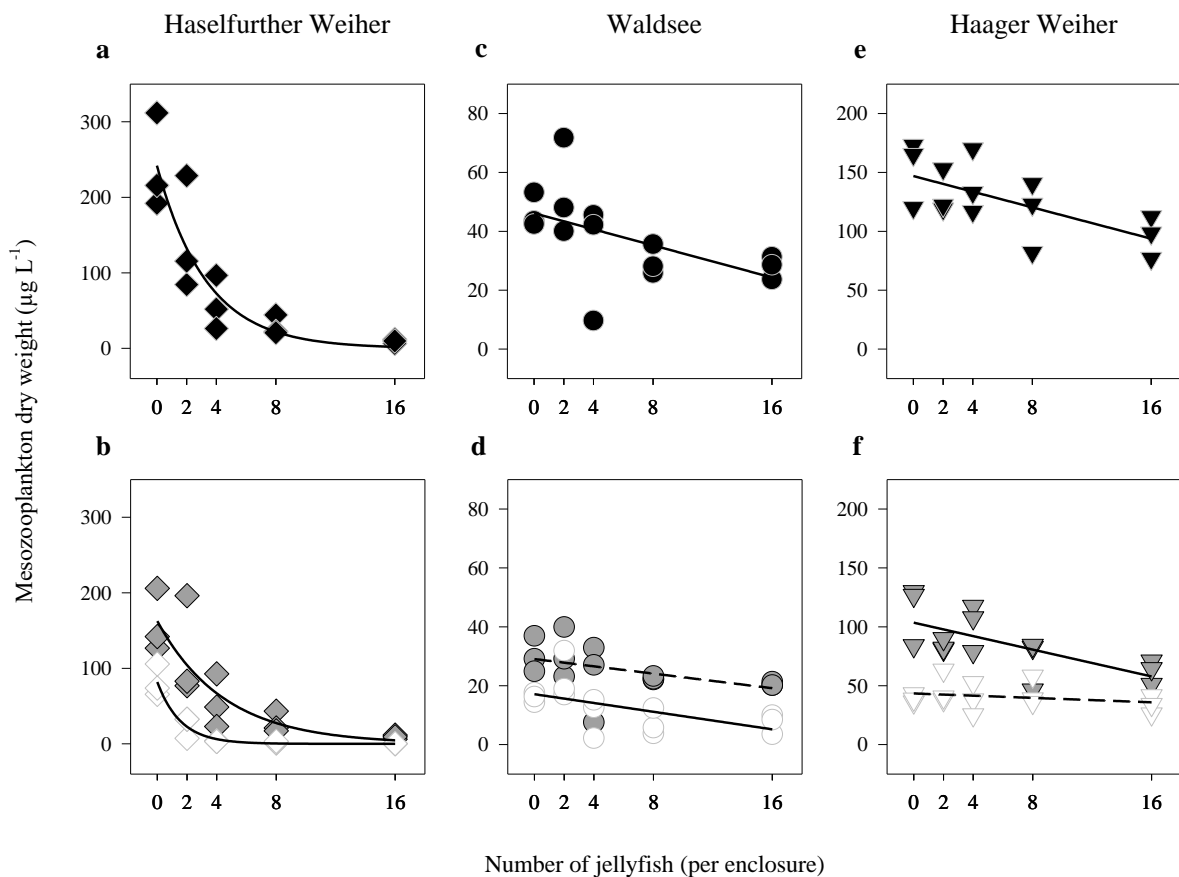


Figure 15: Regression analyses of the total crustacean mesozooplankton dry weight (black symbols), of cladocerans (grey symbols) and of copepods (white symbols) versus jellyfish density in the enclosures of (a, b) Lake Haselfurther Weiher, (c, d) Lake Waldsee and (e, f) Lake Haager Weiher at the end of the experiments. Displayed are significant linear or exponential regression curves (solid, $p < 0.05$) and insignificant trends (dashed lines).

Results

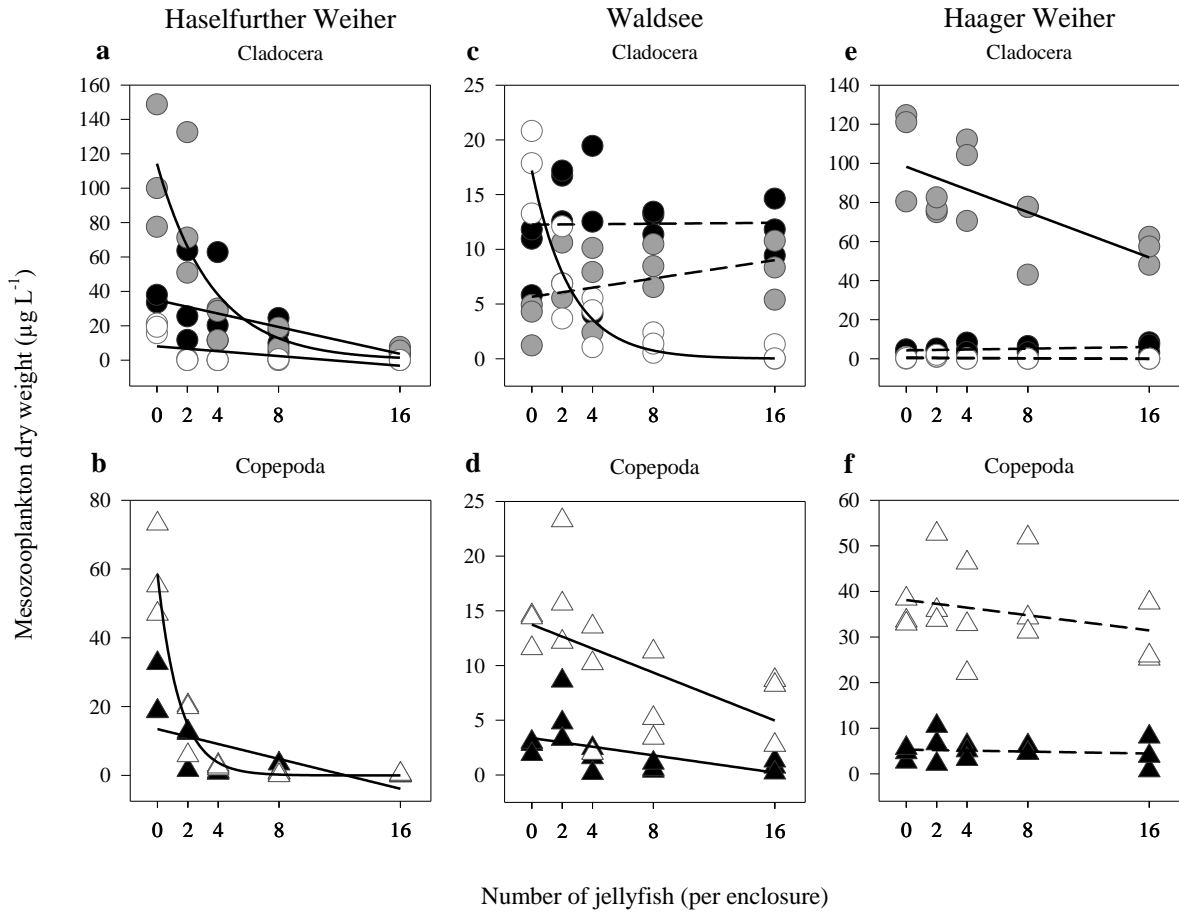


Figure 16: Regression analyses of dry weight ($\mu\text{g L}^{-1}$) of *Bosmina sp.* (●), *Ceriodaphnia sp.* (◐), *Daphnia sp.* (○), calanoid copepods (▲) and of cyclopoid copepods (△) versus jellyfish density in the enclosures of (a,b) Lake Haselfurther Weiher, (c,d) Lake Waldsee, (e,f) Lake Haager Weiher at the end of the experiments. Displayed are significant linear or exponential regression curves (solid, $p < 0.05$) and insignificant trends (dashed lines).

Table 10: Summary of the regression analyses of the dry weight ($\mu\text{g L}^{-1}$) of total crustacean mesozooplankton, of taxonomical groups and of single taxa as functions of jellyfish density in the enclosures of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher at the end of the experiments. Applied regression models are linear or exponential fits. Significant p-values are highlighted ($p < 0.05$).

	Haselfurther Weiher			Waldsee			Haager Weiher		
	p	R ²	equation	p	R ²	equation	p	R ²	equation
Total dry weight	0.0005	0.82	$y = 241.89 e^{(-0.30 \cdot x)}$	0.0352	0.30	$y = -1.36 x + 46.14$	0.0072	0.44	$y = -3.32 x + 146.90$
Cladocera	0.0026	0.74	$y = 162.52 e^{(-0.22 \cdot x)}$	0.0811	0.22	$y = -0.62 x + 29.02$	0.0060	0.45	$y = -2.85 x + 103.49$
<i>Bosmina</i> sp.	0.0197	0.35	$y = -1.95 x + 34.98$	0.9562	0.0002	$y = 0.01 x + 12.26$	0.1875	0.13	$y = 0.11 x + 4.30$
<i>Ceriodaphnia</i> sp.	0.0030	0.75	$y = 114.31 e^{(-0.27 \cdot x)}$	0.1288	0.17	$y = 0.21 x + 5.66$	0.0050	0.47	$y = -2.90 x + 98.25$
<i>Daphnia</i> sp.	0.0417	0.28	$y = -0.71 x + 8.06$	0.0001	0.87	$y = 17.20 e^{(-0.39 \cdot x)}$	0.0676	0.23	$y = -0.05 x + 0.64$
<i>Diaphanosoma</i> sp.	-	-	-	-	-	-	0.1765	0.14	$y = -0.01 x + 0.30$
Copepoda	0.0001	0.91	$y = -3.67 x + 44.33$	0.0264	0.33	$y = -0.75 x + 17.12$	0.3415	0.07	$y = -0.47 x + 43.41$
calanoid	0.0096	0.41	$y = -1.08 x + 13.47$	0.0459	0.27	$y = -0.20 x + 3.37$	0.6488	0.02	$y = -0.05 x + 5.31$
cyclopoid	<0.0001	0.94	$y = 58.51 e^{(-0.69 \cdot x)}$	0.0288	0.32	$y = -0.55 x + 13.74$	0.3232	0.08	$y = -0.42 x + 38.10$

Results

To compare the effect of jellyfish on the dry weight of the total zooplankton and of single mesozooplankton taxa of the three experiments, effect sizes were calculated. A strong jellyfish dependent negative effect was shown on the total mesozooplankton dry weight of Haselfurther Weiher, similar weaker negative effects occurred in the other two lakes (Figure 17 f). Across all three experiments, a clear negative effect on total zooplankton dry weight was visible in the highest jellyfish treatment. No taxon-specific effect of jellyfish density was detected across the three experiments (Figure 17). However, great effects are shown for *Daphnia sp.* already at low jellyfish densities of two individuals per enclosure (Figure 17 c). Also neutral to positive effects were observed for *Bosmina sp.* and *Ceriodaphnia sp.* (Figure 17 a, b). Strongest effects were observed for cyclopoid copepods in Lake Haselfurther Weiher (Figure 17 e).

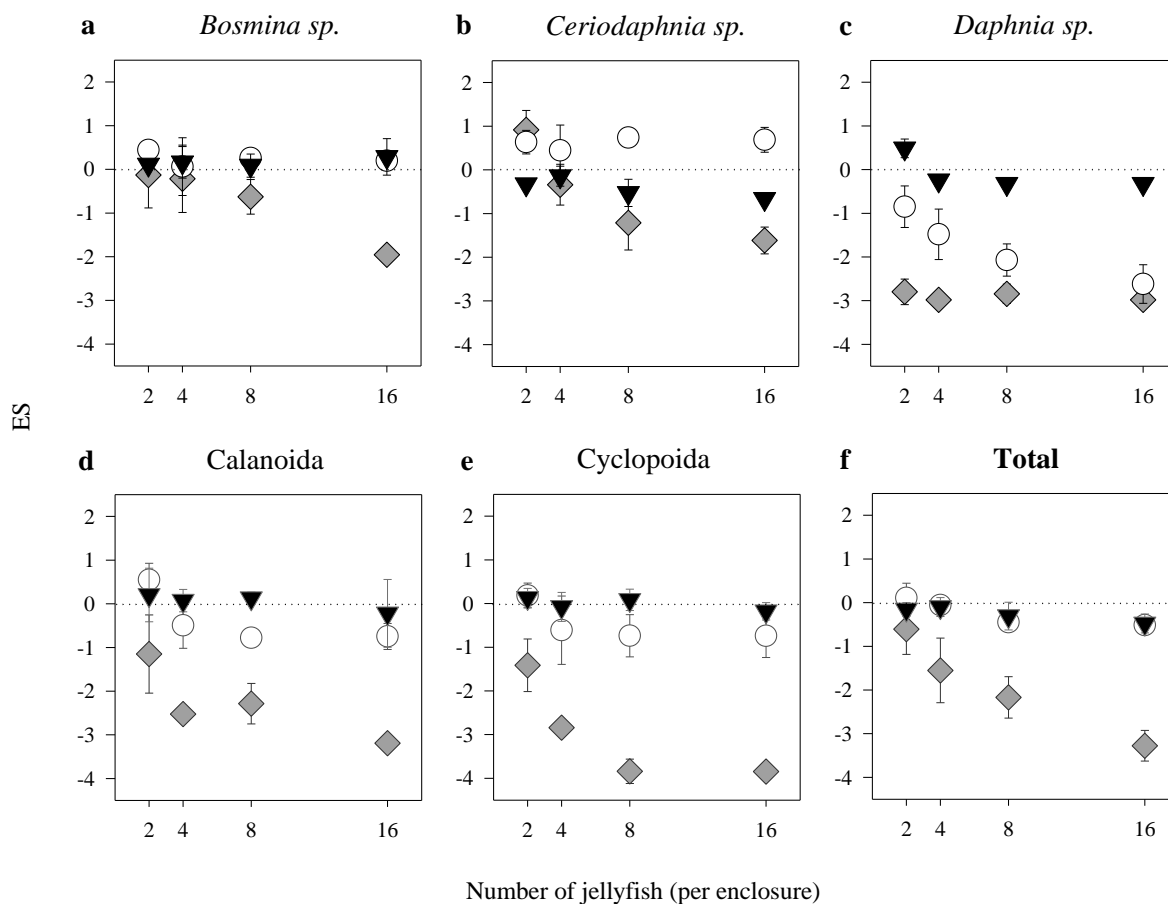


Figure 17: Effects (ES) of jellyfish on the dry weight of (a) *Bosmina sp.*, (b) *Ceriodaphnia sp.*, (c) *Daphnia sp.*, (d) calanoid copepods, (e) cyclopoid copepods and on (f) the whole crustacean mesozooplankton community in relation to jellyfish density in the enclosures of Lake Haselfurther Weiher (◆), Waldsee (○) and Haager Weiher (▼) at the end of the experiments. Displayed are mean values \pm 95% CI, dashed line indicates zero effect.

Results

Comparison of mesozooplankton community composition

In all three experiments, assemblages of crustacean mesozooplankton differed among treatments at the end of the experiments. Results of analyses of similarity (ANOSIM) showed that differences were strongest in enclosures of Haselfurther Weiher (Global R = 0.747, p = 0.001). Smaller differences were observed between communities of Waldsee (Global R = 0.455, p = 0.001). Almost no differences were detected among zooplankton assemblages in enclosures of Haager Weiher (Global R = 0.053, p = 0.312). In Lake Haselfurther Weiher a clear separation of the jellyfish-free and the maximum density treatment was observed (Figure 18), mainly due to differences in the abundance of *Ceriodaphnia sp.* that contributed 56.3 % to the dissimilarity. In Lake Waldsee this dissimilarity was mainly due to *Bosmina sp.* (40.9 %) and in Lake Haager Weiher it was due to *Ceriodaphnia sp.* (72.9 %).

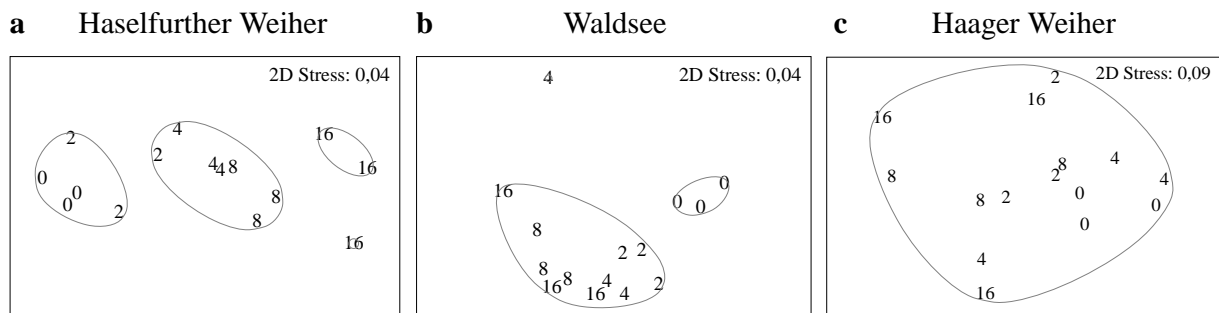


Figure 18: Non-metric multidimensional scaling (nMDS) plots showing differences in assemblages of crustacean mesozooplankton at the end of the mesocosm experiments in (a) Lake Haselfurther Weiher, (b) Lake Waldsee and (c) Lake Haager Weiher. Each number represents the zooplankton assemblage in an individual mesocosm according to the jellyfish density treatments. The proximity of the symbols indicates the degree of similarity between assemblages; ellipses indicate an 80 % similarity between assemblages.

Changes in mesozooplankton growth rates

Growth rates of crustacean mesozooplankton taxa were changed by jellyfish presence. Especially in Lake Haselfurther Weiher, these changes contributed to changes in competitiveness (Figure 19 a). In jellyfish-free treatments, *Ceriodaphnia sp.* had the highest growth rates with 0.05 ± 0.02 ind $L^{-1} d^{-1}$ (mean \pm standard error). In the highest jellyfish density treatments, the growth rate was on average -0.17 ± 0.04 ind $L^{-1} d^{-1}$, indicating that *Ceriodaphnia sp.* was less competitive than calanoid copepods ($-0.12 \pm 0.98 \cdot 10^{-17}$ ind $L^{-1} d^{-1}$) and *Daphnia sp.* (-0.08 ± 0.00 ind $L^{-1} d^{-1}$). The lowest growth rates were exhibited by cyclopoid copepods with a growth rate of $-0.29 \pm 0.23 \cdot 10^{-2}$ ind $L^{-1} d^{-1}$. In Lake Waldsee, the

Results

opposite was observed for *Daphnia sp.*. This taxon had the lowest growth rate in the maximum jellyfish treatment with 16 jellyfish per enclosure ($-0.17 \pm 0.43 \cdot 10^{-2}$ ind $L^{-1} d^{-1}$) and was the least competitive organism observed (Figure 19 b). In Lake Haager Weiher, growth rates changed slightly with jellyfish density (Figure 19 c).

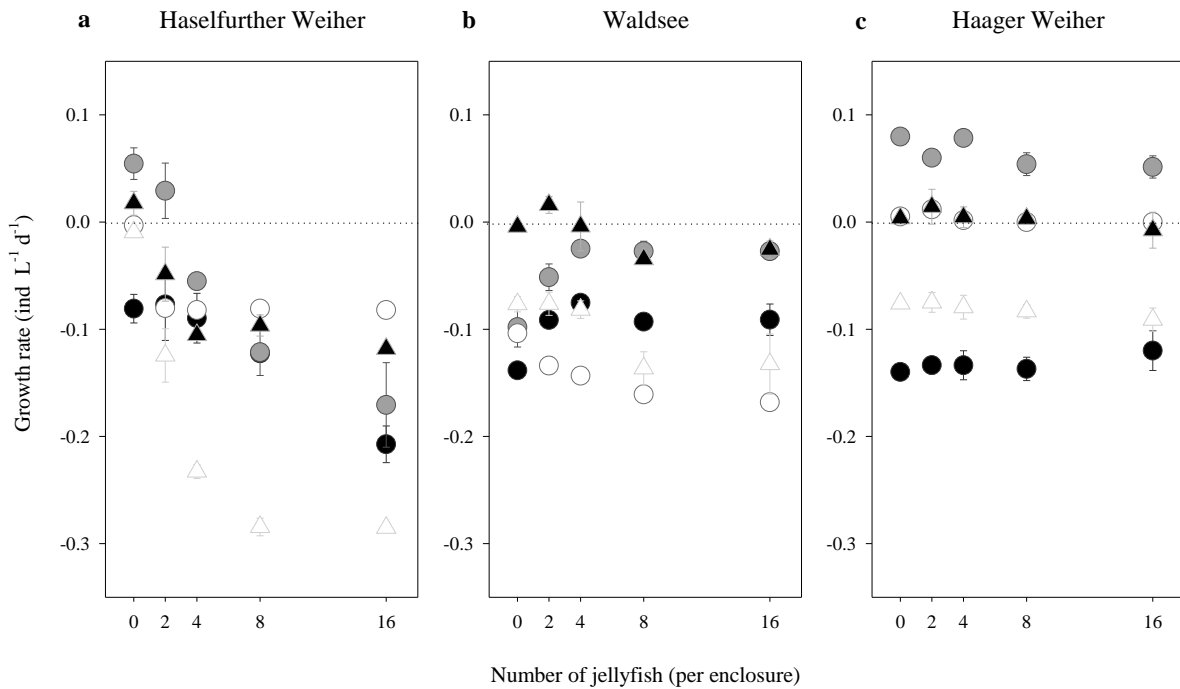


Figure 19: Growth rates (ind $L^{-1} d^{-1}$) of *Bosmina sp.* (●), *Ceriodaphnia sp.* (●), *Daphnia sp.* (○), calanoid copepods (▲) and cyclopoid copepods (Δ) in relation to jellyfish density in the enclosures of (a) Lake Haselfurther Weiher, (b) Lake Waldsee, (c) Lake Haager Weiher. Displayed are mean values \pm standard errors, the dashed line indicates zero growth.

Changes in mesozooplankton diversity

The presence of medusae had a variable influence on the zooplankton diversity in the three experiments (Figure 20). Shannon diversity H' significantly declined with increasing jellyfish densities in Lake Haselfurther Weiher and in Lake Waldsee as a function of altered evenness (Figure 20 a, b, Table 11). A linear relation for treatments with a maximum of eight jellyfish was observed. Enclosures with eight medusae showed the greatest change in species diversity of crustacean mesozooplankton. A similar pattern could be observed for Pielou's evenness J' . In Lake Haager Weiher, Shannon diversity H' of the crustacean mesozooplankton correlated positively with the jellyfish density (Figure 20 c, Table 11).

Results

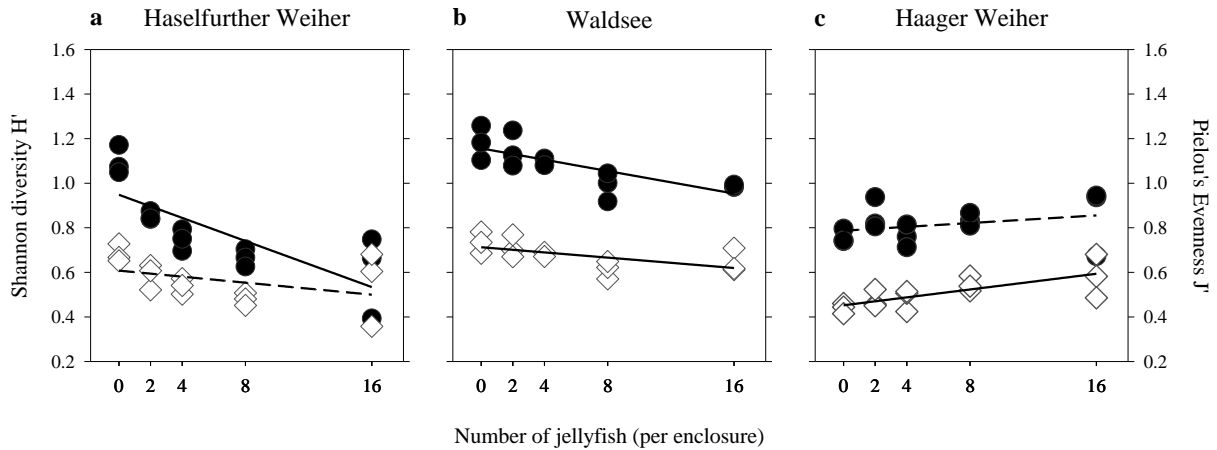


Figure 20: Shannon diversity H' (●) and Pielou's evenness J' (◇) of the crustacean mesozooplankton community as a function of jellyfish density in the enclosures of (a) Lake Haselfurther Weiher, (b) Lake Waldsee and (c) Lake Haager Weiher at the end of the experiments. Displayed are significant linear regression curves (solid, $p < 0.05$) and insignificant trends (dashed lines).

Table 11: Summary of regression analyses of Shannon diversity (H') and of Pielou's evenness (J') of the crustacean mesozooplankton community as a function of increasing jellyfish density at the end of the mesocosm experiments. Applied regression models are linear fits. Significant p -values are highlighted ($p < 0.05$).

	Haselfurther Weiher			Waldsee			Haager Weiher		
	p	R²	equation	p	R²	equation	p	R²	equation
H'	0.0008	0.60	$y = -0.03x + 0.95$	0.0014	0.59	$y = -0.01x + 1.16$	0.2674	0.09	$y = 0.004x + 0.79$
J'	0.1419	0.16	$y = -0.01x + 0.61$	0.0282	0.34	$y = -0.01x + 0.71$	0.0021	0.53	$y = 0.01x + 0.45$

3.3.3 Phytoplankton

Time course of phytoplankton

A common trend in all three mesocosm experiments (Lake Haselfurther Weiher, Lake Waldsee, Lake Haager Weiher) was a decline of at least 50% in chlorophyll a (chl a) during the first two to three days (Figure 21). Different trends of chlorophyll a in relation to the jellyfish densities were observed. The phytoplankton communities in jellyfish-free treatments remained low in biomass and were not able to fully recover after the decline. In Lake Haselfurther Weiher and in Lake Waldsee, a growth plateau of phytoplankton was already reached after four and seven days, respectively. In Lake Haager Weiher the chl a

Results

concentrations in control treatments continued declining until the end of the experiment. All predation treatments showed a similar pattern of growth over time. In all experiments, the highest phytoplankton growth was reached in enclosures with 16 jellyfish (Suppl. Figures 1, 2, 3). In Lake Haselfurther Weiher, a peak of phytoplankton growth was reached at day nine, afterwards the chl *a* concentrations decreased constantly (Suppl. Figure 1). In Lake Waldsee a peak of chl *a* occurred at day 11 and phytoplankton growth saturation was reached (Suppl. Figure 2). In Lake Haager Weiher, the highest chl *a* concentrations were measured at the end of the experiment (Suppl. Figure 3).

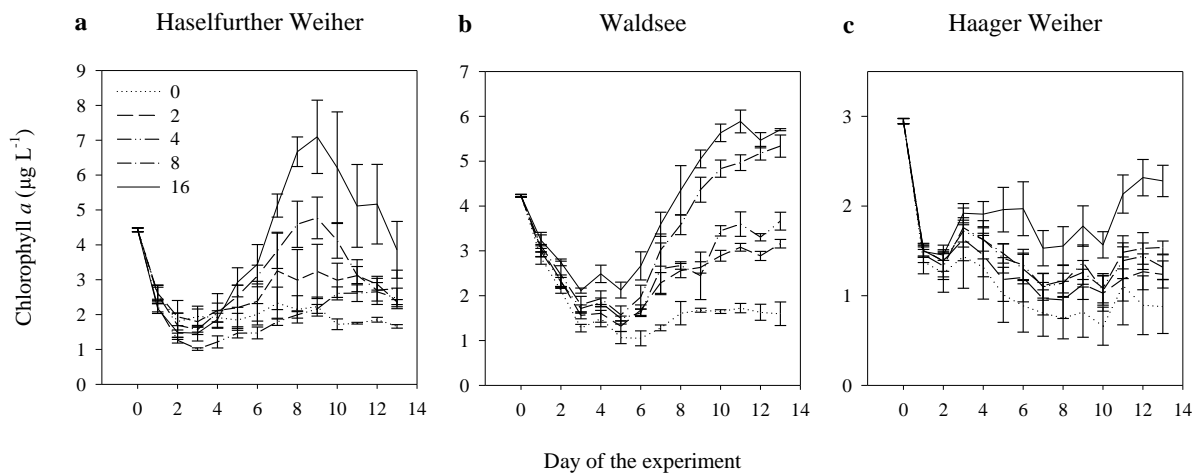


Figure 21: Development of chl *a* ($\mu\text{g L}^{-1}$) over the experimental duration of 13 days in the three mesocosm experiments. Displayed are average chl *a* concentrations with standard errors of each of the five jellyfish density treatments (0, 2, 4, 8, 16 jellyfish per enclosure; see legend) for (a) Lake Haselfurther Weiher, (b) Lake Waldsee and (c) Lake Haager Weiher.

Relationship between phytoplankton growth and jellyfish density

In all three experiments, a significant positive relationship of phytoplankton biomass (measured as chl *a*) and jellyfish density was observed. This correlation started after the first decline phase and lasted until the end of the experiment (Suppl. Figures 1, 2, 3). At day 13, the total chl *a* concentration in treatments with the highest density of jellyfish increased up to fourfold in comparison to the jellyfish-free treatments (Figure 22). A linear relationship of jellyfish density and phytoplankton biomass was observed in all three experiments (Figure 22, Table 12). This linear trend was mainly due to a linear increase of diatoms/ dinoflagellates and of green algae (Figure 22, Table 12). On the contrary, cryptophytes slightly decreased with increasing jellyfish densities in Lake Waldsee (Table 12). No trends were observed for the blue-green algae (Table 12).

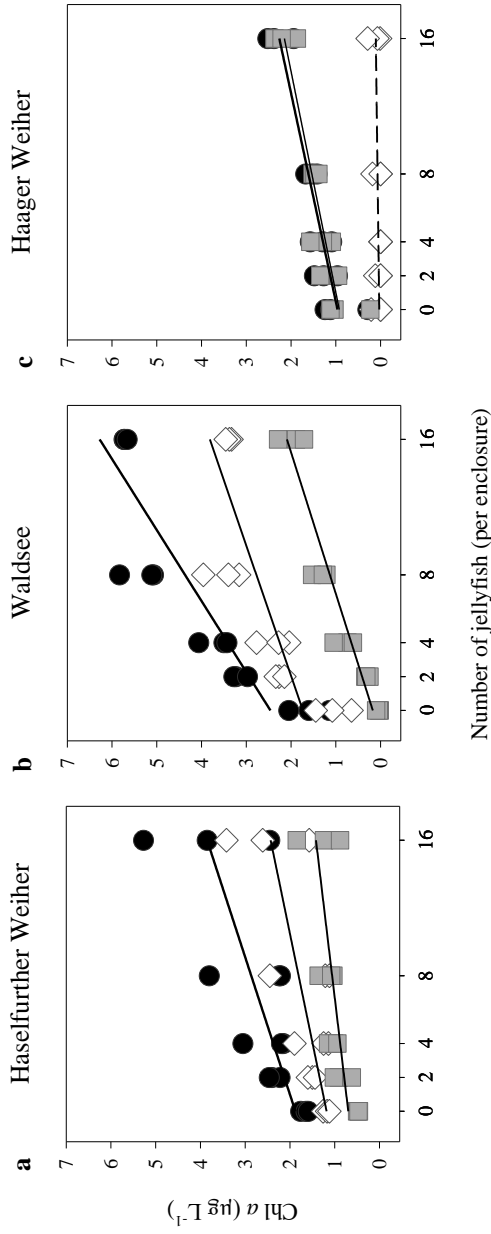


Figure 22: Regression analyses of the chl *a* concentrations of (●) the whole community and of the two functional groups (◇) green algae and (■) diatoms/dinoflagellates versus jellyfish density in enclosures of (a) Lake Haselfurther Weiher, (b) Lake Waldsee and (c) Lake Haager Weiher at the end of the experiments. Displayed are significant linear regression curves (solid, $p < 0.05$) and insignificant trends (dashed lines).

Table 12: Summary of the regression analyses of chl *a* concentrations ($\mu\text{g L}^{-1}$) versus the jellyfish density treatments in enclosures of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher at the end of the experiments. Applied regression models are linear fits, significant *p*-values are highlighted ($p < 0.05$).

	Haselfurther Weiher	Waldsee	Haager Weiher	
	p	p	p	
	R²	R²	R²	
	equation	equation	equation	
Total chlorophyll <i>a</i>	0.0022	<0.0001	<0.0001	$y = 0.12 x + 1.88$ $y = 0.24 x + 2.46$ $y = 0.08 x + 0.96$
Green algae	0.0055	0.0004	0.2849	$y = 0.08 x + 1.18$ $y = 0.13 x + 1.73$ $y = 0.01 x + 0.03$
Blue-green algae	-	0.6959	-	$y = -0.001 x + 0.24$ -
Diatoms/dinoflagellates	0.0028	<0.0001	<0.0001	$y = 0.05 x + 0.70$ $y = 0.12 x + 0.17$ $y = 0.08 x + 0.92$
Cryptophytes	-	0.0028	-	$y = -0.01 x + 0.31$ -

Results

Effect of jellyfish density on total phytoplankton and functional algal groups

The effect of jellyfish density on the phytoplankton abundance was similar in Lake Haselfurther Weiher (0.57 ± 0.34) and in Lake Haager Weiher (0.55 ± 0.12) at the highest jellyfish densities. The largest effects were observed in Lake Waldsee, where the effect size was $0.95 \pm 0.64 \cdot 10^{-2}$ in the highest jellyfish density treatment (Figure 23 a). This effect was mainly the result of a high effect of jellyfish on diatoms/dinoflagellates in all three experiments (Figure 23 c). Secondly, the effects of jellyfish on the green algae group were highly positive (Figure 23 b). The effect of jellyfish on green algae was only in Lake Haager Weiher not found to be significant (Figure 23 b).

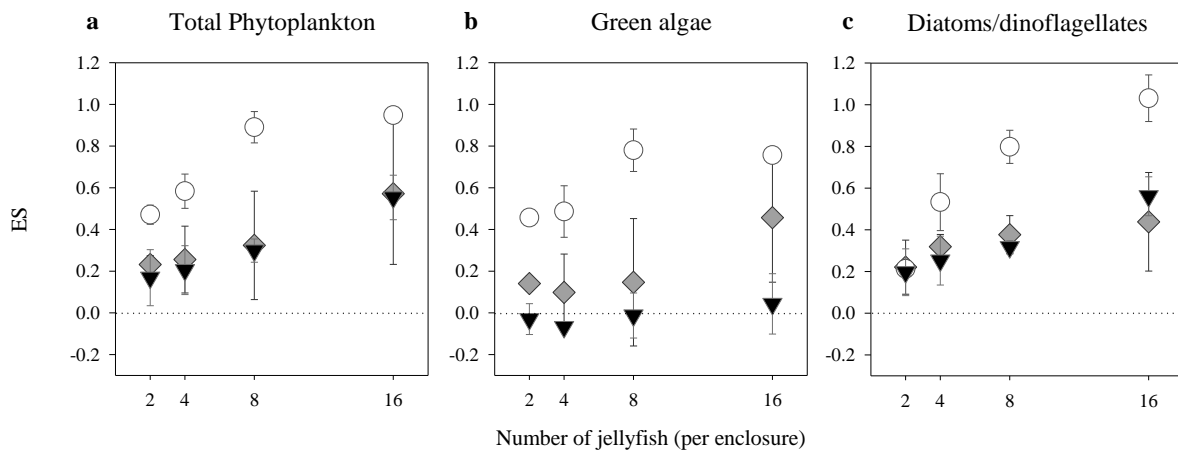


Figure 23: Effects of jellyfish on (a) the total chl *a* concentration and on the chl *a* concentration of (b) green algae and (c) diatoms/dinoflagellates. Shown are the effects for the experiments of (◆) Lake Haselfurther Weiher, (○) Lake Waldsee and (▼) Lake Haager Weiher. Displayed are mean values \pm 95% CI, dashed line indicates zero effect.

Jellyfish effects on seston stoichiometry

Statistical analyses of seston stoichiometry data revealed inconsistent trends in the three experiments. The only significant trend was observed for the seston C:P ratio in Lake Waldsee (Figure 26 b, Table 15). The increasing jellyfish density resulted in a decrease of seston C:P ratio. A similar decreasing, but insignificant trend, was observed in Lake Haager Weiher (Figure 26 c, Table 15). On the contrary, in lake Haselfurther Weiher the seston C:P ratio showed an increasing trend with increasing density of jellyfish (Figure 26 a), albeit not significantly (Table 15).

Results

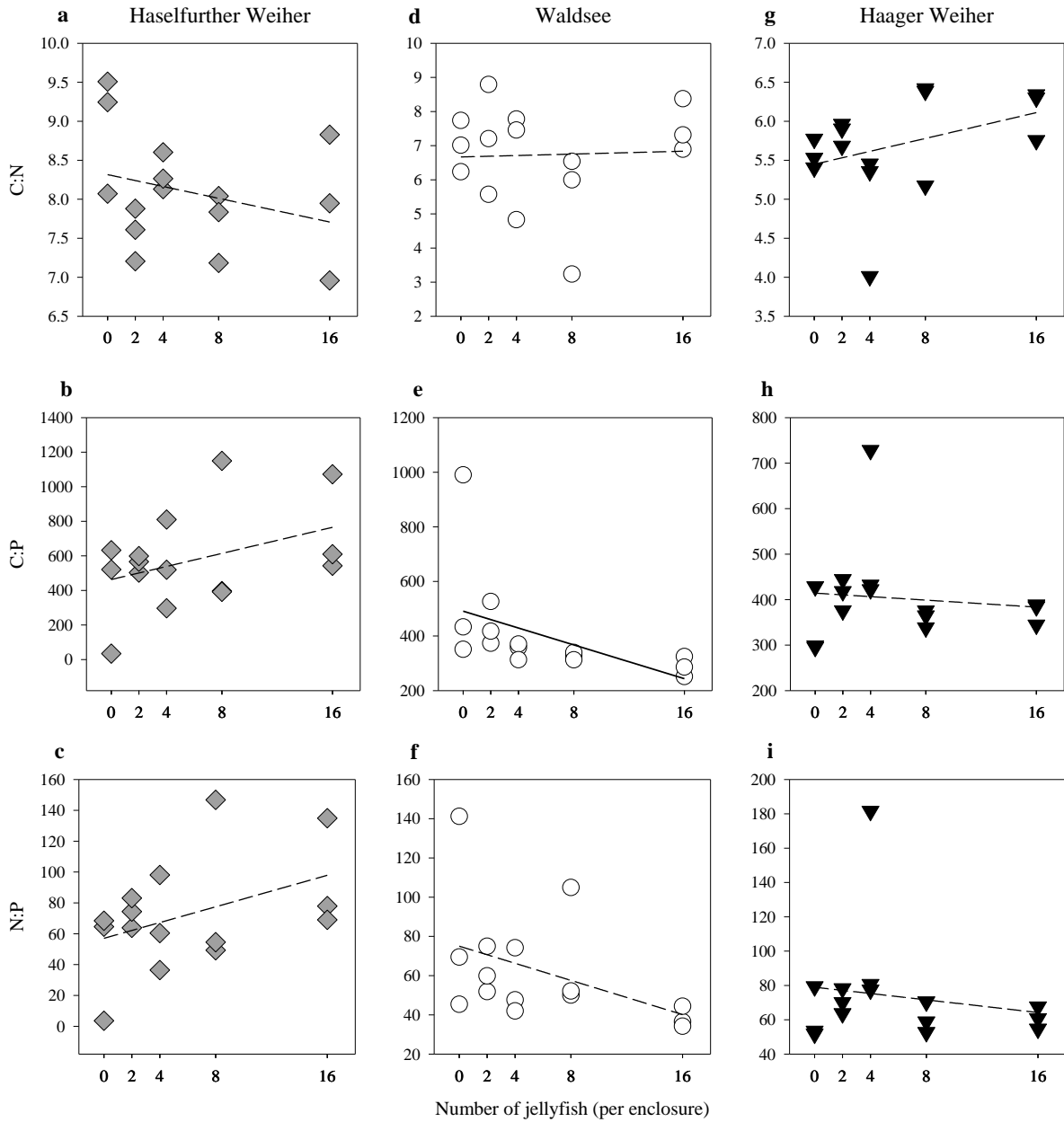


Figure 24: Responses of seston stoichiometry ratios (C:N, C:P and N:P) to an increasing number of jellyfish after 13 days for (a, b, c) Lake Haselfurther Weiher, (d, e, f) Lake Waldsee and (g, h, i) Lake Haager Weiher. Displayed are significant linear regression curves (solid, $p < 0.05$) and insignificant trends (dashed lines).

Results

Table 13: Summary of the regression analyses of seston stoichiometry ratios (C:N, C:P and N:P) in relation to jellyfish density in enclosures of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher at the end of the experiments. Applied regression models are linear fits, significant p-values are highlighted ($p < 0.05$).

	Haselfurther Weiher			Waldsee			Haager Weiher		
	p	R ²	equation	p	R ²	equation	p	R ²	equation
C:N	0.2683	0.09	$y = -0.04 * x + 8.32$	0.8779	0.002	$y = 0.01 * x + 6.67$	0.1466	0.12	$y = 0.04 * x + 5.45$
C:P	0.1427	0.16	$y = 18.89 * x + 463.03$	0.0507	0.26	$y = -15.45 * x + 491.03$	0.6932	0.01	$y = -1.92 * x + 414.22$
N:P	0.1154	0.18	$y = 2.55 * x + 57.04$	0.0956	0.20	$y = -2.18 * x + 74.98$	0.5435	0.03	$y = -0.92 * x + 78.93$

Jellyfish effects on nutrient and phytoplankton interactions

The total chl *a* content as a function of total phosphorus (TP) showed a positive linear trend within each experiment and in Lake Waldsee this was significant (Figure 24, Table 13). The resulting residuals showed significant positive linear relationships with increasing density of jellyfish (Figure 24, Table 13).

In all three experiments, soluble reactive phosphorus (SRP) as a function of TP showed a positive linear trend, which was significant in Lake Waldsee (Figure 25, Table 14). The resulting residuals showed negative linear relationships to increasing density of jellyfish (Figure 25, Table 14).

Results

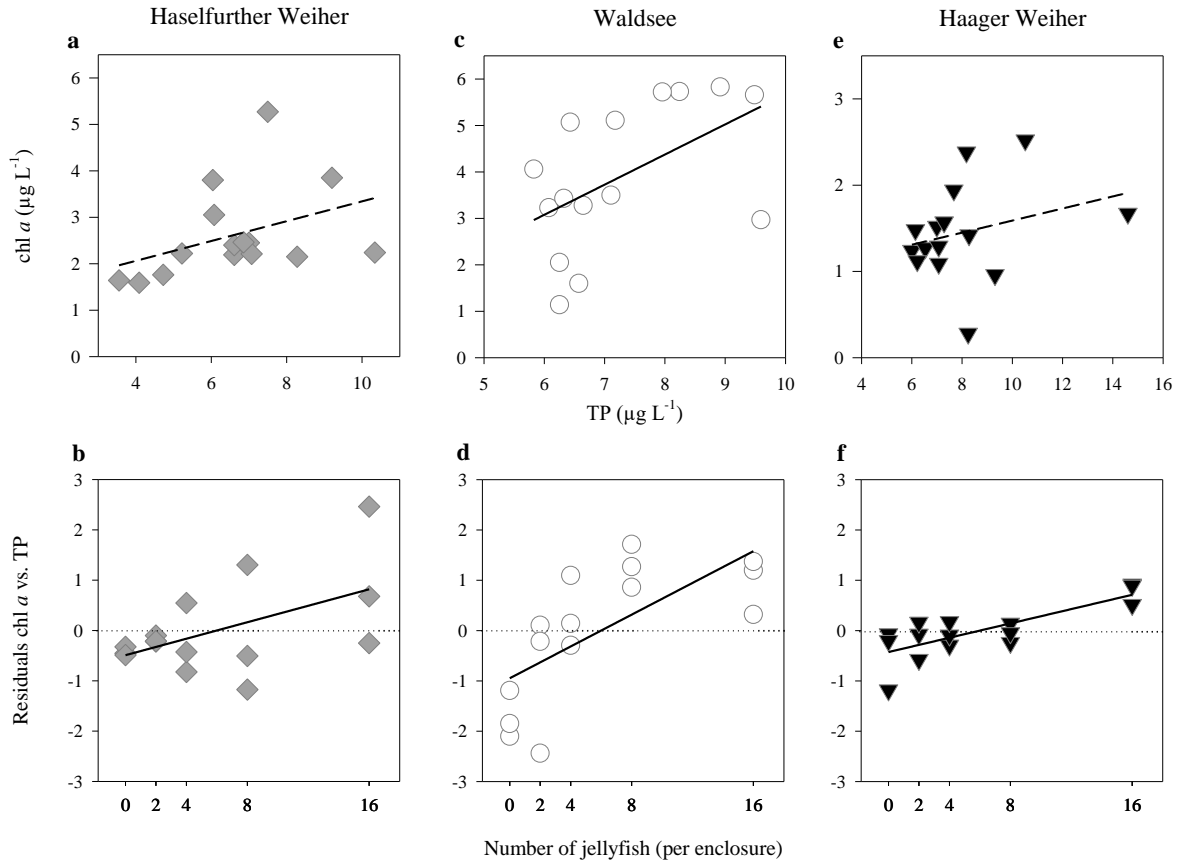


Figure 25: Relationship of (a, b, c) chl *a* and TP and (b, d, f) the resulting residuals as a function of jellyfish density in the enclosures of (◆) Lake Haselfurther Weiher, (○) Lake Waldsee and (▼) Lake Haager Weiher at the end of the experiments. Displayed are significant linear regression curves (solid, $p < 0.05$) and insignificant trends (dashed lines).

Table 14: Summary of the regression analyses of relationships of chl *a* vs. TP to jellyfish density and of the resulting residual plots in enclosures of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher at the end of the experiments. Applied regression models are linear fits, significant p-values are highlighted ($p < 0.05$).

	Haselfurther Weiher			Waldsee			Haager Weiher		
	p	R ²	equation	p	R ²	equation	p	R ²	equation
chl <i>a</i> vs. TP	0.1497	0.15	$y = 0.21 x + 1.21$	0.0458	0.27	$y = 0.65 x - 0.82$	0.3135	0.08	$y = 0.07 x + 0.89$
Residual plot chl <i>a</i> vs. TP	0.0452	0.27	$y = 0.08 x - 0.49$	0.0046	0.47	$y = 0.16 x - 0.95$	0.0005	0.62	$y = 0.07 x - 0.43$

Results

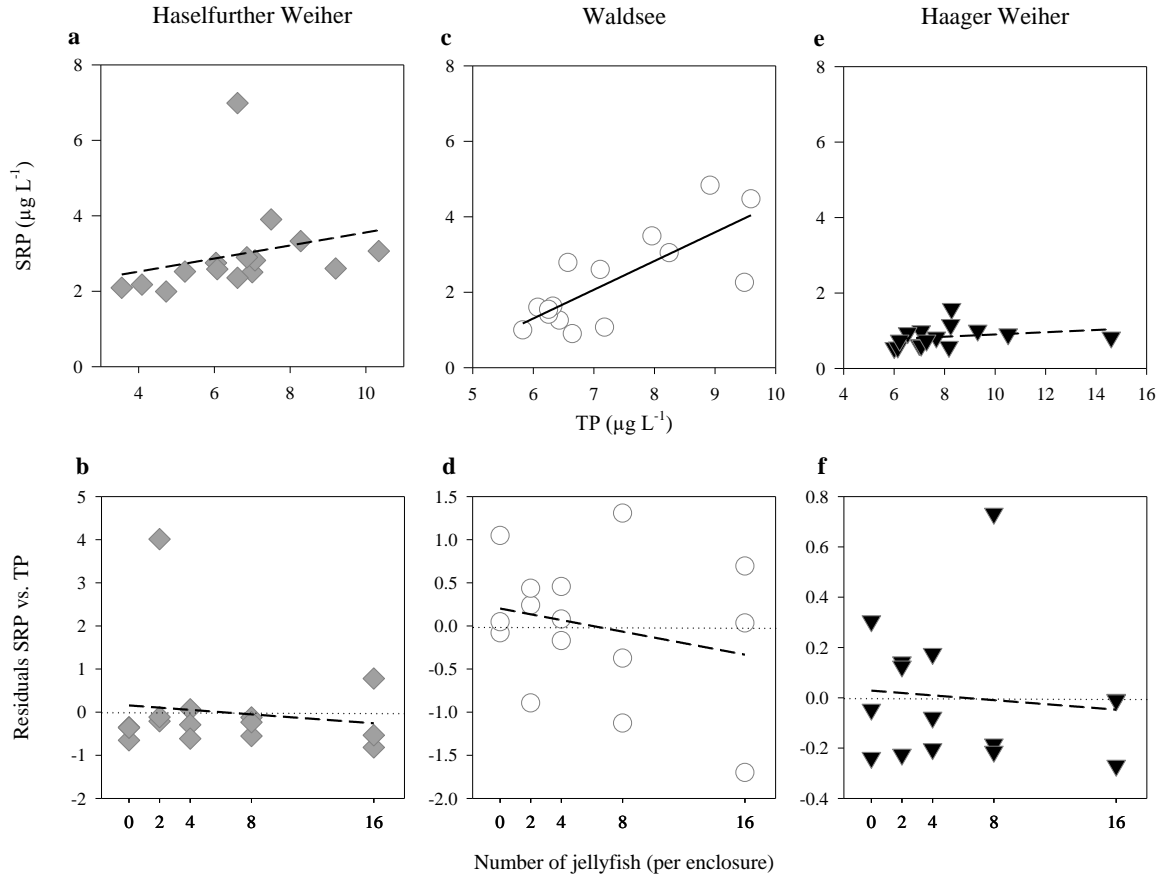


Figure 26: Relationship of (a, b, c) SRP and TP in the enclosures and (b, d, f) the resulting residuals as a function of jellyfish density in the enclosures of (◆) Lake Haselfurther Weiher, (○) Lake Waldsee and (▼) Lake Haager Weiher at the end of the experiments. Displayed are significant linear regression curves (solid, $p < 0.05$) and insignificant trends (dashed lines).

Table 15: Summary of the regression analyses of relationships of SRP vs. TP to jellyfish density and of the resulting residual plots in enclosures of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher at the end of the experiments. Applied regression models are linear fits, significant p-values are highlighted ($p < 0.05$).

	Haselfurther Weiher			Waldsee			Haager Weiher		
	p	R ²	equation	p	R ²	equation	p	R ²	equation
SRP vs. TP	0.3501	0,07	$y = 0.17 x + 1.83$	0.0008	0.60	$y = 0.76 x - 3.27$	0.3942	0.06	$y = 0.03 x + 0.60$
Residual plot SRP vs. TP	0.6457	0.02	$y = -0.03 x + 0.16$	0.3771	0.06	$y = -0.03 x + 0.20$	0.7137	0.01	$y = -0.01 x + 0.03$

3.4 Jellyfish and Phosphorus Distribution

Indoor mesocosm experiments were conducted to investigate the impact of the freshwater jellyfish *C. sowerbii* on the phosphorus distribution in a defined water column. These jellyfish effects were compared with the effects of the pelagic insect larvae *Chaoborus spp.* and of natural crustacean zooplankton. These experiments were conducted with medusae of *C. sowerbii type 1*, the dominant *Craspedacusta* species in all investigated European lakes at the present stage (topic 1).

3.4.1 Experiments with *C. sowerbii*

The net upward phosphorus transport in the experimental water columns induced by jellyfish was substantial and phosphorus concentrations in the upper 140 cm of the columns were significantly different to control treatments after 24 h (Figure 27). At the top 20 cm, $68.18 \pm 16.48 \mu\text{g}$ total phosphorus (TP) L^{-1} (mean \pm standard error; $N = 7$) was measured in jellyfish treatments, which was about four times higher compared to control treatments ($18.59 \pm 3.93 \mu\text{g}$ TP L^{-1} ; $N = 7$).

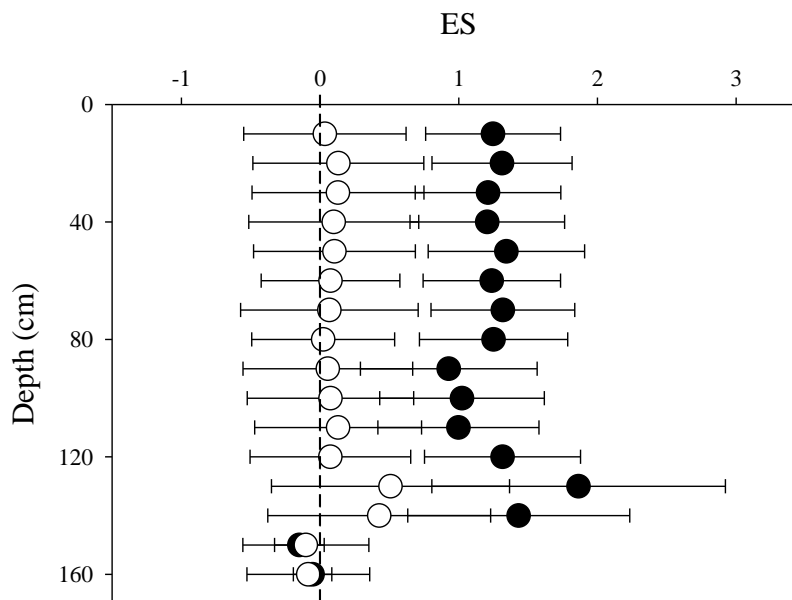


Figure 27: Effects (ES) of *C. sowerbii* (●, $N = 7$) and *Chaoborus spp.* larvae (○, $N = 4$) on the vertical distribution of total phosphorus in the columns after 24 hours. Error bars indicate 95% CI, dashed vertical line indicates zero effect.

Results

The magnitude of the upward phosphorus transport in the experimental water columns induced by jellyfish was a function of jellyfish density (Figure 28 a). Higher jellyfish density resulted in higher phosphorus concentrations at the top of the experimental water column (Figure 28 a; $y = 23.68 x + 28.72$; $R^2 = 0.70$; $p = 0.0774$). On average, one jellyfish per column resulted in an hourly net phosphorus shift of $1.04 \mu\text{g TP L}^{-1}$ to the top of the column. This resulted in an overall transport of $24.89 \mu\text{g TP L}^{-1}$ within 24 h.

3.4.2 Experiments with Pelagic *Chaoborus* spp. Larvae

Pelagic *Chaoborus* larvae had no significant effect on phosphorus distribution in the experimental water columns (24 h sampling, Figure 27). After 24 h, the phosphorus concentration in the top 20 cm of the columns was on average $24.67 \pm 4.05 \mu\text{g TP L}^{-1}$ in columns with *Chaoborus* larvae and $17.50 \pm 1.07 \mu\text{g TP L}^{-1}$ in columns without *Chaoborus*.

3.4.3 Experiment with a Crustacean Zooplankton Gradient

The effect of crustacean zooplankton on upward phosphorus transport in the experimental water columns was related to zooplankton density. Higher zooplankton densities resulted in higher phosphorus concentrations in the upper 20 cm of the columns (Figure 28 b; $y = 0.39 x + 16.30$; $R^2 = 0.84$; $p = 0.0278$). On average, the net upward transport of phosphorus by the zooplankton community at a natural density (8 ind L^{-1}) was $3.12 \mu\text{g TP L}^{-1}$ within 24 hours.

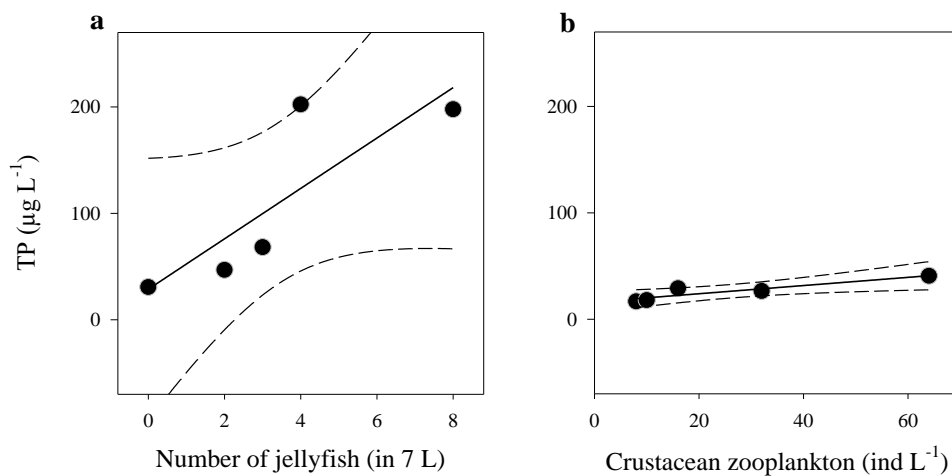


Figure 28: Total phosphorus transported to the top of each column by the migration of (a) *C. sowerbii* and (b) crustacean zooplankton after 24 hours. Solid lines represent linear regressions; dashed lines indicate 95% CIs.

3.5 Evidence of Jellyfish Food Web Effects in the Field

The PCA analysis on 11 environmental variables revealed three components with eigenvalues > 1. The first two components explained 56.7 % of the total variance in the data. The respective factor-loading plot shows that the environmental parameters were similar among most lakes with and without *Craspedacusta medusae* (Figure 29). Lake Neuer Baarer Weiher (BW) was divergent from other jellyfish lakes, mainly due to differences in nitrate and nitrite concentrations, temperature and pH.

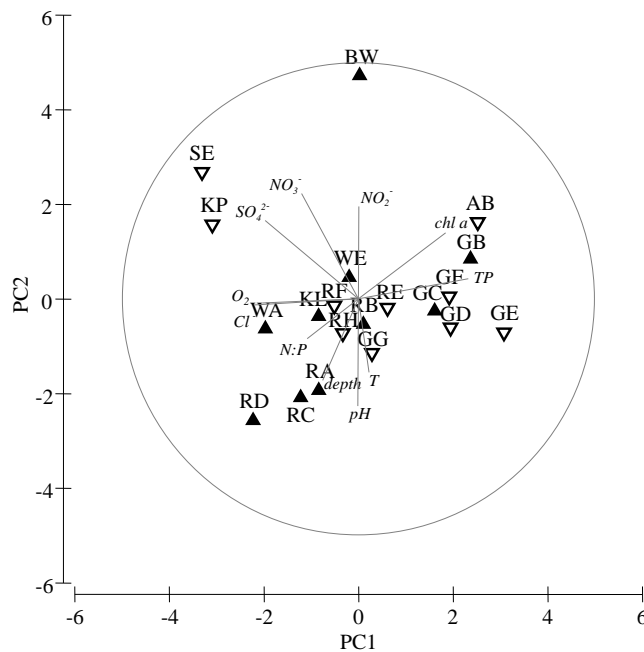


Figure 29: Principal-Component Analysis (PCA) of the environmental data of lakes with (▲) and without (▼) medusae. Letters next to symbols refer to Lake ID, see Table 4. The clustering of the data along the primary (PC1: 30.9 % of the variance) and secondary (PC2: 25.9 % of the variance) axes represent 56.7 % of the total variance. The maximum possible strength of all correlations is indicated by the grey circle.

The relationship of chl *a* and TP of all investigated lakes (with and without jellyfish) showed a linear trend ($y = 2.08 x - 8.08$, $R^2 = 0.62$, $p < 0.0001$, Figure 30 a). The residuals showed a higher scattering in lakes with jellyfish as they show in lakes without jellyfish (Figure 30 b). The mean of residuals of lakes with jellyfish showed a negative value, the mean of residuals of lakes without jellyfish showed a positive value, albeit the difference between residuals of the two categories was not significant (Mann-Whitney rank sum test; $p = 0.162$). A significant linear trend was shown for the relationship of SRP and TP ($y = 0.24 x - 1.18$; $R^2 = 0.36$, $p =$

Results

0.0048, Figure 30 c), but the difference between the residuals of the two categories was insignificant (Mann-Whitney rank sum test, $p = 0.910$; Figure 30 d). No differences between lakes with and without jellyfish were found in seston stoichiometry (p -values for C:P = 0.618, for N:P = 1.000, for C:N = 0.429; Figure 31).

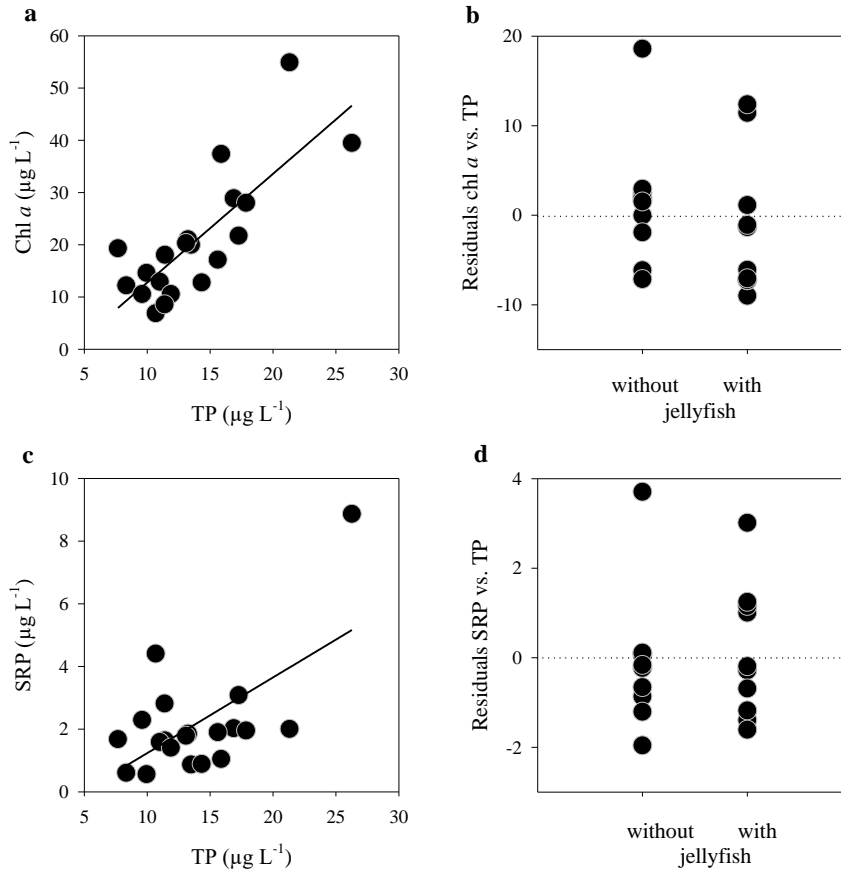


Figure 30: (a) Relationship of chl *a* and TP in lakes with and without jellyfish and (b) the resulting residual plot separated for lakes without ($N = 10$) and with ($N = 10$) jellyfish; (c) relationship of SRP and TP and (d) the resulting residual plot. Solid lines indicate significant linear relationships ($p < 0.05$).

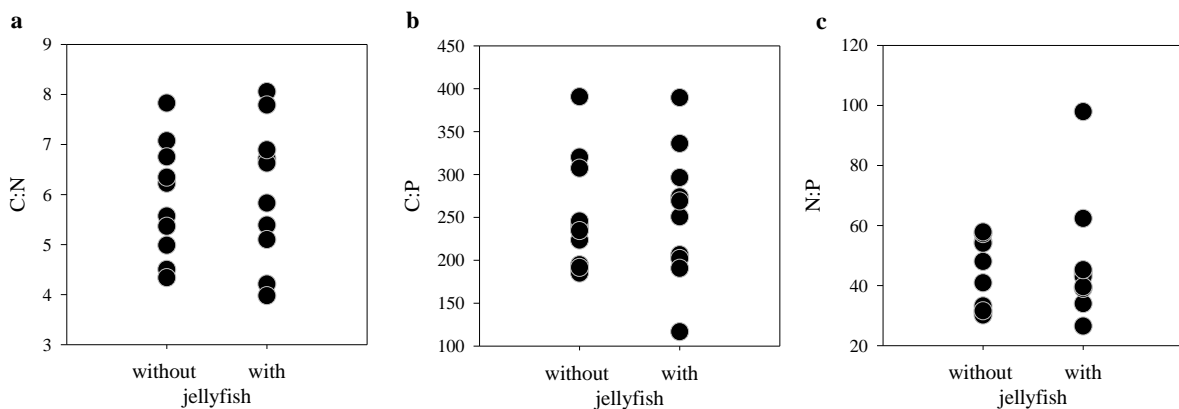
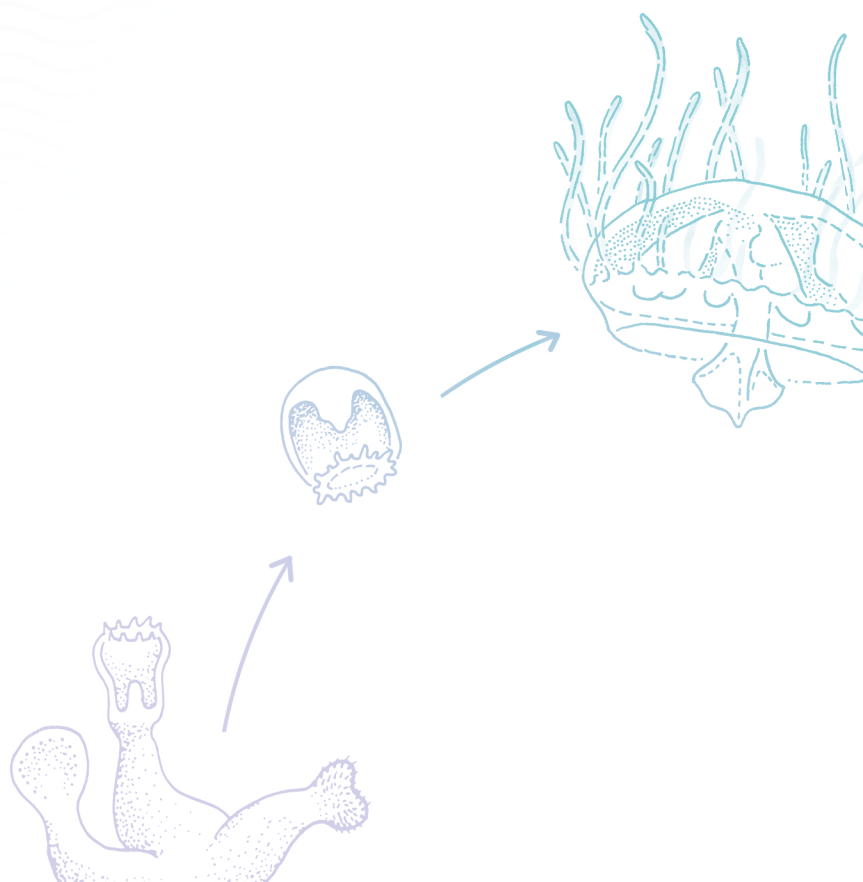


Figure 31: Seston stoichiometry ratios: (a) C:N, (b) C:P, (c) N:P in lakes with ($N=10$) and without ($N=10$) *C. sowerbii* medusae during the lake survey.

4 Discussion



4.1 Genetic Diversity of *Craspedacusta*

4.1.1 Two *Craspedacusta* Species Invaded Europe

Results from the newly obtained mitochondrial DNA sequence data from *Craspedacusta* are consistent with recent reports that more than one genetic lineage invaded Europe (Fritz et al. 2009, Karaouzas et al. 2015, Schifani et al. 2019). Two divergent lineages, which in the past were presumed to represent “*C. sowerbii*” due to morphological similarities among medusae, are now recognized as separate species by molecular evidence (Karaouzas et al. 2015, Schifani et al. 2019). However, in the present study, the two *Craspedacusta* species that invaded Europe are labeled *C. sowerbii* type 1 and *C. sowerbii* type 2 and are not assigned to specific species names. This is due to several discrepancies between molecularly defined species identity and associated species names in previous studies, suggesting that a taxonomic revision is needed.

4.1.2 Haplotype Diversity

New findings from the present study are that each of the two species comprised two species-specific lines and that altogether four distinct major mitochondrial haplotype lines invaded Europe. Notably, no more than three haplotype lines had been previously supported worldwide for “*C. sowerbii*” (Schifani et al. 2019), including all singleton variants in GenBank (e.g. Cai et al. unpubl.). An additional and frequent fourth haplotype line (type 1.2) was for the first time detected in the present study. This type was dominant among polyps, but surprisingly medusae of this type had been found in three lakes only within this study. Because previous genetic studies were based on low sample sizes and on the medusae stage only (Collins et al. 2008, Zhang et al. 2009, Fritz et al. 2009, Zou et al. 2012, Karaouzas et al. 2015, Fuentes et al. 2019, Schifani et al. 2019), the fourth haplotype line could simply have been below the detection level because of insufficient sampling. This hypothesis is supported by the fact that in a former study, also conducted with samples from Germany and Austria, only one COI mtDNA-haplotype had been detected among medusae (Fritz et al. 2009). Three haplotype lines emerged in later studies including individuals from Greece and Italy (Karaouzas et al. 2015, Schifani et al. 2019). With increased sampling intensity, in total four

haplotype lines were found among individuals from Germany. At the present stage, it seems that the fourth type is restricted to Europe.

4.1.3 Association between Haplotype, Life Stage and Sex of Medusae

Since it had been suggested that there might be strains of polyps that have lost the ability to produce medusae (Acker and Muscat 1976), greater haplotype diversity could be expected in the polyp stage. The data of the present study show that this is not the case, as the same four haplotypes were found among polyps and medusae across space and time. Even with an increased sampling intensity of polyps at Lake Langwieder See, no further haplotype lines were discovered. This contrasts with other invasive cnidarians such as *Aurelia aurita*, where a recent COI study revealed 50 haplotypes among polyps in contrast to only 36 haplotypes among medusae (Dawson et al. 2015, Van Walraven et al. 2016).

Joint analyses of haplotype and sex of medusae revealed a surprising finding: medusae of type 1.1 and of type 2.2 were all female and medusae of type 1.2 and of type 2.1 were all male. This strict relationship between sex and haplotype in both species might indicate a complex mode of mitochondrial DNA inheritance, the doubly uniparental inheritance (DUI), which is so far only described for several bivalve species (Skibinski et al. 1994, Zouros et al. 1994, Hoeh et al. 1996, Passamonti and Scali 2001, Curole and Kocher 2002, Hoeh et al. 2002, Serb and Lydeard 2003, Passamonti 2007, Theologidis et al. 2008). In those species two types of mtDNA exist, one that is transmitted through the eggs to both female and male offspring (the maternal genome) and another that is transmitted through the sperm only to male offspring (the paternal genome). In adult males, the paternal genome predominates in the gonads and the maternal genome in the somatic tissues (Stewart et al 1995, Sutherland et al. 1998). These two distinct mtDNA lineages with different distributions in female and male tissues make DUI in principle easy to detect (Theologidis et al. 2008). In the present study, only gonad tissue was used for DNA analyses. Further analyses also of somatic tissue in combination with the sequencing of the potential female and male genomes of both species are needed to decide about the presence of this inheritance mode in *Craspedacusta* species.

4.1.4 Phylogenetic Analysis, Species Assignment and Species Names

Joint phylogenetic analyses of the newly obtained mitochondrial 16S rRNA and COI sequence data with formerly published *Craspedacusta* sequences showed that the two species

Discussion

of the present study corresponded to the two *C. "sowerbii"* species clades already reported from European *Craspedacusta* medusae. *C. sowerbii type 1* corresponds to "*C. sowerbii kiatingi*" and *C. sowerbii type 2* corresponds to "*C. sowerbyi / C. sowerbii*" (Fritz et al. 2009, Schifani et al. 2019).

Based on COI data, a minimum uncorrected p-distance of 14.0 % between the two species *C. sowerbii type 1* and *C. sowerbii type 2* was found, which is similar to the value given in the study of Karaouzas et al. (2015). In addition, also the minimum uncorrected p-distance between mitochondrial 16S rRNA gene sequences of these two species clades was calculated in the present study, which was 3.7 %. There is no agreed level of genetic differentiation that would decisively indicate independent species status for two individuals (Folino-Rorem et al. 2009). However, the genetic distances among clades are in the range of thresholds for species discrimination in other hydrozoans regarding both mtDNA loci COI and 16S (Schuchert 2005, Folino-Rorem et al. 2009, Montano et al. 2015, Maggioni et al. 2016, Cunha et al. 2017). For example, data from a recent taxonomic revision of the hydrozoan genus *Cordylophora* revealed a genetic differentiation between two species clades of 6.04 % (16S) and 12.35 % (COI; Folino-Rorem et al. 2009). Similar genetic distances were also found between two species of the hydrozoan genus *Pteroclava* with uncorrected p-distances of 7.5 (16S) and 16.0 (COI; Maggioni et al. 2016). Additionally, as a common rule for species discrimination, inter-specific genetic distances should be about ten times higher compared to intra-specific distances (Hebert et al. 2004). Relying on that classification criterion, the two major genetic mtDNA lineages in *Craspedacusta* represent two distinct species. For *Craspedacusta*, the K2P-distance between the two main clades was about 13 times greater than within clades based on COI (Table 6). The distance was about 10 times higher based on 16S, which suggests a lower discriminatory power of that locus (Table 7). Thus, the commonly recommended mitochondrial 16S rRNA gene as a preferred DNA barcode for Hydrozoan species identification (Miglietta et al. 2009, Moura et al. 2011, Moura et al. 2012, Zheng et al. 2014, Moura et al. 2018) has been shown to be less discriminatory regarding *Craspedacusta*, although the recognition of separated lineages was consistent with both loci. Therefore, the levels of genetic divergence observed within *Craspedacusta* indicate the use of COI sequences in phylogenetic studies.

Importantly, morphology-based species identification within the genus *Craspedacusta* is ambiguous (Jankowski 2001, Pope 2007, Fritz et al. 2009, Zhang et al. 2009, Jankowski and Anokhin 2019) due to insufficient species descriptions, ignoring age- and sex-specific

morphological variation of traits. The naming of now genetically-defined *Craspedacusta* species remains therefore problematic. Notably, the original species names and species descriptions in Chinese literature are primarily based on the origin of the individuals and the respective name of the lake or region with low attention to species-diagnostic traits, which contributes to the confusion. In many cases, new descriptions of *Craspedacusta* later turned out being a local variation of a formerly described species (Bouillon and Boero 2000, Jankowski 2001). This explains the problems with species names such as “*C. kiatingi*”, a species, which has originally been described as a variant of *C. sowerbii* only (Gaw and Kung 1939) but which is treated as a “species” (e.g. in Jankowski and Anokhin 2019, Schifani et al. 2019) also in GenBank entries. That the morphology of genetically-defined *C. kiatingi* specimens from Europe did not correspond to “species-diagnostic” morphological traits of the species (Fritz et al. 2009) underlines the confusion.

Molecular analyses of COI from type material (holotypes) of the morphologically defined species would be useful to determine species names. The holotype of *C. sowerbii* (Lankester 1880) probably does not exist, but for example a specimen of *C. sowerbii* from London from 1883 and type material from *C. sinensis* (Gaw and Kung 1939), *C. ziguensis* (He and Xu 1985) and of *C. kiatingi* (Gaw and Kung 1939) is available (see Jankowski 2001 and Smithsonian National Museum of Natural History, USA). In case of low quality of DNA of these specimens due to formalin-preservation, an alternative approach would be the detailed morphological description of individuals of the genetically-defined species *C. sowerbii type 1* and *C. sowerbii type 2* and the determination of morphological diagnostic characters. Assessing morphological similarities and differences for additional samples of *Craspedacusta* from around the world in conjunction with molecular species identification would further allow addressing the role of morphological plasticity in the taxonomy of this hydrozoa and is recommended for the two life stages, polyp and medusa.

4.1.5 Genetic and Sexual Structure of Medusae Populations

Intense population samplings at three remote lakes (Lake near Jílové/Držkova, Lake Schwarzlsee, Lake Waldsee) showed that medusae individuals within lakes were fixed for a specific haplotype and sex. While the female-type 1.1 was found in two lakes, the male type 1.2 was found only once among medusae. Overall, the female type 1.1 was the most frequent one in the 25 jellyfish-lakes screened in this study. This finding is consistent with the frequently described occurrence of unisexual and mainly female medusae populations of

Craspedacusta within European lakes (Boecker 1905, Dejdar 1934, Germain 1934, Stadel 1961, Lundberg et al. 2005, Pérez-Bote et al. 2006).

Only in one lake, Lake Baarer Weiher (Germany), haplotypes of both species and both sexes were found simultaneously in population samples of the sexually reproducing medusa life stage in 2016 and 2017. Male haplotypes from the two species (type 1.2 and 2.1) were found across years and medusae with the female haplotype 2.2 at least in one of the years (Suppl. Table 1). The coexistence of female and male medusae of both species in Lake Baarer Weiher shows that the two species are theoretically able to reproduce sexually and that even hybridization between the two species is possible. Nevertheless, regarding the high degree of unisexual medusae populations within almost all investigated lakes in this and in previous studies, it has to be assumed that bisexual reproduction of both *Craspedacusta* species is highly limited within Europe. But in case this happens, each sexually produced offspring will be characterized by its unique genetic combination which will differ from parents and all siblings recreating genetic diversity. Similarly, in the case of hybridization, a high level of genetic diversity will be created and among those hybrid genomes, few might be better adapted to novel environments than each of the parental species (Seehausen 2004).

4.1.6 Sex Determination

The perfect association between the sex of medusae and haplotype in both *Craspedacusta* species constitutes a first strong indication, that the sex of medusae is genetically defined. This genetic sex determination of descendants has already been described for other cnidarians like *Aurelia* or the sea anemone *Actinia* (Ayre 1988, Liu et al. 2018). In contrast, in some other hydrozoan genera, environmental parameters such as water temperature or food availability play a role in the sex determination of descendants, like in *Clythia* or *Hydra* (Littlefield 1994, Carré and Carré 2000). For example, when *Clythia* colonies were raised at lower temperatures of about 15°C, the released medusae were mainly male in contrast to predominantly female medusae, when they were budded and cultured at higher temperatures (24°C; Carré and Carré 2000). Such a mechanism for sex determination of the medusa stage cannot be totally excluded for *Craspedacusta* at the present stage but is less likely than the genetic determination by the mother polyp because of the perfect coupling of haplotype and sex in the present study. Notably, males and females were found at the same sampling date within a specific lake and individuals were similar in size (pers. obs.), indicating that they were produced at a similar time point.

4.1.7 Ecology and Genetic Diversity

The finding that haplotypes from the two species co-occurred within many European lakes, at least in the polyp stage, indicates rather broad than narrow ecological requirements of these four types for a successful establishment. However, that only four haplotypes managed to spread could mean that only a few haplotypes are able to cope with the environmental conditions outside China. Only three subvariants of the four major haplotypes showed a mutation: two 16S singletons and one rare COI haplotype were detected among six individuals across all data sets (481 individuals). Each subvariant was restricted to a specific lake. The question arises, if these are newly evolved haplotypes or if they have also been introduced from China in the past. That few generalist haplotypes can be highly invasive, has recently been shown for *Daphnia galeata* from the *D. longispina* complex, where identical lines spread between China and Europe (Yin et al. 2018).

Coexistence of mtDNA haplotypes in the polyp and in the medusa stage

When the focus is on the polyp stage, several examples of haplotype and species coexistence within the same lake were found in the present study. With increased sampling intensity detection also increased notably. Polyps from two species and three different haplotypes in Lake Langwieder See were detected even on a single stone (type 1.1, 1.2 and 2.2; dataset 3). This proposes that with even higher sampling intensity all known haplotypes might be found within specific lakes. On the contrary, species coexistence and even coexistence of haplotypes from the same species seems to be the exception in the medusa life stage, also when sample size was increased. Type 1.2 was the most frequent one among polyps while it was rare among medusae. In contrast, haplotype 1.1 was the most abundant among medusae but rare among polyps. These differences in haplotype frequencies among polyps and among medusae, which come along with rare coexistence of medusae with different haplotypes (and sex), can have several reasons. For example, external factors such as temperature, food, light, pH and CO₂ (reviewed in Acker and Muscat 1976) that trigger medusae budding in polyps might be haplotype-specific (Van Walraven et al. 2016). Another explanation could be that the released newborn medusae have haplotype-specific requirements to reach the adult medusa stage. Their successful development may, for example, depend on the availability of preferred food provided by local communities in the different lakes. In this way, only a few lakes could meet the requirements for species and haplotype coexistence in the medusa stage.

Geographical distribution of species – Subtropical and temperate species?

At the species level, *C. sowerbii* type 2 was much rarer than *C. sowerbii* type 1 in both life stages in the European samples of the present study. This suggests different invasion success of the two species. An alternative explanation for the biased species abundances could be that *C. sowerbii* type 1 was just the earlier invader and is for that reason more abundant. Finally, the two species might also differ in ecological requirements, being more generalists or specialists. Schifani et al. (2019) speculated that *C. kiatingi* (corresponding to *C. sowerbii* type 1) seems to be better adapted to continental or temperate climates, while *C. sowerbii* (corresponding to *C. sowerbii* type 2) may find its optimum in warmer climates. The obvious dominance of *C. sowerbii* type 1 in European countries with a temperate climate (Austria, Czech-Republic, Germany and Switzerland) and of *C. sowerbii* type 2 in countries with a temperate Mediterranean and subtropical climate (Chile, Greece, Italy, and Uruguay) support this idea. Additionally, medusae of *C. sowerbii* type 2 were more common among German samples in the extraordinarily hot season 2018 (Imbery et al. 2018) compared to the years 2015-2017 (S. Gießler, pers. comm.). It is likely that *C. sowerbii* type 2 is better adapted to warmer conditions, which notably also includes an adaption to specific food web communities and dynamics of these lakes. This could also mean that *C. sowerbii* type 2 could increase its range in regions with usually temperate climates when temperatures further increase. However, the hypothesis that the invasion success of the two species is linked to climatic conditions should be tested based on a much wider sampling of the *Craspedacusta* populations occurring worldwide.

It has to be noted that the newly obtained 16S sequences of polyps from Lake Tanganyika are the first molecular data for *Craspedacusta* from the African continent. Medusae of *Craspedacusta* were formerly recorded from southern Africa (Rayner 1988, Rayner and Appleton 1989, Rayner and Appleton 1992). However, the newly sampled and genotyped polyps are the first evidence that Lake Tanganyika contains both limnomedusan genera *Limnocyclus* and *Craspedacusta*. Polyp density in this African lake was low in the searched regions (pers. obs.), but two polyps could be analyzed, which showed mtDNA haplotypes 1.1 and 2.2. Therefore, two *Craspedacusta* species coexist with *L. tanganyicae* at least in the polyp stage. However, if this coexistence already exists since long time is not known. Further molecular investigations are recommended to test species-specific or even haplotype-specific ecological adaptations and to examine if the potentially sub-/tropical *C. sowerbii* type 2 predominates among *Craspedacusta* polyps in Lake Tanganyika.

4.1.8 Large-scale Dispersal and Multiple Introductions

Joint phylogenetic analyses of the two loci COI and 16S revealed that the two species *C. sowerbii type 1* and *C. sowerbii type 2* succeeded to invade freshwater ecosystems worldwide. Although only a few *Craspedacusta* medusae samples from around the world had been analyzed by molecular markers thus far (Table 1), a worldwide spread of three specific haplotypes outside Europe emerged: type 1.1 was found in Africa (own data), type 2.1 was found in China (Zou et al. 2012) and type 2.2 was found in North and South America (Collins et al. 2008, Fuentes et al. 2019, Martinez unpubl.) and on the African continent (own data; data set 2).

The current data are insufficient to reconstruct the invasion history of *Craspedacusta* because of low sample sizes, but the wide geographic distribution of the same *Craspedacusta* mtDNA haplotypes indicates that there must have been multiple introductions of specimens. It has been demonstrated that multiple introductions may be the rule rather than the exception for many aquatic invasive species (Folino-Rorem et al. 2009). For instance, several species, such as *Dreissena polymorpha* and *Dreissena bugensis*, were probably introduced multiple times by ballast water from the Pontio-Caspian to the North American Great Lakes (Colautti et al. 2005, Stepien et al. 2005, Stepien and Tumeo 2006). Especially recurrent human-mediated vectors are important for multiple and long-distance dispersals by creating high connectivity among habitats over space and time (e.g. Puth and Post 2005, Riccardi 2015, Bullock et al. 2018) and should be considered as main factors also in the distribution of *Craspedacusta*.

Despite low sample sizes, haplotypes from both species have been reported in two individuals from China, the country of origin: one species-specific haplotype from *C. sowerbii type 2* (type 2.1) and another Chinese haplotype, which was placed in the species cluster from *C. sowerbii type 1* by phylogenetic analyses. That haplotypes have spread from China and that multiple introductions occurred is also supported by ITS-phylogenies including more Chinese individuals; again, two species clusters emerged where sequences from China were grouped together with sequences from different geographic origin, from Europe and Chile (Fritz et al. 2009, Fuentes et al. 2019, Schifani et al. 2019).

The co-occurrence of different haplotypes within Europe may be the result either of multiple independent introductions or co-introduction of multiple lineages. Based on morphological identifications, several *Craspedacusta* species/lineages co-occur in the native range, especially in the Yangtze River System, even within the same enclosed water body

Discussion

(Kramp 1950). It is therefore likely that these lineages were transported together as benthic life stages (polyps, frustules, podocysts) attached to the same vector such as ornamental plants, mussels or stones. The finding of polyps of three different haplotypes on the same stone at Lake Langwieder See supports this suggestion. Colonies composed of individuals from different species might have been transported in such a way repeatedly over time.

The finding of all four haplotypes among young lakes only a few kilometers apart (see also Figure 5 c) further indicates that specimen of all four haplotypes must be highly effective in post-introduction population expansion. For example, Lake Baarer Weiher (types 1.2, 2.1, 2.2) was excavated between 1968 and 1989, Lake Waldsee (type 1.1) was excavated in 1967 and "Reichertshofen Lake D" (type 2.2) was built between 1983 and 1998. It remains, however, unclear to what extent the observed distribution within this region is the result of natural dispersal or repeated human-mediated distribution.

4.1.9 Conclusion

In this study, the genetic population structure of European *Craspedacusta* polyps and medusae based on mtDNA data was addressed. One unexpected finding was missing haplotype diversity among male and female medusae, which needs further attention. However, the fact that only four haplotypes have been found does not mean that populations are composed of few clones. Since genetic diversity at the nuclear level also seems to be low as derived from ITS-data (Fritz et al. 2009, Zheng et al. 2009, Schifani et al. 2019), a predominant clonal population structure of *Craspedacusta* in freshwater environments is likely. Additional analyses with nuclear codominant markers (such as microsatellites) are needed to decide about predominant clonal population structure. The resulting cyto-nuclear genotypes will allow tracing the extent of genetic recombination within species and potential hybridization between species.

4.2 Feeding Ecology and Trophic Position of Polyps

The polyp stage is the important life cycle element for the establishment of *Craspedacusta* in a newly invaded habitat and *Hydra* polyps are potential native cnidarian competitors as they have similar dietary niches and can co-occur on the same substrate (Dodds and Hall 1984, Koetsier and Bryan 1989, Stanković and Ternjej 2010, Folino-Rorem 2015).

4.2.1 Functional and Numerical Response Analyses of *Craspedacusta* and *Hydra*

A comparative functional response methodology was used to assess the relative use of resources by the invasive polyp *Craspedacusta* and the native *Hydra sp.* Results have shown that both polyps can ingest a considerable number of rotifers (*Brachionus calyciflorus*) over time and that both polyps ingested increasing numbers of prey with increasing concentration of the prey. It was difficult to decide on the appropriate type of functional response because saturation was not reached for both predator-prey systems and the data were also well described by a linear function. This observation of non-saturation is common in experiments with cnidarians (Purcell 1997), which are considered to be a type of “functional” filter-feeders (Jeschke et al. 2004). Nevertheless, an indication for saturation occurred at prey levels higher than $0.6 \mu\text{g C L}^{-1}$ for both predators *Craspedacusta* and *Hydra* and a functional response type 2 (Holling 1959) was therefore applied.

The functional response analyses further showed that the maximum ingestion of prey items by a single *Hydra* polyp ($8.60 \pm 5.10 \mu\text{g C d}^{-1}$) was higher as for a single *Craspedacusta* polyp ($3.86 \pm 0.87 \mu\text{g C d}^{-1}$). Sessile polyps like *Hydra* and *Craspedacusta* are ‘sit-and-wait-predators’ (Kaliszewicz 2013), in which the effectiveness of their strategy is based on both the ability of the predator to catch prey and the probability of prey coming in reach of the predator. A high number of tentacles had been observed to increase predation and prey-holding efficiency in some other ‘sit-and-wait’ predators like corals (Sebens 1987). It is likely that the presence of tentacles in *Hydra* and the absence of tentacles in *Craspedacusta* are the reason for observed differences. A lower prey handling time was formerly described as being a characteristic trait of successful invasive crustaceans in comparison to the handling time of similar native species (Dick et al. 2013). The present data show, that this is not necessarily a characteristic trait of the polyps of invasive *Craspedacusta* and it seems that *Hydra* has an advantage considering the maximum intake of prey items.

Discussion

However, the average dry weight of pooled samples of polyps within this study revealed that one polyp of *Hydra* was on average ten times heavier in terms of dry weight and carbon content as one individual of *Craspedacusta*. Hence, the ingestion rate in relation to the body carbon of the predator (mass-specific ingestion rate) showed an opposite pattern as the feeding rates per individuals. The daily mass specific ingestion rate of *Craspedacusta* was higher as the one of *Hydra*. Polyps of *Craspedacusta* were able to ingest up to 18 times their own body carbon per day and a single *Hydra* polyp ingested four times its own body carbon per day at the maximum prey density. A daily food uptake which is higher than the body weight has also been shown for other cnidarians like the hydrozoan medusae *Sarsia tubulosa* (Daan 1986), *Sarsia geminifera* (Stibor et al. 2004) or the ctenophore *Pleurobrachia bachei* (Hirota 1972). Less is known about daily mass specific ingestion rates of sessile cnidarians, but for example, the marine hydroid *Tubularia larynx* is able to capture a mean of 4.15 mg dry weight of prey per day, which represents between 70 and 110% of the dry weight of a single hydranth (Gili et al. 1996). So far, this value was seen as the highest reported from any hydroid or other cnidarians (Gili et al. 1996) but the present study indicates that the ingestion rates of polyps of *Craspedacusta* are much higher.

Related to the high daily mass specific ingestion rate of *Craspedacusta* was the fast and high numerical response of the polyps. *Hydra* was not able to use the ingested prey for offspring reproduction, independent on the tested food levels. Even at the highest food level of 1 μg carbon per ml, no asexual reproduction was observed. This indicates that *Craspedacusta* polyps can use ingested food more efficiently for asexual reproduction compared to *Hydra* polyps. However, various factors can contribute to the growth of *Hydra* including the surrounding medium, temperature, pH, dissolved oxygen and ionic balance (Quinn et al. 2012). Laboratory experiments using *H. littoralis* and *H. vulgaris* have for example demonstrated that *Hydra* may require defined ranges of these factors, including temperatures of 20-30°C and daily feeding of *Artemia* in order to achieve logarithmic growth (Loomis 1953, Fu et al. 1991). That offspring production, especially frustules budding of polyps, depends on feeding rate has also been shown in former studies on *Craspedacusta* (Lytle 1961, Acker and Muscat 1976, Folino-Rorem et al. 2015) and are in accordance with the results in the present study. *Craspedacusta* produced up to three times more offspring from the same available food source than *Hydra*. The present results further indicate that increased prey densities caused by nutrient enrichment could trigger a very fast numerical response from

Craspedacusta polyps and that they could be greater beneficiaries from enrichment of benthic food webs than it might be the case for *Hydra*.

4.2.2 Isotopic Niche Differentiation of *Craspedacusta* and *Hydra*

Co-occurrence of polyps from both genera *Craspedacusta* and *Hydra*, is reported even on the same substrate, such as dreissenid mussels (Stanković and Ternjej 2010, Folino-Rorem 2015). Therefore, the significance of dietary niches partitioning was investigated with a comparative stable isotope methodology. Stable isotope analyses are important tools for comparative studies of trophic niche widths and trophic positions (Peterson and Fry 1987, Bearhop et al. 2004, Grey 2006, Cucherousset et al. 2012). Ratios of nitrogen isotopes ($^{15}\text{N}:$ ^{14}N) serve to index relative trophic levels because ^{15}N tends to become enriched upon increased trophic levels. On the other hand, ratios among carbon isotopes ($^{13}\text{C}:$ ^{12}C) are used to identify the sources of basal carbon suppliers in freshwater systems (Post 2002, Finlay and Kendall 2007). It is important to point out that pelagic carbon sources in lakes are usually characterized by relatively low $^{13}\text{C}:$ ^{12}C ratios compared to littoral carbon sources (France 1995). A dry weight of about 0.2 mg is required for measurement accuracy of stable isotopes (T. Hansen, pers. comm.), therefore a corresponding number of individuals needed to be pooled for each taxon of interest. As a consequence, the number of replicates per taxon is low (usually three). However, it should be noted that each sample already reflects the average values of carbon and nitrogen signatures of a large number of individuals, which increases the degree of reliability. For instance, a single data point of *Craspedacusta* represents the average carbon and nitrogen signatures of 20 individual polyps.

The first common feature was that *Hydra* and *Craspedacusta* showed a similar trophic position. It is generally expected that $\delta^{15}\text{N}$ values will be enriched at each trophic transfer by an increase of approximately 2.8 to 3.4 ‰ (e.g. Minagawa and Wada 1984), but $\delta^{15}\text{N}$ values of the two polyp genera were on average only 0.92 ‰ different. These low differences support the assumption that the two polyp genera are similar in their trophic level and clearly predatory. The $\delta^{15}\text{N}$ values of the two polyp genera were around 1 to 1.5 trophic positions higher as the ones for herbivore benthic filter-feeder *Dreissena polymorpha* or herbivore pelagic filter-feeder *Daphnia longispina* (Barnett et al. 2007). This relationship shows that polyps of the two genera are functionally similar predators and could indeed be competitors for food.

Discussion

However, mean $\delta^{13}\text{C}$ values of the two different polyps were significantly different and the isotopic niche widths never overlapped. This clearly shows that the two polyp types have different dietary carbon sources and that they must be specialized on different food types. This implies that they are not competing for the same food and that dietary niche separation enables their coexistence. In detail, *Craspedacusta* polyps had consistently heavier carbon signals than the *Hydra* polyps. The $\delta^{13}\text{C}$ values of *Hydra* were in general closer to $\delta^{13}\text{C}$ values of the free-swimming medusa of *Craspedacusta* and the filter-feeding cladocerans *Sida crystallina*, *Alona sp.* and *Daphnia longispina*. The carbon sources of these taxa are predominantly pelagic (Dejdar 1934, Barnett et al. 2007), reflected by their relatively lighter $\delta^{13}\text{C}$ values compared to mainly benthic grazers like the cladoceran species *Pleuroxus truncatus* (Casper 2012) or gastropods like *Lymnea stagnalis* (Reavell 1980). As the $\delta^{13}\text{C}$ signature of *Craspedacusta* was similar to the values of these benthic grazers, it can be concluded that the carbon source of the polyp is also mostly benthic. The results show that neither lake specific nor seasonal differences were reasons for dietary niche separation of *Craspedacusta* and *Hydra* polyps. The general pattern could rather be explained by the morphological differences of the two polyp genera. Due to the mobility and the highly flexible and elongated body with tentacles, *Hydra* polyps might be able to catch pelagic prey. Due to the smaller body size and the lack of tentacles compared to *Hydra*, polyps of *Craspedacusta* are limited to benthic prey organisms. Such a resource partitioning based on morphology as observed in these investigations is a known mechanism that enables the coexistence of competing species (Leyequi n et al. 2007).

These morphological differences might also explain the observed higher generalistic feeding behavior of *Hydra* compared to *Craspedacusta*. The trophic niche of *Hydra* seems to be larger in spring (May) compared to July or October as seen by a larger ellipse area in the seasonal sampling approach at Lake Langwieder See. The reason for a broader trophic niche might be due to the already mentioned mobility and tentacle length of *Hydra* and additionally to higher abundances of different crustacean species in spring compared to summer or autumn, when this prey type is reduced by high predation pressure by fish (Sommer et al. 1986, Sommer et al. 2012). The seasonal samplings at Lake Langwieder See showed that the size of the dietary niche of both polyps varied with the season and influences the strength of dietary niche separation.

4.2.3 Conclusion

The joint analyses of resource use efficiencies and stable isotopes analyses have shown that coexistence of both functionally similar polyps of *Craspedacusta* and of *Hydra* within the same benthic food web should be possible in a long-term perspective. Given solely the functional and numerical response analyses it seems that *Craspedacusta* has an advantage because of its higher resource use efficiency and the fast and high reproduction at low food densities. The stable isotope analyses, however, have shown that the two polyp genera occupy separate dietary niches independently of season and lake type, which enables their coexistence in the same benthic food web. For that reason, an establishment of *Craspedacusta* should not be affected by competition for food with the resident *Hydra* polyps.

4.3 Trophic Cascades Mediated by Jellyfish

In marine systems, gelatinous predators are more common compared to freshwater systems and several studies describe cascading effects of jellyfish down to phytoplankton growth (Stibor et al. 2004, Pitt et al. 2007, West et al. 2009). In freshwater systems, the hydrozoan jellyfish *Craspedacusta sowerbii* can form big blooms of medusae during summer. In a mesocosm experiment, Jankowski et al. (2005) were able to measure a decrease of zooplankton biomass and an increase of chlorophyll *a*, a measure for phytoplankton biomass, within a mesocosm experiment. The authors compared the effect of a very high jellyfish density to the effect of no predation on the community of a hypertrophic lake. However, jellyfish can occur in different densities in lakes and within a specific lake, medusae density can vary seasonally. Furthermore, zooplankton and phytoplankton communities differ among lakes and a higher diversity of taxa and a higher number of trophic interactions within a lake potentially influence trophic cascades (Shurin et al. 2002, Stibor et al. 2004). For these reasons, the effect of different jellyfish densities (0, 2, 4, 8, 16 medusae per 140 L enclosures) on the natural summer plankton community of three different oligotrophic lakes were tested within the present study to figure out general mechanisms of food web dynamics mediated by jellyfish in this lake type.

The results show that *C. sowerbii* was able to significantly reduce the amount of crustacean mesozooplankton and to indirectly induce a significant increase of phytoplankton. The strong positive effect of zooplankton removal on algal biomass indicates a three-link trophic cascade in all investigated plankton communities.

4.3.1 Direct Jellyfish Effects on Mesozooplankton

Density-dependent jellyfish effect on zooplankton abundance

At the end of all three mesocosm experiments, a strong negative relationship between jellyfish density and mesozooplankton biomass was observed. This inverse relationship between medusa densities and their prey has also been found in several studies with marine jellyfish species and supports this result (e.g. Möller 1984, Brewer 1989, Behrends and Schneider 1995). Within the experimental duration of 13 days, in treatments with highest jellyfish density (16 jellyfish per 140 L enclosure) the mean reduction of zooplankton biomass ranged

Discussion

between 37 and 96 % whereas in low density treatments (2 jellyfish per 140 L enclosure) the values were between 5 and 41 % in comparison to control treatments. Such high reduction of zooplankton indicates that predation by *C. sowerbii* can be substantial already at much lower densities (0.014 ind L⁻¹ to 0.114 ind L⁻¹) compared to densities described by Jankowski et al. (2005; 0.5 ind L⁻¹). The strong reduction of mesozooplankton biomass supports the former suggestions that *C. sowerbii* is able to decrease zooplankton standing stocks in lakes (Davis 1955, Green 1998, Jankowski and Ratte 2001, Smith and Alexander 2008).

Changes of zooplankton community composition

Across all three experiments, jellyfish had a significant negative effect on all crustacean mesozooplankton groups and taxa. The investigated zooplankton communities contained cladocerans of the genera *Bosmina*, *Ceriodaphnia*, *Daphnia* and *Diaphanosoma*, and both calanoid and cyclopoid copepods. Similar diets, including a variety of cladocerans and copepods, have been reported previously (e.g. Davis 1955, Dodson and Cooper 1983, Spadinger and Maier 1999, Boothroyd et al. 2002). These taxa and groups are the most common members of freshwater pelagic communities and known to be phytoplankton grazers (Barnett et al. 2007). Consequently, jellyfish are not dependent on a specific prey type and could potentially cause increased algal growth by reducing zooplankton in a variety of lakes.

No preference of jellyfish for a specific taxon or group was found, but the strength of negative effects on the different taxa varied and, in some cases, also a slight positive effect on specific taxa was observed. Higher effect sizes by predation of jellyfish were measured for bigger and active prey such as *Daphnia* and cyclopoid copepods, already at low jellyfish densities (2 jellyfish per 140 L enclosure). Size and activity of prey being important factors for feeding preferences of jellyfish have been already noted in former studies about *C. sowerbii* (Dodson and Cooper 1983, Spadinger and Maier 1999, Boothroyd et al. 2002). Especially selectivity coefficients calculated based on stomach analyses of *C. sowerbii* medusae support the food preference for bigger and active prey (Spadinger and Maier 1999).

The effect on smaller taxa such as *Bosmina* and *Ceriodaphnia*, which are considered to be at the lower limit of prey size for *C. sowerbii* (Spadinger and Maier 1999), varied among the experiments. The indifferent effects of *C. sowerbii* on the abundance of *Bosmina* due to decreased encounter rate have also been shown by Smith and Alexander (2008). Since the feeding mode of *C. sowerbii* may be passive, the result of encountering prey while sinking down through the water column with expanded tentacles is likely to be related to the

abundance and size of prey. Other factors, such as thick exoskeletons, powerful escape movements and, immunity to nematocyst toxins could reduce the likelihood of being preyed upon for certain groups of zooplankton (Boothroyd et al. 2002). This observed feeding of *C. sowerbii* in response to zooplankton body-size and overall prey abundance further resulted in a change in community composition in comparison to jellyfish-free treatments. Changes of zooplankton community composition can have further effects on filtration rates, recycling processes or predation risk by size-selective predators such as visually feeding fish.

Changes of zooplankton diversity

Predation by *C. sowerbii* also had consequences for zooplankton diversity. A reduction of diversity of zooplankton communities in terms of reduced evenness in two of the investigated zooplankton communities (Lake Haselfurther Weiher, Lake Waldsee) was observed. In the third community, the opposite effect was visible, diversity/evenness increased (Lake Haager Weiher). In this community, zooplankton taxa were more equally represented with higher jellyfish predation. Consequently, the initial zooplankton community composition is crucial for the direction of jellyfish predation effects on the diversity of crustacean mesozooplankton.

If the initial community is dominated by one or a few groups (low evenness) and jellyfish will preferably feed on the dominant group, then zooplankton evenness might increase and thereby also diversity. In case that the initial mesozooplankton community is composed evenly and that jellyfish selectively feed on one specific taxon, evenness might decrease and thereby also mesozooplankton diversity. Diversity of herbivore consumers can also have far-reaching consequences for ecosystem dynamics as consumer diversity might influence its function as predator of primary producers but also its role as prey for higher trophic levels (Gamfeldt et al. 2005, Hillebrand and Shurin 2005, Striebel et al. 2012).

4.3.2 Indirect Jellyfish Effects on Phytoplankton

Density-dependent jellyfish effect on phytoplankton

In all three experiments, phytoplankton biomass increased significantly with increasing jellyfish abundance, suggesting that jellyfish stimulate primary production indirectly by zooplankton reduction. Such clear trophic cascades induced by jellyfish top-down effects were visible on average three days after the start of the experiments and were more or less pronounced until the end. In all three experiments, chl *a* was on average two to three times

Discussion

higher in treatments containing the maximum number of jellyfish (16 per enclosure) compared to jellyfish-free treatments. The strong positive effect of zooplankton removal on algal biomass indicates a three-link trophic cascade, as it is usually observed in freshwater systems with planktivorous fish as top-predator (Carpenter et al. 1985, Vanni and Findlay 1990, Vanni et al. 1997). This contrasts with observed trophic cascades induced by marine jellyfish, where jellyfish presence can also result in lower phytoplankton growth, due to alternative trophic pathways in relation to the dual role of copepods (Stibor et al. 2004). In marine systems, copepods are the dominant functional group, but in freshwater, cladocerans usually dominate the zooplankton community in terms of abundance, species number and biomass (Sommer and Stibor 2002, Walseng et al. 2006). As described above, *C. sowerbii* reduced both functional groups and feed on specific prey taxa more or less in proportion to their abundance. A general cascading effect of jellyfish predation on phytoplankton growth should for that reason be true for a broad variety of freshwater lakes. Additionally, it has been shown that the combined impact of both functional zooplankton groups, cladocerans (filter-feeder) and copepods (selective feeder), led to a substantial decline in phytoplankton biomass in contrast to the impact of a single functional group (Sommer et al. 2001, Sommer et al. 2003). Consequently, a reduction of members of both groups by jellyfish predation should lead to stronger cascading effects than the reduction of only one of the two groups.

In earlier experiments with *C. sowerbii* described by Jankowski et al. (2005), similar effects on phytoplankton growth were observed; the phytoplankton biomass was about three times higher with the in treatments with highest jellyfish densities compared to jellyfish-free treatments (Jankowski et al. 2005). However, the experimental jellyfish density described in the study of Jankowski et al. (2005) exceed by far (4 times) the jellyfish densities in the present experiments. The present results therefore clearly show that *C. sowerbii* can have strong cascading effects on phytoplankton already at low jellyfish densities. Consequently, not only big jellyfish blooms, but also a moderate occurrence of jellyfish could have measurable cascading effects in pelagic food webs.

The difference in the strength of cascading effects on phytoplankton biomass between the present three experiments and the study of Jankowski et al. (2005) could be explained by obvious differences in community composition of zooplankton. In the study of Jankowski et al. (2005) younger life stages of copepods and small cladocerans (bosminids) dominated in the lake and in the diet of jellyfish. In the present study, initial communities and diet of jellyfish were more diverse and also larger cladocerans, such as *Daphnia* were included. As it

Discussion

was shown in a series of studies, especially large cladoceran species and individuals are very efficient grazers and may strongly suppress algal biomass (Gliwicz 1977, 1980). Therefore, these cladocerans play a key role in trophic cascades. This is supported by the stronger link between jellyfish density and phytoplankton biomass in the experiment of Lake Waldsee in comparison to the other two experiments; probably due to a higher proportion of larger cladocerans in the initial zooplankton community and a strong reduction of these by *C. sowerbii*.

Jellyfish effect on phytoplankton composition

Not only total biomass of phytoplankton was indirectly increased by jellyfish predation on zooplankton, but the composition of phytoplankton was also changed. The dominance of a specific group was stable across treatments for a specific experiment (green algae in Haselfurther Weiher and Waldsee, diatoms/dinoflagellates in Haager Weiher), but the functional groups diatoms/dinoflagellates and green algae benefited the most from the presence of jellyfish across all experiments. A change of phytoplankton composition was further attributed to a neutral or negative indirect effect of jellyfish on blue-green algae and cryptophytes, when present. Such changes in the community composition of phytoplankton also change edibility and quality of phytoplankton as a food source for zooplankton.

The size of phytoplankton is one of the most fundamental traits for feeding relationships between phytoplankton and zooplankton. A change of community composition could be accompanied by a shift in phytoplankton size and therefore the edibility for grazers could be affected as well. Especially the size range of diatoms and dinoflagellates, the groups which benefited the most by jellyfish predation on zooplankton, is large (Litchman et al. 2009, Le Bescot et al. 2015). Cell volumes of freshwater diatoms, for example, vary <6 orders of magnitude with the largest cells being approximately $10^6 \mu\text{m}^3$ (Litchman et al. 2009). Bigger taxa would be inedible for most cladocerans, as the size range of food items ingestible for cladocerans is determined by the filter mesh-size and the opening width of the mandibles and the carapace gap (Sommer and Stibor 2002). For example, *Daphnia spp.* has lower size limits of approximately 1 mm and upper ones of around 30 mm (Gliwicz and Siedlar 1980, Geller and Müller 1981, Gophen and Geller 1984). Copepods generally can ingest larger food items than cladocerans, although a wide overlap in the food spectrum is generally found (Geller and Müller 1981, Kleppel 1993, Adrian and Schneider-Olt 1999, Sommer et al. 2000, 2001), and could have an advantage in phytoplankton communities dominated by bigger taxa.

Discussion

Phytoplankton is able to synthesize essential fatty acids, amino acids, and sterols, so the biochemical composition varies considerably among phytoplankton taxa (Sommer et al. 2012). Zooplankton, however, must obtain these macromolecules from their diet (Sommer et al. 2012). Cyanobacteria and Chlorophyta are deficient in polyunsaturated fatty acids (PUFA) and sterols, whereas diatoms and most flagellate taxa are in PUFA- and sterol-rich primary producers and thus, nutritionally rich for zooplankton (Müller-Navarra et al. 2004). The observed changes in phytoplankton composition mediated by indirect jellyfish effects could therefore result in altered availability of essential macromolecules to zooplankton. This would have critical consequences for zooplankton reproduction and recruitment (Arts et al. 2009). Dietary levels of fatty acids, amino acids and sterols had been positively correlated to growth, egg production and egg hatching, as well as other physiological functions in zooplankton (Brett and Müller-Navarra 1997, Guisande et al. 2000, Arts et al. 2009, Mariash et al. 2011).

Jellyfish effect on seston stoichiometry

The Redfield-Ratio defines optimal molar elemental stoichiometry of phytoplankton as C:N:P=106:16:1 (Redfield 1934). According to measures of classical Redfield seston stoichiometry, the initial phytoplankton community of all three lakes was phosphorus limited ($C : P > 100$) and nitrogen was not limiting ($C : N < 7$). At the end of the experiments, no clear relationship between jellyfish density and nutrient limitation based on seston stoichiometry was observed. Only Lake Waldsee phytoplankton showed a significant decrease of P limitation with increasing jellyfish density, based on their biomass stoichiometry. This indicates that the stoichiometric composition of phytoplankton can be affected by the presence of jellyfish. Such changes can have further bottom-up effects on higher trophic levels, up to zooplankton, jellyfish, planktivorous fish and piscivores. Organisms of higher trophic levels are usually much more constrained in their stoichiometry. Hence, if food stoichiometry is very different from consumer stoichiometry a so-called stoichiometric trophic mismatch can occur. For example, phytoplankton C : P ratios above 300 can result in P limitation of the growth of *Daphnia*, which usually has C : P ratios around 105 (Urabe and Watanabe 1992, DeMott et al. 2001, Hessen et al. 2004). In lake Waldsee, the C : P ratio decreases from an average value of 500 in control treatments to 300 in treatments with the highest jellyfish density. An improvement of phytoplankton quality indirectly by jellyfish predation is visible, but it seems that zooplankton growth is still potentially affected by P limitation.

Discussion

Potential reasons for this observed effect of decreasing P limitation with increasing jellyfish density could be that nutrients are released directly during the feeding process by “sloppy feeding” of the jellyfish (loss of carbon and nutrients during feeding process) or by the jellyfish’s excretion, as it was also shown for some marine jellyfish (Pitt et al. 2007, Pitt et al. 2009, West et al. 2009). Moreover, jellyfish may also contribute indirectly to nutrient cycling via a process known as biogenic mixing (Katija and Dabiri 2009, Katija et al. 2012), which is studied in this thesis and confirmed for *C. sowerbii* by laboratory experiments (topic 4, see page 108). To what extent a combination of these factors contributes to changes in seston stoichiometry and maybe supports primary production, as it was found for marine jellyfish already (Pitt et al. 2009), should be further investigated for systems with *Craspedacusta*.

Jellyfish effect on nutrient and phytoplankton interactions

In all three experiments, phytoplankton (chl *a*) increased with total phosphorus (TP). However, the residual variance of the linear relationship of chl *a* and TP was influenced by jellyfish density. The chl *a* to TP ratio was higher in treatments with high jellyfish abundances compared to treatments with low and zero jellyfish abundances. This indicates a lower predation pressure of zooplankton on phytoplankton and thereby a higher amount of phytoplankton per unit available phosphorus in high jellyfish density treatments. Hence, the measured chl *a* in treatments with high jellyfish abundances deviated from classical nutrient-predicted chl *a* concentrations (e.g. Sakamoto 1966, Dillon and Rigler 1974, OECD 1982, McCauley et al. 1989, Prairie et al. 1989, Champion and Currie 2000, Raike et al. 2003, Hakanson et al. 2005). This finding is in accordance with the cascading trophic interaction theory (Carpenter et al. 1985) and supports the finding of jellyfish mediated trophic cascades down to phytoplankton. Further support was the measured lower soluble phosphorus concentrations per unit total phosphorus with increasing jellyfish abundances. Reduced zooplankton grazing pressure on phytoplankton in treatments with jellyfish resulted in higher standing stocks of phytoplankton and thereby higher phosphorus uptake and consequently lower dissolved phosphorus levels in the water.

4.3.3 Conclusion

The observed cascading effects by jellyfish on mesozooplankton assemblages were clearly density-dependent. The results show that not only big jellyfish blooms but also a moderate occurrence of jellyfish could have measurable cascading effects in pelagic food webs.

Discussion

However, it is very difficult to estimate “average” natural abundances of jellyfish in lakes as jellyfish distributions are very patchy and variable (Boulenger and Flower 1928, Milne 1938, Deacon and Haskell 1967, Graham et al. 2001). A swarm of jellyfish occurring in a small area of a lake may have strong local impacts on zoo- and phytoplankton but it will be very difficult to estimate the effect sizes of such a local swarm for entire lake plankton communities. It is important to note that mesocosm experiments in general detect short-term cascade effects within days to weeks (Benndorf 1990). Support for the results of the mesocosm experiments by field analyses would be useful to predict cascading effects by jellyfish *in situ*.

4.4 Jellyfish and Phosphorus Dynamics

It was hypothesized that *Craspedacusta* as the “new” jellyfish member of freshwater food webs could also have strong “biomixing” effects such as seen in marine jellyfish and thereby supply phosphorus to nutrient-depleted surface layers by upward migrations.

Strong effects of *Craspedacusta* medusae on the net upward phosphorus transport in experimental water columns were measured in the present study. Within one hour, one jellyfish transported about 0.1 % of the injected P-concentration from the bottom of the experimental water column to the top of the column. As no phytoplankton and almost no bacteria were left after filtration of lake water (0.2 μm) at the beginning of each experiment, the nutrient redistribution due to excretion and swimming of zooplankton was very small (see own data). Therefore, the main reason for the nutrient increase at the top of the columns was most likely the swimming behavior of the jellyfish. By moving upwards, the pulsation mode of the medusae sets large starting vortexes into motion (contraction phase), which are stopped with a second vortex ring during expansion (Lucas et al. 2013). This process sets big packages of water into motion (Colin et al. 2006) and could have largely contributed to the measured upward transport of phosphorus. The medusae are moving downwards more passively by sinking and thereby exposing tentacles upwards as a filter mechanism for catching their prey (Boulenger and Flower 1928, Milne 1938). Therefore, the downward transport of phosphorus by sinking medusae is probably very low.

The effect of the freshwater medusa on nutrient transport was compared with that of native crustacean and non-crustacean zooplankton. The predatory insect larvae of *Chaoborus spp.* is distributed in both temperate and tropical lakes and can be present in high numbers (Dusoge 1983, Xie et al. 1998). The larvae diurnally migrate, during the daytime they bury themselves in the sediment and at night they feed at the surface (Berg 1937, Voss and Mumm 1999, Gosselin and Hare 2003). As *Chaoborus spp.* larvae are one of the biggest zooplankton representatives that migrate diurnally (Lorke et al. 2004), the aim of the present study was to measure the biogenic nutrient transport of a native zooplankton species comparable in size to the jellyfish. In this study, an effect of the pelagic insect larvae of *Chaoborus spp.* on the phosphorus distribution was not measurable. A possible explanation is the torpedo-shaped body and floating swimming mechanism of *Chaoborus spp.* larvae; they migrate via passive

Discussion

buoyancy using air sacks (McGinnis et al. 2017), which likely creates only a very small motion of the surrounding water.

In treatments with natural crustacean zooplankton from a nearby lake a measurable but much smaller effect on nutrient (P) upward transport was measured. There was a clear dose – effect relationship visible, meaning that a linear increase in P transport could be observed with increasing zooplankton abundances. In the present experiments a crustacean zooplankton community with 8 ind L^{-1} transported within one hour 0.01 % of the injected P from the bottom to the top of the column. The observation of a small but measurable upward transport of P by crustacean zooplankton is in line with earlier measurements of Haupt et al. (2010) who also measured a small but detectable increase of phosphorus concentration in the epilimnion of experimental plankton towers by *Daphnia* diel vertical migration. They stated that the increase was most probably mainly due to excretion of *Daphnia* and in a range that could already result in an increase of primary production. A recent modeling study supports the idea that small organisms (mm-cm) such as vertically migrating crustacean zooplankton can induce biogenic mixing of stratified fluids even at intermediate Reynolds numbers (Wang and Ardekani 2015). The results of the present study show that biological upward nutrient transport mediated by migrating jellyfish of *Craspedacusta* from deeper water layers could probably be much stronger, resulting not mainly from excretion but from water movements induced by the swimming behavior of jellyfish. Light is usually sufficient in upper water layers to support photosynthesis, the biogenic nutrient input will therefore immediately result in nutrient uptake by phytoplankton and thereby enhance primary production.

4.5 Evidence of Jellyfish Food Web Effects in the Field

C. sowerbii is known in freshwaters for about 100 years. If the jellyfish plays a functional role, then lakes, which contain jellyfish, should show different food web dynamics compared to lakes with similar environmental factors (nutrients, morphometry, water column stratification) that do not contain jellyfish. In the present study strong indirect positive effects of jellyfish on phytoplankton biomass were measured in outdoor mesocosm experiments (topic 3). This phytoplankton increase could even be enhanced by the upward nutrient (phosphorus) transport mediated by jellyfish movements, as it was measured in columns in the laboratory (topic 4). If differences would be already visible in the field, higher phytoplankton abundances (measured as chl *a*) per unit of growth-limiting nutrient (P) in lakes containing jellyfish compared to jellyfish-free lakes were expected. However, no differences in the Chl-TP relationship between the two lake categories with and without jellyfish were detected. This can have different reasons.

The mesocosm experiments (topic 3) have shown that trophic cascades mediated by jellyfish are density-dependent. However, similar as described for marine jellyfish the jellyfish density of *Craspedacusta* within a lake is hard to determine because of high patchiness of jellyfish occurrence and of vertical migration patterns (Boulenger and Flower 1928, Milne 1938, Deacon and Haskell 1967, Graham et al. 2001). High patchiness during the survey was also observed in all the examined lakes and the total jellyfish density of each lake was not determined. Indeed, higher chl *a* values might occur within such patches, but these values might not be big enough to change whole lake dynamics reflected in an altered Chl-TP relationship. The highest deviation of the general Chl to TP regression among jellyfish-lakes was calculated for Lake Waldsee, and as a very subjective estimate, the jellyfish density in that lake was the highest. This supports the hypothesis that jellyfish densities of *Craspedacusta* in the examined lakes were in general rather too low to result in measurable changes of Chl-TP relationships.

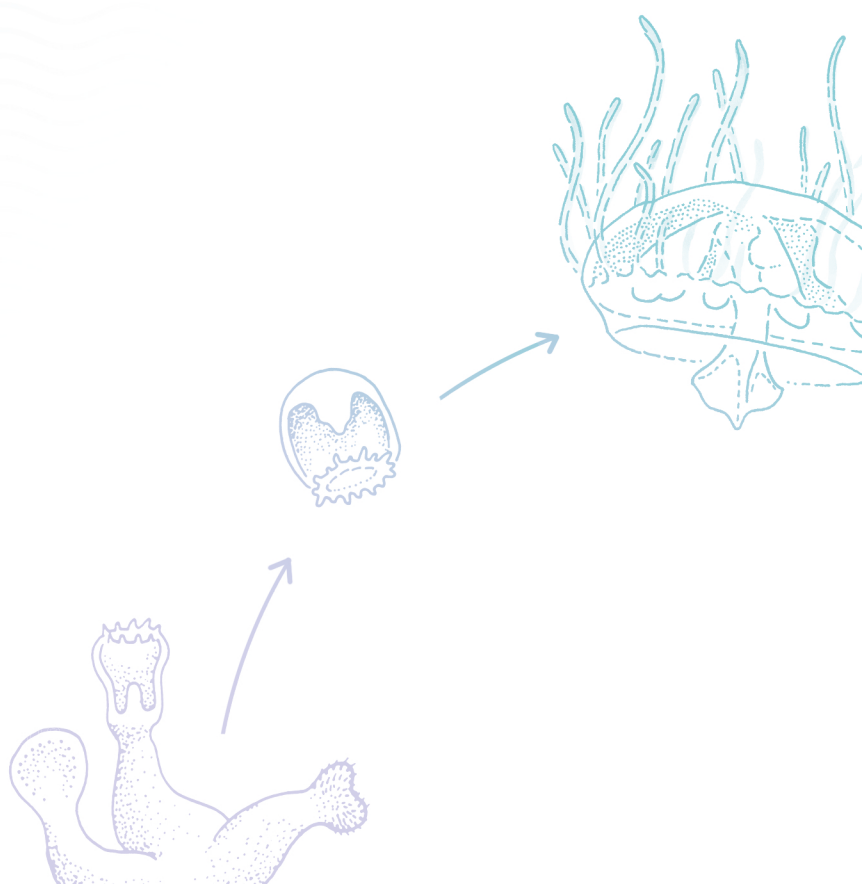
Additionally, it is not possible to discriminate cascading effects mediated by fish and by jellyfish within a single lake. It is known, that *Craspedacusta* medusae can co-occur with fish (Dodson and Cooper 1983, Jankowski et al. 2005). However, it is hard to determine, if jellyfish-lakes have lower fish biomass compared to jellyfish-free lakes and information about that relationship is completely missing. It could be possible that jellyfish can only develop in

Discussion

lakes which contain only small amounts of fish and thereby enough zooplankton for jellyfish growth. In this case, the relatively high zooplankton content may also reduce phytoplankton growth and the positive effect of jellyfish on phytoplankton growth might be invisible. Furthermore, if fish have a disadvantage by jellyfish presence, then Chl-TP relationships might not differ among lakes with and without jellyfish, because fish effects might be reduced and be replaced by jellyfish effects. If jellyfish and fish can co-occur undisturbed, then the jellyfish effect should be visible as positive deviations of Chl-TP regressions. According to Dodson and Cooper (1983), there should be no risk of competition between *Craspedacusta* and fish, as the predation effect of jellyfish on zooplankton is considered to be too low for strong competition with fish. Furthermore, according to Jankowski et al. (2005) both food chains of roach (planktivorous fish) and of jellyfish can co-occur and have simultaneous impacts on the zooplankton community structure. However, further studies are needed to investigate co-occurrence and the possible food web effects of different densities of fish and jellyfish in the field.

Chl-TP regression models are often applied in lake management to manipulate TP levels to control algal biomass (Håkanson et al. 2005). Therefore, the Chl-TP regression models that have been presented so far (e.g. Sakamoto 1966, Dillon and Rigler 1974, OECD 1982, McCauley et al. 1989, Prairie et al. 1989, Champion and Currie 2001, Räike et al. 2003, Hakanson et al. 2005) should be analysed whether modifications for lakes containing jellyfish are needed assuming further increasing jellyfish abundances.

5 Outlook



5.1 Tolerance Range and Dispersal Limitation of the Polyp Stage

The polyp sampling for genetic and ecological analyses in this thesis showed that both species of *C. sowerbii* are by far more common than estimated from medusae observations only. These observations indicate that the dispersal rate of the polyps must be high, because polyps were found in nearly all the investigated lakes, even with low sampling effort. Surprisingly, globally known mtDNA-haplotypes were found close together within lakes, indicating that the likelihood of their dispersal is similar. Their unbalanced frequencies, however, suggest different colonization success and future research should address the adaptive potentials of the different haplotypes. To investigate differences in survival, growth and reproduction of polyp haplotypes, laboratory experiments manipulating important environmental factors such as temperature, light and food (quantity and quality) should be conducted. Polyp tolerance curves for these factors should be quantified for the different haplotypes, which can help to understand observed population dynamics in different aquatic systems and seasons.

Additionally, the colonization success of the genetically different polyps can further be influenced by substrate type. Polyps were so far only collected from stones and not from other potentially inhabited substrates such as macrophytes, wood or mussels (Acker and Muscat 1976, Park 1998, Stanković and Ternjej 2010, Folino-Rorem 2015). The genetic population structure of polyps sampled from different substrates should be investigated in the future and frequencies of haplotypes should be compared. In laboratory experiments, it could also be tested if polyps of different types actively prefer specific substrates.

5.2 Mechanisms Regulating Medusae Production and Sex Determination

Understanding the interaction between an organism's life history and environmental factors is an essential task in ecology. In spite of the observed presence of two species of *C. sowerbii*, it is even more important to close existing gaps in understanding how the phase transition of the benthic polyp to the pelagic medusa is influenced by multiple environmental factors. For example, external factors such as temperature, food, light, pH and CO₂ are considered to trigger medusa budding in polyps (reviewed in Acker and Muscat 1976). If the transition of polyp to medusa depends on haplotype-specific triggers should be systematically tested within laboratory experiments.

Outlook

It should further be investigated, if the sex of medusae is linked to their mtDNA-haplotype as indicated by the results of topic 1. To rule out the role of thermal conditions in sex determination of *Craspedacusta*, laboratory experiments similar to the studies in *Aurelia* by Liu et al. (2018) are needed. There it has been shown that the sex of *Aurelia* medusae was determined at the polyp stage independent of temperature and that all medusae originating from a given polyp are, phenotypically, of the same sex. Moreover, the temperature did not induce a switch between sexes in older medusae (Liu et al. 2018). The question if sex is genotypically defined is of high evolutionary importance because selection will act primarily on the polyp stage and in case of a linkage, founder effects would favor sex-biased populations, such as observed in the wild.

5.3 Jellyfish and the Pelagic-Benthic Couplings of Fluxes of Energy and Matter

Mesocosm experiments described within topic 3 have revealed that the reduction of zooplankton biomass by jellyfish predation is high. In contrast to other plankton guilds, no important pelagic predators of the medusa are known, and the medusa can be seen as a potential “dead-end” in pelagic food webs. Interestingly, benthic crayfish of the genus *Orconectes* were reported to prey actively on *C. sowerbii* in a laboratory experiment (Dodson and Cooper 1983) and are considered to be the only predator of the medusae after their sedimentation following death. Hence, jellyfish are most probably remineralized in the sediment. This has been also shown for marine environments, where dead jellyfish were efficiently removed by benthic detritivores (Titelman et al. 2006, Pitt et al. 2008). For that reason, freshwater jellyfish may represent an important element of pelagic-benthic couplings in invaded lakes. This jellyfish mediated flux, respectively redirection of fluxes, of energy and matter from the pelagic into benthic environments would be new for European freshwater environments and should be investigated in more detail.

5.4 Migration Patterns of Jellyfish

Within nutrient distribution experiments of topic 4, a clear migratory pattern of freshwater jellyfish between deeper water layers and the surface was observed in indoor water columns. Under natural conditions, medusae have often been observed near the water surface in the

Outlook

morning or in the afternoon (Spadinger and Maier 1999) and during the day, they have often been found near the bottom (Dumont 1994, Spadinger and Maier 1999), indicating that freshwater jellyfish perform diel vertical migration as most other mesozooplankton. Details about the rhythm of the synchronized migrations are, however, contradictory. Deacon and Haskell (1967) found *C. sowerbii* specimens near the surface during daytime and suggested that positive phototaxis regulates jellyfish migration. One explanation for the ambivalent observations could be an overlooked difference in migratory drivers such as temperature, light intensity and UV exposure (Williamson et al. 2011). Synchronized migrations would have stronger effects on the resident food web, as, for example, nutrient redistribution correlated with jellyfish density in the present thesis (topic 4). It is therefore important to examine the effect of specific drivers on vertical positioning and migration patterns of freshwater jellyfish for example within controlled laboratory experiments and *in situ*. Potential behavioral differences between the two *Craspedacusta* species in European lakes should be taken into account.

5.5 Future Importance of Jellyfish as Members of Freshwater Food Webs

In marine ecosystems the effects of eutrophication coupled with ocean warming have been related with an increase in the frequency of blooms of invasive jellyfish (including Cnidaria and Ctenophora), with relevant adverse consequences for local and regional biodiversity (Purcell 2005, Brotz et al. 2012, Duarte et al. 2013). Recent studies have shown that medusae of *C. sowerbii* are UV sensitive to a certain extent (Caputo et al. 2018), indicating that especially the medusa stage may further benefit from “browning” and eutrophication processes that decrease UV penetration (Huovinen et al. 2000, Huovinen and Goldman 2000). Such processes and future changes in the timing and length of seasons might lead to an increase of population sizes and further expansions of both *C. sowerbii* species within European freshwater systems, similar as it is also presumed for marine jellyfish (Purcell 2012). For that reason, the focus on jellyfish as an important component in freshwater ecosystems may increase in the future and the relevance of a “gelatinous food chain” for freshwater systems. A recent, so far unique case of cutaneous poisoning to humans caused by *C. sowerbii* in Europe (Loeuillet et al. 2017) shows the potential dangers of invasion by at least one of these species and supports the need to improve the knowledge about these invasive freshwater jellyfish.

References

- Acker T.S. and Muscat A.M. (1976) Ecology of *Craspedacusta sowerbii* Lankester, a freshwater hydrozoan. *Am. Midl. Nat.*, **95**, 323-336.
- Adrian R. and Schneider-Olt B. (1999) Top-down effects of crustacean zooplankton on pelagic microorganisms in a mesotrophic lake. *J. Plankton Res.*, **21**, 2175-2190.
- Allredge A., Robison B., Fleminger A., Torres J., King J. and Hamner W. (1984) Direct sampling and in situ observation of a persistent copepod aggregation in the mesopelagic zone of the Santa Barbara Basin. *Mar. Biol.*, **80**, 75-81.
- Arbačiauskas K. and Lesutienė J. (2005) The freshwater jellyfish (*Craspedacusta sowerbii*) in Lithuanian waters. *Acta Zool. Litu.*, **15**, 54-57.
- Arts M.T., Brett M.T. and Kainz M. (2009) *Lipids in aquatic ecosystems*, Springer Science & Business Media.
- Augustin H., Foissner W. and Adam H. (1987) A sewage plant as a remarkable new habitat of the fresh-water polyp *Craspedacusta sowerbii* (Hydrozoa: Coelenterata). *Limnologica Jena*, **18**, 225-226.
- Ayre D. and Willis B. (1988) Population structure in the coral *Pavona cactus*: clonal genotypes show little phenotypic plasticity. *Mar. Biol.*, **99**, 495-505.
- Barnett A.J., Finlay K. and Beisner B.E. (2007) Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshw. Biol.*, **52**, 796-813.
- Beckett D.C. and Turanchik E.J. (1980) Brief Note: Occurrence of the Freshwater Jellyfish *Craspedacusta Sowerbyi* Lankester in the Ohio River. *Ohio J. Sci.*, **80**, 95-96.
- Behrends G. and Schneider G. (1995) Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). *Mar. Ecol. Prog. Ser.*, **127**, 39-45.
- Benndorf J. (1990) Conditions for effective biomanipulation; conclusions derived from whole-lake experiments in Europe. In: *Biomanipulation Tool for Water Management* pp. 187-203. Springer.
- Berg K. (1937) Contributions to the biology of *Corethra* (Meigen) (*Chaoborus* Lichtenstein), Biologiske Meddeling, Levin & Munsgaard, Kobenhavn.
- Boecker E. (1905) Über das Vorkommen von *Limnocoedium* im Münchener Botanischen Garten. *Biol. Zbl.*, **25**, 605-606.
- Boothroyd I.K.G., Etheredge M.K. and Green J.D. (2002) Spatial distribution, size structure, and prey of *Craspedacusta sowerbyi* Lankester in a shallow New Zealand lake. *Hydrobiologia*, **468**, 23-32.
- Bouillon J., Castiaux P. and Vandermeerssche G. (1957) Quelques aspects histologiques de *Limnocoidea tanganyicae*: Observations de coupes ultrafines au microscope électronique. *Exp. Cell Res.*, **13**, 529-544.
- Bouillon J. and Boero F. (2000) Synopsis of the families and genera of the Hydromedusae of the world, with a list of the worldwide species. *Thalassia Salent.*, **24**, 47-296.
- Boulenger C. and Flower W. (1928) The Regent's Park Medusa, *Craspedacusta sowerbii*, and its Identity with *C. (Microhydra) ryderi*. In: *Proc. Zool. Soc. Lond.*, pp. 1005-1014. Wiley Online Library.

References

- Bray J.R. and Curtis J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.*, **27**, 325-349.
- Brett M. and Müller-Navarra D. (1997) The role of highly unsaturated fatty acids in aquatic foodweb processes. *Freshw. Biol.*, **38**, 483-499.
- Brewer R.H. (1989) The annual pattern of feeding, growth, and sexual reproduction in *Cyanea* (Cnidaria: Scyphozoa) in the Niantic River estuary, Connecticut. *Biol. Bull.*, **176**, 272-281.
- Brotz L., Cheung W.W., Kleisner K., Pakhomov E. and Pauly D. (2012) Increasing jellyfish populations: trends in large marine ecosystems. In: *Jellyfish Blooms IV*, pp. 3-20. Springer.
- Bullock J.M., Bonte D., Pufal G., Da Silva Carvalho C., Chapman D.S., García C., García D., Matthysen E. and Delgado M.M. (2018) Human-mediated dispersal and the rewiring of spatial networks. *Trends Ecol. Evol. (Amst.)*, **33**, 958-970.
- Bushnell Jr J.H. and Porter T.W. (1967) The occurrence, habitat, and prey of *Craspedacusta sowerbyi* (particularly polyp stage) in Michigan. *Trans. Amer. Microsc. Soc.*, **86**, 22-27.
- Caputo L., Huovinen P., Sommaruga R. and Gómez I. (2018) Water transparency affects the survival of the medusa stage of the invasive freshwater jellyfish *Craspedacusta sowerbii*. *Hydrobiologia*, **817**, 179-191.
- Carpenter S., Kitchell J. and Hodgson J. (1985) Cascading trophic interactions and lake productivity. *Bioscience*, **35**, 634-639.
- Carré D. and Carré C. (2000) Origin of germ cells, sex determination, and sex inversion in medusae of the genus *Clytia* (Hydrozoa, Leptomedusae): the influence of temperature. *J. Exp. Zool.*, **287**, 233-242.
- Casper S.J. (2012) *Lake Stechlin: A temperate oligotrophic lake*, Springer Science & Business Media.
- Champion M. and Currie D. (2000) Phosphorus - chlorophyll relationships in lakes, rivers and estuaries. *Verh. - Int. Ver. Theor. Angew. Limnol.*, **27**, 1986-1989.
- Clarke K. and Green R. (1988) Statistical design and analysis for a "biological effects" study. *Mar. Ecol. Prog. Ser.*, **46**, 213-226.
- Clarke K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.*, **18**, 117-143.
- Clement M., Posada D. and Crandall K.A. (2000) TCS: a computer program to estimate gene genealogies. *Mol. Ecol.*, **9**, 1657-1659.
- Colautti R.I. and MacIsaac H.J. (2004) A neutral terminology to define 'invasive' species. *Div. Dist.*, **10**, 135-141.
- Colautti R.I., Manca M., Viljanen M., Ketelaars H.A., Buergi H., MacIsaac H.J. and Heath D.D. (2005) Invasion genetics of the Eurasian spiny waterflea: evidence for bottlenecks and gene flow using microsatellites. *Mol. Ecol.*, **14**, 1869-1879.
- Colin S.P., Costello J.H. and Kordula H. (2006) Upstream foraging by medusae. *Mar. Ecol. Prog. Ser.*, **327**, 143-155.
- Collins A.G., Winkelmann S., Hadrys h. and Schierwater B. (2005) Phylogeny of (Cnidaria, Hydrozoa) in light of mitochondrial 16S rRNA data. *Zool. Scr.*, **34**, 91-99.
- Collins A.G., Schuchert P., Marques A.C., Jankowski T., Medina M. and Schierwater B. (2006) Medusozoan phylogeny and character evolution clarified by new large and

References

- small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. *Syst. Biol.*, **55**, 97-115.
- Collins A.G., Bentlage B., Lindner A., Lindsay D., Haddock S.H., Jarms G., Norenburg J.L., Jankowski T. and Cartwright P. (2008) Phylogenetics of Trachylina (Cnidaria: Hydrozoa) with new insights on the evolution of some problematical taxa. *J. Mar. Biol. Assoc. UK*, **88**, 1673-1685.
- Costello J., Bayha K., Mianzan H., Shiganova T. and Purcell J. (2012) Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: a review. *Hydrobiologia*, **690**, 21-46.
- Cucherousset J., Boulêtreau S., Martino A., Roussel J.M. and Santoul F. (2012) Using stable isotope analyses to determine the ecological effects of non-native fishes. *Fish. Manag. Ecol.*, **19**, 111-119.
- Cunha A.F., Collins A.G. and Marques A.C. (2017) Phylogenetic relationships of Proboscoida Broch, 1910 (Cnidaria, Hydrozoa): Are traditional morphological diagnostic characters relevant for the delimitation of lineages at the species, genus, and family levels? *Mol. Phylogen. Evol.*, **106**, 118-135.
- Cunningham C.W. and Buss L.W. (1993) Molecular evidence for multiple episodes of paedomorphosis in the family Hydractiniidae. *Biochem. Syst. Ecol.*, **21**, 57-69.
- Curole J.P. and Kocher T.D. (2002) Ancient sex-specific extension of the cytochrome c oxidase II gene in bivalves and the fidelity of doubly-uniparental inheritance. *Mol. Biol. Evol.*, **19**, 1323-1328.
- Daan R. (1986) Food intake and growth of *Sarsia tubulosa* (Sars, 1835), with quantitative estimates of predation on copepod populations. *J. Sea. Res.*, **20**, 67-74.
- Davis C.C. (1955) Notes on the food of *Craspedacusta sowerbii* in Crystal Lake, Ravenna, Ohio. *Ecology*, **36**, 364-366.
- Dawson M.N., Cieciel K., Decker M.B., Hays G.C., Lucas C.H. and Pitt K.A. (2015) Population-level perspectives on global change: genetic and demographic analyses indicate various scales, timing, and causes of scyphozoan jellyfish blooms. *Biol. Invasions*, **17**, 851-867.
- Deacon J.E. and Haskell W.L. (1967) Observations on the ecology of the freshwater jellyfish in Lake Mead, Nevada. *Am. Midl. Nat.*, **78**, 155-166.
- Dejdar E. (1934) Die Süßwassermeduse *Craspedacusta sowerbii* Lankester in monographischer Darstellung. *Z. Morphol. Okol. Tiere*, **28**, 595-691.
- DeMott W.R., Gulati R.D. and Van Donk E. (2001) *Daphnia* food limitation in three hypereutrophic Dutch lakes: Evidence for exclusion of large-bodied species by interfering filaments of cyanobacteria. *Limnol. Oceanogr.*, **46**, 2054-2060.
- DeVries D.R. (1992) The freshwater jellyfish *Craspedacusta sowerbyi*: a summary of its life history, ecology, and distribution. *J. Freshw. Ecol.*, **7**, 7-16.
- Dexter R.W., Surrarrer T.C. and Davis C.W. (1949) Some recent records of the fresh-water jellyfish *Craspedacusta sowerbii* from Ohio and Pennsylvania. *Ohio J. Sci.*, **49**, 235-241.
- Dick J.T., Gallagher K., Avlijas S., Clarke H.C., Lewis S.E., Leung S., Minchin D., Caffrey J., Alexander M.E. and Maguire C. (2013) Ecological impacts of an invasive predator explained and predicted by comparative functional responses. *Biol. Invasions*, **15**, 837-846.
- Dillon P.J. and Rigler F. (1974) The phosphorus-chlorophyll relationship in lakes 1, 2. *Limnol. Oceanogr.*, **19**, 767-773.

References

- Dodd J.A., Dick J.T., Alexander M.E., Macneil C., Dunn A.M. and Aldridge D.C. (2014) Predicting the ecological impacts of a new freshwater invader: functional responses and prey selectivity of the 'killer shrimp', *Dikerogammarus villosus*, compared to the native *Gammarus pulex*. *Freshw. Biol.*, **59**, 337-352.
- Dodds R.B. and Hall K.D. (1984) Environmental and Physiological Studies of the Freshwater Jellyfish *Craspedacusta sowerbyi*. *Bios*, 75-83.
- Dodson S.I. and Cooper S.D. (1983) Trophic relationships of the freshwater jellyfish *Craspedacusta sowerbyi* Lankester 1880. *Limnol. Oceanogr.*, **28**, 345-351.
- Duarte C.M., Pitt K.A., Lucas C.H., Purcell J.E., Uye S.-I., Robinson K., Brotz L., Decker M.B., Sutherland K.R. and Malej A. (2013) Is global ocean sprawl a cause of jellyfish blooms? *Front. Ecol. Environ.*, **11**, 91-97.
- Duggan I.C. and Eastwood K.R. (2012) Detection and distribution of *Craspedacusta sowerbii*: Observations of medusae are not enough. *Aquat. Invasions*, **7**, 271-275.
- Dumont H.J. (1994) The distribution and ecology of the fresh- and brackish-water medusae of the world. *Hydrobiologia*, **272**, 1-12.
- Dunham D.W. (1941) Studies on the ecology and physiology of the freshwater jellyfish, *Craspedacusta sowerbii*. The Ohio State University.
- Dusoge K. (1983) Biotic structure and processes in the lake system of R. Jorka watershed (Masurian Lakeland, Poland) VIII. Biomass and distribution of benthos in profundal and littoral zones. *Ekol. Pol.*, **32**, 747-760.
- Finlay J.C. and Kendall C. (2007) Stable isotope tracing of temporal and spatial variability in organic matter sources to freshwater ecosystems. In: *Stable isotopes in ecology and environmental science*, John Wiley and Sons, **2**, 283-333.
- Fish G.R. (1971) *Craspedacusta sowerbyi* Lankester (Coelenterata: Limnomedusae) in New Zealand lakes. *N. Z. J. Mar. Freshwat. Res.*, **5**, 66-69.
- Folino-Rorem N.C., Darling J.A. and D'Ausilio C.A. (2009) Genetic analysis reveals multiple cryptic invasive species of the hydrozoan genus *Cordylophora*. *Biol. Invasions*, **11**, 1869-1882.
- Folino-Rorem N.C. (2015) Phylum Cnidaria. In: *Thorp and Covich's Freshwater Invertebrates.*, pp. 159-179. Elsevier.
- Folino-Rorem N.C., Reid M. and Peard T. (2015) Culturing the freshwater hydromedusa, *Craspedacusta sowerbii* under controlled laboratory conditions. *Invertebr. Reprod. Dev.*, **60**, 17-27.
- Folmer O., Black M., Hoeh W., Lutz R. and Vrijenhoek R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.*, **3**, 294-299.
- France R.L. (1995) Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnol. Oceanogr.*, **40**, 1310-1313.
- France S.C. and Hoover L.L. (2002) DNA sequences of the mitochondrial COI gene have low levels of divergence among deep-sea octocorals (Cnidaria: Anthozoa). *Hydrobiologia*, **471**, 149-155.
- Fritz G.B., Pfannkuchen M., Reuner A., Schill R.O. and Brummer F. (2009) *Craspedacusta sowerbii*, Lankester 1880 - population dispersal analysis using COI and ITS sequences. *J. Limnol.*, **68**, 46-52.
- Fu L.-J., Staples R. and Stahl Jr R. (1991) Application of the *Hydra attenuata* assay for identifying developmental hazards among natural waters and wastewaters. *Ecotoxicol. Environ. Saf.*, **22**, 309-319.

References

- Fuentes R., Cárdenas L., Abarzua A. and Caputo L. (2019) Southward invasion of *Craspedacusta sowerbii* across mesotrophic lakes in Chile: geographical distribution and genetic diversity of the medusa phase. *Freshw. Sci.*, **38**, 193-202.
- Funk J.L. and Vitousek P.M. (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature*, **446**, 1079.
- Galarce L.C., Riquelme K.V., Osman D.Y. and Fuentes R.A. (2013) A new record of the non-indigenous freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 (Cnidaria) in Northern Patagonia (40 S, Chile). *Bioinvasions Rec.*, **2**, 263-270.
- Gamfeldt L., Hillebrand H. and Jonsson P. (2005) Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecol. Lett.*, **8**, 696-703.
- Gasith A., Gafny S., Hershkovitz Y., Goldstein H. and Galil B.S. (2011) The invasive freshwater medusa *Craspedacusta sowerbii* lankester, 1880 (Hydrozoa: Olindiidae) in Israel. *Aquat. Invasions*, **6**, 147-152.
- Gause G.F. (1934) Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science*, **79**, 16-17.
- Gaw H. and Kung L. (1939) Studies on the freshwater medusa found in Kiatingi, Szechuen. *Sci. Rep. Nat. Wuhan Univ. Biol*, **1**, 1-12.
- Geller W. and Müller H. (1981) The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. *Oecologia*, **49**, 316-321.
- Germain H. (1934) Sur la présence d'une méduse, *Craspedacusta sowerbyi* Lankester, dans la Mayenne. *Bull. Soc. Zool. Fr*, **59**, 85-87.
- GESAMP (IMO/FAO/UNESCO-IOC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Pollution) (1997) Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. *GESAMP reports and studies no. 58.*, International Maritime Organization, London.
- Ghabooli S., Shiganova T.A., Zhan A., Cristescu M.E., Eghtesadi-Araghi P. and MacIsaac H.J. (2011) Multiple introductions and invasion pathways for the invasive ctenophore *Mnemiopsis leidyi* in Eurasia. *Biol. Invasions*, **13**, 679-690.
- Gili J.M., Hughes R.G. and Alvà V. (1996). A quantitative study of feeding by the hydroid *Tubularia larynx* Ellis and Solander, 1786. *Sci. Mar.*, **60**, 43-54.
- Gliwicz Z. (1977) Food size selection and seasonal succession of filter feeding zooplankton in an eutrophic lake. *Ecologia Polska*, **25**, 179-225.
- Gliwicz Z.M. (1980) Filtering rates, food size selection, and feeding rates in cladocerans-another aspect of interspecific competition in filter-feeding zooplankton. In: *Evolution and ecology of zooplankton communities*. University of New England Press, Hanover, N.H., pp. 282-291.
- Gliwicz Z. and Siedlar E. (1980) Food size limitation and algae interfering with food collection in *Daphnia*. *Arch. Hydrobiol.*, **88**, 155-177.
- Gomes-Pereira J.N. and Dionísio G. (2013) *Craspedacusta sowerbii* Lankester, 1880 in southern Portugal. *Bioinvasions Rec.*, **2**, 133-136.
- Gophen M. and Geller W. (1984) Filter mesh size and food particle uptake by *Daphnia*. *Oecologia*, **64**, 408-412.
- Gosselin A. and Hare L. (2003) Burrowing behavior of *Chaoborus flavicans* larvae and its ecological significance. *J. N. Am. Benthol. Soc.*, **22**, 575-581.

References

- Graham W.M., Pagès F. and Hamner W.M. (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia*, **451**, 199-212.
- Graham W.M., Gelcich S., Robinson K.L., Duarte C.M., Brotz L., Purcell J.E., Madin L.P., Mianzan H., Sutherland K.R. and Uye S.-I. (2014) Linking human well-being and jellyfish: ecosystem services, impacts, and societal responses. *Front. Ecol. Environ.*, **12**, 515-523.
- Grange L.J., Smith C.R., Lindsay D.J., Bentlage B. and Youngbluth M.J. (2017) High abundance of the epibenthic Trachymedusa *Ptychogastria polaris* Allman, 1878 (Hydrozoa, Trachylina) in subpolar fjords along the West Antarctic Peninsula. *PLoS one*, **12**, e0168648.
- Green J. (1998) Plankton associated with medusae of the freshwater jellyfish *Craspedacusta sowerbyi* (Lankester) in a Thames backwater. In: *Freshwat. Forum*, pp. 69-76.
- Grey J. (2006) The use of stable isotope analyses in freshwater ecology: current awareness. *Polish J. Ecol.*, **54**, 563-584.
- Guisande C., Riveiro I. and Maneiro I. (2000) Comparisons among the amino acid composition of females, eggs and food to determine the relative importance of food quantity and food quality to copepod reproduction. *Mar. Ecol. Prog. Ser.*, **202**, 135-142.
- Håkanson L., Blenckner T., Bryhn A.C. and Hellström S.-S. (2005) The influence of calcium on the chlorophyll–phosphorus relationship and lake Secchi depths. *Hydrobiologia*, **537**, 111-123.
- Hall T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp. Ser.*, **41**, 95-98.
- Hansen T. and Sommer U. (2007) Increasing the sensitivity of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ abundance measurements by a high sensitivity elemental analyzer connected to an isotope ratio mass spectrometer. *Rapid Comm. Mass Spectr.*, **21**, 314-318.
- Haupt F., Stockenreiter M., Reichwaldt E.S., Baumgartner M., Lampert W., Boersma M. and Stibor H. (2010) Upward phosphorus transport by *Daphnia* diel vertical migration. *Limnol. Oceanogr.*, **55**, 529-534.
- Hays G.C., Doyle T.K. and Houghton J.D. (2018) A paradigm shift in the trophic importance of jellyfish? *Trends Ecol. Evol. (Amst.)*, **33**, 874-884.
- He Z. (2003) A revision of the genus *Craspedacusta* in China (Limnomedusae, Olindiidae). *Acta Zoo. Sinica*, **28**, 20-23.
- He Z. and Xu R. (1985) A new species of freshwater medusa from Hubei (Limnomedusae: Olindiidae). *Acta Zoo. Sinica*, **10**, 341-343.
- Hebert P.D., Stoeckle M.Y., Zemlak T.S. and Francis C.M. (2004) Identification of birds through DNA barcodes. *PLoS Biol.*, **2**, 313-321.
- Hedges L.V., Gurevitch J. and Curtis P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150-1156.
- Hessen D.O., Ågren G.I., Anderson T.R., Elser J.J. and De Ruiter P.C. (2004) Carbon sequestration in ecosystems: the role of stoichiometry. *Ecology*, **85**, 1179-1192.
- Hessen D.O. and Kaartvedt S. (2014) Top–down cascades in lakes and oceans: different perspectives but same story? *J. Plankton Res.*, **36**, 914-924.
- Hillebrand H. and Shurin J.B. (2005) Biodiversity and aquatic food webs. In: *Aquatic food webs: An ecosystem approach*, pp. 184-197. New York, Oxford Univ. Press.

References

- Hirota J. (1972) Laboratory culture and metabolism of the planktonic ctenophore, *Pleurobrachia bachei* A. Agassiz. In: Takenouti, A. Y. (ed.) *Biological oceanography of the northern North Pacific Ocean*. Idemitsu Shoten, Tokyo, pp. 465-484.
- Hoeh W.R., Stewart D.T., Sutherland B.W. and Zouros E. (1996) Multiple origins of gender-associated mitochondrial DNA lineages in bivalves (Mollusca: Bivalvia). *Evolution*, **50**, 2276-2286.
- Hoeh W., Stewart D. and Guttman S. (2002) High fidelity of mitochondrial genome transmission under the doubly uniparental mode of inheritance in freshwater mussels (Bivalvia: Unionoidea). *Evolution*, **56**, 2252-2261.
- Holling C.S. (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.*, **91**, 293-320.
- Holling, C.S. (1966). The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.*, **98**, 5-86.
- Hubschman J.H. and Kishler W.J. (1972) *Craspedacusta sowerbyi* Lankester 1880 and *Cordylophora lacustris* Allman 1871 in Western Lake Erie (Coelenterata). *Ohio J. Sci.*, **72**, 318-321.
- Huovinen P.S. and Goldman C.R. (2000) Inhibition of phytoplankton production by UV-B radiation in clear subalpine Lake Tahoe, California-Nevada. *Verh. - Int. Ver. Theor. Angew. Limnol.*, **27**, 157-160.
- Huovinen P., Penttilä H. and Soimasuo M. (2000) Penetration of UV radiation into Finnish lakes with different characteristics. *Int. J. Circumpolar Health*, **59**, 15-21.
- Hyman L.H. (1940) *The invertebrates: Protozoa through Ctenophora vol. 1*, The McGraw-Hill Companies.
- Imbery F., Friedrich K., Haeseler S., Koppe C., Janssen W. and Bissollo P. (2018) Vorläufiger Rückblick auf den Sommer 2018 – eine Bilanz extremer Wetterereignisse. Stand: 03.08.2018. *Deutscher Wetterdienst, Abteilung für Klimaüberwachung und Agrarmeteorologie*.
- Jackson A.L., Inger R., Parnell A.C. and Bearhop S. (2011) Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.*, **80**, 595-602.
- Jackson J.B.C. (2008) Ecological extinction and evolution in the brave new ocean. *Proc. Natl. Acad. Sci. USA*, **105**, 11458-11465.
- Jackson M., Wasserman R., Grey J., Ricciardi A., Dick J.T. and Alexander M. (2017) Novel and disrupted trophic links following invasion in freshwater ecosystems. In: *Adv. Ecol. Res.* pp. 55-97. Elsevier.
- Jankowski T. (2000) Chemical composition and biomass parameters of a population of *Craspedacusta sowerbii* Lank1880 (Cnidaria: Limnomedusa). *J. Plankton Res.*, **22**, 1329-1340.
- Jankowski T. (2001) The freshwater medusae of the world - a taxonomic and systematic literature study with some remarks on other inland water jellyfish. *Hydrobiologia*, **462**, 91-113.
- Jankowski T. and Ratte H.-T. (2001) On the influence of the freshwater jellyfish *Craspedacusta sowerbii* on the zooplankton community. *Int. Ver. Theor. Angew. Limnol.*, **27**, 3287-3290.
- Jankowski T., Collins A.G. and Campbell R. (2008) Global diversity of inland water cnidarians. *Hydrobiologia*, **595**, 35-40.

References

- Jankowski T., Strauss T. and Ratte H.T. (2005) Trophic interactions of the freshwater jellyfish *Craspedacusta sowerbii*. *J. Plankton Res.*, **27**, 811-823.
- Jankowski T. and Anokhin B. (2019) Phylum Cnidaria. In: *Thorp and Covich's Freshwater Invertebrates*, pp. 93-111. Elsevier.
- Jeffrey S.T. and Humphrey G. (1975) New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanz.*, **167**, 191-194.
- Jeschke J.M., Kopp M. and Tollrian R. (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biol. Rev.*, **79**, 337-349.
- Kaliszewicz A. (2013) Is larger better in sit-and-wait predators? Competitive superiority in *Hydra*. *Hydrobiologia*, **714**, 105-114.
- Karaouzas I., Zogaris S., Lopes-Lima M., Froufe E., Varandas S., Teixeira A. and Sousa R. (2015) First record of the freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 in Greece suggests distinct European invasion events. *Limnology*, **16**, 171-177.
- Katija K. and Dabiri J.O. (2009) A viscosity-enhanced mechanism for biogenic ocean mixing. *Nature*, **460**, 624-627.
- Katija K. (2012) Biogenic inputs to ocean mixing. *J. Exp. Biol.*, **215**, 1040-1049.
- Kleppel G. (1993) On the diets of calanoid copepods. *Mar. Ecol. Prog. Ser.*, **99**, 183-183.
- Knowler D. (2005) Reassessing the costs of biological invasion: *Mnemiopsis leidyi* in the Black Sea. *Ecol. Econ.*, **52**, 187-199.
- Koetsier P. and Bryan C.F. (1989) Winter and spring macroinvertebrate drift in an outpocketing of the lower Mississippi River, Louisiana (USA). *Hydrobiologia*, **185**, 205-209.
- Kolar C.S. and Lodge D.M. (2001) Progress in invasion biology: predicting invaders. *Trends Ecol. Evol. (Amst.)*, **16**, 199-204.
- Kotler B.P., Brown J.S. and Subach A. (1993) Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. *Oikos*, **67**, 548-556.
- Kramp P.L. (1950) Freshwater Medusae in China. *Proc. Zool. Soc. Lond.*, **120**, 165-184.
- Krebs, C. J. (1985). In: *Ecology: The experimental analysis of distribution and abundance*. Third edition. Harper and Row, New York, USA.
- Kumar S., Stecher G. and Tamura K. (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Mol. Biol. Evol.*, **33**, 1870-1874.
- Lankester E.R. (1880) On a new jelly-fish of the order Trachomedusae, living in fresh water. *Science*, **1**, 34.
- Le Bescot N., Mahé F., Audic S., Dimier C., Garet M.J., Poulain J., Wincker P., De Vargas C. and Siano R. (2015) Global patterns of pelagic dinoflagellate diversity across protist size classes unveiled by metabarcoding. *Environ. Microbiol.*, **18**, 609-626.
- Leyequién E., De Boer W.F. and Cleef A. (2007) Influence of body size on coexistence of bird species. *Ecol. Res.*, **22**, 735-741.
- Litchman E., Klausmeier C. and Yoshiyama K. (2009) Contrasting size evolution in marine and freshwater diatoms. *Proc. Natl. Acad. Sci. USA*, **106**, 2665-2670.
- Littlefield C.L., Finkemeier C. and Bode H.R. (1991) Spermatogenesis in *Hydra oligactis*: II. How temperature controls the reciprocity of sexual and asexual reproduction. *Dev. Biol.*, **146**, 292-300.

References

- Littlefield C.L. (1994) Cell-cell interactions and the control of sex determination in *Hydra*. *Semin. Dev. Biol.*, **5**, 13-20.
- Liu C., Gu Z., Xing M., Sun Y., Chen S. and Chen Z. (2018) Sex determination and differentiation in *Aurelia sp. I*: the absence of temperature dependence. *J. Oceanol. Limnol.*, **36**, 457-464.
- Lockwood J.L., Cassey P. and Blackburn T. (2005) The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol. (Amst.)*, **20**, 223-228.
- Lodge D.M. (1993) Biological invasions: lessons for ecology. *Trends Ecol. Evol. (Amst.)*, **8**, 133-137.
- Loeuillet E., Nowaczyk A., Faucher A.-C., Duhamelle A. and Labadie M. (2017) Envenimation par une méduse d'eau douce (*Craspedacusta sowerbii*) en France métropolitaine. *Toxicologie Analytique et Clinique*, **29**, 325-330.
- Loomis W.F. (1953) The cultivation of *Hydra* under controlled conditions. *Science*, **117**, 565-566.
- Lorke A., McGinnis D.F., Spaak P. and Wüest A. (2004) Acoustic observations of zooplankton in lakes using a Doppler current profiler. *Freshw. Biol.*, **49**, 1280-1292.
- LUBW Landesanstalt für Umwelt, Messungen und Naturschutz Baden-Württemberg (2012) Projekt Zooplankton. Zählen, Bestimmen, Auswerten. Bericht des Instituts für Seenforschung.
- Lucas K., Colin S.P., Costello J.H., Katija K. and Klos E. (2013) Fluid interactions that enable stealth predation by the upstream-foraging Hydromedusa *Craspedacusta sowerbyi*. *Biol. Bull.*, **225**, 60-70.
- Lundberg S., Svensson J.-E. and Petrusek A. (2005) *Craspedacusta* invasions in Sweden. *SIL Proceedings, 1922-2010*, **29**, 899-902.
- Lytle C. (1961) Patterns of budding in the freshwater hydroid *Craspedacusta*. In: *Biology of Hydra and some other Colenterates*, pp. 317-336. University of Miami Press.
- Maggioni D., Montano S., Seveso D. and Galli P. (2016) Molecular evidence for cryptic species in *Pteroclava krempfi* (Hydrozoa, Cladocorynidae) living in association with alcyonaceans. *Syst. Biodivers.*, **14**, 484-493.
- Mariash H.L., Cazzanelli M., Kainz M.J. and Rautio M. (2011) Food sources and lipid retention of zooplankton in subarctic ponds. *Freshw. Biol.*, **56**, 1850-1862.
- Martínez D., Iñiguez A., Percell K., Willner J., Signorovitch J. and Campbell R. (2010) Phylogeny and biogeography of *Hydra* (Cnidaria: Hydridae) using mitochondrial and nuclear DNA sequences. *Mol. Phylogenetics Evol.*, **57**, 403-410.
- Massaro F.C., Negreiros N.F. and Rocha O. (2013) A search for predators and food selectivity of two native species of *Hydra* (Cnidaria: Hydrozoa) from Brazil. *Biota Neotrop.*, **13**, 35-40.
- Matthews D.C. (1963) Freshwater jellyfish *Craspedacusta sowerbyi* Lankester in Hawaii. *Trans. Amer. Microsc. Soc.*, **82**, 18-22.
- McCauley E. (1984) The estimation of the abundance and biomass of zooplankton in samples. In: *A manual on methods for the assessment of secondary productivity in fresh waters*, pp. 228-265. Blackwell, Oxford, UK.
- McCauley E., Downing J.A. and Watson S. (1989) Sigmoid relationships between nutrients and chlorophyll among lakes. *Can. J. Fish. Aquat. Sci.*, **46**, 1171-1175.
- McClary A. (1959) The effect of temperature on growth and reproduction in *Craspedacusta sowerbii*. *Ecology*, **40**, 158-162.

References

- McClary A. (1960) Food ingestion in *Craspedacusta sowerbii*. *Trans. Wis. Acad. Sci. Arts Lett.*, **49**, 149-156.
- McGinnis D.F., Flury S., Tang K.W. and Grossart H.-P. (2017) Porewater methane transport within the gas vesicles of diurnally migrating *Chaoborus spp.*: An energetic advantage. *Sci. Rep.*, **7**, 44478.
- Meyerson L.A. and Mooney H.A. (2007) Invasive alien species in an era of globalization. *Front. Ecol. Environ.*, **5**, 199-208.
- Miglietta M.P., Schuchert P. and Cunningham C.W. (2009) Reconciling genealogical and morphological species in a worldwide study of the Family Hydractiniidae (Cnidaria, Hydrozoa). *Zool. Scr.*, **38**, 403-430.
- Milne L.J. (1938) Some aspects of the behavior of the fresh-water jellyfish, *Craspedacusta sp.* *Am. Nat.*, **72**, 464-472.
- Minagawa M. and Wada E. (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim. Cosmochim. Acta*, **48**, 1135-1140.
- Möller H. (1984) Reduction of a larval herring population by jellyfish predator. *Science*, **224**, 621-622.
- Montano S., Maggioni D., Arrigoni R., Seveso D., Puce S. and Galli P. (2015) The hidden diversity of *Zanclaea* associated with scleractinians revealed by molecular data. *PLoS one*, **10**, e0133084.
- Moreno-Leon M.A. and Ortega-Rubio A. (2009) First record of *Craspedacusta sowerbyi* Lankester, 1880 (Cnidaria: Limnomedusae: Olindiidae) in Mexico (Adolfo Lopez Mateos reservoir), with notes on their feeding habits and limnological dates. *Biol. Invasions*, **11**, 1827-1834.
- Moura C.J., Cunha M.R., Porteiro F.M. and Rogers A.D. (2011) The use of the DNA barcode gene 16S mRNA for the clarification of taxonomic problems within the family Sertulariidae (Cnidaria, Hydrozoa). *Zool. Scr.*, **40**, 520-537.
- Moura C.J., Cunha M.R., Porteiro F.M. and Rogers A.D. (2012) Polyphyly and cryptic diversity in the hydrozoan families Lafoeidae and Hebellidae (Cnidaria: Hydrozoa). *Invertebr. Syst.*, **25**, 454-470.
- Moura C.J., Lessios H., Cortés J., Nizinski M.S., Reed J., Santos R.S. and Collins A.G. (2018) Hundreds of genetic barcodes of the species-rich hydroid superfamily Plumularioidea (Cnidaria, Medusozoa) provide a guide toward more reliable taxonomy. *Sci. Rep.*, **8**, 17986.
- Müller-Navarra D.C., Brett M.T., Park S., Chandra S., Ballantyne A.P., Zorita E. and Goldman C.R. (2004) Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes. *Nature*, **427**, 69.
- Múrias Dos Santos A., Cabezas M.P., Tavares A.I., Xavier R. and Branco M. (2015) tcsBU: a tool to extend TCS network layout and visualization. *Bioinformatics*, **32**, 627-628.
- Nicholas K. and Frid C. (1999) Occurrence of hydromedusae in the plankton off Northumberland (western central North Sea) and the role of planktonic predators. *J. Mar. Biol. Assoc. UK*, **79**, 979-992.
- Nishimiya-Fujisawa C. and Kobayashi S. (2012) Germline stem cells and sex determination in Hydra. *Int. J. Dev. Biol.*, **56**, 499-508.
- OECD (1982) Eutrophication of Waters. Monitoring, Assessment and Control. Paris, 154 p.

References

- Oscoz J., Tomas P. and Duran C. (2010) Review and new records of non-indigenous freshwater invertebrates in the Ebro River basin (Northeast Spain). *Aquat. Invasions*, **5**, 263-284.
- Osenberg C.W., Sarnelle O. and Cooper S.D. (1997) Effect size in ecological experiments: The application of biological models in meta-analysis. *Am. Nat.*, **150**, 798-812.
- Pace M.L., Cole J.J., Carpenter S.R. and Kitchell J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol. (Amst.)*, **14**, 483-488.
- Page B., McKenzie J. and Goldsworthy S.D. (2005) Dietary resource partitioning among sympatric New Zealand and Australian fur seals. *Mar. Ecol. Prog. Ser.*, **293**, 283-302.
- Park J.H. (1998) First record of a freshwater jellyfish, *Craspedacusta sowerbii* Lankester, 1880 (Limnomedusae, Olindiidae) from reservoirs in Korea. *Korean J. Biol. Sci.*, **2**, 303-308.
- Passamonti M. and Scali V. (2001) Gender-associated mitochondrial DNA heteroplasmy in the venerid clam *Tapes philippinarum* (Mollusca Bivalvia). *Curr. Genet.*, **39**, 117-124.
- Passamonti M. (2007) An unusual case of gender-associated mitochondrial DNA heteroplasmy: the mytilid *Musculista senhousia* (Mollusca Bivalvia). *BMC Evol. Biol.*, **7**, S7.
- Payne F. (1924) A study of the fresh-water medusa, *Craspedacusta ryderi*. *J. Morphol.*, **38**, 387-429.
- Payne F. (1926) Further studies on the life history of *Craspedacusta ryderi*, a fresh-water hydromedusan. *Biol. Bull.*, **50**, 433-443.
- Pennak R.W. (1956) The freshwater jellyfish *Craspedacusta* in Colorado with some remarks on its ecology and morphological degeneration. *Trans. Amer. Microsc. Soc.*, **75**, 324-331.
- Pérez-Bote J.L., Muñoz A., Morán R., Roso R. and Romero A.J. (2006) First record of *Craspedacusta sowerbyi* Lankester, 1880 (Cnidaria: Limnomedusae: Olindiidae) in the Proserpina Reservoir (Extremadura, SW Spain) with notes on their feeding habits. *Belg. J. Zool.*, **136**, 163.
- Perrings C., Dehnen-Schmutz K., Touza J. and Williamson M. (2005) How to manage biological invasions under globalization. *Trends Ecol. Evol. (Amst.)*, **20**, 212-215.
- Peterson B.J. and Fry B. (1987) Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.*, **18**, 293-320.
- Pielou E.C. (1966) The measurement of diversity in different types of biological collections. *Journal Theor. Biol.*, **13**, 131-144.
- Pitt K.A., Kingsford M.J., Rissik D. and Koop K. (2007) Jellyfish modify the response of planktonic assemblages to nutrient pulses. *Mar. Ecol. Prog. Ser.*, **351**, 1-13.
- Pitt K.A., Clement A.-L., Connolly R.M. and Thibault-Botha D. (2008) Predation by jellyfish on large and emergent zooplankton: implications for benthic–pelagic coupling. *Estuar. Coast. Shelf Sci.*, **76**, 827-833.
- Pitt K.A., Welsh D.T. and Condon R.H. (2009) Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. *Hydrobiologia*, **616**, 133-149.
- Pitt K.A. and Lucas C.H. (2014) *Jellyfish blooms*, Springer.
- Polis G.A., Sears A.L., Huxel G.R., Strong D.R. and Maron J. (2000) When is a trophic cascade a trophic cascade? *Trends Ecol. Evol. (Amst.)*, **15**, 473-475.

References

- Pope L.G. (2007) Sexual dimorphism and symmetry variation in the freshwater jellyfish, *Craspedacusta sowerbii* (Lankester), Southern Illinois University at Carbondale.
- Post D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**, 703-718.
- Prairie Y.T., Duarte C.M. and Kalff J. (1989) Unifying nutrient–chlorophyll relationships in lakes. *Can. J. Fish. Aquat. Sci.*, **46**, 1176-1182.
- Purcell J.E. (1997) Pelagic cnidarians and ctenophores as predators: Selective predation, feeding rates, and effects on prey populations. *Ann. Inst. Oceanogr.*, **73**, 125-137.
- Purcell J.E. (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. *J. Mar. Biol. Assoc. UK*, **85**, 461-476.
- Purcell J.E. and Decker M.B. (2005) Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987-2000. *Limnol. Oceanogr.*, **50**, 376-387.
- Purcell J.E., Uye S.-I. and Lo W.-T. (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar. Ecol. Prog. Ser.*, **350**, 153-174.
- Purcell J.E. (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annu. Rev. Mar. Sci.*, **4**, 209-235.
- Puth L.M. and Post D.M. (2005) Studying invasion: have we missed the boat? *Ecol. Lett.*, **8**, 715-721.
- Quinn B., Gagné F. and Blaise C. (2012) *Hydra*, a model system for environmental studies. *Int. J. Dev. Biol.*, **56**, 613-625.
- R Development Core Team (2013) *RA Lang. Environ. Stat. Comput.*, **55**, 275-286.
- Räike A., Pietiläinen O.-P., Rekolainen S., Kauppila P., Pitkänen H., Niemi J., Raateland A. and Vuorenmaa J. (2003) Trends of phosphorus, nitrogen and chlorophyll a concentrations in Finnish rivers and lakes in 1975–2000. *Sci. Total Environ.*, **310**, 47-59.
- Raposeiro P.M., Ramos J. and Costa A.C. (2011) First record of *Craspedacusta sowerbii* Lankester, 1880 (Cnidaria: Limnomedusae) in the Azores. *Arquipelago Life and Marine Sciences*, **28**, 11-13.
- Rayner N.A. (1988) First record of *Craspedacusta sowerbyi* Lankester (Cnidaria: Limnomedusae) from Africa. *Hydrobiologia*, **162**, 73-77.
- Rayner N.A. and Appleton C.C. (1989) Occurrence of introduced *Craspedacusta sowerbii* and indigenous *Limnognathia tanzanica* (Cnidaria: Limnomedusae) in Southern Africa. *Environ. Conserv.*, **16**, 267-270.
- Rayner N.A. and Appleton C. (1992) A new record of *Craspedacusta sowerbii* (Cnidaria: Limnomedusae) from southern Africa. *Afr. Zool.*, **27**, 143-145.
- Reavell P. (1980) A study of the diets of some British freshwater gastropods. *J. Conchol.*, **30**, 253-271.
- Redfield A.C. (1934) On the proportions of organic derivatives in sea water and their relation to the composition of plankton. *James Johnstone memorial volume*, 176-192.
- Reisinger E. (1957) Zur Entwicklungsgeschichte und Entwicklungsmechanik von *Craspedacusta* (Hydrozoa, limnotrachylina). *Z. Morph. u. Ökol. Tiere*, **45**, 656-698.
- Reusch T.B., Bolte S., Sparwel M., Moss A.G. and Javidpour J. (2010) Microsatellites reveal origin and genetic diversity of Eurasian invasions by one of the world's most notorious marine invader, *Mnemiopsis leidyi* (Ctenophora). *Mol. Ecol.*, **19**, 2690-2699.

References

- Reynoldson T.B. and Association F.B. (1978) *A key to the British species of freshwater triclads (Turbellaria, Paludicola)*. FBA Scientific Publication, 23. Freshwater Biological Association, Ambleside.
- Ricciardi A. (2015) Ecology of invasive alien invertebrates. In: *Thorp and Covich's Freshwater Invertebrates*, pp. 83-91. Elsevier.
- Ricciardi A. and Cohen J. (2007) The invasiveness of an introduced species does not predict its impact. *Biol. Invasions*, **9**, 309-315.
- Rice N.E. (1958) Occurrence of both sexes of the fresh-water medusa, *Craspedacusta sowerbii* Lankester, in the same body of water. *Am. Midl. Nat.*, **59**, 525-526.
- Richardson D.M., Pysek P., Rejmánek M., Barbour M.G., Panetta F.D., West C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Div. Dist.*, **6**, 93-107.
- Richardson A.J., Bakun A., Hays G.C. and Gibbons M.J. (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol. (Amst.)*, **24**, 312-322.
- Rivera-De La Parra L., Sarma S. and Nandini S. (2016) Effects of predation by *Hydra* (Cnidaria) on cladocerans (Crustacea: Cladocera). *J. Limnol.*, **75**, 39-47.
- Saadalla H.a.A. (2006) First record of the freshwater medusa *Craspedacusta* sp. (Cnidaria, Hydrozoa) from an artificial lake in Baghdad, Iraq. *Zool. Middle East*, **37**, 107-110.
- Sakai A.K., Allendorf F.W., Holt J.S., Lodge D.M., Molofsky J., With K.A., Baughman S., Cabin R.J., Cohen J.E. and Ellstrand N.C. (2001) The population biology of invasive species. *Annu. Rev. Ecol. Syst.*, **32**, 305-332.
- Sakamoto M. (1966) Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. *Arch. Hydrobiol.*, **62**, 1-28.
- Schifani E., Viviano A., Viviano R., Naselli-Flores L. and Marrone F. (2019) Different lineages of freshwater jellyfishes (Cnidaria, Olindiidae, Craspedacusta) invading Europe: another piece of the puzzle from Sicily, Italy. *Limnology*, **20**, 143-151.
- Schlesinger A., Kramarsky-Winter E., Rosenfeld H., Armoza-Zvoloni R. and Loya Y. (2010) Sexual plasticity and self-fertilization in the sea anemone *Aiptasia diaphana*. *PLoS One*, **5**, e11874.
- Schneider C.A., Rasband W.S. and Eliceiri K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods*, **9**, 671.
- Schuchert P. (2005) Species boundaries in the hydrozoan genus *Coryne*. *Mol. Phylogen. Evol.*, **36**, 194-199.
- Schuchert P. (2010) The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata part 2. *Rev. Suisse Zool.*, **117**, 337-555.
- Sebens K.P. (1987) The ecology of indeterminate growth in animals. *Annu. Rev. Ecol. Syst.*, **18**, 371-407.
- Seehausen O. (2004) Hybridization and adaptive radiation. *Trends Ecol. Evol. (Amst.)*, **19**, 198-207.
- Serb J.M. and Lydeard C. (2003) Complete mtDNA sequence of the North American freshwater mussel, *Lampsilis ornata* (Unionidae): an examination of the evolution and phylogenetic utility of mitochondrial genome organization in Bivalvia (Mollusca). *Mol. Biol. Evol.*, **20**, 1854-1866.

References

- Shurin J.B., Borer E.T., Seabloom E.W., Anderson K., Blanchette C.A., Broitman B., Cooper S.D. and Halpern B.S. (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.*, **5**, 785-791.
- Siebert S. and Juliano C.E. (2017) Sex, polyps, and medusae: Determination and maintenance of sex in cnidarians. *Mol. Reprod. Dev.*, **84**, 105-119.
- Simoncelli S., Thackeray S.J. and Wain D.J. (2017) Can small zooplankton mix lakes? *Limnol. Oceanogr. Lett.*, **2**, 167-176.
- Siquier M., Alanis W. and Debat C.M. (2017) First record of *Craspedacusta sowerbii* Lankester, 1880 (Hydrozoa, Limnomedusae) in a natural freshwater lagoon of Uruguay, with notes on polyp stage in captivity. *Braz. J. Biol.*, **77**, 665-672.
- Skibinski D., Gallagher C. and Beynon C. (1994) Sex-limited mitochondrial DNA transmission in the marine mussel *Mytilus edulis*. *Genetics*, **138**, 801-809.
- Smith A.S. and Alexander J.E., Jr. (2008) Potential effects of the freshwater jellyfish *Craspedacusta sowerbii* on zooplankton community abundance. *J. Plankton Res.*, **30**, 1323-1327.
- Systat Software (2008) SigmaPlot for Windows, version 11.0. Systat Software Chicago, IL.
- Solomon M. (1949) The natural control of animal populations. *J. Anim. Ecol.*, **18**, 1-35.
- Sommer U., Gliwicz Z.M., Lampert W. and Duncan A. (1986) The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.*, **106**, 433-471.
- Sommer F., Stibor H., Sommer U. and Velimirov B. (2000) Grazing by mesozooplankton from Kiel Bight, Baltic Sea, on different sized algae and natural seston size fractions. *Mar. Ecol. Prog. Ser.*, **199**, 43-53.
- Sommer U., Sommer F., Santer B., Jamieson C., Boersma M., Becker C. and Hansen T. (2001) Complementary impact of copepods and cladocerans on phytoplankton. *Ecol. Lett.*, **4**, 545-550.
- Sommer U. and Stibor H. (2002) Copepoda–Cladocera–Tunicata: the role of three major mesozooplankton groups in pelagic food webs. *Ecol. Res.*, **17**, 161-174.
- Sommer U., Stibor H., Katechakis A., Sommer F. and Hansen T. (2002) Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production: primary production. In: *Sustainable increase of marine harvesting: fundamental mechanisms and new concepts*, pp. 11-20. Springer.
- Sommer U., Adrian R., De Senerpont Domis L., Elser J.J., Gaedke U., Ibelings B., Jeppesen E., Lüring M., Molinero J.C. and Mooij W.M. (2012) Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. *Annu. Rev. Ecol. Evol. Syst.*, **43**, 429-448.
- Spadinger R. and Maier G. (1999) Prey selection and diel feeding of the freshwater jellyfish, *Craspedacusta sowerbyi*. *Freshw. Biol.*, **41**, 567-573.
- Spigel R.H. and Imberger J. (1987) Mixing processes relevant to phytoplankton dynamics in lakes. *N. Z. J. Mar. Freshwat. Res.*, **21**, 361-377.
- Stadel O. (1961) Neuere Kenntnisse über Ökologie und Verbreitung der Süßwassermeduse *Craspedacusta sowerbii*. *Abh. Verh. Naturwiss. Ver. Hamburg*, **5**, 157-192.
- Stanković I. and Ternjej I. (2010) New ecological insight on two invasive species: *Craspedacusta sowerbii* (Coelenterata: Limnomedusae) and *Dreissenia polymorpha* (Bivalvia: Dreissenidae). *J. Nat. Hist.*, **44**, 2707-2713.

References

- Stefani F., Leoni B., Marieni A. and Garibaldi L. (2010) A new record of *Craspedacusta sowerbii*, Lankester 1880 (Cnidaria, Limnomedusae) in Northern Italy. *J. Limnol.*, **69**, 189-192.
- Stepien C.A., Brown J.E., Neilson M.E. and Tumeo M.A. (2005) Genetic diversity of invasive species in the Great Lakes versus their Eurasian source populations: insights for risk analysis. *Risk Anal.*, **25**, 1043-1060.
- Stepien C.A. and Tumeo M.A. (2006) Invasion genetics of Ponto-Caspian gobies in the Great Lakes: a 'cryptic' species, absence of founder effects, and comparative risk analysis. *Biol. Invasions*, **8**, 61-78.
- Stewart D.T., Saavedra C., Stanwood R.R., Ball A.O. and Zouros E. (1995) Male and female mitochondrial DNA lineages in the blue mussel (*Mytilus edulis*) species group. *Mol. Biol. Evol.*, **12**, 735-747.
- Stibor H., Vadstein O., Diehl S., Gelzleichter A., Hansen T., Hantzsche F., Katechakis A., Lippert B., Loseth K., Peters C., Roederer W., Sandow M., Sundt-Hansen L. and Olsen Y. (2004) Copepods act as a switch between alternative trophic cascades in marine pelagic food webs. *Ecol. Lett.*, **7**, 321-328.
- Stich H.-B. and Lampert W. (1981) Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature*, **293**, 396-398.
- Striebel M., Singer G., Stibor H. and Andersen T. (2012) „Trophic overyielding”: Phytoplankton diversity promotes zooplankton diversity. *Ecology*, **93**, 2719-2727.
- Sutherland B., Stewart D., Kenchington E.R. and Zouros E. (1998) The fate of paternal mitochondrial DNA in developing female mussels, *Mytilus edulis*: implications for the mechanism of doubly uniparental inheritance of mitochondrial DNA. *Genetics*, **148**, 341-347.
- Theologidis I., Fodelianakis S., Gaspar M.B. and Zouros E. (2008) Doubly uniparental inheritance (DUI) of mitochondrial DNA in *Donax trunculus* (Bivalvia: Donacidae) and the problem of its sporadic detection in Bivalvia. *Evolution*, **62**, 959-970.
- Titelman J., Riemann L., Sørnes T.A., Nilsen T., Griekspoor P. and Båmstedt U. (2006) Turnover of dead jellyfish: stimulation and retardation of microbial activity. *Mar. Ecol. Prog. Ser.*, **325**, 43-58.
- Urabe J. and Watanabe Y. (1992) Possibility of N or P limitation for planktonic cladocerans: an experimental test. *Limnol. Oceanogr.*, **37**, 244-251.
- Väinölä R. (2002) The freshwater jellyfish *Craspedacusta sowerbii* in Finland. *Memo. Soc. Fauna Flora Fenn.*, **78**, 13-15.
- Van Walraven L., Driessen F., Van Bleijswijk J., Bol A., Luttikhuisen P.C., Coolen J.W., Bos O.G., Gittenberger A., Schrieken N. and Langenberg V.T. (2016) Where are the polyps? Molecular identification, distribution and population differentiation of *Aurelia aurita* jellyfish polyps in the southern North Sea area. *Mar. Biol.*, **163**, 172.
- Vanni M.J. and Findlay D.L. (1990) Trophic cascades and phytoplankton community structure. *Ecology*, **71**, 921-937.
- Vanni M.J., Layne C.D. and Arnott S.E. (1997) “Top-down” trophic interactions in lakes: effects of fish on nutrient dynamics. *Ecology*, **78**, 1-20.
- Verity P.G. and Smetacek V. (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol. Prog. Ser.*, **130**, 277-293.
- Vinogradov M., Shushkina E., Musaeva E. and Sorokin P.Y. (1989) A newly acclimated species in the Black Sea: the ctenophore *Mnemiopsis leidyi* (Ctenophora: Lobata). *Oceanology*, **29**, 220-224.

References

- Voss S. and Mumm H. (1999) Where to stay by night and day: Size-specific and seasonal differences in horizontal and vertical distribution of *Chaoborus flavicans* larvae. *Freshw. Biol.*, **42**, 201-213.
- Walseng B., Hessen D.O., Halvorsen G. and Schartau A.K. (2006) Major contribution from littoral crustaceans to zooplankton species richness in lakes. *Limnol. Oceanogr.*, **51**, 2600-2606.
- Walsh E.J., Salazar M., Ramirez J., Moldes O. and Wallace R.L. (2006) Predation by invertebrate predators on the colonial rotifer *Sinantherina socialis*. *Invertebr. Biol.*, **125**, 325-335.
- Wang S. and Ardekani A.M. (2015) Biogenic mixing induced by intermediate Reynolds number swimming in stratified fluids. *Sci. Rep.*, **5**, 17448.
- West E.J., Pitt K.A., Welsh D.T., Koop K. and Rissik D. (2009) Top-down and bottom-up influences of jellyfish on primary productivity and planktonic assemblages. *Limnol. Oceanogr.*, **54**, 2058-2071.
- Wetzel R.G. and Likens G.E. (1991) Inorganic Nutrients: Nitrogen, Phosphorus, and Other Nutrients. In: *Limnological Analyses*, pp. 81-105. Springer New York.
- Williamson M. (1996) *Biological Invasions*, Chapman & Hall, London, UK.
- Williamson C.E., Fischer J.M., Bollens S.M., Overholt E.P. and Breckenridge J.K. (2011) Toward a more comprehensive theory of zooplankton diel vertical migration: integrating ultraviolet radiation and water transparency into the biotic paradigm. *Limnol. Oceanogr.*, **56**, 1603-1623.
- Xie P., Iwakuma T. and Fujii K. (1998) Studies on the biology of *Chaoborus flavicans* (Meigen) (Diptera: Chaoboridae) in a fish-free eutrophic pond, Japan. *Hydrobiologia*, **368**, 83-90.
- Yin M., Wang X., Ma X., Gießler S., Petrussek A., Griebel J., Hu W. and Wolinska J. (2018) Cytonuclear diversity and shared mitochondrial haplotypes among *Daphnia galeata* populations separated by seven thousand kilometres. *BMC Evol. Biol.*, **18**, 130.
- Zhang L.Q., Wang G.T., Yao W.J., Li W.X. and Gao Q. (2009) Molecular systematics of medusae in the genus *Craspedacusta* (Cnidaria: Hydrozoa: Limnomedusae) in China with the reference to the identity of species. *J. Plankton Res.*, **31**, 563-570.
- Zhang Y.-W., Xiao-Fu P., Xiao-Ai W., Jiang W.-S., Qian L. and Jun-Xing Y. (2016) Effects of osmotic pressure, temperature and stocking density on survival and sexual reproduction of *Craspedacusta sowerbii*. *Zool. Res.*, **37**, 90.
- Zheng L., He J., Lin Y., Cao W. and Zhang W. (2014) 16S rRNA is a better choice than COI for DNA barcoding hydrozoans in the coastal waters of China. *Acta Oceanol. Sin.* **33**, 55-76.
- Zou H., Zhang J., Li W.X., Wu S.G. and Wang G.T. (2012) Mitochondrial genome of the freshwater jellyfish *Craspedacusta sowerbyi* and phylogenetics of medusozoa. *PLoS One*, **7**, e51455.
- Zouros E., Ball A.O., Saavedra C. and Freeman K.R. (1994) An unusual type of mitochondrial DNA inheritance in the blue mussel *Mytilus*. *Proc. Natl. Acad. Sci. USA*, **91**, 7463-7467.
- Maps in Figure 5 were generated in QGIS Geographic Information System (v. 3.6.3, 2019), Open Source Geospatial Foundation Project, <http://qgis.osgeo.org>.

Index of Figures

- Figure 1: Worldwide distribution of *Craspedacusta sowerbii* (light gray) and of *Limnocnida tanganyicae* (dark grey; with permission from Jankowski et al. 2008)..... 12
- Figure 2: Schematic life cycle of *Craspedacusta sowerbii* (modified after Lundberg et al. 2005) with pictures of the different life stages and of gonadal tissue of adult male and female medusae. 14
- Figure 3: Simplified (a) marine (adapted with permission from Sommer et al. 2002) and (b) freshwater pelagic food web with fish and jellyfish as top-predator. Please note that the arrows indicate a bottom-up perspective for the marine food web in opposite to a top-down perspective for the freshwater food web. Organisms are not to scale. 20
- Figure 4: (a) Particle tracks and in the flow (arrows indicate the distance that particles travelled over 0.1 s) and (b) schematic flow (dotted lines) surrounding *C. sowerbii* during contraction and relaxation phases of the swimming cycle (adapted with permission from Colin et al. 2006). 23
- Figure 5: Sampling sites of *Craspedacusta* ▲ polyps, ● medusae and of ■ both life stages for genetic analyses (topic 1). (a) Overview of the sampling area (without sampling site Lake Marathon (Greece)). (b) Detailed view of Bavarian sampling sites. Lakes HW, HS, LW and WE are part of topic 2. Lakes HA, HW and WA are included in topic 3. BS, KS and HW are included in topic 4. (c) Detailed view of Ingolstadt area. Lakes with IDs in italics are included in topic 5 (jellyfish-free lakes = dark grey). (d) Sampling sites (A, B and C) of polyps at Lake Langwieder See (topic 1, data set 4)..... 28
- Figure 6: TCS-parsimony network based on concatenated COI and mitochondrial 16S rRNA gene regions from *Craspedacusta* individuals from 53 lakes in Europe. Six mtDNA haplotypes (types 1.1, 1.2, 1.2.1, 2.1, 2.1.1 and 2.2) are arranged in two separated networks (90% cut-off). Circle-size relates to the number of individuals with a specific haplotype. White color specifies polyps, grey color refers to female medusae and grey color with black dots refers to male medusae. For sample size see Table 5. 50
- Figure 7: Maximum likelihood phylogenies including all available unique COI sequences of *Craspedacusta* and *Limnocnida*. Representative sequences for the six mtDNA haplotypes of newly generated *Craspedacusta* sequences (data set 1) are indicated by type 1.1, 1.2, 1.2.1, 2.1, 2.1.1 and 2.2; other sequences were obtained from GenBank (Table 1). Percent bootstrap support is shown at nodes. Scale bars indicate Kimura 2-parameter distances. 53
- Figure 8: Maximum likelihood phylogenies including all available unique mitochondrial 16S rRNA gene sequences of *Craspedacusta* and *Limnocnida*. Representative sequences for the six mtDNA haplotypes of newly generated *Craspedacusta* sequences (data set 1) are indicated by type 1.1, 1.2, 1.2.1, 2.1, 2.1.1 and 2.2; all other sequences besides the two African *C. sowerbii* sequences were obtained from GenBank (see Table 1). Percent bootstrap support is shown at nodes. Scale bars indicate Kimura 2-parameter distances. 55
- Figure 9: TCS parsimony network based on concatenated COI and mitochondrial 16S rRNA gene regions from *Craspedacusta* medusa samples from four different lakes. Five mtDNA haplotypes (type 1.1, 1.1.1, 1.2, 2.1 and 2.2) are arranged in two separated networks (90% cut-off). Circle-size relates to the number of individuals with a certain haplotype. Shades and colors refer to medusae from different lakes. Grey color = Lake

Index of Figures

- Neuer Baarer Weiher (N = 42, samples in 2016 and 2017), crosses = lake near Jílové/Držkova (N = 40), dots = Lake Schwarzlsee (N = 40), white = Lake Waldsee (N = 40)..... 57
- Figure 10: TCS-parsimony network based on concatenated COI and mitochondrial 16S rRNA gene regions from *Craspedacusta* polyp samples from Lake Langwieder See (Germany). Three mtDNA haplotypes (type 1.1, 1.2, 2.1 and 2.2) are arranged in two separated networks (90% cut-off). Circle-size relates to the number of individuals with a specific haplotype. Colors indicate polyps from three different sites, which were sampled in 2015: Grey = site A, white = site B, black = site C. Numbers from 1 to 7 refer to polyps from seven different stones at site B, which were sampled in 2016. 59
- Figure 11: Functional response of the (a) polyp of *Craspedacusta* and of the (b) polyp of *Hydra*. The relationship between prey density (*Brachionus calyciflorus*) and ingestion rate is described by the function: (a) $y = (3.86 \pm 0.87) x / (0.65 \pm 0.28) + x$, $R^2 = 0.49$, $p < 0.0001$; (b) $y = (8.61 \pm 5.10) x / (1.62 \pm 1.38) + x$, $R^2 = 0.39$, $p < 0.0001$. Dashed lines represent 95% confidence intervals..... 60
- Figure 12: Numerical response of polyps of *Craspedacusta* observed at (a) day 6 and (b) day 9 after the end of functional response experiments. The relationship between prey density and offspring production is described by the function: (a) $y = (3.41 \pm 0.32) x / (0.87 \pm 0.27) + x$, $R^2 = 0.63$, $p < 0.0001$; and (b) $y = (3.93 \pm 0.46) x / (1.20 \pm 0.40) + x$, $R^2 = 0.63$, $p < 0.0001$. Dashed lines indicate 95% confidence intervals. 61
- Figure 13: Mean \pm standard error (SE) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of (○) polyps of *Craspedacusta* and of (●) *Hydra* from (a) Langwieder See 2, (b) Hartsee, (c) Langwieder See 3, (d) Haselfurther Weiher, (e) Langwieder See 1 and (f) Weicheringer See. Isotopic values of (▼) *Alona sp.*, (Δ) *Bosmina sp.*, (▲) *Daphnia longispina*, (☆) *Dreissena polymorpha*, (▲) *Lymnea stagnalis*, (◇) *Pleuroxus truncatus*, (◆) *Polyphemus pediculus*, (∇) *Sida crystallina*, (□) Calanoida, (■) Cyclopoida, (■) Copepoda, (◆) *Dugesia sp.* and of (●) medusae of *Craspedacusta*. 63
- Figure 14: Stable isotope bi-plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of (○) polyps of *Craspedacusta* and of (●) *Hydra* from (a) Langwieder See 2, (b) Hartsee, (c) Langwieder See 3, (d) Haselfurther Weiher, (e) Langwieder See 1 and (f) Weicheringer See. Ellipses depict the 95% confidence intervals (SIBER). No overlap of ellipses indicates significant differences of the isotopic niches between *Craspedacusta* and *Hydra* polyps. 64
- Figure 15: Regression analyses of the total crustacean mesozooplankton dry weight (black symbols), of cladocerans (grey symbols) and of copepods (white symbols) versus jellyfish density in the enclosures of (a, b) Lake Haselfurther Weiher, (c, d) Lake Waldsee and (e, f) Lake Haager Weiher at the end of the experiments. Displayed are significant linear or exponential regression curves (solid, $p < 0.05$) and insignificant trends (dashed lines)..... 67
- Figure 16: Regression analyses of dry weight ($\mu\text{g L}^{-1}$) of *Bosmina sp.* (●), *Ceriodaphnia sp.* (●), *Daphnia sp.* (○), calanoid copepods (▲) and of cyclopoid copepods (Δ) versus jellyfish density in the enclosures of (a,b) Lake Haselfurther Weiher, (c,d) Lake Waldsee, (e,f) Lake Haager Weiher at the end of the experiments. Displayed are significant linear or exponential regression curves (solid, $p < 0.05$) and insignificant trends (dashed lines)..... 68
- Figure 17: Effects (ES) of jellyfish on the dry weight of (a) *Bosmina sp.*, (b) *Ceriodaphnia sp.*, (c) *Daphnia sp.*, (d) calanoid copepods, (e) cyclopoid copepods and on (f) the whole crustacean mesozooplankton community in relation to jellyfish density in the enclosures

Index of Figures

- of Lake Haselfurther Weiher (◆), Waldsee (○) and Haager Weiher (▼) at the end of the experiments. Displayed are mean values ± 95% CI, dashed line indicates zero effect. .. 70
- Figure 18: Non-metric multidimensional scaling (nMDS) plots showing differences in assemblages of crustacean mesozooplankton at the end of the mesocosm experiments in (a) Lake Haselfurther Weiher, (b) Lake Waldsee and (c) Lake Haager Weiher. Each number represents the zooplankton assemblage in an individual mesocosm according to the jellyfish density treatments. The proximity of the symbols indicates the degree of similarity between assemblages; ellipses indicate an 80 % similarity between assemblages. 71
- Figure 19: Growth rates (ind L⁻¹ d⁻¹) of *Bosmina* sp. (●), *Ceriodaphnia* sp. (●), *Daphnia* sp. (○), calanoid copepods (▲) and cyclopoid copepods (Δ) in relation to jellyfish density in the enclosures of (a) Lake Haselfurther Weiher, (b) Lake Waldsee, (c) Lake Haager Weiher. Displayed are mean values ± standard errors, the dashed line indicates zero growth. 72
- Figure 20: Shannon diversity H' (●) and Pilon's evenness J' (◇) of the crustacean mesozooplankton community as a function of jellyfish density in the enclosures of (a) Lake Haselfurther Weiher, (b) Lake Waldsee and (c) Lake Haager Weiher at the end of the experiments. Displayed are significant linear regression curves (solid, p < 0.05) and insignificant trends (dashed lines). 73
- Figure 21: Development of chl *a* (μg L⁻¹) over the experimental duration of 13 days in the three mesocosm experiments. Displayed are average chl *a* concentrations with standard errors of each of the five jellyfish density treatments (0, 2, 4, 8, 16 jellyfish per enclosure; see legend) for (a) Lake Haselfurther Weiher, (b) Lake Waldsee and (c) Lake Haager Weiher. 74
- Figure 22: Regression analyses of the chl *a* concentrations of (●) the whole community and of the two functional groups (◇) green algae and (■) diatoms/dinoflagellates versus jellyfish density in enclosures of (a) Lake Haselfurther Weiher, (b) Lake Waldsee and (c) Lake Haager Weiher at the end of the experiments. Displayed are significant linear regression curves (solid, p < 0.05) and insignificant trends (dashed lines). 75
- Figure 23: Effects of jellyfish on (a) the total chl *a* concentration and on the chl *a* concentration of (b) green algae and (c) diatoms/dinoflagellates. Shown are the effects for the experiments of (◆) Lake Haselfurther Weiher, (○) Lake Waldsee and (▼) Lake Haager Weiher. Displayed are mean values ± 95% CI, dashed line indicates zero effect. 76
- Figure 24: Responses of seston stoichiometry ratios (C:N, C:P and N:P) to an increasing number of jellyfish after 13 days for (a, b, c) Lake Haselfurther Weiher, (d, e, f) Lake Waldsee and (g, h, i) Lake Haager Weiher. Displayed are significant linear regression curves (solid, p < 0.05) and insignificant trends (dashed lines). 77
- Figure 25: Relationship of (a, b, c) chl *a* and TP and (b, d, f) the resulting residuals as a function of jellyfish density in the enclosures of (◆) Lake Haselfurther Weiher, (○) Lake Waldsee and (▼) Lake Haager Weiher at the end of the experiments. Displayed are significant linear regression curves (solid, p < 0.05) and insignificant trends (dashed lines). 79
- Figure 26: Relationship of (a, b, c) SRP and TP in the enclosures and (b, d, f) the resulting residuals as a function of jellyfish density in the enclosures of (◆) Lake Haselfurther Weiher, (○) Lake Waldsee and (▼) Lake Haager Weiher at the end of the experiments. Displayed are significant linear regression curves (solid, p < 0.05) and insignificant trends (dashed lines). 80

Index of Figures

- Figure 27: Effects (ES) of *C. sowerbii* (●, N = 7) and *Chaoborus spp.* larvae (○, N = 4) on the vertical distribution of total phosphorus in the columns after 24 hours. Error bars indicate 95% CI, dashed vertical line indicates zero effect. 81
- Figure 28: Total phosphorus transported to the top of each column by the migration of (a) *C. sowerbii* and (b) crustacean zooplankton after 24 hours. Solid lines represent linear regressions; dashed lines indicate 95% CIs..... 82
- Figure 29: Principal-Component Analysis (PCA) of the environmental data of lakes with (▲) and without (▽) medusae. Letters next to symbols refer to Lake ID, see Table 4. The clustering of the data along the primary (PC1: 30.9 % of the variance) and secondary (PC2: 25.9 % of the variance) axes represent 56.7 % of the total variance. The maximum possible strength of all correlations is indicated by the grey circle. 83
- Figure 30: (a) Relationship of chl *a* and TP in lakes with and without jellyfish and (b) the resulting residual plot separated for lakes without (N =10) and with (N =10) jellyfish; (c) relationship of SRP and TP and (d) the resulting residual plot. Solid lines indicate significant linear relationships ($p < 0.05$). 84
- Figure 31: Seston stoichiometry ratios: (a) C:N, (b) C:P, (c) N:P in lakes with (N=10) and without (N=10) *C. sowerbii* medusae during the lake survey..... 84

Index of Tables

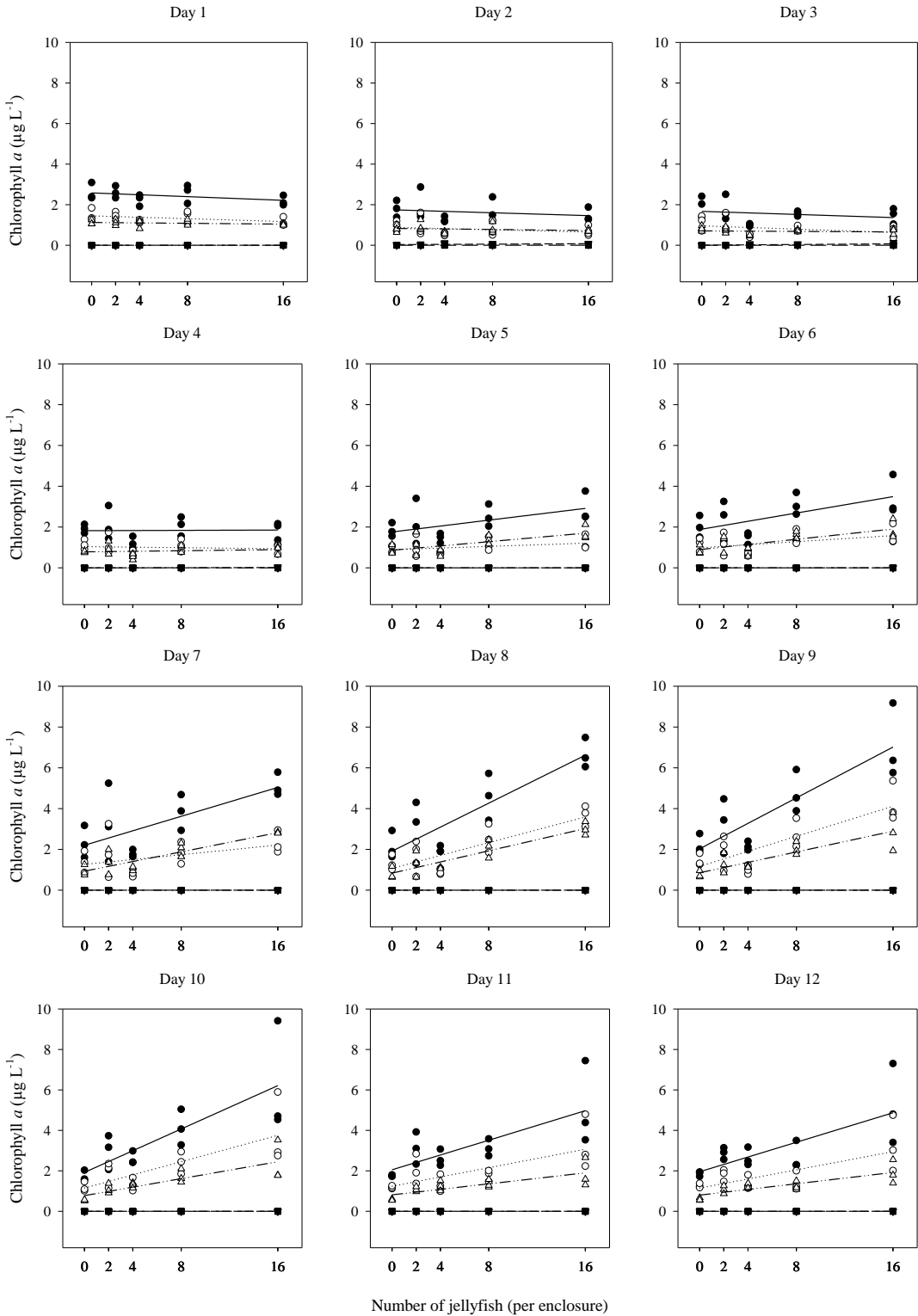
Table 1: All available COI and mitochondrial 16S rRNA gene sequences of medusae of <i>Craspedacusta</i> and <i>Limnocnida</i> published in GenBank, listed with accession numbers (na: information is missing).	32
Table 2: Samplings of <i>Craspedacusta</i> polyps, <i>Hydra</i> polyps and of other invertebrates for stable isotope analyses. Superscript numbers refer to three different sampling dates at Langwieder See. Main habitat and trophic group affiliations of invertebrates (according to Dejdar 1934, Reavell 1980, Barnett et al. 2007, Reynoldson and Association 1978, Casper 2012) are shown in parentheses.	39
Table 3: Sampling sites for investigation of trophic cascade effects mediated by <i>C. sowerbii</i> medusae in three separate outdoor mesocosm experiments.....	40
Table 4: Sampling sites (*indicate closest town to lake) for investigations of jellyfish effects in the field survey. Samples were taken of ten lakes with and of ten lakes without jellyfish observations during sampling in summer 2017.	47
Table 5: Assignment of <i>Craspedacusta</i> polyp (P) and medusa (M) haplotypes from 53 lakes to four types based on parsimony network analysis of concatenated COI and 16S sequences (*: closest town to lake, #: two sampling dates of medusae, \$: three sampling dates of medusae, f: female medusae, m: male medusae). Type 1.2 includes subtype 1.2.1 (LB3) and type 2.1 includes subtype 2.1.1 (KR743), see Figure 6.....	51
Table 6: Genetic distances among COI sequences (600 bp) of <i>C. sowerbii type 1</i> (n=5) and <i>type 2</i> (n=7) and <i>L. tanganicæ</i> (n=1) included in the ML tree in Figure 7. Kimura 2-Parameter (K2P) distances (below diagonal) and the uncorrected p-distances (shown in bold, above the diagonal) are displayed as mean value ± standard error. Distances within <i>C. sowerbii type 1</i> and within <i>C. sowerbii type 2</i> were the same for both distance estimators (shown in italics).....	53
Table 7: Genetic distances among mitochondrial 16S rRNA gene sequences (604 bp) of <i>C. sowerbii type 1</i> (n=5), <i>C. sowerbii type 2</i> (n=7), <i>C. sinensis</i> (n=1), <i>C. ziguiensis</i> (n=1) and <i>L. tanganicæ</i> (n=2) shown in the ML tree in Figure 8. Kimura 2-Parameter (K2P) distances (below diagonal) and the uncorrected p-distances (shown in bold, above the diagonal) are displayed as mean value ± standard error. Distances within <i>C. sowerbii type 1</i> and within <i>C. sowerbii type 2</i> were the same for both parameters (shown in italics).....	55
Table 8: Summary of statistical comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among polyps of <i>Craspedacusta</i> and of <i>Hydra</i> . Shown are mean values ± standard errors (SE), significant p-values are indicated by bold numbers.....	62
Table 9: Initial composition of the plankton communities and related seston stoichiometry in mesocosm experiments of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher.....	65
Table 10: Summary of the regression analyses of the dry weight ($\mu\text{g L}^{-1}$) of total crustacean mesozooplankton, of taxonomical groups and of single taxa as functions of jellyfish density in the enclosures of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher at the end of the experiments. Applied regression models are linear or exponential fits. Significant p-values are highlighted ($p < 0.05$).....	69
Table 11: Summary of regression analyses of Shannon diversity (H') and of Pielou's evenness (J') of the crustacean mesozooplankton community as a function of increasing jellyfish	

Index of Tables

density at the end of the mesocosm experiments. Applied regression models are linear fits. Significant p-values are highlighted ($p < 0.05$).....	73
Table 12: Summary of the regression analyses of chl <i>a</i> concentrations ($\mu\text{g L}^{-1}$) versus the jellyfish density treatments in enclosures of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher at the end of the experiments. Applied regression models are linear fits, significant p-values are highlighted ($p < 0.05$).	75
Table 13: Summary of the regression analyses of seston stoichiometry ratios (C:N, C:P and N:P) in relation to jellyfish density in enclosures of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher at the end of the experiments. Applied regression models are linear fits, significant p-values are highlighted ($p < 0.05$).....	78
Table 14: Summary of the regression analyses of relationships of chl <i>a</i> vs. TP to jellyfish density and of the resulting residual plots in enclosures of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher at the end of the experiments. Applied regression models are linear fits, significant p-values are highlighted ($p < 0.05$).	79
Table 15: Summary of the regression analyses of relationships of SRP vs. TP to jellyfish density and of the resulting residual plots in enclosures of Lake Haselfurther Weiher, Lake Waldsee and Lake Haager Weiher at the end of the experiments. Applied regression models are linear fits, significant p-values are highlighted ($p < 0.05$).	80

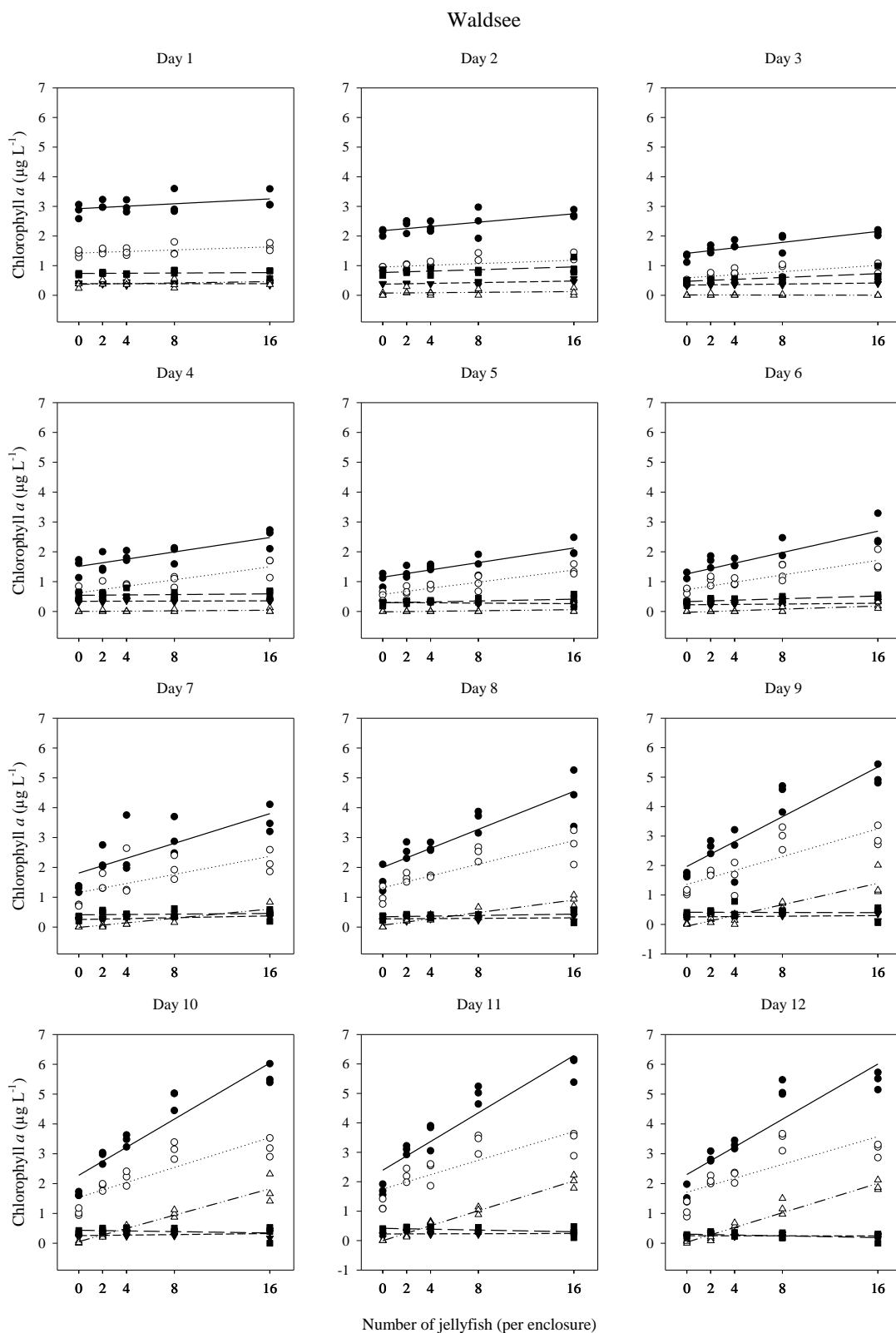
Supplementary Figures

Haselfurther Weiher



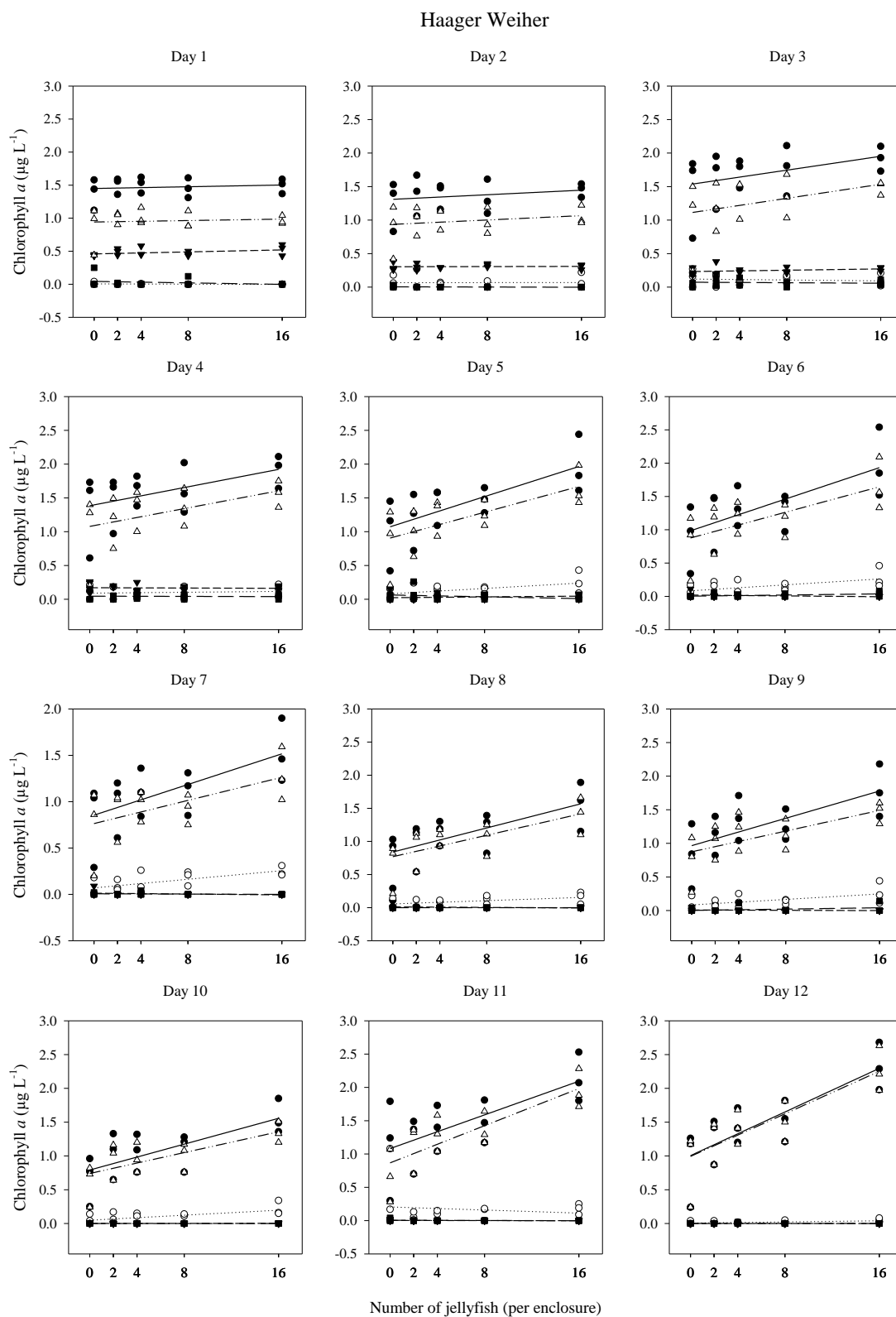
Suppl. Figure 1: Regression analyses of daily measurements of chl *a* concentrations of (●) the whole community and of the functional groups (○) green algae, (△) diatoms/dinoflagellates, (■) blue-green algae and (▼) cryptophytes versus the jellyfish density treatments in enclosures of Lake Haselfurther Weiher.

Supplementary Figures



Suppl. Figure 2: Regression analyses of daily measurements of chl *a* concentrations of (●) the whole community and of the functional groups (○) green algae, (△) diatoms/dinoflagellates, (▼) blue-green algae and (■) cryptophytes versus the jellyfish density treatments in enclosures of Lake Waldsee.

Supplementary Figures



Suppl. Figure 3: Regression analyses of daily measurements of chl *a* concentrations of (●) the whole community and of the functional groups (○) green algae, (△) diatoms/dinoflagellates, (▼) blue-green algae and (■) cryptophytes versus the jellyfish density treatments in enclosures of Lake Haager Weiher.

Supplementary Tables

Suppl. Table 1: List of altogether 481 *Craspedacusta* samples of polyps (P) and medusae (M) used in topic 1. All samples from Czech-Republic were provided by A. Petrušek, samples from “Alte Donau Wien” were provided by A. Schagerl, Swiss samples were provided by P. Schuchert. Population samples are in italics, * closest town to lake.

	Sample ID	Lake	Latitude	Longitude	Country	Sampling date	Stage	Sex	type	data set
1	ADA141	Alte Donau Wien, oxbow lake, site A	48.2292	16.4353	Austria	190815	M	f	1.1	1
2	ADA142	Alte Donau Wien, oxbow lake, site A	48.2292	16.4353	Austria	190815	M	f	1.1	1
3	ADB290	Alte Donau Wien, oxbow lake, site B	48.2493	16.4060	Austria	210815	M	f	1.1	1
4	ADB291	Alte Donau Wien, oxbow lake, site B	48.2493	16.4060	Austria	210815	M	f	1.1	1
5	ADB292	Alte Donau Wien, oxbow lake, site B	48.2493	16.4060	Austria	210815	M	f	1.1	1
6	ADB293	Alte Donau Wien, oxbow lake, site B	48.2493	16.4060	Austria	210815	M	f	1.1	1
7	ADB294	Alte Donau Wien, oxbow lake, site B	48.2493	16.4060	Austria	210815	M	f	1.1	1
8	AL1	Altenhain*	51.3013	12.6797	Germany	060715	P	-	1.2	1
9	AL2	Altenhain*	51.3013	12.6797	Germany	060715	P	-	1.2	1
10	AL3	Altenhain*	51.3013	12.6797	Germany	060715	P	-	1.2	1
11	AS1	Aldrian See	46.8198	15.5299	Austria	130815	P	-	1.2	1
12	AS2	Aldrian See	46.8198	15.5299	Austria	130815	P	-	1.2	1
13	AS3	Aldrian See	46.8198	15.5299	Austria	130815	P	-	1.2	1
14	BD1	Bodensee	47.6381	9.3899	Germany	140916	P	-	1.1	1
15	BD2	Bodensee	47.6381	9.3899	Germany	140916	P	-	1.2	1
16	BD3	Bodensee	47.6381	9.3899	Germany	140916	P	-	1.1	1
17	BK356	Borecká skalka *	49.7922	15.5800	Czech-Republic	120915	M	f	1.1	1
18	BK357	Borecká skalka *	49.7922	15.5800	Czech-Republic	120915	M	f	1.1	1
19	BK358	Borecká skalka *	49.7922	15.5800	Czech-Republic	120915	M	f	1.1	1
20	BK359	Borecká skalka *	49.7922	15.5800	Czech-Republic	120915	M	f	1.1	1
21	BK360	Borecká skalka *	49.7922	15.5800	Czech-Republic	120915	M	f	1.1	1
22	BL300	Blansko *	49.3496	16.6499	Czech-Republic	101014	M	m	1.2	1
23	BR558	Blatná - Řečice *	49.4349	13.8619	Czech-Republic	101014	M	f	1.1	1
24	BR559	Blatná - Řečice *	49.4349	13.8619	Czech-Republic	101014	M	f	1.1	1
25	BR560	Blatná - Řečice *	49.4349	13.8619	Czech-Republic	101014	M	f	1.1	1
26	BR561	Blatná - Řečice *	49.4349	13.8619	Czech-Republic	101014	M	f	1.1	1
27	BR562	Blatná - Řečice *	49.4349	13.8619	Czech-Republic	101014	M	f	1.1	1
28	BR750	Blatná - Řečice *	49.4349	13.8619	Czech-Republic	280816	M	f	1.1	1
29	BR751	Blatná - Řečice *	49.4349	13.8619	Czech-Republic	280816	M	f	1.1	1
30	BR752	Blatná - Řečice *	49.4349	13.8619	Czech-Republic	280816	M	f	1.1	1
31	BR753	Blatná - Řečice *	49.4349	13.8619	Czech-Republic	280816	M	f	1.1	1
32	BR754	Blatná - Řečice *	49.4349	13.8619	Czech-Republic	280816	M	f	1.1	1
33	BA1016	Brandsee	48.6802	11.5235	Germany	150917	M	f	1.1	1
34	BA1917	Brandsee	48.6802	11.5235	Germany	150917	M	f	1.1	1
35	BA1018	Brandsee	48.6802	11.5235	Germany	150917	M	f	1.1	1
36	BA1019	Brandsee	48.6802	11.5235	Germany	150917	M	f	1.1	1
37	BA1020	Brandsee	48.6802	11.5235	Germany	150917	M	f	1.1	1
38	BS1	Brunnensee	47.9842	12.4362	Germany	250315	P	-	1.2	1
39	BS2	Brunnensee	47.9842	12.4362	Germany	250315	P	-	1.2	1
40	BS3	Brunnensee	47.9842	12.4362	Germany	250315	P	-	1.2	1
41	BW651	Neuer Baarer Weiher	48.6770	11.4911	Germany	170816	M	m	1.2	1, 3

Supplementary Tables

Suppl: Table 1 continued

	Sample ID	Lake	Latitude	Longitude	Country	Sampling date	Stage	Sex	type	data set
42	BW652	Neuer Baarer Weiher	48.6770	11.4911	Germany	170816	M	m	1.2	1, 3
43	BW653	Neuer Baarer Weiher	48.6770	11.4911	Germany	170816	M	m	1.2	1, 3
44	BW654	Neuer Baarer Weiher	48.6770	11.4911	Germany	170816	M	m	1.2	1, 3
45	BW655	Neuer Baarer Weiher	48.6770	11.4911	Germany	170816	M	m	1.2	1, 3
46	BW144	Neuer Baarer Weiher	48.6770	11.4911	Germany	110916	M	m	2.1	3
47	BW656	Neuer Baarer Weiher	48.6770	11.4911	Germany	170816	M	m	1.2	3
48	BW657	Neuer Baarer Weiher	48.6770	11.4911	Germany	170816	M	m	1.2	3
49	BW658	Neuer Baarer Weiher	48.6770	11.4911	Germany	170816	M	m	1.2	3
50	BW674	Neuer Baarer Weiher	48.6770	11.4911	Germany	170816	M	m	1.2	3
51	BW675	Neuer Baarer Weiher	48.6770	11.4911	Germany	230816	M	m	1.2	3
52	BW676	Neuer Baarer Weiher	48.6770	11.4911	Germany	230816	M	m	1.2	3
53	BW678	Neuer Baarer Weiher	48.6770	11.4911	Germany	230816	M	m	1.2	3
54	BW872	Neuer Baarer Weiher	48.6770	11.4911	Germany	070817	M	m	1.2	3
55	BW917	Neuer Baarer Weiher	48.6770	11.4911	Germany	140817	M	m	1.2	3
56	BW1062	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	m	1.2	3
57	BW1063	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	m	1.2	3
58	BW1064	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	f	2.2	3
59	BW1065	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	m	1.2	3
60	BW1066	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	m	1.2	3
61	BW1067	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	f	2.2	3
62	BW1068	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	f	2.2	3
63	BW1069	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	m	1.2	3
64	BW1070	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	f	2.2	3
65	BW1071	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	f	2.2	3
66	BW1072	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	m	1.2	3
67	BW1073	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	m	1.2	3
68	BW1074	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	m	1.2	3
69	BW1075	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	f	2.2	3
70	BW1076	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	f	2.2	3
71	BW1077	Neuer Baarer Weiher	48.6770	11.4911	Germany	080917	M	m	1.2	3
72	BW1118	Neuer Baarer Weiher	48.6770	11.4911	Germany	150917	M	m	1.2	3
73	BW1119	Neuer Baarer Weiher	48.6770	11.4911	Germany	150917	M	m	1.2	3
74	BW1120	Neuer Baarer Weiher	48.6770	11.4911	Germany	150917	M	m	1.2	3
75	BW1125	Neuer Baarer Weiher	48.6770	11.4911	Germany	161017	M	m	2.1	3
76	BW1126	Neuer Baarer Weiher	48.6770	11.4911	Germany	161017	M	f	2.2	3
77	BW1127	Neuer Baarer Weiher	48.6770	11.4911	Germany	161017	M	m	2.1	3
78	BW1128	Neuer Baarer Weiher	48.6770	11.4911	Germany	161017	M	m	2.1	3
79	BW1129	Neuer Baarer Weiher	48.6770	11.4911	Germany	161017	M	m	2.1	3
80	BW1130	Neuer Baarer Weiher	48.6770	11.4911	Germany	161017	M	m	2.1	3
81	BW1131	Neuer Baarer Weiher	48.6770	11.4911	Germany	161017	M	m	2.1	3
82	BW1132	Neuer Baarer Weiher	48.6770	11.4911	Germany	161017	M	m	2.1	3
83	CC1	Copacabana	46.9776	15.4573	Austria	130815	P	-	2.2	1
84	CC2	Copacabana	46.9776	15.4573	Austria	130815	P	-	1.2	1
85	CC3	Copacabana	46.9776	15.4573	Austria	130815	P	-	1.2	1
86	CS1	Chiemsee	47.8712	12.4538	Germany	190715	P	-	1.2	1
87	CS2	Chiemsee	47.8712	12.4538	Germany	190715	P	-	1.2	1
88	CS3	Chiemsee	47.8712	12.4538	Germany	190715	P	-	1.2	1
89	CS677	Chiemsee	47.8712	12.4538	Germany	180816	M	f	1.1	1
90	DW1	Danglweiher	48.7587	12.9190	Germany	210715	P	-	1.1	1
91	DW2	Danglweiher	48.7587	12.9190	Germany	210715	P	-	1.1	1
92	DW3	Danglweiher	48.7587	12.9190	Germany	210715	P	-	1.1	1
93	DW151	Danglweiher	48.7587	12.9190	Germany	060815	M	f	1.1	1
94	DW152	Danglweiher	48.7587	12.9190	Germany	060815	M	f	1.1	1
95	DW153	Danglweiher	48.7587	12.9190	Germany	060815	M	f	1.1	1
96	DW154	Danglweiher	48.7587	12.9190	Germany	060815	M	f	1.1	1
97	DW155	Danglweiher	48.7587	12.9190	Germany	060815	M	f	1.1	1

Supplementary Tables

Suppl: Table 1 continued

	Sample ID	Lake	Latitude	Longitude	Country	Sampling date	Stage	Sex	type	data set
98	FA1	Fasaneriesee	48.2042	11.5291	Germany	050716	P	-	1.2	1
99	FA2	Fasaneriesee	48.2042	11.5291	Germany	050716	P	-	1.2	1
100	FK1	Feldkirchner Badensee IV	48.3260	14.0689	Austria	060815	P	-	1.1	1
101	FK2	Feldkirchner Badensee IV	48.3260	14.0689	Austria	060815	P	-	1.1	1
102	FK3	Feldkirchner Badensee IV	48.3260	14.0689	Austria	060815	P	-	1.1	1
103	FK176	Feldkirchner Badensee IV	48.3260	14.0689	Austria	181115	M	f	1.1	1
104	FK177	Feldkirchner Badensee IV	48.3260	14.0689	Austria	181115	M	f	1.1	1
105	FK178	Feldkirchner Badensee IV	48.3260	14.0689	Austria	181115	M	f	1.1	1
106	FK179	Feldkirchner Badensee IV	48.3260	14.0689	Austria	181115	M	f	1.1	1
107	FK180	Feldkirchner Badensee IV	48.3260	14.0689	Austria	181115	M	f	1.1	1
108	FS1	Feldmochinger See	48.2134	11.5143	Germany	160615	P	-	1.2	1
109	FS2	Feldmochinger See	48.2134	11.5143	Germany	160615	P	-	1.1	1
110	FS3	Feldmochinger See	48.2134	11.5143	Germany	160615	P	-	1.1	1
111	GA1	Geisenfeld* Lake A	48.7047	11.5551	Germany	291014	P	-	1.1	1
112	GA2	Geisenfeld* Lake A	48.7047	11.5551	Germany	291014	P	-	1.1	1
113	GA3	Geisenfeld* Lake A	48.7047	11.5551	Germany	291014	P	-	1.1	1
114	GB862	Geisenfeld* Lake B	48.7017	11.5566	Germany	310717	M	f	1.1	1
115	GB863	Geisenfeld* Lake B	48.7017	11.5566	Germany	310717	M	f	1.1	1
116	GB864	Geisenfeld* Lake B	48.7017	11.5566	Germany	310717	M	f	1.1	1
117	GB865	Geisenfeld* Lake B	48.7017	11.5566	Germany	310717	M	f	1.1	1
118	GB866	Geisenfeld* Lake B	48.7017	11.5566	Germany	310717	M	f	1.1	1
119	GC976	Geisenfeld* Lake C	48.7019	11.5530	Germany	220817	M	f	1.1	1
120	GC977	Geisenfeld* Lake C	48.7019	11.5530	Germany	220817	M	f	1.1	1
121	GC978	Geisenfeld* Lake C	48.7019	11.5530	Germany	220817	M	f	1.1	1
122	GC979	Geisenfeld* Lake C	48.7019	11.5530	Germany	220817	M	f	1.1	1
123	GC980	Geisenfeld* Lake C	48.7019	11.5530	Germany	220817	M	f	1.1	1
124	GS1	Griessee	47.9858	12.4423	Germany	300715	P	-	1.2	1
125	GS2	Griessee	47.9858	12.4423	Germany	300715	P	-	1.2	1
126	GS3	Griessee	47.9858	12.4423	Germany	300715	P	-	1.2	1
127	HA873	Haager Weiher	48.4503	11.8283	Germany	070817	M	f	1.1	1
128	HA874	Haager Weiher	48.4503	11.8283	Germany	070817	M	f	1.1	1
129	HA875	Haager Weiher	48.4503	11.8283	Germany	070817	M	f	1.1	1
130	HA876	Haager Weiher	48.4503	11.8283	Germany	070817	M	f	1.1	1
131	HA877	Haager Weiher	48.4503	11.8283	Germany	070817	M	f	1.1	1
132	HB1	Halfinger Badensee	47.9434	12.2775	Germany	291015	P	-	1.2	1
133	HB2	Halfinger Badensee	47.9434	12.2775	Germany	291015	P	-	1.2	1
134	HB3	Halfinger Badensee	47.9434	12.2775	Germany	291015	P	-	1.2	1
135	HS1	Hartsee	47.9268	12.3671	Germany	010616	P	-	1.2	1
136	HS2	Hartsee	47.9268	12.3671	Germany	010616	P	-	1.2	1
137	HW1	Haselfurther Weiher	48.4820	12.0130	Germany	070716	P	-	1.2	1
138	HW2	Haselfurther Weiher	48.4820	12.0130	Germany	070716	P	-	1.2	1
139	HW280	Haselfurther Weiher	48.4820	12.0130	Germany	230815	M	f	1.1	1
140	HW281	Haselfurther Weiher	48.4820	12.0130	Germany	230815	M	f	1.1	1
141	HW282	Haselfurther Weiher	48.4820	12.0130	Germany	230815	M	f	1.1	1
142	HW283	Haselfurther Weiher	48.4820	12.0130	Germany	230815	M	f	1.1	1
143	HW284	Haselfurther Weiher	48.4820	12.0130	Germany	230815	M	f	1.1	1
144	HW461	Haselfurther Weiher	48.4820	12.0130	Germany	110716	M	f	1.1	1
145	HW462	Haselfurther Weiher	48.4820	12.0130	Germany	110716	M	f	1.1	1
146	HW463	Haselfurther Weiher	48.4820	12.0130	Germany	110716	M	f	1.1	1
147	HW464	Haselfurther Weiher	48.4820	12.0130	Germany	110716	M	f	1.1	1
148	HW465	Haselfurther Weiher	48.4820	12.0130	Germany	110716	M	f	1.1	1
149	JD411	Jílové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	1, 3
150	JD412	Jílové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	1, 3
151	JD413	Jílové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	1, 3
152	JD414	Jílové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	1, 3
153	JD415	Jílové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	1, 3

Supplementary Tables

Suppl: Table 1 continued

	Sample ID	Lake	Latitude	Longitude	Country	Sampling date	Stage	Sex	type	data set
154	JD416	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
155	JD417	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
156	JD418	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
157	JD419	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
158	JD420	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
159	JD421	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
160	JD422	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
161	JD423	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
162	JD424	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
163	JD425	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
164	JD426	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
165	JD427	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
166	JD428	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
167	JD429	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
168	JD430	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
169	JD431	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
170	JD432	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
171	JD433	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
172	JD434	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
173	JD435	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
174	JD436	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
175	JD437	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
176	JD438	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
177	JD439	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
178	JD440	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
179	JD441	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
180	JD442	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
181	JD443	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
182	JD444	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
183	JD445	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
184	JD446	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
185	JD447	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
186	JD448	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
187	JD449	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
188	JD450	Jilové/Držkova*	50.6691	15.2893	Czech-Republic	041015	M	m	2.1	3
189	KE7	Kesselsee	47.9161	12.3528	Germany	030616	P	-	1.2	1
190	KF1	Karlsfelder See	48.2368	11.4682	Germany	080715	P	-	1.2	1
191	KF2	Karlsfelder See	48.2368	11.4682	Germany	080715	P	-	1.2	1
192	KF3	Karlsfelder See	48.2368	11.4682	Germany	080715	P	-	1.2	1
193	KL847	Kleiner Leitner Weiher	48.7051	11.3211	Germany	180717	M	f	1.1	1
194	KL848	Kleiner Leitner Weiher	48.7051	11.3211	Germany	180717	M	f	1.1	1
195	KL849	Kleiner Leitner Weiher	48.7051	11.3211	Germany	180717	M	f	1.1	1
196	KL850	Kleiner Leitner Weiher	48.7051	11.3211	Germany	180717	M	f	1.1	1
197	KL851	Kleiner Leitner Weiher	48.7051	11.3211	Germany	180717	M	f	1.1	1
198	KO301	Kojetice*	50.2407	14.5157	Czech-Republic	120915	M	f	1.1	1
199	KO302	Kojetice*	50.2407	14.5157	Czech-Republic	120915	M	f	1.1	1
200	KO303	Kojetice*	50.2407	14.5157	Czech-Republic	120915	M	f	1.1	1
201	KO304	Kojetice*	50.2407	14.5157	Czech-Republic	120915	M	f	1.1	1
202	KO305	Kojetice*	50.2407	14.5157	Czech-Republic	120915	M	f	1.1	1
203	KR740	Klicava reservoir	50.0706	13.9311	Czech-Republic	260916	M	m	2.1	1
204	KR741	Klicava reservoir	50.0706	13.9311	Czech-Republic	260916	M	m	2.1	1
205	KR742	Klicava reservoir	50.0706	13.9311	Czech-Republic	260916	M	m	2.1	1
206	KR743	Klicava reservoir	50.0706	13.9311	Czech-Republic	260916	M	m	2.1.1	1
207	KR744	Klicava reservoir	50.0706	13.9311	Czech-Republic	260916	M	m	2.1	1
208	KS1	Klostersee	47.9746	12.4523	Germany	030616	P	-	1.2	1
209	LB1	Langbürgner See	47.9015	12.3517	Germany	290715	P	-	1.2	1

Supplementary Tables

Suppl: Table 1 continued

	Sample ID	Lake	Latitude	Longitude	Country	Sampling date	Stage	Sex	type	data set
210	LB2	Langbürgner See	47.9015	12.3517	Germany	290715	P	-	1.2	1
211	LB3	Langbürgner See	47.9015	12.3517	Germany	290715	P	-	1.2.1	1
212	LE2	Lerchenauersee	48.1974	11.5374	Germany	040716	P	-	1.2	1
213	LE4	Lerchenauersee	48.1974	11.5374	Germany	040716	P	-	2.2	1
214	LGX01	Lake Geneva	46.4500	6.4858	Switzerland	170613	P	-	1.2	1
215	LM1	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	1.2	1
216	LM2	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	1.2	1
217	LM3	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	1.2	1
218	LM4	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	1.2	1
219	LM5	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	2.1	1
220	LM6	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	2.1	1
221	LM7	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	2.1	1
222	LM8	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	1.2	1
223	LM9	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	1.2	1
224	LM10	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	1.2	1
225	LM11	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	1.2	1
226	LM12	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	1.2	1
227	LM13	Lake Marathon	38.1655	23.8975	Greece	150617	P	-	1.2	1
228	LTP1	Lake Tanganyika	-8.6227	31.2004	Africa	310316	P	-	2.2	2
229	LTP2	Lake Tanganyika	-8.6227	31.2004	Africa	310316	P	-	1.1	2
230	LU1	Luberweiher	48.7838	13.0103	Germany	210715	P	-	1.1	1
231	LU2	Luberweiher	48.7838	13.0103	Germany	210715	P	-	1.1	1
232	LU3	Luberweiher	48.7838	13.0103	Germany	210715	P	-	1.1	1
233	LU162	Luberweiher	48.7838	13.0103	Germany	060815	M	f	1.1	1
234	LU163	Luberweiher	48.7838	13.0103	Germany	060815	M	f	1.1	1
235	LU164	Luberweiher	48.7838	13.0103	Germany	060815	M	f	1.1	1
236	LU165	Luberweiher	48.7838	13.0103	Germany	060815	M	f	1.1	1
237	LU166	Luberweiher	48.7838	13.0103	Germany	060815	M	f	1.1	1
238	LWA1	Langwieder See, site A	48.1935	11.4188	Germany	191115	P	-	1.2	1, 4
239	LWA2	Langwieder See, site A	48.1935	11.4188	Germany	191115	P	-	1.2	1, 4
240	LWA3	Langwieder See, site A	48.1935	11.4188	Germany	191115	P	-	1.2	1, 4
241	LWA4	Langwieder See, site A	48.1935	11.4188	Germany	191115	P	-	1.1	4
242	LWA5	Langwieder See, site A	48.1935	11.4188	Germany	191115	P	-	1.2	4
243	LWB1	Langwieder See, site B	48.1969	11.4166	Germany	191115	P	-	1.2	4
244	LWB2	Langwieder See, site B	48.1969	11.4166	Germany	191115	P	-	1.2	4
245	LWB3	Langwieder See, site B	48.1969	11.4166	Germany	191115	P	-	1.2	4
246	LWB4	Langwieder See, site B	48.1969	11.4166	Germany	191115	P	-	1.2	4
247	LWB5	Langwieder See, site B	48.1969	11.4166	Germany	191115	P	-	1.2	4
248	LWC1	Langwieder See, site C	48.1983	11.4129	Germany	191115	P	-	1.2	4
249	LWC2	Langwieder See, site C	48.1983	11.4129	Germany	191115	P	-	2.2	4
250	LWC3	Langwieder See, site C	48.1983	11.4129	Germany	191115	P	-	1.2	4
251	LWC4	Langwieder See, site C	48.1983	11.4129	Germany	191115	P	-	1.2	4
252	LWC5	Langwieder See, site C	48.1983	11.4129	Germany	191115	P	-	2.2	4
253	LWS1_1	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
254	LWS1_2	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
255	LWS1_3	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
256	LWS1_4	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
257	LWS1_5	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
258	LWS1_6	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
259	LWS1_7	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
260	LWS1_8	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
261	LWS1_9	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
262	LWS1_10	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
263	LWS1_11	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
264	LWS1_12	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
265	LWS1_13	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4

Supplementary Tables

Suppl: Table 1 continued

	Sample ID	Lake	Latitude	Longitude	Country	Sampling date	Stage	Sex	type	data set
266	LWS1_14	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
267	LWS1_15	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
268	LWS1_16	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
269	LWS1_17	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
270	LWS1_18	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
271	LWS1_19	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
272	LWS1_20	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
273	LWS1_21	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
274	LWS1_22	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
275	LWS1_23	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
276	LWS1_24	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
277	LWS1_25	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
278	LWS1_26	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
279	LWS1_27	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
280	LWS1_28	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
281	LWS1_29	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
282	LWS1_30	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
283	LWS2_1	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.1	4
284	LWS2_3	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.1	4
285	LWS2_4	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
286	LWS2_5	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
287	LWS2_6	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
288	LWS2_7	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
289	LWS2_8	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
290	LWS2_9	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
291	LWS2_10	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
292	LWS2_11	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
293	LWS2_12	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
294	LWS2_13	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
295	LWS2_14	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
296	LWS2_15	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
297	LWS2_16	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
298	LWS2_17	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
299	LWS2_18	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
300	LWS2_19	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
301	LWS2_20	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
302	LWS2_21	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
303	LWS2_22	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
304	LWS2_23	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
305	LWS2_25	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	2.2	4
306	LWS2_26	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
307	LWS2_27	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
308	LWS3_1	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
309	LWS3_2	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
310	LWS3_3	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
311	LWS3_4	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
312	LWS3_5	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
313	LWS3_6	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
314	LWS3_7	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
315	LWS4_1	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
316	LWS4_2	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
317	LWS4_3	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
318	LWS4_4	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
319	LWS4_5	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
320	LWS5_1	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
321	LWS5_2	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4

Supplementary Tables

Suppl: Table 1 continued

	Sample ID	Lake	Latitude	Longitude	Country	Sampling date	Stage	Sex	type	data set
322	LWS5_3	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
323	LWS5_4	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
324	LWS5_5	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.1	4
325	LWS5_6	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.1	4
326	LWS5_7	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.1	4
327	LWS5_8	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.1	4
328	LWS5_9	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.1	4
329	LWS5_10	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.1	4
330	LWS6_1	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
331	LWS6_2	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
332	LWS6_3	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
333	LWS7_1	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
334	LWS7_2	Langwieder See, site B	48.1969	11.4166	Germany	081216	P	-	1.2	4
335	OS1	Olchinger See	48.2090	11.3565	Germany	160615	P	-	1.2	1
336	OS2	Olchinger See	48.2090	11.3565	Germany	160615	P	-	1.2	1
337	OS3	Olchinger See	48.2090	11.3565	Germany	160615	P	-	1.2	1
338	PH1	Pelhamer See	47.9337	12.3502	Germany	020615	P	-	1.2	1
339	PH2	Pelhamer See	47.9337	12.3502	Germany	020615	P	-	1.2	1
340	PH3	Pelhamer See	47.9337	12.3502	Germany	020615	P	-	1.2	1
341	RA679	Reichertshofen* Lake A	48.6911	11.5237	Germany	290916	M	f	2.2	1
342	RA680	Reichertshofen* Lake A	48.6911	11.5237	Germany	290916	M	f	2.2	1
343	RA681	Reichertshofen* Lake A	48.6911	11.5237	Germany	290916	M	f	2.2	1
344	RA682	Reichertshofen* Lake A	48.6911	11.5237	Germany	290916	M	f	2.2	1
345	RA683	Reichertshofen* Lake A	48.6911	11.5237	Germany	290916	M	f	2.2	1
346	RA802	Reichertshofen* Lake A	48.6911	11.5237	Germany	120717	M	f	2.2	1
347	RA803	Reichertshofen* Lake A	48.6911	11.5237	Germany	120717	M	f	2.2	1
348	RA804	Reichertshofen* Lake A	48.6911	11.5237	Germany	120717	M	f	2.2	1
349	RA805	Reichertshofen* Lake A	48.6911	11.5237	Germany	120717	M	f	2.2	1
350	RA806	Reichertshofen* Lake A	48.6911	11.5237	Germany	120717	M	f	2.2	1
351	RB852	Reichertshofen* Lake B	48.6931	11.5244	Germany	250717	M	f	1.1	1
352	RB853	Reichertshofen* Lake B	48.6931	11.5244	Germany	250717	M	f	1.1	1
353	RB854	Reichertshofen* Lake B	48.6931	11.5244	Germany	250717	M	f	1.1	1
354	RB855	Reichertshofen* Lake B	48.6931	11.5244	Germany	250717	M	f	1.1	1
355	RB856	Reichertshofen* Lake B	48.6931	11.5244	Germany	250717	M	f	1.1	1
356	RC933	Reichertshofen* Lake C	48.6911	11.5193	Germany	230817	M	f	1.1	1
357	RC934	Reichertshofen* Lake C	48.6911	11.5193	Germany	230817	M	f	1.1	1
358	RC935	Reichertshofen* Lake C	48.6911	11.5193	Germany	230817	M	f	1.1	1
359	RC936	Reichertshofen* Lake C	48.6911	11.5193	Germany	230817	M	f	1.1	1
360	RC937	Reichertshofen* Lake C	48.6911	11.5193	Germany	230817	M	f	1.1	1
361	RD1078	Reichertshofen* Lake D	48.6887	11.5176	Germany	280817	M	f	2.2	1
362	RD1079	Reichertshofen* Lake D	48.6887	11.5176	Germany	280817	M	f	2.2	1
363	RD1080	Reichertshofen* Lake D	48.6887	11.5176	Germany	280817	M	f	2.2	1
364	RD1081	Reichertshofen* Lake D	48.6887	11.5176	Germany	280817	M	f	2.2	1
365	RD1082	Reichertshofen* Lake D	48.6887	11.5176	Germany	280817	M	f	2.2	1
366	RWX60	Ringwiler Weiher	47.3116	8.8538	Switzerland	051013	P	-	1.2	1
367	SI1	Simssee	47.8718	12.2385	Germany	291015	P	-	1.2	1
368	SI2	Simssee	47.8718	12.2385	Germany	291015	P	-	1.2	1
369	SI3	Simssee	47.8718	12.2385	Germany	291015	P	-	1.2	1
370	SL1	Schliersee	47.7267	11.8603	Germany	200715	P	-	1.2	1
371	SL2	Schliersee	47.7267	11.8603	Germany	200715	P	-	1.2	1
372	SL3	Schliersee	47.7267	11.8603	Germany	200715	P	-	1.2	1
373	SS1	Schwarzlsee	46.9830	15.4254	Austria	050617	P	-	1.2	1
374	SS2	Schwarzlsee	46.9830	15.4254	Austria	050617	P	-	1.2	1
375	SS3	Schwarzlsee	46.9830	15.4254	Austria	050617	P	-	1.2	1
376	SS216	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	1, 3
377	SS217	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	1, 3

Supplementary Tables

Suppl: Table 1 continued

	Sample ID	Lake	Latitude	Longitude	Country	Sampling date	Stage	Sex	type	data set
378	SS218	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	1, 3
379	SS219	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	1, 3
380	SS220	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	1, 3
381	SS221	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
382	SS222	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
383	SS223	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
384	SS224	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
385	SS225	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
386	SS226	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
387	SS227	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
388	SS228	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
389	SS229	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
390	SS230	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
391	SS231	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
392	SS232	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
393	SS233	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
394	SS234	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
395	SS235	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
396	SS236	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
397	SS237	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
398	SS238	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
399	SS239	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
400	SS240	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
401	SS241	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
402	SS242	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
403	SS243	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
404	SS244	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
405	SS245	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
406	SS246	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
407	SS247	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
408	SS248	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
409	SS249	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
410	SS250	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
411	SS251	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
412	SS252	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
413	SS253	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
414	SS254	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
415	SS255	Schwarzlsee	46.9830	15.4254	Austria	120815	M	f	1.1	3
416	ST1	Straß*	47.9168	12.3812	Germany	290715	P	-	1.2	1
417	ST2	Straß*	47.9168	12.3812	Germany	290715	P	-	1.2	1
418	ST3	Straß*	47.9168	12.3812	Germany	290715	P	-	1.2	1
419	TT1	Tüttensee	47.8463	12.5683	Germany	180715	P	-	1.2	1
420	TT2	Tüttensee	47.8463	12.5683	Germany	180715	P	-	1.2	1
421	TT3	Tüttensee	47.8463	12.5683	Germany	180715	P	-	1.2	1
422	WE1	Weicheringer See	48.7036	11.3296	Germany	291014	P	-	1.1	1
423	WE2	Weicheringer See	48.7036	11.3296	Germany	291014	P	-	1.2	1
424	WE3	Weicheringer See	48.7036	11.3296	Germany	291014	P	-	1.1	1
425	WG2	Waldschwaigsee	48.2251	11.4375	Germany	220616	P	-	1.2	1
426	WA1	Waldsee	48.6925	11.5133	Germany	210815	P	-	1.1	1
427	WA2	Waldsee	48.6925	11.5133	Germany	210815	P	-	1.1	1
428	WA3	Waldsee	48.6925	11.5133	Germany	210815	P	-	1.1	1
429	WA049	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	1, 3
430	WA050	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	1, 3
431	WA051	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	1, 3
432	WA052	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	1, 3
433	WA053	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	1, 3

Supplementary Tables

Suppl: Table 1 continued

	Sample ID	Lake	Latitude	Longitude	Country	Sampling date	Stage	Sex	type	data set
434	WA054	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
435	WA055	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
436	WA056	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
437	WA057	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
438	WA058	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
439	WA059	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
440	WA060	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
441	WA061	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
442	WA062	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
443	WA063	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
444	WA064	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
445	WA065	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
446	WA066	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
447	WA067	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
448	WA068	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
449	WA069	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
450	WA070	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
451	WA071	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
452	WA072	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
453	WA073	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
454	WA074	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
455	WA075	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
456	WA076	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
457	WA077	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
458	WA078	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
459	WA079	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
460	WA080	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
461	WA081	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
462	WA082	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
463	WA083	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
464	WA084	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
465	WA085	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
466	WA086	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
467	WA087	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
468	WA088	Waldsee	48.6925	11.5133	Germany	210815	M	f	1.1	3
469	WA601	Waldsee	48.6925	11.5133	Germany	080716	M	f	1.1	1
470	WA602	Waldsee	48.6925	11.5133	Germany	080716	M	f	1.1	1
471	WA603	Waldsee	48.6925	11.5133	Germany	080716	M	f	1.1	1
472	WA604	Waldsee	48.6925	11.5133	Germany	080716	M	f	1.1	1
473	WA605	Waldsee	48.6925	11.5133	Germany	080716	M	f	1.1	1
474	WA762	Waldsee	48.6925	11.5133	Germany	120717	M	f	1.1	1
475	WA763	Waldsee	48.6925	11.5133	Germany	120717	M	f	1.1	1
476	WA764	Waldsee	48.6925	11.5133	Germany	120717	M	f	1.1	1
477	WA765	Waldsee	48.6925	11.5133	Germany	120717	M	f	1.1	1
478	WA766	Waldsee	48.6925	11.5133	Germany	120717	M	f	1.1	1
479	WS1056	Waldsee Schechen	47.9460	12.1530	Germany	300817	M	m	1.2	1
480	WS1057	Waldsee Schechen	47.9460	12.1530	Germany	300817	M	m	1.2	1
481	WS1058	Waldsee Schechen	47.9460	12.1530	Germany	300817	M	m	1.2	1

Supplementary Tables

Suppl. Table 2: Primer sequences for amplifying COI and 16S sequences of *Craspedacusta*, *Limnocyclus* and of other invertebrates.

Primers for COI	Sequence (5' to 3')	Provided by
LimF CoR	TGAGTATTTTCAACAAATCACARAGA AAGTAAGCTCTAGTATCAACRTCCAT	P. Schuchert
CF2 CR2	TCGCTGAGTATTTTCAACAAATC GATTATCATGGTAGCAGACGTG	S. Giebler
CF4 CR4	GAACTCTCTATCTAGTCTTCCGGT GTGATGGGCCCAAACAATGAA	S. Giebler
CF6 CR6	CTTAATTCGCTGAGTATTTTCAAC TTATTCCGAATGCGGGTATG	S. Giebler
CF7 CR7	CGCTGAGTATTTTCAACAAATCAC AACATGTGATGRGCCCAAAC	S. Giebler
LCO1490 HCO2198	GGTCAACAAATCATAAAGATATTGG TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. 1994
Primers for 16S	Sequence (5' to 3')	Provided by
F2 R2	TCGACTGTTTACCAAAAACATAGC ACGGAATGAACTCAAATCATGTAAG	Cunningham and Buss 1993; Collins et al. 2008

Curriculum Vitae

Curriculum Vitae

Publications and Presentations

Publications

Peer reviewed

Petrowski, S., Molis, M., **Schachtl, K.** and Buschbaum, C. (2015). "Do bioturbation and consumption affect coastal Arctic marine soft-bottom communities?" *Polar Biology*, 1-13.

Presentations

Oral Presentations

Schachtl, K., Gießler, S. and Stibor, H. (2017). "Quallen im Süßwasser, es gibt sie wirklich! Einblicke in Ökologie und Genetik." **Talk** within the lecture series "Naturschutz und Umweltforschung" at LMU, Germany.

Schachtl, K., Gießler, S. and Stibor, H. (2017). "Quallen im Süßwasser, es gibt sie wirklich! Einblicke in Ökologie und Genetik." **Talk** within the lecture series "Aquatic Ecology" at LMU, Germany.

Schachtl, K., Gießler, S. and Stibor, H. (2016). "The invasive freshwater jellyfish – what's going on with polyps?" **Talk** at the "Go jelly" meeting, Kiel, Germany.

Schachtl, K., Gießler, S. and Stibor, H. (2016). "Neozoen in heimischen Gewässern: Einblicke in die Ökologie & Populationsgenetik der Süßwasserqualle *Craspedacusta sowerbii*." **Talk** within the lecture series "Naturschutz und Umweltforschung" at LMU, Germany.

Schachtl, K., Gießler, S. and Stibor, H. (2016). "Quallen im Süßwasser - ja, es gibt sie wirklich! - Einblicke in Ökologie und Genetik." **Invited talk** at the University of Graz, Austria.

Schachtl, K., Gießler, S. and Stibor, H. (2015). "The invasive freshwater jellyfish – conspicuous medusa and occult polyps." **Invited talk** at the Limnological Institute at the University of Konstanz, Germany.

Publications and Presentations

Schachtl, K., Gießler, S. and Stibor, H. (2015). Invasive Arten im Plankton heimischer Gewässer – die ökologische Rolle neuer Nahrungsnetzgliedern. **Talk** at the forum for PhD students of the “Studienstiftung des deutschen Volkes”, Heidelberg, Germany.

Poster Presentations

Schachtl, K., Villegas Villegas, S., Gießler, S. and Stibor, H. (2017). “Food web effects of the invasive freshwater jellyfish *Craspedacusta sowerbii*.” **Poster** at the aquatic sciences meeting of the Association for the Sciences of Limnology and Oceanography (ASLO) in Honolulu, USA.

Schachtl, K., Gießler, S. and Stibor, H. (2016). “The invasive freshwater jellyfish – what’s going on with polyps?” **Poster** at the 109th Annual Meeting of the German Zoological Society at the University of Kiel, Germany.

Schachtl, K., Gießler, S. and Stibor, H. (2017). “Genetic and ecological characterization of the freshwater jellyfish *Craspedacusta sowerbii*.” **Poster** at the 17th Annual Meeting of the Gesellschaft für Biologische Systematik at the Museum for Palaeontology Munich, Germany.

Schachtl, K., Gießler, S. and Stibor, H. (2015). “The invasive freshwater jellyfish *Craspedacusta sowerbii* – occult polyps and conspicuous medusae.” **Poster** at the 108th Annual Meeting of the German Zoological Society at the University of Graz, Austria.

Schachtl, K., Gießler, S. and Stibor, H. (2015). “Genetic and ecological characterization of the invasive freshwater jellyfish *Craspedacusta sowerbii*.” **2nd poster prize** at “Fresh Blood for Fresh Water Symposium” in Mondsee, Austria.

Workshop

Hohmann, T. and **Schachtl, K.** (2016). „Was machen standortfremde Arten in unseren Gewässern?“ Workshop for school classes at the „16. Münchner Wissenschaftstage“, Germany.

Acknowledgements

After all, my thesis is finished. Of course there are many people who contributed to this success, who supported and encouraged, me and I like to take this opportunity to say thank you.

First I want to thank Prof. Dr. Herwig Stibor for the opportunity to work in his group and for being part of this interesting and interdisciplinary research project from day one. I enjoyed the freedom of research you gave me, as well as the guidance you offered and our scientific discussions, which were always inspiring. I also want to thank for giving me the chance to attend several national and international conferences. Thank you, Herwig, as well, for the pleasant activities and conversations besides work.

Special thanks I owe to Dr. Sabine Gießler for supervising me in the genetic part of my thesis. Thank you for your good advices, for your infinite patience, the unlimited motivation, for your intense proofreading, the introduction to the scientific community of DZG and for all your support in good and bad times. Together with Herwig, I could not have imagined having better advisors and mentors for my doctoral thesis than you two!

I want to thank all the members of my thesis committee for their comments and suggestions. Special thanks go to Prof. Dr. Gerhard Haszprunar (ZSM) for writing the second report of my thesis and for giving me the permission to conduct the first genetic analyses in his laboratories.

Further thanks go to the German Research Foundation (DFG) for the financial support of the project. I am also very grateful for my PhD scholarship by the Studienstiftung des deutschen Volkes that made this thesis possible at the beginning.

I am very grateful to Dr. Maria Stockenreiter for supporting me during the last years in all matters. Thank you, Mia, especially for your expert knowledge during my ecological experiments, for your enthusiasm and for the funny time.

Another very important person during the last years was Tine Hohmann. Thank you, Tine, for your unlimited help in all experiments, genetic analyses, samplings, for all your patience, the proofreading and for every moment you were there for me, even for non-scientific matters.

I am very grateful also to Margit Feißel, for all the organisational work you took off my shoulders, but also for your help in the laboratory and all the funny moments in between. Special thanks I also have to give to Angelika Wild and Achim Weigert for their strong support during my experiments in Seeon and for making the stay always a pleasure.

Acknowledgements

Further thanks go to Prof. Dr. Gompel for providing me equipment and his laboratories for conducting parts of my genetic analyses. Thanks also to Rita Jänichen for her support in the lab and the cheerful chats in between.

Now, special thanks to all my colleagues at Aquatic Ecology. Thank you for creating this nice atmosphere at work, and for bringing me samples from wherever you were. I enjoyed our funny and sometimes weird talks especially during coffee breaks and mensa times. Thanks to all my office mates, to my “Doktorschwestern” Monika Poxleitner, Felicitas Buchberger and Sara Hammerstein for making my start and the stay at LMU so pleasant, and to Patrick Lorenz and Yuanyuan Wang. Yuanyuan, have further fun with *Craspedacusta*! Outside the Aquatic Ecology I also want to thank Christina Nagler for her advice and help with the scholarship and for her inspiring attitude. A special thank further goes to Semra. Thanks also to the LMU photographer, Carolin Bleese, for making beautiful jellyfish pictures.

Many students did a great job and contributed to the present work. I would like to thank Sarah Villegas, Sheena Weller, Patrick Galvan Estacio, Lukas Schlieder, Botond Polgari, Marlis Fuschlberger, Chieh Lin, Sam Fleming, Alice Wörle and Ramona Klotz. Thank you, Ramona, for helping me with R and QGIS and have further fun with your PhD about the polyp stage!

A special thank goes to Prof. Dr. Christian Sturmbauer (University of Graz), who allowed me to join his Africa excursion and for supporting me in my projects at Lake Tanganyika. Thanks to Tini, Sandra, Max and all the other excursion participants for the unforgettable time and for their enthusiastic help at jellyfishing.

I also have to thank “Landesfischereiverband” and “Bayrischer Rundfunk” for their reports about the jellyfish project. The publicity helped a lot, as many people gave reports of new jellyfish sightings afterwards!

Special thanks go to all the people sampling stones or jellyfish for our project and for helping me with various problems, especially to Prof. Dr. Adam Petrusek, Dr. Michael Schagerl, Dr. Peter Schuchert, Dr. Terry Peard, Frederic Schedel, Klaus Thomas and the Diving Center Schwarzlsee.

Of course life outside work is equally important and I like to thank all those who shared my ups and downs over the last years and who didn't get tired from all my jellyfish stories. Especially Marita, Franzi, Vreni, Kathrin and Jérôme – thank you for cheering me up whenever necessary. Very special thanks go to my cousin Hermann Bauer for making the beautiful life cycle and food web drawings and for helping me with the layout.

Papa, Mama, Eva, Teresa, Felix, Wolfgang and Georges – thank you „für einfach ois“.



Carolin Bleese

Always look on the “jelly“ side of life

Declarations

Eidesstattliche Versicherung

Ich versichere hiermit an Eides statt, dass die vorgelegte Dissertation von mir selbständig und ohne unerlaubte Hilfe angefertigt ist.

München, den 14.11.2019

Katrin Schachtl

Ort, Datum

(Unterschrift)

Erklärung

Hiermit erkläre ich, *

- dass die Dissertation nicht ganz oder in wesentlichen Teilen einer anderen Prüfungskommission vorgelegt worden ist.
- dass ich mich anderweitig einer Doktorprüfung ohne Erfolg **nicht** unterzogen habe.
- dass ich mich mit Erfolg der Doktorprüfung im Hauptfach.....
und in den Nebenfächern.....
bei der Fakultät für.....der.....
unterzogen habe.
- dass ich ohne Erfolg versucht habe, eine Dissertation einzureichen oder mich der Doktorprüfung zu unterziehen.

München, den 14.11.2019

Katrin Schachtl

Ort, Datum

(Unterschrift)

*) Nichtzutreffendes streichen