SHORT COMMUNICATION

Aquatic food web research in mesocosms: a literature survey

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ABSTRACT

Food web research feeds ecology with elementary theoretical concepts that need controlled experimental testing. Mesocosm facilities offer multiple ways to execute experimental food web research in a rigorous way. We performed a literature survey to overview food web research implementing the mesocosm approach. Our goal was to summarise quantitatively how the mesocosm approach has formerly been used and question how to best utilise mesocosms for the emerging topics in food web research in the future. We suggest increasing the number of replicates, extending the duration of the experiments, involving higher trophic levels and addressing the combined effects of multiple stressors.

INTRODUCTION

Experimental research is more challenging in community ecology than in population ecology. The spatio-temporal scales and the complexity of multispecies systems make it almost impossible to test models and theory. This is one of the reasons why mathematical modelling advanced faster, relative to empirical research, in food web studies (Layman *et al*., 2015).

Food web research provides a series of predictions that would need experimental validation. Models based on static network analysis (Lau *et al.,* 2017), structural sensitivity analysis (Dunne *et al.,* 2002) or dynamical simulations (Pimm, 1980; Livi *et al*., 2011) provide a number of results *e.g.* on the strength of indirect effects (Zhao *et al.,* 2016), the roles organisms play in communities (Cirtwill *et al*., 2018) and the general architecture of natural food webs (Sommer *et al.,* 2018). The predictions of these studies could mainly be tested on time-series data (d'Alcalà *et al*., 2004; Gsell *et al.,* 2016) and field experiments (Paine, 1980; Carpenter and Kitchell, 1993), while experimental testing under controlled conditions is missing so far.

Experimental food web research under controlled conditions has been a dream for a long time. In the last couple of decades, technology made mesocosm (Lawton *et al.,* 1993) and microcosm (Drake, 1991) experiments possible and the solution is being outlined. Mesocosms have the volume between 1 m^3 to 1000 m^3 (Bloesch *et al.,* 1988) and provide a unique facility where testing theory, validating models and designing controlled experiments can synergistically help each other.

Following the first successful multispecies experiments in mesocosms (Thompson *et al.,* 1993; Naeem *et al.,* 1994), it seemed necessary to provide an overview on food web studies using the mesocosm approach for future directions. We present a survey based on literature mining, showing the key properties of both the experimental facilities and the experimental designs implemented. Our goal was to summarise quantitatively how the mesocosm approach has formerly been used and to question how to best utilise mesocosms in the future for the emerging topics in food web research. Our purpose was not to evaluate the experiments, the methods or the results but to have an overall view on how the experiments are constructed: what are the most commonly used approaches – concentrating exclusively on the design of the experiments – and what may be missing when studying food webs.

METHODS

We performed a literature survey based on Google Scholar (date: 17 January 2019) using the following

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Key words: Food web; mesocosm; experimental design; freshwater; aquatic ecosystems.

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keywords: "food web"/ "foodweb"/ "food-web" (plus all in plural) combined with the following expressions: "mesocosm", "container", "artificial pond", "experimental aquatic", "experimental community" (plus all in plural), excluding the word "stream". The keywords were chosen to occur in the title of the scientific articles. We did not want to narrow down our search to specific dates, hence no boundaries were selected for the publication date. All in one, we ran the search with the following: "allintitle: mesocosm OR mesocosms OR container OR containers OR "artificial pond" OR "artificial ponds" OR "experimental aquatic" OR "experimental community" "food web" OR "food webs" OR foodweb OR foodwebs OR "food-web" OR "food-webs".

We focused only on scientific articles, hence we excluded books, book reviews, reviews, doctoral theses, posters and conference abstracts. We did not filter for the journal. We considered studies only on aquatic systems and papers published in ISI-referenced journals. After inspecting all the articles, we excluded those that portrayed tidal mesocosm research or food web modelling without information about the experimental design.

First, we extracted basic information on the experimental facilities, including the number of tanks, tank volume, outdoor/indoor facility. Then, we summarised quantitatively the experimental designs focusing on the number of replicates (we define a "replicate" as an experiment under the same conditions as another, previously existing experiment – if the number of experiments is n, the number of replicates is n-1), number of trophic levels involved, manipulated factors, number of different treatments, combined factors, the duration of experiments and the type of the mimicked aquatic ecosystems. In the case of those studies, where there was no specific information on the ecosystem type besides that the experiment was executed in freshwater or in marine environment, we added another two types called "freshwater" and "marine" separate from *e.g.* "shallow lake" or "lagoon" type. If an experiment was performed in both marine and freshwater environment as well, we added a group type called "freshwater and marine". We quantified as many variables as were available in the articles. If an article concluded more than one mesocosm experiment (*e.g.* in different types of mesocosm tanks), we considered those experiments as separate ones in our dataset.

RESULTS

Our search resulted in 34 scientific articles (all listed in the *Appendix*). Overall, we described 38 mesocosm experiments quantitatively. Nine parameters of each mesocosm study were analysed as follows (see also the *Electronic Supporting Material* and more methodological considerations later).

Most of the mesocosm experiments have been run outdoor (33), while only a minority indoor (5). The number of tanks was typically 6, 9 or 12 (Fig. 1a, entire range was 1 to 64). The number of replicates was the most typically 3, 4, or zero (Fig. 2a). The distribution of tank volumes tended to be rather small, except 2 outstandingly large ones (Fig. 1b). In the case of the large tanks, the number of replicates was usually low. The number of trophic levels involved was 2 in the most cases, occasionally 3 (Fig. 2b). In one of the studies they experimented only with one trophic level but modelled the food web with two levels (with added information from literature). Since we were interested in the experimental design, we considered this as a one trophic level study. The type of manipulations was diverse. Nutrients and predators were manipulated the most frequently (Fig. 3a) due to the aims of studying the effects of either the bottom-up or the top-down controls. In most of the cases, only a single factor was manipulated while the combinations of different stressors were studied only in very few cases. The most frequently studied ecosystems

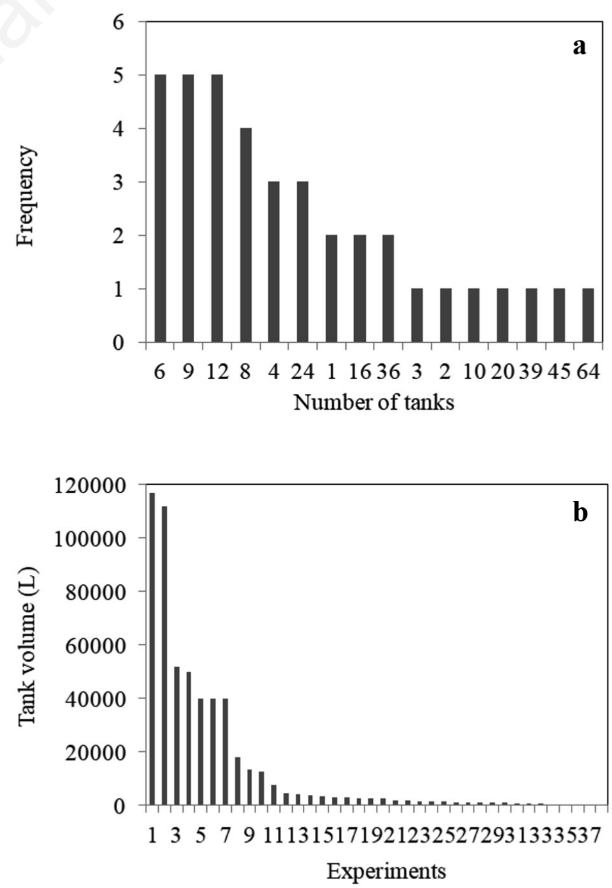

Fig. 1. The distribution of the number of tanks (a) and the volume of the tanks (b) in the surveyed mesocosm food web experiments.

in mesocosm were shallow lakes, while the least studied ecosystem types were the freshwater and marine ecosystems (both ecosystems tested in one study), the estuarine ecosystems, as well as the general freshwater ones (Fig. 3b). According to the duration of the experiments, few-week-long experiments dominated food web research in mesocosms with a minimum of 14 days and a maximum of 60 days (Fig. 3c). Only a very few articles included a year-long or more than one-year-long experiments.

The vast majority of papers were multi-authored and the number of papers published from mesocosm experiments has increased steadily by 1 to 2-3 per a year in the last few years.

DISCUSSION AND CONCLUSIONS

In this study we reviewed papers of mesocosm experiments on food web research in order to support the design of future food web experiments research in a simple but operative way. Our results highlighted some deficiencies in former approaches, which may require some considerations for future food web research.

Ecosystem types

Shallow lakes are overrepresented in our survey compared to other ecosystems types. Since mesocosm tanks are limited in terms of construction (cost) and management (total volume), most of the former studies basically mimicked shallow lake systems or considered the tanks as the homogenous pelagic environment of lakes. One may, however, consider that small volumes represent a higher surface to volume ratio where *e.g.* benthic growth makes difficult to fully reconstruct the pelagic environment. In other words, epiphyte growth on walls can alter food web dynamics, since trophic and non-trophic relationships may appear. In contrast, combined freshwater and marine ecosystems are largely understudied (as well as in most aspects of ecology), while such experiments would be of high interest (Stibor *et al.,* 2004).

Replications

Based on our results, we would suggest increasing the number of replicates, if logistics and financial constraints make it possible. While the increasing number of treatments increases the number of samples substantially (especially in full factorial design), modern approaches, such as eDNA, genomics, or bioinformatics make possible to deal with such constraints (Barnes *et al.*, 2014; Piredda *et al.*, 2016). Also, using such advanced approaches the time for data acquisition may be reduced, plus the number of replicates could be increased in time.

Of course these modern approaches do not supersede the classical methods but can provide us with different, additional information about the communities. Meaning, the modern techniques do not solve the question of increasing the replication number completely, but can be a part of the solution: we can look into different questions (*e.g.* gene sequences) in higher replication number.

This may be especially important in the case of short-term studies, where the aim would be to repeat experiments multiple times within a year (during different

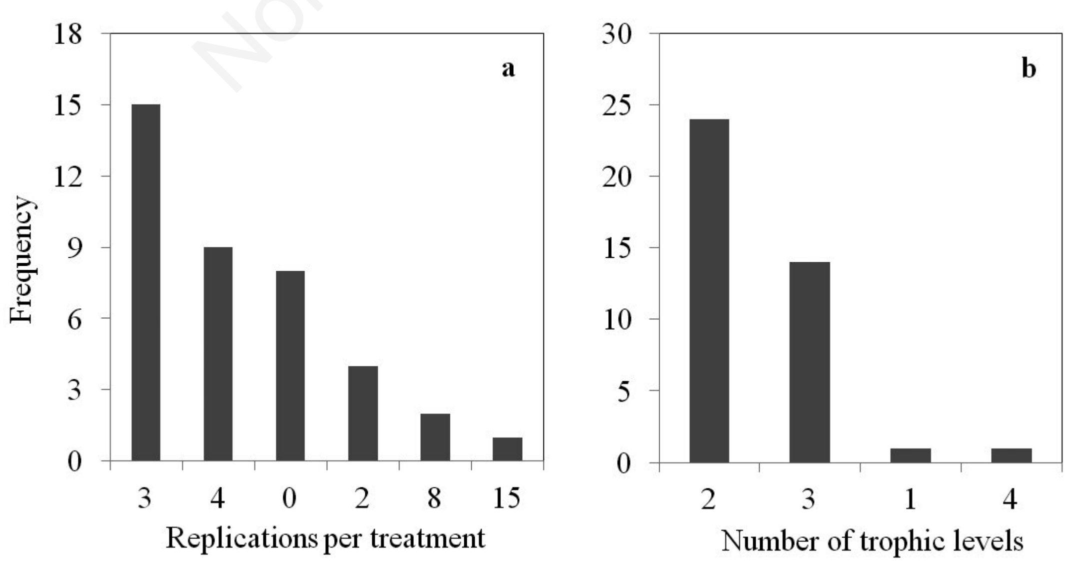

Fig. 2. The distribution of the number of replications per treatment (a) and the number of trophic levels involved (b) in the surveyed experiments.

seasons) or along the same season during the subsequent years. Additionally, the former example would exclude the effect of phenology on the tested organisms, since species may respond to the same stress distinctly during a year (*e.g.* differences in the relative species abundance rate), due to the seasonal differences (Chiba *et al.,* 2008, Aberle *et al.,* 2012, Mackas *et al.,* 2012).

Duration of studies

We further conclude that longer-term studies would also be necessary to study the lasting effects of treatments and their combinations over time on the different components of the food webs. Apart from the bottom-up and top-down experimental designs, it would be highly desirable to perform manipulations more frequently at the

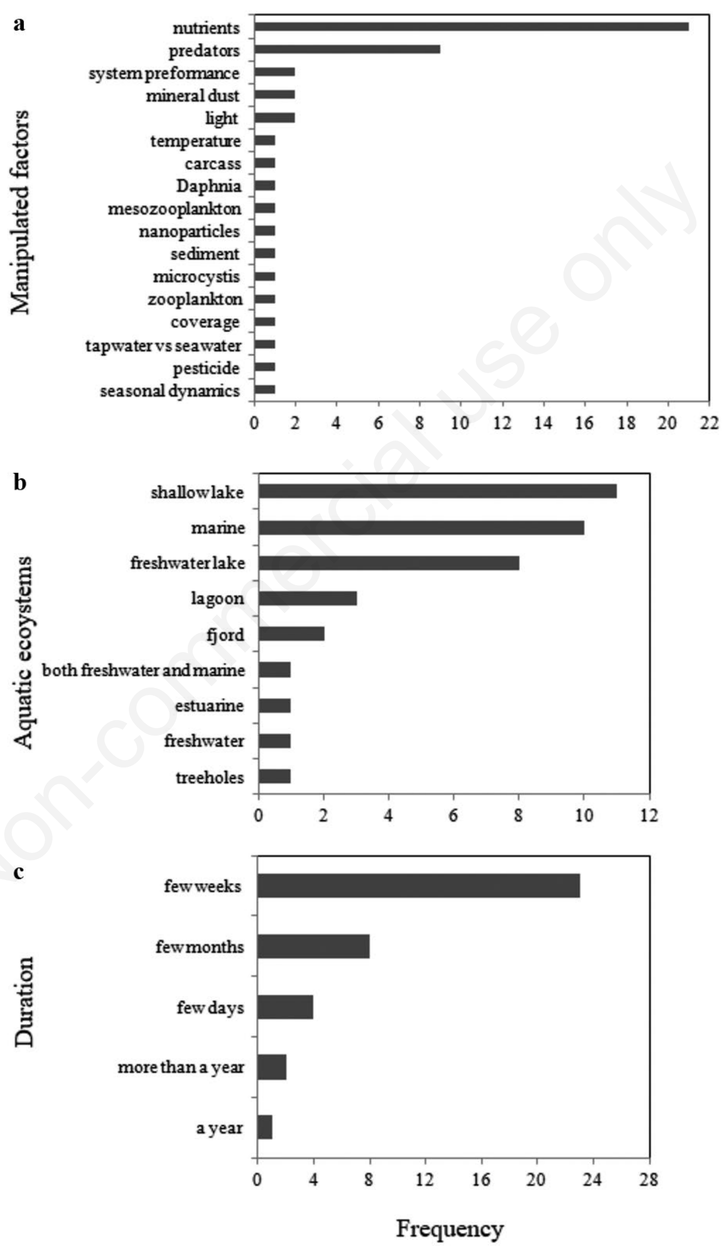

Fig. 3. The distribution of manipulated factors (a), the ecosystems modelled (b) and the duration of the experiments (c) in the surveyed mesocosm studies. In the case of the manipulated factors (a), nutrient manipulations included the manipulations of N, P, Si, S, C in different compounds and dissolved organic matter (DOM), separately or combined. In one study only Daphnia was manipulated, therefore a separate group was created from zooplankton where the whole zooplankton level was manipulated. In the case of the mimicked aquatic ecosystems (b) a separate group for freshwater involves those studies exclusively, where there was no additional information on the ecosystem besides that it was conducted in freshwater

intermediate trophic levels (Lafferty *et al.,* 2006) and study their effects on the food web functioning. Central problems in community ecology (*e.g.* the interaction between bottom-up and top-down control; the typical trophic level of the keystone species; how to infer dynamics from the structure) can all be addressed if speciose food webs can be experimentally manipulated.

Additionally, since the demography of species differs, the type of studied organisms is predetermined by the length of the experiment. Therefore, prolonging the mesocosm experiment would mean extending the possibility of including different species than in a short-term study (*e.g.* fish). Also, conducting long-term studies in open systems – where the continuous water flow is guaranteed – enable long-term natural processes (*e.g.*, interaction chain effect) to be examined (Wootton, 1993).

Treatments

It may be challenging but very useful to better study the combined effects of different factors (*e.g.*, the effect of nutrient load and the invasion of non-native species). Interactions of different drivers can create various effects (De Laender *et al.,* 2016) on the different sections/components of the food webs. These effects often appear in the intermediate trophic levels, thus can be easily overseen when narrowing down experiments only to 1-2 trophic levels. Even though in the articles overviewed here the effects of multi-stressors on ecosystems were studied rarely, nowadays it seems there is a growing interest in aiming this direction (Garzke *et al.,* 2016, Kaldy *et al.,* 2017, Wahl *et al.,* 2020).

Facilities

Ultimately, we would like to emphasize that conducting mesocosm research clearly requires excellent team work in these expensive experimental systems, explaining the great deal of multi-authored papers. During the last couple of decades 2 or 3 papers on food web studies from mesocosm experiments are published every year as a result of increasing financial resources (*e.g.*, the AQUACOSM and the AQUACOSM-Plus – EU funded infrastructures to promote international collaborations). Publications on mesocosm studies originate mainly from well-established groups within a network of institutes in aquatic ecology. The extension of such networks towards groups with outstanding expertise in food web ecology may benefit future aquatic research.

Future mesocosm experiments

Based on our findings future mesocosm experiments in the context of food web ecology may benefit from the following summarized suggestions: i) increasing the number of replicates (>3), ii) extending the duration of the experiments, iii) involving higher trophic levels and/or more taxonomic groups, and iv) studying the combined effects of multiple factors on food web functioning.

An additional aspect for future experiments is the use of longitudinal, high-resolution samplings to track various alterations along the progression of the experiment. This may be important to characterize the features of planktonic blooms, providing phenological information and revealing shifts in the food web due to different stressors (Moustaka-Gouni *et al.,* 2016).

As an example, a recently established outdoor mesocosm facility at the Balaton Limnological Institute (Tihany, Hungary) is characterized by a relatively large number (12) of fully controlled tanks with a relatively large volume (5000 L). The discussed criteria will be applied in performing experiments in the near future, especially running experiments with multiple replicates over extended time-scales (months) with at least 3 trophic levels involved. Implicitly, the number of manipulated factors combined with high replicate number will shortly exceed the capacity of the mesocosm system. Resolving this limitation we suggest either examining the factors separately (or using gradients) or running an experiment that can be repeated several times. We recommend these limitations and the offered possible solutions to be taken into consideration in order to fill the methodological gaps occurring in experimental food web research. Yet, we recognize that it is still a long way to go until experimental research will routinely be chosen and statistically highly valuable in aquatic food web studies.

Methodological constraints

Searching for relevant articles we used Google Scholar, since it is freely accessible and is considered to be the world's largest academic search engine. On the other hand, it also has a disadvantage: searching for keywords in the abstracts is only possible for the articles added in the recent years. Since we did not want to narrow down our research to specific dates (in this case the articles published in 2018 and 2019) we excluded this option and we searched for keywords within the titles. Searching for keywords in the whole text resulted in more than ten thousand of results, which would have been impossible to process within a limited time frame. We are aware that we missed articles that did not include our keywords in their title – *e.g.* leaving out papers on food web studies using the mesocosm approach that concentrate on pelagic systems, resulting in our conclusion that marine ecosystems are underrepresented. However, we chose the keywords consequently and could review published articles on aquatic food webs using the mesocosm approach, highlighting it also within the title. Therefore our review gives an instrumental overview open for further analyses on a potentially extended data set.

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