# Size Spectra as a tool to understand structures and processes of aquatic communities

### DISSERTATION

zur Erlangung des akademischen Grades Doctor rerum naturalium (Dr. rer. nat.)

eingereicht an der Lebenswissenschaftlichen Fakultät der Humboldt-Universität zu Berlin

von M.Res. Lisa-Marie Braun

Präsidentin der Humboldt-Universität zu Berlin Prof. Dr. Julia von Blumenthal

Dekan der Lebenswissenschaftlichen Fakultät der Humboldt-Universität zu Berlin Prof. Dr. Dr. Christian Ulrichs

Gutachter/innen: 1. PD. Dr. Thomas Mehner 2. Prof. Dr. Jens Krause 3. Prof. Meryem Beklioglu

Tag der mündlichen Prüfung: 14. 10. 2022



### LISA-MARIE BRAUN

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Humboldt University Berlin, Faculty of Life Sciences

Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Department of Fish Biology, Fisheries and Aquaculture

Germany, February 2023

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### Summary

Aquatic communities are highly body-size structured with an exponential decline of abundance with increasing body size, which is referred to as the size spectrum (SS). The importance of body size as a principal and simplifying framework within aquatic communities, has led to a high number of theoretical and empirical studies on energy fluxes in food webs and predatorprey interactions using Size Spectra. These size-based approaches offer a rather simple and inexpensive method to answer complex ecological questions. However, conflicting findings on the key drivers of SS highlight the need for further studies.

To address some of these conflicting conclusions, I investigated a range of questions within the fields of limnology and coral reef ecology. In this thesis size-based approaches such as SS were employed to explore (i) what drives zooplankton size distribution and whether zooplanktivorous fish (top-down) or resource availability and environmental condition (bottom-up) determine zooplankton community SS, (ii) whether traditional midwater trawling or modern hydroacoustic methods more reliably represent fish SS, and (iii) coral reef fish community SS and habitat structural complexity and their relationship across site-specific anthropogenic stressors.

By analysing long term data, I first found that neither top-down or bottom-up forces drove the zooplankton community size distribution. Zooplankton SS seem robust against predation effects but a sensitive indicator for lake-wide energy availability and transfer efficiency in the food web. Then I found that hydroacoustic methods reliably represent pelagic fish community SS, making it a great alternative to traditional and more invasive fish removal sampling methods. Finally, I discovered that coral reef fish SS slope and structural complexity of the reef exhibited a significant negative relationship on two of the examined reef sites which are least exposed to anthropogenic disturbances. A consistent pattern of fish SS and reef complexity was missing, indicating that other environmental factors may also impact the assessed parameters.

Overall, my studies show the range of applications of SS to effectively answer universal questions from trophic interactions and the importance of habitat characteristics in a community to a methodological comparison of fish sampling methods. The high variability of SS behaviour and the influence of environmental conditions further underlines the importance to include data on a large temporal scale. Community information, such as taxonomic identity and consideration of species-specific feeding and habitats preferences, for example, are still beneficial in some cases to answer ecologically questions extensively.

## Zusammenfassung

Aquatische Gemeinschaften sind stark körpergrößenstrukturiert mit einer exponentiellen Abnahme der Häufigkeit der Individuen mit zunehmender Körpergröße, die als Größenspektrum (SS) bezeichnet wird. Körpergrößenbasierte Ansätze bieten eine einfache und kostengünstige Methode zur Beantwortung komplexer ökologischer Fragestellungen in aquatischer Forschung. Widersprüchliche Ergebnisse zu den wichtigsten Faktoren, die Größenspektren beeinflussen unterstreichen jedoch die Notwendigkeit weiterer Studien.

Um einige dieser widersprüchlichen Schlussfolgerungen anzugehen, habe ich eine Reihe von Fragen in den Bereichen Limnologie und Korallenriffökologie untersucht. In dieser Dissertation wurden größenbasierte Ansätze wie SS verwendet, um zu untersuchen, (i) was die Größenverteilung von Zooplankton beeinflusst und ob Zooplankton-fressende Fische (topdown) oder Ressourcenverfügbarkeit und Umweltbedingungen (bottom-up) die SS der Zooplanktongemeinschaft bestimmen, (ii) ob traditionelle Schleppnetze oder moderne hydroakustische Methoden Fisch-SS zuverlässiger darstellen, und (iii) ob SS von Korallenriff-Fischgemeinschaften und die strukturelle Komplexität der Korallen bzw. deren Beziehung zueinander sich unter verschiedenen anthropogenen Stressoren verändert.

Zuallererst konnte ich zeigen, dass weder Top-down- noch Bottom-up-Kräfte stark die Größenverteilung der Zooplanktongemeinschaft beeinflussten. Zooplankton SS scheinen robust gegenüber Prädationseffekten zu sein, aber ein empfindlicher Indikator für die Energieverfügbarkeit und Transfereffizienz im Nahrungsnetz des untersuchten Sees. Des Weiteren konnten meine Studien bestätigen, dass hydroakustische Methoden die SS von pelagischen Fischgemeinschaften zuverlässig darstellen, was sie zu einer kostengünstigen und minimalinvasiven Alternative zu traditionellen Fischentnahmemethoden macht. Ich konnte jedoch kein allgemeingültiges Muster hinsichtlich der Größenverteilung von Korallenrifffischen und der strukturellen Komplexität der Korallen in Beziehung zu unterschiedlichen anthropogenen Stressoren finden.

Insgesamt zeigt die Dissertation das weite Anwendungsspektrum von SS, um Strukturen und Prozesse in aquatischen Gemeinschaften und Fischfangmethoden zu untersuchen. Die hohe Variabilität von Größenspektren und der Einfluss von Umweltbedingungen unterstreicht weiter die Wichtigkeit, Daten über einen langen Zeitraum einzubeziehen. Darüber hinaus unterstreichen die Ergebnisse dieser Arbeit auch die Grenzen der Anwendung von SS, da für die Beantwortung mancher ökologischer Fragestellungen artenspezifische Informationen, wie Lebensraum- und Nahrungspräferenzen benötigt werden.

# **Chapter 1**

## **General introduction**

### Aquatic Ecosystems in the Anthropocene

There is rising recognition that functionally intact and biologically complex aquatic ecosystems deliver numerous economically valuable commodities to humanity. Freshwater and marine ecosystems provide essential ecosystem services (Barbier 2017; Vári et al. 2022) that underpin global water and food security, as well as economic productivity (Hanjra and Qureshi 2010). However, intensifying exploitation of aquatic resources to meet the requirements of a rapidly growing global population place ecosystem functions at risk. Additionally, climate change is suggested to have detrimental effects on freshwater and marine ecosystems by altering thermal regimes of ecosystems (Wernberg et al. 2016; Ciszewski et al. 2022) and further enhancing eutrophication processes through warming (Jeppesen et al. 2010; Trolle et al. 2011). Numerous coastal marine systems have already been degraded by centuries of overfishing and pollution, while rising water temperatures are exerting additional stress (Hughes et al. 2003; Pandolfi et al. 2003; Hoegh-Guldberg et al. 2007; Heron et al. 2016). Similarly, freshwater systems are in alarming condition and their biodiversity is threatened by anthropogenic impacts (Dudgeon et al. 2006; Reid et al. 2019). Changes in aquatic systems become evident at different levels of biological organization, spanning from the individual to the ecosystem level with associated consequences for a range of services to society. Thus, emphasising the growing need for an improved understanding of these valuable ecosystems and the effects of potential stressors for effective conservation and management purposes.

### Importance of body size in ecology

Despite the great complexity of aquatic communities, observations have revealed that organisms' size distributions tend to exhibit a high regularity in different ecosystems, with many small and a few large sized organisms (e.g. White et al., 2007). The size of an organism strongly influences its metabolism, growth, mortality, reproduction (Peters 1983; Calder 1984;

Marquet et al. 2005; Woodward et al. 2005), movement and trophic position (Elton 1927; Kleiber 1932). Specifically, the relationship between body size, density and energy utilization of a population are of fundamental interest in ecology (White et al. 2007). In aquatic ecosystems, smaller organisms are typically more abundant than larger ones (Kerr 1974; Sprules et al. 1991; Thiebaux and Dickie 1993). This commonly observed exponential decline of the density of a population with average body size is typical when all individuals share the same resources (Damuth 1981). It was found that the amount of energy accessible to a population directly determines its abundance, which is further governed by the metabolic rate of individuals. The metabolism is determined by body size in combination with temperature and defines the rate of resource uptake and resource allocation to growth and reproduction, described in the metabolic theory of ecology (MTE, Gillooly et al., 2001, 2002; Brown et al., 2004). Size-based communities, as in aquatic systems, show a strong correlation between individual size and trophic level. Most primary productivity is limited to the smallest organisms and trophic interactions are driven by predation of larger individuals on smaller ones. Large predators occupying higher trophic levels are typically less abundant than their smaller prey occupying lower trophic levels, which is due to the energy loss during energy transfer between trophic levels (Lindeman 1942; Borgmann 1987; Brown and Gillooly 2003; Jennings and Mackinson 2003). Therefore, the total energy available to larger individuals is lower than for smaller individuals. The proportion of resource production converted into consumer production is described with the energy transfer within food webs and can be quantified by the trophic transfer efficiency (TTE). It is suggested to be approximately 10% between adjacent trophic levels (Lindeman 1942). Size-based constraints of predation resulting in size-based feeding by individuals further influence the size structure in aquatic food webs (Cohen et al. 1993). Fish are limited by the size of the prey they can engulf as a whole (Hambright 1991; Hairston and Hairston 1993; Christensen 1996; Nilsson and Brönmark 2000), which is due to the lack of jointed appendages that constrain prey handling capacities. Fish gape size typically sets the upper limit of potential prey items that can be swallowed (e.g. Nilsson and Brönmark, 2000). However, many organisms grow through several orders of magnitude in body size throughout their life cycle and therefore shift their diet composition and range of prey size with growth (Wainwright and Richard 1995; Scharf et al. 1997). This process of ontogenetic niche shift is often associated with a change in trophic position (Werner and Guillian 1984; Mittelbach and Persson 1998; Barnes et al. 2010; Gilljam et al. 2011) and also relates body size of individuals to trophic position in aquatic food webs (Jennings et al. 2001; Romanuk et al. 2011; Hussey et al. 2014). This emphasizes the importance for examining size of individuals for a better

understanding of interactions in aquatic communities. Therefore, when one aims to understand ecological interactions and ecosystem processes in aquatic systems, it is suggested that size is often a better predictor of the position of an organism within a food web than, for example taxonomic identity (Brooks and Dodson 1965; Jennings et al. 2001; Woodward et al. 2005; White et al. 2007).

### Size-based approaches for ecosystem understanding and conservation

Size-based approaches are commonly employed to understand impacts ranging from eutrophication to fishing (Trebilco et al. 2013; Sprules and Barth 2016; Blanchard et al. 2017). Size-based models permit a level of simplification of numerous, often poorly known, processes for a vast array of individuals in an aquatic community (Ward et al. 2012). Additionally, size structure is easily estimated, in comparison to other features of an entire assemblage, such as trophic transfer efficiency, predator-prey mass ratios or the mass exponent of growth scaling, while still delivering insights into their combined effects on food web efficiency (Jennings et al. 2002). Therefore, size-based ecosystem assessment and modelling tools have emerged as powerful methods to understand ecosystem function and impacts of human and environmentaldriven changes from individual - to ecosystem level processes. Understanding the processes that govern the structure of communities in ecosystems is an essential objective in ecology and the required baseline for well-informed conservation and management of valuable ecosystems and their services. The conceptual foundation for our understanding of these mechanisms was described by Elton (1927), who noted that the interactions among organisms shape the structure and function of communities; while the nature of these interactions is determined by the identity and the body size of the individuals involved. This still holds true, and body size has since been proposed as the "master trait", as it is the driving force for the structure and dynamic of ecological systems (Brown et al. 2004).

# Community size spectrum – a seemingly universal pattern of abundance size distribution across ecosystems and its implications

The negative relationship between body size and abundance in aquatic communities is often referred to as the community size spectrum (SS), describing the relationship between the logarithm of body mass and the logarithm of abundance (Sheldon et al. 1972; Jensen et al.

2009; Sprules and Barth 2016). This relationship is usually linear and was therefore traditionally described with slopes and intercepts of linear regressions (Sheldon et al. 1972; Kerr and Dickie 2001). The SS intercept reflects the overall abundance of organisms in the community and the slope quantifies the decreasing rate of numerical abundance with increasing body size (Ahrens and Peters 1991). Therefore, both SS intercept and slope represent two indices of food web functions. Essential features of trophic food webs, such as trophic transfer efficiency and energy demand were found to correlate with SS slopes (Mehner et al. 2018; Bartrons et al. 2020). For instance, low energy transfer efficiency is reflected by steepening slopes, i.e. increase relative abundance of small individuals (Kerr and Dickie 2001). Sheldon and colleagues (1972) were the first to describe an universal pattern, spanning from bacteria to whales, of an ecosystems biomass remaining relatively constant when summed within logarithmically equal body mass intervals. Based on their observations, empirical studies supported the existence of a remarkable regularity in shape and slope of the SS for a range of aquatic communities and ecosystems, including fish, invertebrates, plankton and zooplankton communities e.g. in the open ocean (Sheldon et al. 1972; San Martin et al. 2006a), coral reefs (Wilson et al. 2010; Heather et al. 2021) and freshwater systems (Gaedke 1992; Yurista et al. 2014). It was found that in steady state conditions the SS slope has a theoretical value across ecosystems and organisms. Mechanistic models describing size-based feeding and physiological constraints (Blanchard et al. 2017; Andersen 2019), as well as basic scaling theory that encapsulates these procedures via transfer efficiency and predator prey mass ratios (Brown and Gillooly 2003; Jennings and Mackinson 2003) mutually predict SS slopes to be approximately -2 (Normalized abundance SS; e.g. Blanchard et al. 2017). These findings suggest that common processes may regulate the abundances of small and large organisms in distinctive contexts.

The often found empirical consistency of SS slopes across different aquatic systems has led to its utilization as an indicator of ecosystem health at regional and global scale (Shin et al. 2005). While SS have first emerged as indicators of fishing impacts in marine systems, they are now also applied to freshwaters to detect effects of exploitation. This is due to SS slopes sensitivity to the effects of fishing (Shin et al. 2005; Petchey and Belgrano 2010) and the removal of the largest individuals leading to steeper SS slopes (more negative) in fish communities (Rice and Gislason 1996). Interestingly, systematic changes in SS similar to those that occur in exploited fisheries are also found in systems that are under other types of environmental pressure (Reuman et al. 2008). It was found that the SS slope varies consistently in response to environmental gradients, including temperature and productivity (Emmrich et al. 2011; Arranz

et al. 2016) or biotic factors, such as invasions (Broadway et al. 2015; Arranz et al. 2021), and thus has been proposed as an indicator of ecosystem functioning (e.g. productivity), health and environmental changes (e.g. human induced disturbances; Sprules and Goyke 1994; Daan et al. 2005; Petchey and Belgrano 2010). Therefore, size-based approaches not only allow insights into ecological interactions of aquatic communities but also enable us to understand the effects of various anthropogenic stressors and natural factors (Trebilco et al. 2013; Sprules and Barth 2016; Blanchard et al. 2017) that have been shown to impact the size distribution of organisms. In the following paragraphs I will describe in more detail the factors that affect freshwater and marine systems, specifically in lake and coral reef ecosystems.

### Factors affecting community size distributions in lake systems

A multitude of abiotic and biotic factors are known to influence the size structure of freshwater communities. Metabolism regulating factors such as temperature (Tordesillas et al. 2016) and food availability (Liu et al. 2015) are known to influence the growth of zooplankton populations (Tordesillas et al. 2016). Rising temperatures regularly favour small organisms (Atkinson et al. 2003; Havens et al. 2015; Andersen et al. 2016) and therefore result in a shift towards smaller body sizes in communities (Gardner et al. 2011), which leads to steeper SS slopes and a reduced size diversity. In contrast, greater resource availability may cause increases in the relative abundance of large organisms and therefore flatter SS slopes (Gaedke et al. 2004; Sprules and Barth 2016). Rises of overall zooplankton community abundances are often caused by higher food availability resulting from increases in total phosphorus (TP) concentration in the water (Hanson and Peters 1984; Pinto-Coelho et al. 2005). In addition, top-down predation effects from fish (Jeppesen et al. 1997; Zhang et al. 2013) are also known to strongly affect biomass and body size distribution of zooplankton communities (Brooks and Dodson 1965; Badosa et al. 2007), causing a reduced size diversity (Brucet et al. 2010).

Similarly, lake fish assemblage and size structure are known to be influenced by various natural and anthropogenic factors. Specifically, anthropogenic eutrophication, a severe problem in lake systems, was found to lead to a disproportional dominance of smaller individuals. This is due to a higher turnover and increased reproductive rates and small fish production (Emmrich et al. 2011; Brucet et al. 2013; Chu et al. 2016). Particularly, a dominance of small-bodied cyprinids and a decline of the abundance of piscivore fish with increasing nutrient levels was noted (Jeppesen et al. 2000; Olin et al. 2002; Mehner et al. 2005). Concerning are also findings

that show increasing temperatures to cause a change in the thermal regime of lakes, which can result in significant alterations of lake fish assemblage size structure (e.g. Sahoo and Schladow 2008). Warming results in an increase and a dominance of warmwater species and a greater proportion of small (and younger) individuals (Lehtonen 1996; Daufresne et al. 2009; Jeppesen et al. 2012; van Dorst et al. 2019) resulting in steeper slopes of the fish SS (Audzijonyte et al. 2020; Gårdmark and Huss 2020). This is due to the faster growth and higher reproduction rates of small organisms than large ones at higher temperatures.

However, it is challenging to elucidate which of these factors exhibit the greatest effect on trophic interactions and therefore the size structure in aquatic communities. The impact of these factors occur simultaneously and their interactive effects can be very complex (Shurin et al. 2012; Liu et al. 2020). Specifically, trophic interaction in the pelagic area of lake systems is a fundamental topic in classical and modern limnological ecology, with many scientific studies centred around the opposing effects of fish feeding (top-down) and phytoplankton biomass (bottom-up) on zooplankton communities (Brooks and Dodson 1965; Carpenter et al. 1985; McQueen et al. 1986). Recent studies have also recognised the importance of the environmental conditions at which top-down or bottom-up effects dominate (Carpenter et al. 2016). Due to the numerous factors influencing these complex interactions, it is not surprising that to date, studies on pelagic food chains have not identified a single 'master' mechanism, which drives the zooplankton community composition and biomass in the pelagic area of all lakes. However, applying a size-based approach and analysing comprehensive long-term data with numerous potentially important abiotic and biotic factors may offer the opportunity to detect the drivers of these complex pelagic interactions. Understanding the drivers influencing trophic interactions and the importance of specific environmental conditions is critical in regards to the increasing direct and indirect anthropogenic impacts that threaten aquatic systems.

### Factors affecting coral reef fish size distributions

In marine systems, SS parameters were traditionally employed as indicators for ecosystemlevel changes driven by fishing impacts on fish assemblages (Blanchard et al. 2017). However, physical characteristics of an individual's habitat, such as the three-dimensional structure of coral reefs is known to affect the size distribution of fish communities as well (e.g. Luckhurst and Luckhurst, 1978; Hoegh-guldberg and Bruno, 2016; Ferrari et al., 2018). Structural complexity directly provides prey refugia for small-bodied fish to avoid predation (Steele 1999; Holbrook and Schmitt 2002) and offers protection from physical stress, such as water flow (Johansen et al. 2008). A reduced structural complexity (with e.g. no/ few caves, overhangs or vertical reliefs) is associated with fewer small bodied fish and therefore shallower SS slopes in the Seychelles (Graham et al. 2007), Fiji (Wilson et al. 2010), Cozumel (Alvarez-Filip et al. 2011) and the Bahamas (Rogers et al. 2014). Many previous studies on the relationship of fish size structure and coral reef structural complexity were undertaken in regions where fishing is also occurring (e.g. Carvalho et al., 2021) or on very pristine and undisturbed coral reefs (Robinson and Baum 2016). To my knowledge, information on the relationship between structural complexity and fish SS slope in relation to differing exposure to touristic activities, such as divers and snorkelers is missing in regions without any fishing impacts. SCUBA diving and snorkelling are particularly popular at holiday destinations that harbour coral reefs (Cope 2003). However, divers often collide with corals, which is a great threat to the vulnerable coral reef structure (Harriott et al. 1997; Hawkins et al. 1999; Walters and Samways 2001). It is suggested that the extent of damage to the reef is directly linked to the intensity of site use by divers and snorkelers (Dixon et al. 1993; Hawkins et al. 1999, 2005). It is difficult to convolute the signals from a combination of human-induced stressors such as fishing, pollution and physical habitat destruction occurring at different scales and acting at the same time (Chabanet et al. 2005). Therefore, assessing the impacts of touristic activities without other direct sources of anthropogenic disturbances, such as fishing, may allow for a better understanding of the fish community SS slope and reef structural complexity and their relationship among reef sites that are exposed to different intensities of recreational activities.

### Sampling techniques to describe the fish size spectrum

The assessment and monitoring of aquatic systems, specially of fish communities requires comparability across sampling years of the same site and between systems to precisely examine the effect of stressors. Traditionally, SS of fish communities have been derived from catch data in order to assess fish stocks and fishing impacts (e.g. Rice and Gislason 1996a; Emmrich et al. 2011). However, it is suggested that virtually all types of sampling gears can be considered species- and size-selective (Gulland 1980; Prchalová et al. 2008; Olin et al. 2009). Methods to catch fish, such as trawling, gillnetting and electrofishing are inherently size selective and may consequently introduce a bias in the analyses of SS by under and/or overrepresenting certain

size classes (Hamley 1975; Jensen 1986; Bonvechio et al. 2008). Specifically, avoidance and escapement are problems relevant to all types of nets, while the size of the net and mesh size was found to determine the size and the species of fish being collected (Pearcy 1980; Kashkin and Parin 1983). For example large trawls often collect larger and more active fish, because small individuals have higher chances to escape through large meshes (Pearcy 1980). Further problems with net methods are the associated high fish mortality as well as the high labour and investment costs (Chopin and Arimoto 1995; Emmrich et al. 2011). In contrast to fishing, scientific hydroacoustic methods can offer a less size-selective, less cost-intensive and less destructive method to document SS of fish communities in lakes. The relevant hard- and software for scientific hydroacoustics have evolved rapidly in recent years (Simmonds and MacLennan 2008), making it a promising method to overcome the drawbacks of netting techniques in estimating SS (Simmonds and MacLennan 2008). This non-destructive fish sampling technique has a widespread applicability (e.g. Godlewska et al. 2004; de Kerckhove et al. 2016) while avoiding some of the selectivity issues encountered with traditional net sampling gear types (Kubečka et al. 1998; Knudsen and Sægrov 2002; Mehner et al. 2003; Wheeland and Rose 2015). Fish community SS can be successfully determined based on acoustic methods if the majority of fish are recorded within the acoustic beam and consequently measured as single targets (Wheeland and Rose 2016). However, hydroacoustic methods are limited almost entirely to deep (> 10 m) pelagic areas, and usually information on fish species composition and age estimation still requires additional catching of fish. Furthermore, the echo sounder system utilized and the methods of data processing and analysing affect the results and differ between studies and monitoring programs. The reliability of acoustically estimated fish densities is subject to large variations caused by the timing of the survey and the resulting changes in distributional patterns of fishes in the water column (Malinen and Tuomaala 2005). Clearly, more studies are needed, which examine the applicability of hydroacoustics for generating size distributions of fish communities and correspondence between fish density estimates based on acoustic and netting techniques to give a baseline for a standardised method of data analysis.

### Inconsistencies of size spectra based on empirical findings

Besides the remarkable consistencies observed in previously mentioned empirical SS studies (e.g. Sprules and Barth 2016), considerable deviations can occur. Empirical studies are solely

a snapshot of a system, frequently not in a steady state. Many processes can affect the underlying assumptions of mechanistic models and scaling theory and add to the variation around the theoretical slope of - 2 (Trebilco et al. 2016; Eddy et al. 2021). For instance, it is commonly assumed that SS slopes are steeper at higher temperatures based on the interrelationships of body size, temperature and metabolic rate (Brown et al. 2004). However, divergent findings from empirical studies in coastal marine systems (García-Comas et al. 2014) show that this is not always the case. Furthermore, the theoretical slope of -2 is not consistently found for SS of reef fish communities, which often display shallower slopes (e.g. -1.13 to 1.95 Robinson et al. 2017; -1.75, Ackerman et al. 2004; -1.58, Robinson and Baum 2016). This is suggested to be due to seasonal competition for resources (Edgar 1994), energetic subsidies (Trebilco et al. 2016; Morais and Bellwood 2019), relatively high abundances of herbivorous fish (Steneck et al. 2017) or structural complexity and size-dependent habitat refugia (Rogers et al. 2014). Similarly, oligotrophic systems were suggested to exhibit steeper slopes (Jennings and Mackinson 2003), which seems to apply to freshwater systems (Sprules and Munawar 1986) but not to the ocean (San Martin et al. 2006a, b; Kenitz et al. 2018). Currently there are still conflicting ideas and no general consensus on the major factors driving SS slopes. Inconsistent findings and conclusions on the behaviour of SS may result from variations in environmental variability or methodological inconsistencies (Quinones et al. 2003), thus emphasising the demand for further empirical studies. Specifically long-term data with the potential to offer insights on a wider scale and to average out underlying observed variabilities are needed.

### Thesis outline and objectives

In this thesis, I used size-based methods such as SS to (i) infer information on trophic interactions of the pelagic community in a temperate lake, (ii) compare traditional net sampling and modern hydroacoustic methods applicability in representing fish community SS, and (iii) examine structural complexity and fish community size distribution and their relationship on tropical coral reefs among sites with differing exposure levels to touristic activities. More specifically, in **chapter 2**, I examined the size structure, including spectral slope and intercept, of a pelagic zooplankton community in a deep mesotrophic lake across 13 sampling years. It was assessed how changes in abiotic factors, such as resource availability, water temperature and nutrient level, as well as the size structure and biomass of planktivorous fish affect the size

structure of the zooplankton community. In **chapter 3**, the reliability to describe the SS of a pelagic fish community was compared using three methodological approaches across 12 sampling years: a traditional net sampling technique, pelagic midwater trawling, and two modern scientific hydroacoustic methods. Finally, in **chapter 4**, I assessed the relationship of reef fish community SS slopes and reef structural complexity among coral reef sites in the northern Gulf of Aqaba in the Red Sea.

Specifically the research objectives analysed in the following 3 chapters of this thesis were:

- I) To examine if the zooplankton community size structure in the pelagic is driven by bottom up factors, including water temperature, resource availability and nutrient concentration or top down factors, such as pelagic planktivorous fish size distribution and biomass using long-term data of 13 sampling years (chapter 2)
- II) To methodologically compare pelagic fish SS based on simultaneously collected midwater trawl catches and two methods of hydroacoustic based sampling techniques, namely single echo detections (SEDs) and tracked echo groups (TEGs) across 12 years of sampling (chapter 3)
- III) To compare reef fish SS slopes and reef structural complexity and examine their relationship among five coral reef sites with differing site specific anthropogenic disturbances (chapter 4)

### Size spectra in lake systems - study site and data sets

The first two studies (chapter 2 and 3) were conducted in Lake Stechlin, located in a nature reserve approximately 120 km north of Berlin (Germany). The basin of the lake was formed during the last continental glaciation about 12,000 years ago. The drainage of the lake is almost completely covered by forest (95%), while its shoreline is relatively undeveloped with no notable infrastructure. This temperate mesotrophic lake covers about 4.25 km<sup>2</sup> with mean and maximum depths of 22.3 m and 69 m, respectively (see Figure 1 a, Koschel and Adams 2003). A total of 13 fish species inhabit the lake, but the pelagic fish community is dominated by two sympatric species of ciscoes, Coregonus albula and C. fontanae (more than 95% of fish abundance; Mehner and Schulz 2002; Schulz and Freyhof 2003; Helland et al. 2007). Coregonid fishes are known to disperse by diel vertical migration from dense deep water aggregations during the day to a more even spatial distribution over the entire water depth at night (Mehner et al. 2007). Therefore, coregonids are easily detectable as single echoes during hydroacoustic surveys at night, and can be caught by midwater trawling likewise. They show strong variations in year-class strength and annual growth rates resulting in strongly differing abundances between subsequent years (Helminen and Sarvala 1994; Auvinen et al. 2000; Viljanen et al. 2004; Mehner et al. 2011). The average stock exploitation rate by the single commercial fishery at Lake Stechlin is 0.08 (Wanke et al. 2017), suggesting no strong effect of fish removal on fish abundance differences between years. Lake Stechlin has been studied intensively since 1958 by different research institutions with extensive long-term data available on the pelagic fish community, as well crustaceans and environmental descriptors.

**Chapter 2** is based on fish data, including counts and individual body wet mass (in g) from a pelagic midwater trawl collected annually at the end of June between 2005 and 2018 (n=13 years, data for 2016 missing due to net malfunction). Simultaneously to trawling, hydroacoustic surveys were performed to obtain pelagic fish mean mass (in g) and biomass (kilogram per hectare, see Figure 1b). Furthermore, data on crustacean plankton were included, which were collected by vertical tows in the upper depth layer from 0 - 22 m and the lower depth layer from 22.1 - 65 m at the deepest location of the lake (NE basin, 69.5 m). Since fish data were exclusively collected in summer, we similarly considered only zooplankton samples collected during summer months between 2005 and 2018 (13 years, excl. 2016). Therefore, from June to August, the lake was sampled twice a month except 2014 (one sampling in August), 2015 (each month sampled only once) and 2018 (one sampling in August) resulting

in a total of 148 zooplankton samples (74 samplings x 2 depth layers). Physical and chemical data were also recorded at the deepest site of the lake, simultaneously with the crustacean data. Vertical profiles of water temperature (°C), TP (mg L<sup>-1</sup>) concentrations and Chl a (mg L<sup>-1</sup>) concentration as an indicator of resource availability were also recorded.

Similarly, in **chapter 3**, fish counts and individual body wet mass (in g) were estimated annually every June between the 6<sup>th</sup> and 29<sup>th</sup> from 2006 to 2019 using pelagic midwater trawl (n=12 years, data for 2016 missing due to net malfunction) and hydroacoustic surveys (n=12 years, data for 2007 missing due to malfunction of hydroacoustic equipment) simultaneously. The surveys were conducted during complete darkness starting 1 h after sunset. Pelagic midwater trawl surveys covering several depth layers could be conducted only in the deep central and northern basin (from here on central basin, CB) of Lake Stechlin. The morphometry of the lake (horizontal extension of certain depth layers per basin) is very variable (see Figure 1a), and hence hauls with minimum of 500 m towed distance in depths deeper than about 15 m could be realized only in one part of the lake. Therefore, to address potential spatial heterogeneity in fish distribution between the basins, we calculated hydroacoustics SS from either all transects (whole lake, WL) or only from the transects overlapping spatially with the trawl surveys (CB; see Figure 1b).



**Figure 1.** Bathymetric map of Lake Stechlin (a) and diagram with transects from hydroacoustic surveys of whole lake (WL; black), midwater trawling (grey) and with transects from hydroacoustic surveys in the central and northern basin (CB) that overlap with trawling transects (green, b).

### Size spectra in coral reef systems – study site

The **4<sup>th</sup> chapter** of this thesis is based on visual census surveys of the fish community and habitat structural complexity on five coral reef sites along the Israelian coastline in the northern Gulf of Aqaba, Red Sea (see Figure 2). The survey sites span from the north to the south of Eilat and differ in their level of exposure to anthropogenic disturbances. The three sites in the south, Reserve A, Japanese Gardens and IUI are officially protected and part of the in 1964 declared Eilat Coral Beach Nature Reserve, which is managed by the Nature and Parks Authority. Generally, the fringing reef along the Israeli coastline is easily accessible from shore for swimmers, snorkelers and divers. Because of the ease of access, Eilat's coral reefs are among the most heavily visited with ~6 million tourists annually and >300,000 divers per year along the entire 12 km coastline (Tynyakov et al. 2017). Therefore, particularly sensitive areas, such as the reef table and core parts at Japanese Gardens, are considered closed, while at the surrounding area of Japanese Gardens the number of daily visitors is restricted (Israel Nature Parks Authority 2021). The other two sites, Reserve A and IUI are open to visitors without strong restrictions. The sites Dekel and Katza are not officially protected. However, Katza was closed to the public until 2017, as it was used as a fuelling station for tankers.



**Figure 2**: The study sites along the coast of Israel in the northern tip of the Gulf of Aqaba (Red Sea) with the level of protection from touristic activities indicated in brackets (1 - 5 = highest to lowest level of protection), including Japanese Gardens (1), Katza (2), Reserve A (3), IUI (4) and Dekel (5).

# Chapter 2

# Top-down and bottom-up effects on zooplankton size distribution in a deep stratified lake

Braun, Lisa-Marie, Brucet, Sandra, Mehner, Thomas

Aquatic Ecology, 55:527-543 (2021); https://doi.org/10.1007/s10452-021-09843-8

### ABSTRACT

Trophic interactions in the pelagic area of lakes and the opposing effects of fish feeding (topdown) and phytoplankton biomass (bottom-up) on zooplankton communities are central topics in limnology. We hypothesized that zooplankton size distributions should be a more sensitive approach to disentangle top-down and bottom-up effects than the commonly measured zooplankton biomass. We examined zooplankton size distributions from 148 samples collected during summer months in the upper and lower pelagic layers of a deep mesotrophic lake among 13 years of sampling. Top-down effects, namely fish size and biomass, and bottom-up effects, including water temperature and total phosphorus and chlorophyll a concentrations, were considered. To add robustness to our analyses, we expressed the zooplankton size distributions as size spectra based on log-binning, as continuous size spectra and by the size diversity, a measure that has been developed to mimic taxonomic diversity indices. Among numerous regressions tested, significant top-down or bottom-up effects could rarely been detected. Our results indicate that the overall zooplankton size distribution was not significantly affected by fish predation and lake productivity measured as total phosphorus or chlorophyll a concentration. However, we found negative correlations between fish biomass and the preferred zooplankton prey, including Bosmina longirostris, Daphnia cucullata and nauplii in the upper depth layer. However, due to their small body size, low biomass and therefore relative small contribution to the zooplankton size distribution, predation on preferred zooplankton species did not translate into a statistically significant modification of the entire size spectrum. Consequently, the size spectrum seems to be relatively robust against predation effects, but might reflect the lake-wide energy availability and transfer efficiency in the food web.

Keywords: zooplankton size spectra, pelagic, top-down, bottom-up

### INTRODUCTION

Trophic interactions in the pelagic area of lakes are one of the cornerstones of classical and modern limnology. Many scientific studies centred around the opposing effects of fish feeding (top-down) and phytoplankton biomass (bottom-up) on zooplankton communities (Brooks and Dodson 1965; Carpenter et al. 1985; McQueen et al. 1986), while recent studies have also recognised the importance of the conditions at which top-down and bottom-up effects dominate (Carpenter et al. 2016). Zooplankton are an integral part of aquatic ecosystems, playing a crucial role in linking primary producers and higher trophic levels such as fish. In turn, zooplankton communities are sensitive to changes of their resources and their predators, and therefore mirror a balance of food web processes by their body size distribution and taxonomic composition (Mills and Schiavone 1982; Hansson et al. 2007).

However, detecting bottom-up and top-down effects on zooplankton becomes complicated because the zooplankton community is not a homogenous group, but is composed of several taxonomic and functional groups (e.g., cladocerans vs. copepods; filter-feeders vs. particulate feeders; herbivorous vs. omnivorous or carnivorous species). Accordingly, both the selective feeding of zooplankton on phytoplankton and the selective feeding of zooplanktivorous fish on zooplankton may modify the relative densities of zooplankton taxa and subsequently the strength of competitive interactions within the zooplankton community. It is therefore not surprising that studies on pelagic food chains have not identified a single 'master' mechanism, which drives the zooplankton community composition and biomass in the pelagic area of all lakes.

In contrast, it might be possible that the zooplankton size distribution is a more sensitive reflection of the strength of bottom-up or top-down effects in pelagic layers. The body size of individuals is a simple metric to collect, while it is a key characteristic correlated with physiological and ecological properties. The size of an organism scales with traits such as metabolic rate, growth (Marquet et al. 2005; Woodward et al. 2005), life span (Peters 1983; Calder 1984) and trophic position. In aquatic ecosystems, smaller organisms are typically more abundant than larger ones (Kerr 1974; Sprules et al. 1991; Thiebaux and Dickie 1993). This negative relationship between size and abundance emerges from organism traits and ecological interactions (Sprules and Barth 2016) and is often referred to as a community size spectrum (SS). The SS describes the relationship between the logarithm of size and the logarithm of

abundance, which is usually linear and can therefore be characterized by slopes and intercepts of linear regressions (Sheldon et al. 1972; Kerr and Dickie 2001). The intercept reflects the overall abundance of organism in the community and the slope mirrors the relative abundances of small and large organism (Ahrens and Peters 1991). Therefore, SS are a highly effective approach to summarize and compare the size structure of aquatic communities (Cottingham 1999; Cózar et al. 2003) and might be useful to evaluate resource availability for and selective predation on zooplankton communities.

A combination of abiotic and biotic factors influences zooplankton community size structure. Growth of zooplankton populations reflects factors regulating the metabolism, including temperature (Tordesillas et al. 2016) and food availability (Liu et al. 2015). Rising temperatures favour small organisms (Atkinson et al. 2003; Havens et al. 2015; Andersen et al. 2016) and therefore result in a shift towards smaller body size (Gardner et al. 2011), reflected in more negative SS slopes and lower size diversity, whereas greater resource availability leads to an increase in relative abundance of large organisms and therefore flatter SS slopes (Gaedke et al. 2004; Sprules and Barth 2016). Specifically, increases in total phosphorus (TP) lead to increases of overall zooplankton community abundances via higher food availability (Hanson and Peters 1984; Pinto-Coelho et al. 2005). However, top-down predation effects from fish (Jeppesen et al. 1997; Zhang et al. 2013) strongly affect biomass and body size distribution of zooplankton communities (Brooks and Dodson 1965; Badosa et al. 2007), leading to a reduced size diversity (Brucet et al. 2010). It is challenging to elucidate, which of these factors exhibit the greatest effect on trophic levels and therefore population dynamics and size structure, as the impact of each occurs simultaneously (Shurin et al. 2012; Liu et al. 2020) and interactive effects of these factors can be very complex.

In the present study, we used zooplankton SS to evaluate the strength of bottom-up and topdown directed effects on zooplankton size distributions in a deep mesotrophic lake. We examined the zooplankton size distribution from 148 samples collected exclusively during summer months among 13 years in the upper and lower pelagic layers of a deep mesotrophic lake. To add robustness to our analyses, we expressed the size distributions as SS based on logbinning, as continuous SS and by the size diversity, a measure that has been developed to mimic taxonomic diversity indices (Brucet et al. 2006, 2010, 2017; Quintana et al. 2008, 2016). We expected that both annually varying predation by the dominant pelagic planktivorous fish and resource availability via phytoplankton biomass would affect the year-to-year variation of the zooplankton size distributions. Therefore, we explored whether TP, chlorophyll a (chl a) concentrations and water temperature modified the size distribution of zooplankton. In turn, we tested whether the size distribution of fish and their biomasses as obtained by two different fishing methods had an effect on zooplankton size distributions. The lake is dominated by coregonid fishes, which show strong variations in year-class strength and annual growth rates resulting in strongly differing abundances between subsequent years (Helminen and Sarvala 1994; Auvinen et al. 2000; Viljanen et al. 2004; Mehner et al. 2011). Accordingly, strong interannual effects on their zooplankton prey can be expected. We hypothesized that the size distributions of zooplankton would show strong differences between years, which reflect the relative contributions of fish predation and resource availability. Therefore, we aimed to demonstrate that the size distribution of pelagic zooplankton communities is a superior and easy-to-generate metric that informs about the major structuring forces in the pelagic area of deep lakes.



**Fig. 1** Bathymetric map of Lake Stechlin indicating water depth (a) and map with transect lines from trawling (in grey) and hydroacoustic surveys (in black, b)

### **MATERIALS AND METHODS**

### Study site and sampling

This study was conducted in Lake Stechlin, located approximately 120 km north of Berlin (Germany). This mesotrophic lake covers about 4.25 km<sup>2</sup> with mean and maximum depths of 22.3 m and 69 m, respectively (see Figure 1a, Koschel and Adams 2003). A total of 13 fish species inhabit the lake, but the pelagic fish community is dominated by two sympatric species of ciscoes, *Coregonus albula* and *C. fontanae* (more than 95% of fish abundance; Mehner and Schulz 2002; Schulz and Freyhof 2003; Helland et al. 2007). Furthermore, the average stock exploitation rate by the single commercial fishery is 0.08 (Wanke et al. 2017), suggesting no strong effect of fish removal on fish abundance differences between years. We estimated counts and individual body wet mass (in g) of fish using a pelagic midwater trawl annually at the end of June between 2005 and 2018 (n=13 years, data for 2016 missing due to net malfunction). Trawling is commonly employed for SS studies on fish but its inherent size selectivity (Klein et al. 2019) may result in an overrepresentation of medium-sized fish. Therefore, simultaneously to trawling, we also performed hydroacoustic surveys to obtain pelagic fish mean mass (in g) and biomass (kilogram per hectare, see Figure 1b).

#### Crustacean assessment

Crustacean plankton was collected by vertical tows in the upper depth layer from 0 - 22 m and the lower depth layer from 22.1 - 65 m, using a cone-shaped closing net (mesh size 90 µm, opening 27 cm<sup>2</sup>; length 1.2 m, Hydrobios, Kiel, Germany) at the deepest location of the lake (NE basin, 69.5 m). Since fish data were exclusively collected in summer, we similarly considered only zooplankton samples collected during summer months between 2005 and 2018 (13 years, excl. 2016). Therefore, from June to August, the lake was sampled twice a month except 2014 (one sampling in August), 2015 (each month sampled only once) and 2018 (one sampling in August) resulting in a total of 148 zooplankton samples (74 samplings x 2 depth layers). Samples were preserved in a 4% sugar-formaldehyde solution. Taxa were identified according to Flößner (1972, 2000), Kiefer and Fryer (1978), Einsle (1993) and Lieder (1996). A sub-sample containing at least 100 individuals of the dominating species or groups was counted (abundance in Ind m<sup>-3</sup>) using an inverted microscope at 60-fold magnification. Mean length of zooplankton was estimated by measuring approximately 15 individuals per each

frequent group (species level in most cases; see Table 1 in Appendix for list) and then transformed to carbon body mass ( $\mu$ g C Ind<sup>-1</sup>) using species-specific allometric equations from published studies (Bottrell et al. 1976; Kasprzak 1984). To examine the taxon-specific proportions from the entire zooplankton community in the upper and lower depth layers, we calculated the biomass of each taxon group for each depth layer. Abundance (Ind m<sup>-3</sup>) was multiplied with the carbon body mass for each taxon and the group-specific annual average biomass was determined from the individual samples.

### Fish assessment - trawling

A pelagic trawl with 28/20/10 mm mesh size, 10 mm mesh size in the cod-end and a total length of 14.8 m (stretched on land) was utilized. The net with an opening area of approximately 10 m<sup>2</sup> (opening width 3.5 m) was towed by a boat (length 7 m, width 2 m), which was driven by a 60 hp engine over four longitudinal transects in the deepest lake basins (see Figure 1b). Trawling speed (mean  $\pm$  SD) was 6.5  $\pm$  0.6 km h<sup>-1</sup> (1.8  $\pm$  0.2 m s<sup>-1</sup>), while towed distance, as the product of trawling speed and trawling time, ranged between 500 m and 1600 m (mean 840 m) with an average towing time ( $\pm$ SD) of 7.8 min ( $\pm$ 1.9). During each survey, a total of four hauls were conducted at approximately  $12 \text{ m} \pm 0.65 \text{ m}$ ,  $15 \text{ m} \pm 1.09 \text{ m}$ ,  $25 \text{ m} \pm 2.08 \text{ m}$  and  $32 \text{ m} \pm 0.90 \text{ m}$  (mean  $\pm \text{SD}$ ), whereby the two deeper hauls had shorter trawling times and slightly slower hauling speeds. Due to limited spatial extension of water layers with more than 35 m depth, deeper hauls could not be performed. The actual sampling depth was recorded with a diving computer attached on the trawl's head rope. The depth variability during each tow never exceeded 3 m. At the end of each haul, the trawl was quickly lifted by hydraulic winches at speeds comparable to the trawling speeds, thus preventing escapement of fish from the net. Fish were counted, and individually measured to determine total length (TL, nearest centimetre) and body mass (wet mass, wm, nearest gram). Only subsamples were measured and weighed when catches were too large. The abundance of fish (ind. 1000 m<sup>-3</sup>) was estimated from the towed distance and the opening area of the trawl. Due to the shorter hauled distance in the deeper layers, the overall size distribution per year calculated as the total sum of all fish caught by the four hauls would have been biased towards the size of fish in the upper water layers. Therefore, we employed a weighting factor to calculate a weighted mean abundance and size distribution across the four depth layers. The weighting factor (WF) was calculated as the ratio between the maximum volume fished by one among the four hauls in this year and the volume fished in the respective depth. Accordingly,

the WF equals the abundance and size distribution per depth layer to identical fished volumes. Some size distribution analyses require fish numbers per size class as integers; then the weighting factor was rounded to the nearest half integer (see Table 2 in Appendix for an example).

#### Fish assessment - hydroacoustics

Hydroacoustic surveys were completed as a series of transects using a SIMRAD (Kongsberg) EY60 split-beam hydroacoustic unit (120 kHz, circular transducers, beam width 7° x 7°, pulse duration 128 ms, ping rate 3 pings s<sup>-1</sup>). After calibration with standard spheres provided by the manufacturer, the surveys were conducted during complete darkness starting 1 h after sunset every June between the 6<sup>th</sup> and 29<sup>th</sup>. Surveys were performed with vertical beaming along 20 transects (total distance about 12 km) across this tri-basin lake, with transect length ranging from 635 m to 1332 m (see Figure 1b). Data were stored in a computer, processed and analysed by the postprocessing Sonar 5 Pro software (version 6.0.4-R340, Balk and Lindem 2017). The lower target strength (TS) threshold (as a measure of fish body length in dB) was set to -55 dB for the echogram corresponding to fish of an approximate total length of 4.2 cm and 0.42 g wm. Parameters for amplitude echograms were set 6 dB lower (-61 dB) to accept targets out of the half power edge of the sound beam. The TS (dB) of the targets was converted into fish total length (cm) and body wm (g) using the equation obtained for *Coregonus* spp. from Lake Stechlin by Mehner (2006):

(1) TL (cm) = 
$$10^{\left(\frac{(TS + 70.9)}{25.5}\right)}$$
  
(2) wet mass (g) = 0.00507 x (TL (cm)<sup>3.088</sup>)

The records from all 20 sampled transects were combined and averaged for each year. Fish biomass (kg ha<sup>-1</sup>) was obtained by echointegration, by using the size-frequency distribution of the detected individual targets per transect.

### **Environmental descriptor assessment**

Physical and chemical data were recorded at the deepest site of the lake, simultaneously with the crustacean data. Vertical profiles of water temperature (°C) were determined every 5 meters between the surface and 65 m, while TP (mg L<sup>-1</sup>) concentrations were measured from samples at 0, 5, 10, 40, 60 and 65 m depth photometrically. TP was measured after wet digestion of

unfiltered subsamples in an autoclave (potassium peroxodisulfate, 30 min., 134 °C). TP content was determined by flow analysis and spectrometric detection (Foss FIAstar 5000 Analyzer). Chl a (mg L<sup>-1</sup>) concentration was measured at 0, 5 and 10 m depth using photometric determination (Hitachi spectrophotometer U-2900). The arithmetic means of temperature and TP per year were determined for the upper (0 - 20 m) and lower (21 - 65 m) layers separately, while the mean chl a concentration was only based on samples from the upper layer. However, since chl a concentration in shallower depths may have an effect on processes of the entire water column, the determined chl a mean was also utilized as a predictor for dependent variables in the lower layer.

### Data analyses

Zooplankton abundances (Ind m<sup>-3</sup>) were classified into a total of 17 body mass size classes, ranging from 0.1 to 25  $\mu$ g C Ind<sup>-1</sup> (log<sub>2</sub> range: -3.36 – 4.63) and logarithmically transformed (base 2) for each sampling in the upper and lower depth layer (total of 148). The arithmetic mean zooplankton abundances per size class based on all samplings in the upper or lower depth layers for each year were determined and log transformed. Therefore, zooplankton SS were calculated for each depth layer separately per year (total of 26 SS, 2 for each of the 13 years). We utilized the LT (log-transform) method where the log<sub>2</sub> mean counts were aggregated in log<sub>2</sub> size bins of constant width and plotted against the midpoint of the size interval. Ordinary least square regression (OLS) method was used to estimate the SS slope and intercept (Rice and Gislason 1996). The intercept of size spectra is a general measure of total organism abundance. Normality of data was visually examined and tested with a Shapiro-Wilk normality test.

For scrutiny, we also used the maximum likelihood estimation when fitting zooplankton size spectra (Edwards et al. 2017). Here individual zooplankton body masses were not binned, but utilized in continuous form. The exponent of the individual size distribution (b), known to be positively related to the slope of the SS, was determined for each summer sampling in the upper and lower layers. Then the arithmetic mean of exponent b and the confidence interval were determined for each depth layer per year from these samplings. Furthermore, we determined zooplankton size diversity ( $\mu$ ) as based on carbon body mass ( $\mu$ g C), calculated from each sample and then averaged for each depth layer per year following Quintana et al. (2008), employing the Shannon diversity expression but adapted for body size as a continuous variable. Finally, we calculated the total biomass and median body mass of only those zooplankton taxa

that are commonly included in *Coregonus* diet, which encompasses mainly cladocerans, including *Daphnia* spp., *Bosmina* spp., *Chydorus sphaericus, Diaphanosoma brachyrum, Ceriodaphnia quandrangula* and nauplii (Schulz et al. 2003) in each depth layer as a response variable. However, we did not calculate SS for the limited prey taxa as these only represent a fraction of the sizes of the entire community. Therefore, one cannot expect a negative relationship between size and abundance as predicted by SS theory for the entire zooplankton community.

Fish size distribution from trawling was comparably described as continuous SS using maximum likelihood estimation of b, which is the recommended method for fitting fish SS (Edwards et al. 2017). This was based on depth-weighted fish abundances. In addition, the arithmetic mean biomass (g 1000 m<sup>-3</sup>, depth-weighted average from four trawl hauls) was calculated for each year. Finally, fish biomass as kilogram per hectare (kg ha<sup>-1</sup>) and mean mass (in g) of fish were calculated from the hydroacoustic surveys.

To identify relationships between zooplankton community parameters (size distribution) and size or biomass of fish and mean TP, chl a and temperature, we utilized multiple regression analyses (see Table 3). Response variables tested in the multiple regressions were zooplankton slope and intercept (estimated by OLS) and zooplankton mean size diversity index, both per depth layer and year, annual summer averages of exponent b (estimated by MLE) of the SS, median body mass (µg C) and mean abundance (Ind m<sup>-3</sup>) of potential prey taxa in the upper and lower layer. As independent variables we utilized the exponent b of the fish SS (estimated by MLE) and the mean fish biomass (g 1000 m<sup>-3</sup>, both from trawling), as well as mean mass (g) and biomass (kg ha<sup>-1</sup>) as based on hydroacoustic surveys. Water temperature and mean chl a and TP concentrations were also included as environmental and productivity predictors, respectively, in all regressions. Only predictor variables that were not strongly cross-correlated (Pearson correlation coefficient below 0.5, and Variance Inflation Factor (VIF) below 2) were included in the analyses (Belsley et al. 1980), as multicollinearity can result in inflated variance among predictors in the model. Automatic stepwise backwards selection and the Akaike information criterion (AIC) were used to select the variables in the final model by accounting for increasing complexity (as seen in Akaike 1974). The most parsimonious model obtained was the combination of variables that produced the lowest AIC. Residual partial plots for each significant variable were plotted to show the relationship between the predictor and the response variables. All statistical analyses and plots were conducted with the software R (version 4.0.0; R Core Team 2020). Specifically the MLE's of fish and zooplankton size

spectra were performed by the provided R code and package (sizeSpectra) from Edwards et al.

(2017; 2020).

**Tab. 3** Individual response variables and independent variables included in the multiple regression analyses for the upper and lower depth layer (\*indicates annual mean values based on all summer samplings)

Response Variable				
Zooplankton		Fish	Environmental descriptors	
SS Slope (OLS)		SS average the (MLE)		
SS Intercept (OLS)	tuarrilina	SS exponent b (MLE)		
SS exponent b (MLE)*	trawning	Biomass (g 1000 m <sup>-3</sup> )	Chl a + TP+	
Prey Taxa total abundance (Ind m <sup>3</sup> )*			Temp.	
Prey Taxa Median Body Mass (C ug)*	hydro-	Mean mass (g)		
Size diversity*	acoustics	Biomass (kg ha <sup>-1</sup> )		
Abbreviations: SS, Size Spectra; OLS ordinary least square regression; MLE, Maximum Likelihood Estimation; Chl a,				

Abbreviations: SS, Size Spectra; OLS ordinary least square regression; MLE, Maximum Likelihood Estimation; Chl Chlorophyll a; TP, total phosphorus; Temp., Temperature

### RESULTS

### Zooplankton community structure, abundance and biomass (2005-2018, excl. 2016)

During the summer months, the zooplankton community of Lake Stechlin was numerically dominated by copepod nauplii and *Bosmina longirostris*. Nauplii were most abundant (grand mean across all samples and years = 20170 Ind. m<sup>-3</sup> ± 8915) and *Bosmina longirostris* second most abundant ( $\bar{x} = 9540 \pm 9379$  Indm<sup>-3</sup>) in the upper layer. In contrast, *B. longirostris* was most abundant ( $\bar{x} = 3624 \pm 3428$  Ind m<sup>-3</sup>) and nauplii was the second most abundant group in the lower depth layer ( $\bar{x} = 1420 \pm 1180$  Ind m<sup>-3</sup>; see Figure 2 and Table 4 in Appendix). However, total zooplankton community biomass in the upper layer was clearly dominated by the calanoid copepod *Eudiaptomus gracilis* (10 – 30%), with *Daphnia cucullata* (8 - 24%) and nauplii (12-25%) on the second and third rank. In the lower layer, *Eurytemora lacustris* (27 - 76%) and *Bosmina longirostris* (4 – 47%) contributed most to the overall zooplankton community (see Table 5). The body masses of zooplankton ranged from *Chydorus sphaericus* (0.09 µg C Ind.<sup>-1</sup>) in the upper layer to *Cyclops* spp. (24.80 µg C Ind.<sup>-1</sup>) in the lower depth layer. The mean ( $\pm$  SD) body length and mass of the entire zooplankton communities were higher in the lower ( $\bar{x} 0.54 \pm 0.01$  mm;  $\bar{x} = 1.42 \pm 0.08$  µg C bm) than in the upper depth layer ( $\bar{x} 0.50 \pm 0.007$  mm;  $\bar{x} = 0.95 \pm 0.03$  µg C bm).



**Fig. 2** Mean abundance (Ind m<sup>-3</sup>) of zooplankton taxa grouped as: (i) *Bosmina* spp., (ii) *Chydorus* spp. and *Diaphanosoma* spp., (iii) calanoids, (iv) copepodits and nauplii, and (v) *Daphnia* spp. for 2005-2018 (excl. 2016) in the (a) upper and (b) lower depth layer of Lake Stechlin

**Tab. 5** Biomass proportion (%, grand mean average from all samples between 2005 and 2018 (excl. 2016)) of each taxon group and their totals for taxa included (potential prey) and not included (no prey) in the diet of coregonids in the upper and lower depth layers of Lake Stechlin

		<b>Proportion</b>		
		<u>(%)</u>	<u>Total</u>	
Upp	er depth layer			
	Eudiaptomus gracilis	18.71		
	Eurytemora lacustris	13.19		
ey	Thermocyclops oithonoides	7.04		
o pr	cyclopoid Copepodit stages	3.66	47.80	
ŭ	Cyclops spp.	2.21		
	Copepodit stages	2.04		
	Mesocyclops leuckarti	0.96		
	Daphnia cucullata	17.47		
	Nauplii	15.40		
orey	Bosmina longirostris	6.98		
ial p	Diaphanosoma brachyurum	5.46	52 20	
tent	Daphnia bastard	2.32	52.20	
pot	Ceriodaphnia quadrangula	1.91		
	Bosmina coregoni	1.68		
	Chydorus sphaericus	0.98		
Low	er depth layer			
	Eurytemora lacustris	44.35		
	Cyclops spp.	11.69		
ey	Eudiaptomus gracilis	7.26		
o pr	cyclopoid Copepodit stages	4.53	71.66	
ü	Thermocyclops oithonoides	1.68		
	Copepodit stages	1.14		
	Mesocyclops leuckarti	0.99		
	Bosmina longirostris	15.51		
rey	Nauplii	5.44		
	Daphnia cucullata	3.57		
ial p	Diaphanosoma brachyurum	1.22	28.34	
tent	Daphnia bastard	0.97		
pot	Chydorus sphaericus	0.63		
	Bosmina coregoni	0.57		
	Ceriodaphnia quadrangula	0.44		

### Zooplankton spectral slope and shape and MLE b

The zooplankton size distributions substantially deviated from a linear negative log-log relationship, with only six out of the 26 (2 layers x 13 years) linear regressions being significant (p < 0.05, see Table 6 in Appendix). In most of the years, log size and log mean abundance exhibited a bimodal pattern (see Figures 6-9 in Appendix). The highest mean abundance per body mass size-class was often observed in the log<sub>2</sub> body mass classes -1.75 and -1.25 (0.20 – 0.41 µg C) dominated by *Bosmina longirostris* and nauplii and log<sub>2</sub> body mass class 1.25 and 1.75 (1.68 – 3.35 µg C) dominated by *Eudiaptomus gracilis*, *Daphnia cucullata* and *Eurytemora lacustris* (see Table 4 in Appendix). Zooplankton spectral intercepts differed significantly between both depth layers. The mean intercept in the upper layer was significantly higher compared to the lower layer (t-test:  $t_{(24)} = -15.09$ , p <0.0001). In contrast, mean spectral slopes were identical between upper and lower layers (t-test:  $t_{(26)} = -0.0005$ , p = 0.99). The mean exponent b of the SS estimated by MLE was slightly higher in the upper than in the lower depth layer (t-test:  $t_{(155)} = 0.68$ , p = 0.5). Zooplankton mean size diversity was significantly higher in the lower than in the upper layer (t-test:  $t_{(120)} = 3.52$ , p <0.0006, see Table 7).

**Tab.** 7 Zooplankton size metrices (response variables) mean, minimum, maximum and standard deviation (SD) for the upper (U) and lower (L) depth layers, as well as results from t-tests of individual zooplankton response variables between upper and lower depth layers. "OLS" means size spectrum estimated by ordinary least squares, while MLE indicates fit of continuous size spectrum by maximum likelihood

Response	Denth					Statistica Results	l Analy	yses
Variable	Layer	Mean	Minimum	Maximum	SD	t	df	p-value
	U	-0.57	-1.2	0.01	0.1	-0.0005	26	0.9
Slope (OLS)	L	-0.57	-1.1	-0.02	0.1			
	U	13.7	12.4	14.5	0.2	-15.1	24	< 0.0001
Intercept (OLS)	L	10.4	9.7	11.3	0.1			
	U	-2.43	-7	-0.9	0.1	0.68	155	0.5
b (MLE)	L	-2.3	-7.4	-0.7	0.1			
	U	1.2	0.04	1.7	0.04	3.52	120	0.0006
Size diversity	L	1.5	-0.04	2.3	0.06			

### Fish abundance and range between 2005-2018

Fish size distributions varied strongly between years, while the individual wet mass of fish sampled during trawling ranged from 0.018 g to 103 g. Some years were characterised by numerous small young fish (less than 4 g wet mass, e.g. in 2011 and 2017). In other years, bigger fish (17 - 32 g wet mass) dominated the community (e.g. in 2005 and 2008; see Figure 3). The SS exponent b ranged from -1.6 to 0.42. The steepest slopes and therefore the lowest spectral exponents were found in 2012 and 2017, which were characterised by a relatively high number of small fish in contrast to 2010 and 2014 which were characterised by numerous bigger and older fish (see Figure 10 - 13 in Appendix). Fish biomass (g 1000 m<sup>-3</sup>) based on trawling varied  $\approx$  5 fold (range = 140 - 749 g 1000 m<sup>-3</sup>), and mean biomass (kg ha<sup>-1</sup>) based on hydroacoustics differed  $\approx$  3 fold (range = 93 - 314 kg ha<sup>-1</sup>) across years.



**Fig. 3** Depth-weighted counts of fish distributed into body wet mass (g) classes as obtained from four trawling hauls in Lake Stechlin for each sampling year

### Effect of fish abundance and environmental descriptors on zooplankton community

Among the 48 combinations for 6 response variables and the 4 different fish predictors plus the 3 environmental predictors used in all analyses in two depth layers, the majority (45 out of 48) of the regressions were not significant (see Table 8 in Appendix). Only the mean zooplankton spectral intercept (estimated by OLS) was significantly positively related to the exponent b of the fish SS from trawling, and was positively related to TP and negatively related to chl a in the upper depth layer ( $R^2$ = 0.64: F= 5.5, df=9, p=0.01; see Figure 4). No similar correlations were found for the lower layer. Fish biomass (kg ha<sup>-1</sup>) based on hydroacoustics had a significantly negative effect on median body mass of potential fish prey taxa in the upper ( $R^2$ =0.3, F<sub>(11)</sub> = 4.8, p=0.049) and lower depth layers ( $R^2$ =0.53, F<sub>(11)</sub> = 12.69, p=0.004, see Figure 5).


**Fig. 4** Partial residuals of the dependent variable zooplankton SS intercept from the significantly related independent variables fish size distribution exponent b (a), mean TP (b) and chl a (c) concentration (both mg  $L^{-1}$ ) in the upper depth layer of Lake Stechlin



**Fig. 5** Partial residuals of the dependent variable median body mass of zooplankton taxa constituting coregonid prey and the independent variables fish biomass (kg ha<sup>-1</sup>) from hydroacoustic surveys in the upper (a) and lower (b) depth layers of Lake Stechlin

#### DISCUSSION

In our study we aimed to determine top-down and bottom-up drivers for zooplankton size distribution in the pelagic area of the mesotrophic Lake Stechlin during summer months across 13 years of sampling. We tested seven commonly used parameters to describe the zooplankton community size structure and density from several successive years, by expecting that potentially strong effects from fish size or biomass and the environmental predictors would become visible on all or many of the six zooplankton parameters. Surprisingly, however, we

found almost no effect of annual differences in fish size, biomass, TP, chl a and temperature on the zooplankton size structure. This result seems to be robust because we expressed the zooplankton size structure as linearly binned SS, as continuous SS and as size diversity. Furthermore, the fish size and biomass data were obtained by two independent approaches, midwater trawling and hydroacoustics. We conclude that feeding by the zooplanktivorous coregonids in Lake Stechlin does not affect the size distribution of the entire pelagic zooplankton community. However, the few significant regressions indicate that there is a limited top-down effect on the density and size of those zooplankton taxa that constitute the major prey of the coregonids.

Our analyses have shown that fish size distributions as based on the exponent b of the continuous SS obtained from trawling were significantly positively correlated with the spectral intercept of the zooplankton community in the upper layer of the lake. High b exponents indicate a dominance of larger fish in the size distribution. Therefore, years with a relatively high number of medium and large-sized fish (e.g., in 2014 and 2015) were associated with a high density of zooplankton organisms (reflected by the intercept of the zooplankton SS). In contrast, years characterised by numerous small fish (low exponent b, e.g. in 2012 and 2017) were associated with lower zooplankton densities. This positive relationship between zooplankton density and the contribution of larger coregonids to the size distribution may indicate that zooplankton density might be top-down controlled by fish feeding only in years with a dominance of small coregonids. Furthermore, a direct feeding effect of fish was reflected by the negative correlations between hydroacoustically estimated fish biomass and the median body mass of zooplankton prey taxa. These negative correlations were found in both the upper and lower layers. These results suggest that fish feeding might affect size structure and density of the zooplankton community, but with a stronger effect in the upper layers, and with a stronger effect on those cladocerans that constitute the prey of the coregonids (Schulz et al. 2003).

Cladocerans were more frequently found in the upper than in the lower water layer. Coregonids feed mainly during the day in the deeper hypolimnic layers where light intensity is sufficient to allow for selective feeding (Gjelland et al. 2009; Mehner et al. 2010) and while migrating between the lower and upper hypolimnion close to the thermocline at low light conditions during dusk and dawn (Scheuerell and Schindler 2003; Gjelland et al. 2009). Therefore, coregonids in Lake Stechlin perform diel vertical migration for efficient zooplankton feeding, as the great majority of the cladoceran zooplankton in Lake Stechlin concentrate between the

surface and 25 m depth (Kasprzak and Schwabe 1987). Our data were collected during summer months when the higher water temperatures that fish experience close to the thermocline, may result in higher daily basal energy requirements. It was already suggested by Mehner (2006a) that hungry juvenile coregonids prolong their stay in the shallower water layers, despite higher predation risk, to cope with the increasing energy demands during summer. Therefore, they may control the zooplankton density and size in the upper layers during years with a dominance of juvenile coregonids.

Previous studies in Lake Stechlin suggested that the top-down control of the zooplankton biomass by fish predation was unlikely, as trophic transfer efficiency between zooplankton and fish was determined to be relatively low (6%, Schulz et al. 2004). Although prey taxa dominated the upper layer in numbers, we found that prey and non-prey taxa contributed equal amounts of biomass to the zooplankton community in the upper layer. Furthermore, it was shown in a previous study that specifically in summer months pelagic coregonids feed preferentially upon Bosmina longirostris and B. coregoni (Schulz et al. 2003), whilst these taxa contribute only 9% to the total zooplankton community biomass in the upper layer. Therefore, even if they are eaten by fish, their removal has only a minimal impact on the size distribution of the entire zooplankton community. Even more drastically it can be seen in the lower layer, where prey taxa of coregonids likewise dominate in numbers but they contribute only by 28% to the biomass of the zooplankton community. In contrast, the much bigger Eurytemora lacustris, which is not fed upon by the fish, contributes 44% to the community biomass alone. The data obtained here support that the size distribution of the entire zooplankton community is not top-down controlled by fish feeding. There are signs of negative correlations between zooplankton prey size and biomass of smaller coregonids, but these effects are obviously not strong enough to induce traceable changes in the size structure of the entire zooplankton community. These results support that pelagic trophic cascades are weak in lakes with lower productivity (Elser and Goldman 1991; Persson and Diehl 1992; Sarnelle 1992; Mehner et al. 2008).

As the productivity of Lake Stechlin has increased during the last decade (see Figure 12 in Appendix), we expected that chl a and TP concentrations would likewise affect zooplankton size distributions across the years. However, we found only a weak positive effect by TP on zooplankton density (reflected by the intercept of the size spectra), whereas chl a was negatively correlated with the spectral intercept in the upper layer. This result is in part counterintuitive because we would have expected a positive correlation between zooplankton

resources (phytoplankton biomass expressed as chl a) and zooplankton density. However, a recent long-term study from Lake Stechlin found evidence for a decreasing efficiency in trophic coupling between zooplankton and phytoplankton caused by an increasing dominance of filamentous cyanobacteria in the phytoplankton community (Selmeczy et al. 2019). Cyanobacteria are a known inadequate food source for zooplankton (Gulati and DeMott 1997) and therefore their dominance reduced the resource use efficiency and biomass of zooplankton. This dynamics may explain the significant negative relationship of chl a and zooplankton spectral intercept found in the upper layer in our study. However, these correlations became only visible in the multiple regression when the exponent of the fish SS was likewise included. Therefore, another plausible explanation would be that in years with a dominance of small coregonids, the zooplankton density (primarily cladocerans) is diminished, and the lower cladoceran density cascades down to a higher phytoplankton biomass in the upper layer of Lake Stechlin. Overall, however, there is a long-term signal that the increasing TP concentrations may increase the zooplankton densities via bottom-up control. In a recent comparative study across more than 200 lakes it has been clearly shown that chl a concentrations are more strongly bottom-up correlated with fish production rates, than fish feeding rates affect chl a concentrations negatively in the sense of top-down control (Bartrons et al. 2020).

There are several insights from the results that might be important for food web studies beyond Lake Stechlin. Although coregonids are strictly planktivorous and may achieve high biomasses in deep lakes, they seem to have only a limited capacity to induce pelagic trophic cascades down to phytoplankton. There are two reasons for their weak predation effects. First, coregonids have a relatively small gape size, and hence prefer small zooplankton prey such as *Bosmina* spp. (Schulz et al. 2003). In turn, they do not feed upon the large calanoid and cyclopoid copepods, which often dominate in the colder hypolimnetic layers of deep lakes. This strong size and species selectivity prevents that the total zooplankton density is massively affected by coregonid predation. Second, there is a spatial disconnect between coregonids and their preferred prey. While the coregonids prefer the colder hypolimnetic zones with temperatures around 10 -12 °C and ascend into warmer water only during the night (Mehner et al. 2010), cladocerans grow best in the warm epilimnetic layers (Helland et al. 2007). Therefore, fish have only a limited time window during which they can feed upon their preferred prey. This short feeding period may explain why there is only a weak top-down effect of coregonids even on their preferred prey taxa.

Ultimately, we have to revise our expectation that zooplankton size distributions are sensitive to the feeding effect of fish and to environmental predictors. Although species- and sizeselective feeding of coregonids is likely and has effects on the densities of the preferred taxa, these effects do not translate into a statistically significant modification of the entire SS. Instead, the SS seems to be relatively robust against predation effects, and seems to reflect the lake-wide energy availability and transfer efficiency in the food web (Mehner et al. 2018). This suggests that the classical pelagic food chain from fish to phytoplankton is only part of the lake food web. Creating SS across the majority of the organismal groups in both pelagic and benthic habitats might therefore allow inferring the major drivers of food web configurations. Furthermore, additional information on phytoplankton size distribution and taxonomy would allow a better mechanistic understanding of the interaction between phytoplankton and zooplankton communities. In our study, we used exclusively the chl a concentration as an indicator for phytoplankton biomass. However, many zooplankton species feed in a size- and species-selective way. For example, juvenile daphniids usually avoid green filamentous algae, such as Ulothrix, whereas larger individuals include it in their diet (Chen et al. 2011). Shifts in phytoplankton composition and size structure, such as higher biomass of filamentous cyanobacteria induced by global warming (Selmeczy et al. 2019), may modify the strength of top-down effects of zooplankton on phytoplankton (Ersoy et al. 2017).

Our results are based on correlational evidence, which not necessarily allows implications of causal relationships. In particular, data on stomach content analyses or stable isotopes of fish would allow a better understanding of the strength of trophic links that ultimately affect the size distributions (Brose 2010; Boukal 2014). Furthermore, despite having included data from 13 successive years, in the framework of multiple linear regressions this is a low number of observations, and hence is associated with low statistical power (Hair et al. 2014). Accordingly, the overall surprisingly low number of significant multiple linear regressions here has to be considered cautiously. However, our study on pelagic trophic interactions and drivers of zooplankton SS may inspire others with significantly longer datasets to repeat a critical reconsideration of top-down and bottom-up effects on zooplankton size structure in stratified lakes.

#### ACKNOWLEDGEMENTS

We would like to thank the technical staff of the department Experimental Limnology for taking, analysing and curating the long-term environmental and zooplankton data from Lake Stechlin. This study was financially supported by a grant from the German Research Foundation to TM and SB (DFG, grant number Me 1686/7-1). SB was partially financed by a grant from the Spanish Ministry of Science, Innovation and Universities (grant no. RTI2018-095363-B-I00).



# Size spectra of pelagic fish populations in a deep lake – methodological comparison between hydroacoustics and midwater trawling

Lisa-Marie Braun and Thomas Mehner

Water, 13, 1559 (2021)

https://doi.org/10.3390/w13111559

#### ABSTRACT

Size spectra (SS) of the pelagic fish community in a deep lake were methodologically compared between net sampling by trawling and hydroacoustics across 12 years of sampling. Hydroacoustic SS were generated as based on either single-echo detections (SEDs) or tracked echo groups (TEGs) from 20 cross-lake transects. Trawl SS were obtained by a midwater trawl in four pelagic depth layers. All SS were derived from maximum likelihood estimations of the exponent b of a continuous fish body mass distribution. The arithmetic mean exponent b was similar for all methods, and there were no significant differences of b among the three methods across years. However, visual inspection indicated that the SS differed considerably between trawling and hydroacoustics in some of the years, primarily when high densities of 0+ coregonid fishes were strongly spatially aggregated and hence caught by the trawl. Accordingly, there was no correlation between SS generated by trawling and hydroacoustics. In contrast, SS generated by SEDs and TEGs were significantly correlated, indicating reliability and reproducibility of obtaining SS by hydroacoustics. The SS estimated by TEGs revealed a positive trend of exponents b over the years since 2005, potentially reflecting the recent eutrophication of Lake Stechlin, which may lead to higher fish growth rates. We conclude that hydroacoustics may help generating more precise SS of the pelagic fish community in our study lake than midwater trawling. However, truthfulness of SS estimates cannot be evaluated because of the inherent difficulty to determine the true densities and sizes of fishes in lakes.

Keywords: Size spectra; pelagic; single echo detections; target tracking; trawling; coregonids

#### INTRODUCTION

In aquatic ecosystems, size-based indicators are a well-established management tool to track ecosystem status and exploitation effects (Emmrich et al. 2011; Murry and Farrell 2014). Body size is an essential property of organisms, linked to physiological and ecological rates and processes, such as respiration, ingestion, reproduction (Marquet et al. 2005; Woodward et al. 2005), life span (Peters 1983; Calder 1984) and trophic interactions (Thiebaux and Dickie 1992). Furthermore, in aquatic communities body size dictates the functional role of an organism throughout its lifetime due to ontogenetic shifts (Trebilco et al. 2013).

Community size spectra (Sheldon et al. 1972) have been frequently used for understanding the status and structure of aquatic communities, as this concept represents energy flow through a community regardless of species identity. Size spectra (SS) describe the relationship between the logarithm of size and the logarithm of abundance (or biomass), which is usually expressed as linear regression (Sheldon et al. 1972; Kerr and Dickie 2001; Shin et al. 2005). The intercept of the SS reflects the overall abundance (or biomass) of the system and the slope mirrors the relative abundances of small and large organism (Ahrens and Peters 1991) and therefore functions as an indicator of trophic structure (Murry and Farrell 2014; Sprules and Barth 2016). Monitoring these spectral parameters offers the potential to reveal when ecosystems are experiencing external pressures, such as intensive fishing, eutrophication or climate change (Blanchard et al. 2005; Emmrich et al. 2011). Fisheries are usually size-selective and therefore may lead to a significant removal of large individuals from the system (Bianchi et al. 2000). The resulting changes in size structure are imperative for understanding effects on ecosystem structure. SS are a highly effective approach to summarize and compare the size structure of aquatic communities across years and between systems (Cottingham 1999; Cózar et al. 2003), since they signify the aspect of the system under pressure, including total biomass, specific size classes, or both (Sprules and Barth 2016).

Typically, aquatic net sampling methods, such as trawling and gill netting, have been utilized to assess SS of fish communities but these methods induce high mortality of fish and are labourand cost-intensive (Chopin and Arimoto 1995; Emmrich et al. 2011). Furthermore, net sampling is inherently size-selective and therefore may introduce bias in SS analyses (Bonvechio et al. 2008; Olin et al. 2009; Prchalová et al. 2011). In contrast, relevant hardware and software for scientific hydroacoustics have evolved rapidly in recent years (Simmonds and MacLennan 2008) and hence hydroacoustics provides a non-destructive and cost-effective alternative to estimate fish abundances (Shin et al. 2005). In theory, hydroacoustic methods also offer a less size-selective method than fishing to document SS of fish communities. This sampling method has proven useful in describing fish community SS, if the majority of fish are recorded within the acoustic beam and consequently measured as single targets (Wheeland and Rose 2016). However, the echo sounder system utilized and the methods of data processing and analysing affect the results and differ between studies and monitoring programs. Therefore, more studies are needed, which examine the applicability of hydroacoustics for generating size distribution of fish communities and give a baseline for a standardised method of data analysis for measuring SS (de Kerckhove et al. 2016).

The aim of this study was to methodologically compare the SS of a night pelagic fish community in a deep lake based on net sampling by midwater trawling and hydroacoustics over 12 years. Hydroacoustic SS were generated as based on either single-echo detections (SEDs) or tracked echo groups (TEGs). Trawl SS were obtained by conducting night-time hauls in four pelagic depth layers by a midwater trawl. The lake is dominated by coregonid fishes, which are known to disperse by diel vertical migration from dense deep water aggregations during the day to a more even spatial distribution over the entire water depth at night (Mehner et al. 2007). Therefore, coregonids are easily detectable as single echoes during hydroacoustic surveys at night, and can be caught by midwater trawling likewise. In concordance with SS theory, we expected to find a consistent decline in abundance of pelagic fish with increasing body size. Furthermore, considering previous studies on the reasonably good correspondence of fish biomass estimates between net fishing and hydroacoustic (Emmrich et al. 2010, 2012), and between echo integration and tracking (de Kerckhove et al. 2016; Draštík et al. 2017) we assumed that SS generated by all methods would also be reasonably well correlated. Finally, because Lake Stechlin has shown signs of accelerated eutrophication during the last years (Selmeczy et al. 2016; Braun et al. 2021), we expected that the size distribution would become shallower, reflecting faster growth rates of coregonids in response to higher primary production (compare Bartrons et al. 2020).

#### **MATERIALS AND METHODS**

#### Study site and sampling

This study was conducted in Lake Stechlin, located approximately 120 km north of Berlin (Germany). This mesotrophic lake covers about 4.25 km<sup>2</sup> with mean and maximum depths of 22.3 m and 69 m, respectively (see Figure 1a, (Koschel and Adams 2003)). A total of 13 fish species inhabit the lake (Anwand et al. 2003), but the pelagic fish community is dominated by two sympatric species of ciscoes, Coregonus albula and C. fontanae (more than 95% of fish abundance (Mehner and Schulz 2002; Helland et al. 2007)). Furthermore, the average stock exploitation rate by the single commercial fishery is 0.08 (Wanke et al. 2017), suggesting no strong effect of annual fish removal on fish abundance differences between years. We estimated counts and individual body wet mass (in g) of fish annually every June between the 6<sup>th</sup> and 29<sup>th</sup> from 2006 to 2019 using pelagic midwater trawl (n=12 years, data for 2016 missing due to net malfunction) and hydroacoustic surveys (n=12 years, data for 2007 missing due to malfunction of hydroacoustic equipment) simultaneously. The surveys were conducted during complete darkness starting 1 h after sunset. Pelagic midwater trawl surveys covering several depth layers could be conducted only in the deep central and northern basin (from here on central basin, CB) of Lake Stechlin. The morphometry of the lake (horizontal extension of certain depth layers per basin) is very variable (see Figure 1a), and hence hauls with minimum of 500 m towed distance in depths deeper than about 15 m could be realized only in one part of the lake. Therefore, to address potential spatial heterogeneity in fish distribution between the basins, we calculated hydroacoustics SS from either all transects (whole lake, WL) or only from the transects overlapping spatially with the trawl surveys (CB; see Figure 1b).



**Figure 1.** Bathymetric map of Lake Stechlin (a) and diagram with transects from hydroacoustic surveys of whole lake (WL; black), midwater trawling (grey) and with transects from hydroacoustic surveys in the central and northern basin (CB) that overlap with trawling transects (green, b).

#### Fish assessment - trawling

A pelagic trawl with 28/20/10 mm mesh size, 10 mm mesh size in the cod-end and a total length of 14.8 m (stretched on land) was utilized (for more details of the net construction, see Figure 2 in [26]). The net with an opening area of approximately  $10 \text{ m}^2$  (opening width 3.5 m) was towed by a boat (length 7 m, width 2 m), which was driven by a 60 hp engine over four longitudinal transects in the deepest lake basins. Trawling speed (mean  $\pm$  SD) was 6.5  $\pm 0.6$  km h<sup>-1</sup> (1.8  $\pm 0.2$  m s<sup>-1</sup>), while towed distance, as the product of trawling speed and trawling time, ranged between 500 m and 1600 m (mean 840 m) with an average towing time  $(\pm SD)$  of 7.8 min  $(\pm 1.9)$ . During each survey, a total of four hauls were conducted at approximately 12 m  $\pm$  0.65 m, 15 m  $\pm$  1.09 m, 25 m  $\pm$  2.08 m and 32 m  $\pm$  0.90 m (mean  $\pm$  SD) depth, whereby the two deeper hauls had shorter trawling times and slightly slower hauling speeds. Due to limited spatial extension of water layers with more than 35 m depth, deeper hauls could not be performed. The actual sampling depth was recorded with a diving computer attached on the trawl's head rope. The depth variability during each tow never exceeded 3 m. At the end of each haul, the trawl was quickly lifted by hydraulic winches at speeds comparable to the trawling speeds, thus preventing escapement of fish from the net. Fish were counted, and individually measured to determine total length (TL in mm) and body mass (wet mass, wm in gram). Only subsamples were measured and weighed when catches were too large. The number of fish per 1000 m<sup>3</sup> was estimated from the towed distance and the opening area of the trawl. Due to the shorter hauled distance in the deeper layers, the overall size distribution per year calculated as the total sum of all fish caught by the four hauls would have been biased towards the size of fish in the upper water layers. Therefore, we employed a weighting factor (WF) to calculate a weighted mean abundance and size distribution across the four depth layers. The WF was calculated as the ratio between the maximum volume fished by one of the four hauls in this year and the volume fished in the respective depth layer as:

$$WF = \frac{Maximum Volume (m^3) \text{ fished}}{Individual Volume (m^3) \text{ fished}}$$

The fish abundance from the individual hauls was weighted with the calculated WF in each year. Accordingly, the WF equals the abundance and size distribution per depth layer to identical fished volumes. Some size distribution analyses require fish numbers per size class as integers; then the weighting factor was rounded to the nearest half integer (see Table 1).

**Table 1.** Determination of rounded weighting factors (WF) for fish abundance (e.g. for 2009) from trawling in four water depths where the calculated WF was rounded to the nearest half integer to be used for continuous size distributions. In this example year the maximum volume  $(m^3)$  fished at 14 m depth was divided by the fished volume  $(m^3)$  in the other respective layers to determine the WF, which was then rounded to the nearest half integer.

Year	Depth (m)	Volume [m <sup>3</sup> ]	WF	Rounded (WF)
2009	14	15167	1	1
2009	20	10500	1.44	1
2009	32	5000	3.03	3
2009	40	8000	1.89	2

#### Hydroacoustic fish assessment

Hydroacoustic surveys were completed as a series of transects using a SIMRAD (Kongsberg) EY60 split-beam hydroacoustic unit (120 kHz, circular transducers, beam width 7° x 7°, pulse duration 128 ms, ping rate 3 pings s<sup>-1</sup>). The calibration was done with standard spheres provided by the manufacturer. Surveys were performed with vertical beaming along 20 transects (total distance about 12 km) across this tri-basin lake, with transect length ranging from 635 m to 1332 m (see Figure 1b). Among these 20 transects, nine were selected which overlapped with the area of the trawling surveys for the CB estimates of hydroacoustics SS. Some transects from the north basins were missing in 2006 and 2009 due to malfunction of the GPS. Data were stored in a computer, processed and analysed by the postprocessing Sonar5 Pro software (CageEye AS, Oslo, Norway).

#### Hydroacoustic data processing

The lower target strength (TS) threshold (as a measure of fish body length in dB) was set to -55 dB for the SED echogram corresponding to fish of an approximate total length of 4.2 cm and 0.42 g wm. Parameters for amplitude echograms were set 6 dB lower (-61 dB) to accept targets out of the half power edge of the sound beam. Echograms were manually cleaned of noise and non-fish echoes, while bottom detection was run automatically using the software parameter settings. A backstep margin of 2 m was used. The upper limit of the analysed echogram area was set to 1 m below the surface, while the bottom line was set as the lower limit. Tracked echo groups (TEGs) were generated using the automatic tracking algorithm in the software. Criteria for acceptance of SED and TEG parameters are summarized in Table 2. The TS (dB) of the targets was converted into fish total length (cm) and body wet mass (g) using the equation obtained for *Coregonus* spp. from Lake Stechlin by (Mehner 2006b):

(1) TL (cm) = $10^{\left(\frac{(TS+70.9)}{25.5}\right)}$ ,
(2) wet mass (g) = $0.00507 \text{ x} (\text{TL (cm)}^{3.088})$

<b>Table 2.</b> Single echo detection (SED) and tracked echo group (TEG) parameters used in Sor	1ar5 Pro.
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Parameter	Value		
Single echo detection (SED)			
Target Strength threshold	-55 dB		
Minimum target size	-80 dB		
Minimum echo length	0.5		
Maximum echo length	1.6		
Maximum gain compensation	3.0 dB		
Maximum angle standard deviation	0.80		
Tracked echo group (TEG)			
Minimum number of pings in track	3 pings		
Maximum gap between single targets	1 ping		
Vertical gating range	0.3 m		

#### Hydroacoustic data analysis methods

We compared two analytic methods of hydroacoustic data, SEDs and TEGs (Balk and Lindem 2017), with respect to their suitability to reflect fish SS. SEDs represent acoustic targets based on detection by one acoustic ping. Accordingly, this method may reject echoes from true fish or underestimate the true fish size if the target is not optimally positioned in the acoustic beam. In contrast, TEGs are observations of a single fish (i.e., SEDs) during subsequent echoes, combined by the tracking module if judged to belong to one individual fish. This approach reduces the potential bias of SEDs with respect to echo detection and size estimates (Wheeland and Rose 2016). However, if fish are not fully covered by the hydroacoustic beam, their TS and hence true length and mass can be underestimated. Therefore, we used the maximum TS per fish recorded during TEG detection to account for this potential bias.

#### Fish size distribution

To visualise the size distribution of fish based on the entire lake across all 12 sampling years, a body weight (g) frequency distribution for each survey method was calculated. Only fish within a size range of 6.5 - 17.7 cm were regularly caught by trawling. Thus, to facilitate proper correspondence in the size ranges between trawling and hydroacoustics, our analyses included

only medium-sized fish that were recorded by both methods comparably well, whereas fish < 6 cm (1 g) and > 18 cm (50 g) were excluded.

#### Size Spectra fitting

We compared the SS of the pelagic fishes in the size range of 1 - 50 g body wet mass among the three methods (trawl, SED, TEG) across the entire lake. To account for potential spatial heterogeneity in fish distribution, we tested if hydroacoustic based SS estimations differed significantly between CB and WL. The maximum likelihood estimation (MLE) method was utilized, which is the recommended method for fitting continuous fish size distributions (Edwards et al. 2017). The exponent of the individual fish size distribution (b) estimated by MLE coarsely corresponds to the slope of linear SS, as estimated by ordinary least squares. Maximum likelihood estimates of b require numerical maximisation of the log-likelihood function (Page 1968; Edwards 2011), while the  $x_{min}$  and  $x_{max}$  are the minimum and maximum observed body mass values per method and survey year in the MLEs. The abundance SS per method were expressed as a bounded power law (PLB) distribution that was fit across the range of body mass values utilizing the MLE for b. The fitted PLB model was visualized by a red curve superimposed on the continuous size distribution for each year and method individually (see Appendix Figures A1 - A9). The 95% confidence interval for exponent b for each method and sampling year was calculated utilizing the profile likelihood ratio test (Hilborn and Mangel 1997). The estimate of exponent b per year was tested for normal distribution for each method among years with a Shapiro-Wilk normality test (Shapiro and Wilk 1965). Furthermore, we assessed whether the across-year mean estimates of b differed significantly between trawling, SEDs and TEGs in the WL using a Kruskal-Wallis H test. Pairwise Spearman rank correlations were calculated to examine whether there was correspondence of the b values per year from the individual methods and between WL and CB. All statistical analyses and plots were conducted with the software R (R Core Team 2020). Specifically the MLE's were performed by the provided R code and package (sizeSpectra) from (Edwards et al. 2017, 2020).

#### RESULTS

Over the 12 years from which samples could be compared, we determined the size of 8,170 coregonids caught by trawling (222 to 1,400 per year). The numbers of targets recorded by hydroacoustics were 127,726 SEDs (1,520 to 16,531 per year) and 53,922 TEGs (1,626 to 7,207 per year) across the WL and 89,598 SEDs (873 to 16,516 per year) and 40,338 TEGs (1,432 to 6,140 per year) in the CB. In contrast to fish size distributions based on hydroacoustic surveys, we found that trawl catches do not represent small and large fish very well (see Figure 2). Therefore, all further stated results are based on fish between 1 g and 50 g body weight.

The estimates of 'b' were found to correlate significantly between the WL and CB based on SED (Spearman's  $r_s = 0.98$ , p <0.0001) and TEGs (Spearman's  $r_s = 0.98$ , p <0.0001; see Tables 3 and Figure 3, Appendix Table A1). Therefore, spatial heterogeneity in fish distribution between the lake basins was minor, and we base all subsequent comparisons on the SS from all 20 hydroacoustics transects.

The estimated arithmetic mean of exponent b ( $\pm$  SD) across the 12 sampling years was lowest for SED (WL:  $\bar{x} = -0.73 \pm 0.27$ ), followed by trawling ( $\bar{x} = -0.56 \pm 0.72$ ) and was highest for TEGs (WL:  $\bar{x} = -0.44 \pm 0.24$ ). Due to strong among-year differences, the exponent b was not significantly different among the three methods in the WL across the years ( $\chi^2$  (2)= 4.22, p=0.12). However, there were substantial differences in 'b' estimates between the three methods in some years, with the highest variability found for SS based on trawl catches. Linear regression showed that there was no directional change in exponent b across survey years by trawl and SED (trawl: R<sup>2</sup>= -0.09, F<sub>(10)</sub>= 0.03, p=0.84; SED: R<sup>2</sup>=0.02, F<sub>(10)</sub>=1.667, p=0.27; TEGs: R<sup>2</sup>=0.21, F<sub>(10)</sub>= 3.93, p=0.07; see Figure 4), but there was a weakly significant trend toward shallower b over years when plotting TEGs. Furthermore, the estimates of 'b's did not correlate between trawl catches and TEGs ( $r_s = 0.24$ , p=0.44) or between trawl catches and SEDs (Spearman's  $r_s = 0.43$ , p=0.17). In contrast, the exponents from both hydroacoustic methods, SED and TEGs, were found to correlate significantly (Spearman's  $r_s = 0.67$ , p=0.02, see Figure 5).



**Figure 2.** Frequency distributions based on absolute numbers of all sampled fish within 5 g body weight (g) size classes from hydroacoustic surveys, including single echo detections (SEDs, A), tracked echo groups (TEGs, B) and pelagic midwater trawl catches for survey years between 2006 and 2019 (excl. 2007 and 2016) in Lake Stechlin based on transects of the whole lake (WL).

**Table 3.** Results for size spectra of fish with 1 - 50 g body weight fitted with maximum likelihood estimation with the mean ( $\pm$  SD), minimum and maximum of exponent b for each method, including trawling and hydroacoustics based on single echo detections (SEDs) and tracked echo groups (TEGs) for 2006-2019 (excl. 2007 and 2016) for the whole lake (WL) and only transects that from hydroacoustic surveys that overlap with trawl catches in the central lake basin (CB).

· · ·	Exponent	b		
Method	mean	SD	Min	Max
Trawl	-0.56	0.72	-2.00	0.41
$\mathrm{SED}^{\mathrm{WL}}$	-0.73	0.27	-1.37	-0.36
TEG <sup>WL</sup>	-0.44	0.24	-1.2	-0.05
SED <sup>CB</sup>	-0.63	0.28	-1.25	-0.16
TEG <sup>CB</sup>	-0.45	0.25	-1.03	-0.08



**Figure 3.** Scatter plot and Spearman rank correlation between estimates of 'b' from the whole lake (WL) and central basin (CB) based on single echo detections (SEDs, A) and tracked echo groups (TEGs; B).



**Figure 4.** Size spectra exponents b with lower and upper bounds of the 95% confidence interval of b indicated with error bars, and linear regression line from a weakly significant trend (C) to check for a temporal change of size distributions of fish between 1 - 50 g body weight for survey years between 2006 and 2019 (excl. 2007 and 2016).



**Figure 5.** Scatter plot and Spearman rank correlation of exponents b between trawling and hydroacoustic tracked echo groups (TEGs; A), trawling and hydroacoustic single echo detections (SEDs; B) and between hydroacoustic SEDs and TEGs (C).

#### DISCUSSION

In our study we aimed to determine whether the estimated SS of the night pelagic fish community in Lake Stechlin differed between net sampling by midwater trawling and hydroacoustics as based on either SEDs or TEGs across 12 years of sampling. The arithmetic mean exponent b did not show significant differences of the fish community SS if averaged across years. However, there were considerable differences of the exponent b among the three methods for some years, often coinciding with higher densities of coregonid fish juveniles. Accordingly, the SS were not correlated between trawling and both types of hydroacoustics data, but correlated between SEDs and TEGs. Here, it could be argued that this may be due to

the fact that the TEG data stream is a subset of the SED data stream, therefore missing statistical independence and resulting in inflated r and p-values in the Spearman rank correlation. The SS obtained by TEGs showed a positive trend over the sampling years, potentially reflecting faster growth of the coregonids in response to recent eutrophication of Lake Stechlin.

When comparing the hydroacoustic methods, the overall number of TEGs was substantially lower than the number of recorded SEDs. This can be expected because TEGs are composed of several successive SEDs, which are considered as coming from separate fish in SED-based analyses. The exponent b of the SS calculated from SEDs was always more negative than that obtained by TEG detection, indicating a steeper spectral slope and therefore less large relative to small fishes detected by SEDs. These differences in size spectral estimates between both methods occurred also in years when the fish community was dominated by small fish, such as in 2008, 2011, 2017 and 2019. They suggest that the size distribution of SEDs may be biased towards weaker echoes, certainly because even larger fish are often not ideally positioned in the acoustic beam and hence produce echoes weaker than predicted by the true fish length. Using the maximum echo strength from all successive SEDs within a track partly corrects this bias. Accordingly, the average b from TEG detection was the highest among the three methods, indicating that the size distribution of maximum SEDs per track includes a higher proportion of larger fish than obtained by the two other methods. Specifically fish catches from trawling are known to underestimate large fishes, which is attributed to an increased swimming speed with increasing body size (e.g. (Peck et al. 2006)) relative to the operation speed of the trawl. Furthermore, (Emmrich et al. 2010) demonstrated that the mean swimming speed of the largest vendace (e.g. 2.0 m s<sup>-1</sup> for a 20 cm fish, Schmidt 2009) in the trawl mouth is faster than the mean towing speed (1.8 m s<sup>-1</sup>) performed during trawl surveys. In principle, only hydroacoustic estimates allow for an unbiased measure of fish SS over a wide size range, while also providing insights into fish density over the entire water column, both which are not possible with trawling. Therefore, by considering the biases of the other methods, the TEG approach can be considered being the most reliable method with respect to fish size distributions in Lake Stechlin because it avoids both the size selectivity of net fishing with respect to larger and faster swimming fish and the size bias of SED distributions.

In a study similar to ours, (de Kerckhove et al. 2016) compared pelagic fish SS obtained by netting methods with those obtained by hydroacoustics. They found substantial differences in the frequency of single size classes between net catches and hydroacoustics. These authors furthermore compared the size distributions between echo counting and echo integration, both based on a tracking algorithm that combined single SEDs into a track for one fish. SS from

echo counting were constantly shallower than those from echo integration, explained by the effects of target co-incidence, which leads to an overestimation of the size and numbers of large and underestimation of small fish when fish co-occur in denser aggregations. In Lake Stechlin, the difference between echo counting and echo integration might be less prominent because coregonids strongly disperse spatially while ascending into the upper hypolimnion during the night (Mehner et al. 2007). Therefore, fish shoals are rare at night and the vast majority of fish are recorded as single echoes. These two studies together suggest that hydroacoustic methods may generate reliable SS, in particular if based on TEGs to combine several successive echoes into one trace.

It is not surprising that the size distributions between net catches and hydroacoustics differed, in particular in years when the proportion of small coregonids was high. The exponent b of the SS from trawling was lowest in the year 2017 (-2.0), when we caught an unusually high number of  $0^+$  coregonids in the mass range of 1-3 g just in one haul. We do not know the reason for the strong spatial aggregation of these young fish, but it was obvious that this aggregation was not comparably recorded by the 12 km of hydroacoustic transects from the entire lake because the exponents b of hydroacoustics methods in 2017 were within the range observed also in the other years. Therefore, the exponent b differed most strongly between the methods in this year, and the correlations among the methods would have been much stronger without the 2017 data pairs. Coregonids are well known for strongly varying year-class strengths in response to annual differences in temperature successions of the lake (Helminen and Sarvala 1994; Auvinen et al. 2000; Viljanen et al. 2004; Mehner et al. 2011). Therefore it is likely that monitoring the fish community by trawl net catches as conducted in Lake Stechlin may overestimate the densities of certain size classes if these are spatially aggregated. Due to the morphometry of the lake, trawling can be conducted only in a limited part of the lake (mainly in the central and north basins); hence one could argue that this method is more prone to biases from local aggregations than hydroacoustics, which records the fish density and size all over the lake. However, SS based on transects from only the CB have shown that they do not differ significantly in comparison to estimates of b from the entire lake in individual years. Therefore, hydroacoustics do not reveal any systematic differences in fish size among basins of Lake Stechlin.

The arithmetic mean of the exponent b across all methods was about -0.5. It is difficult to compare this value with SS estimates obtained in other lakes (Kerr and Dickie 2001; Wheeland and Rose 2016). First, we calculated SS as based on fish mass, which have a systematically shallower slope or exponent than those based on fish length (Sprules and Barth 2016). Second,

instead of log-binning, we applied continuous size distributions, by assuming that this approach fits the often curvilinear size distributions (Emmrich et al. 2011; Arranz et al. 2016; de Kerckhove et al. 2016) better than linear SS. However, the exponent b of these continuous distributions is not an exact equivalent of the slope of log-linear size distributions (Edwards et al. 2017). Third, the pelagic fish community in Lake Stechlin is essentially composed of two sympatric coregonid species. In contrast, community SS of fish should ideally include at least both prey and predator species, and may combine prey species with differing feeding modes (e.g., planktivores and benthivores). Only if predator-prey interactions are directly included into the size spectrum, can theoretical assumptions about the slope of log-linear SS be applied because these are based on bioenergetics principles (Peters 1983). For example, if severe predation by numerous piscivorous fishes in Lake Stechlin reduced the proportion of small coregonids in the pelagic area of Lake Stechlin, the slope (or exponent) of the size spectrum would become shallower through the lower number of small (prey) and the higher number or large (predator) fishes. However, earlier studies have shown that the density of piscivorous predators in the pelagic area of Lake Stechlin is very low (Mehner et al. 2010). Therefore, there is no massive predation on the coregonids.

Although no significant trend was observed, the estimates of exponent b based on TEGs became less negative during recent years, indicating that the size distribution of coregonids has gradually changed. This trend was not obvious in the exponent b from the trawl catches, but we indeed recorded a higher number of larger coregonids (>30 g) in trawl catches in recent years and found single individuals with more than 50 g not recorded in any of the previous years since the start of monitoring in 2005. These changes in size distribution may reflect an enhanced growth rate of coregonids, likely caused by the recently accelerated eutrophication of Lake Stechlin (Braun, Brucet and Mehner, 2021). Furthermore, Braun et al. (2021) revealed that hydroacoustically determined fish abundances were negatively correlated with zooplankton taxa forming the diet of the coregonids, whereas no such correlations were found for fish biomasses as obtained by trawling. This could indicate that hydroacoustics may reflect the actual state, including abundance, biomass and size distribution of the fish community better than trawling, allowing for more reliable insights into ecological interactions. More detailed explorations of trophic interactions and the consequences of enhanced eutrophication on Lake Stechlin food webs are necessary, but our hydroacoustic records may be a helpful tool to document the effects of environmental change on the population dynamics of the coregonids in Lake Stechlin.

#### CONCLUSIONS

In conclusion, hydroacoustic methods allow for a faster and more efficient assessment of the pelagic fish community in the deep Lake Stechlin, compared with the monitoring by trawl catches. In contrast to net sampling, hydroacoustics do not induce fish mortality, and larger and shallower areas of the lake can be sampled systematically, while not underestimating large fishes as trawling does. Effects of eutrophication of Lake Stechlin in recent years on fish growth rates were exclusively reflected by hydroacoustic methods. Reliable SS can be obtained from hydroacoustic records (see also de Kerckhove et al. 2016), which may complement SS as obtained from net fishing. These records may help detect and interpret environmental changes occurring in this lake. However, we have to admit that only the accuracy of pelagic community size distributions can be improved if hydroacoustics is applied. Currently, there is no way to evaluate the truthfulness of either fishing or hydroacoustics with respect to their estimations of fish size distribution. Ground-truthing of fish densities and size distributions in lakes is still one of the unresolved challenges in fish ecology and management (Kubečka et al. 2009).

Acknowledgments: We would like to thank Alex Türck, Jan Hallermann, Asja Vogt, Christian Helms, Kathrin Jaeschke, Jeanette Völker and several doctoral students who supported the monitoring of Lake Stechlin fishes over the years.

**Author Contributions:** Contributions of individual authors are follows: Conceptualization, LMB, TM; methodology, LMB, TM; formal analysis, LMB; writing—original draft preparation, LMB.; writing—review and editing, TM; visualization, LMB. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was financially supported by a grant from the German Research Foundation to Thomas Mehner (DFG, grant number Me 1686/7-1).

**Data Availability Statement:.** All data are curated and stored in databases of IGB, and can be made available on request to the authors. Long-term monitoring data of Lake Stechlin are available at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries Freshwater Research and Environmental Database (<u>https://fred.igb-berlin.de/).</u>

**Conflicts of Interest:** The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

### **Chapter 4**

## **Coral reef fish size spectra and structural complexity in relation to different level of anthropogenic disturbances**

Braun, L.M., Belmaker, Y., Buba, H., Gavriel, T., Lazarus and M. Mehner, T.

Manuscript in preparation for submission in Marine Biology

#### ABSTRACT

The importance of habitat complexity as a key driver for ecological processes in marine ecosystems has been recognized. Increasing global reef degradation caused by climate change and other direct and indirect anthropogenic disturbances pose a great threat on these fragile systems. Therefore, understanding the link between coral reef fish assemblage and their physical habitat and the effect of human disturbances is critical. Particularly to predict responses of coral reefs and fish communities to increasing anthropogenic threats and inform management accordingly. In this study, we examined the fish community size distribution and the level of reef structural complexity, as well as the relationship of both variables among coral reefs experiencing different levels of exposure to human disturbances in the Gulf of Aqaba, Red Sea. SCUBA visual census surveys of five reef sites along the coastline of Eilat, Israel, were conducted in 2018 and 2019. Five indices of habitat complexity recommended for the Red Sea were utilized to characterize the structural complexity of the reefs along 25 m x 5 m belt-transects. These data were collected together with estimates of fish counts and fish total body length (cm). Reef fish community size distribution was described with size spectra (SS), estimated by maximum likelihood to determine the SS slope. The SS slope and structural complexity indices were compared among five sites of differing exposure to touristic activities on the reef. The relationship of SS slope and structural complexity were also examined among these survey sites. We found that the fish community SS slope exhibited no significant difference among the survey sites. The complexity index rugosity was significantly higher at the two sites least exposed to human disturbances. The SS slope - complexity relationship at these best protected sites was significantly negative, indicating an association of higher complexity with steeper spectral slopes. This association fits with previous findings from reefs around the globe. A consistent pattern of fish community SS slope and structural complexity in relation to anthropogenic disturbances was missing. Overall our findings indicate that the level of anthropogenic disturbances is not the exclusive driver of coral reef structural complexity and fish assemblage. Other habitat characteristics, such as geomorphological features and reef habitat zonation may require further consideration in studies on the relationships between reef structural complexity and fish size distribution.

Keywords: Size spectra, coral structural complexity, anthropogenic disturbances, ecology

#### INTRODUCTION

Global degradation of coral reef systems is concerning, as these are one of the most productive ecosystems on earth with high importance for food security and the provision of other essential ecosystem services to millions of people (e.g. Moberg and Folke, 1999). However, global warming-induced coral bleaching together with other anthropogenically induced factors cause coral mortality and loss of three-dimensional habitat structure (Hoegh-Guldberg 1999). Numerous coral reef fish are site-attached and reliant on live coral cover (Belmaker et al. 2009). The physical characteristics of an individual's habitat are an essential driver for the ecological processes in the entire community (Airoldi and Balata 2008; Rogers et al. 2014; Alvarez-Filip et al. 2015). Specifically, the three-dimensional structure of coral reefs is known to shape fish communities; and structural complexity was found to exhibit a positive relationship with abundance, biomass and species diversity of reef fishes (Luckhurst and Luckhurst 1978; Gratwicke and Speight 2005; Hoegh-guldberg and Bruno 2016; Ferrari et al. 2018; Lazarus and Belmaker 2021). Reef fish abundance can be predicted by reef structure at spatial scales stretching from the size of single coral colonies (Holbrook and Schmitt 2002) to scales of over 100 meters (Purkis et al. 2008). Various mechanisms explain the effect of coral reef structural complexity on the fish community, including (i) the provision of niche space (Holbrook and Schmitt 2002); (ii) the provision of prey refugia relevant for predator-prey interactions (Steele 1999); (iii) increased food availability for predators and prey (Stewart and Jones 2001; Vergés et al. 2011); (iv) and also provision of shelter from physical stress, such as water flow (Johansen et al. 2008) and ultraviolet radiation (Kerry and Bellwood 2012).

Structurally complex coral reefs are characterised by numerous caves or overhangs or vertical reliefs. It was found that the fish abundance is directly affected by the utilization of appropriately sized crevices as prey refugia (Shulman 1985; Hixon and Beets 1993). A reduced mortality rate results in disproportionally high numbers of fish in certain size classes (Rogers et al. 2014). Lower structural complexity negatively impacts particularly small-bodied fish (Wilson et al. 2010). Coral reef sites with low complexity were found to have fewer small-bodied fish in the Seychelles (Graham et al. 2009), Fiji (Wilson et al 2010), Cozumel (Alvarez-Filip et al. 2011) and Bahamas (Rogers et al. 2014). Alarmingly, habitat degradation is suggested to even magnify effects of fishing on coral reefs as increased exploitation reduces large-bodied target species, while habitat loss leads to a reduced abundance of smaller juveniles

and prey individuals that commonly replenish stocks and provide food resource's for predatory fish (Wilson et al. 2010). Food web models indicate that the loss of coral reef structural complexity resulting from declining coral live cover and density (Alvarez-Filip et al. 2009) may initiate a three-fold reduction of fisheries productivity (Rogers et al. 2014). These trends highlight the great importance to halt, and even reverse, the loss of reef architecture. Hence, this topic has been a key focus of coral reef ecology research and conservation efforts in the past decades (e.g. Luckhurst and Luckhurst 1978; Graham et al. 2009; Stella et al. 2011; Rogers et al. 2014; Richardson et al. 2017).

The ultimate causes of live coral cover loss and coral reef degradation in most regions of the world are not clear. Global stressors, such as climate change, as well as local stressors, including overfishing, coastal pollution and other symptoms of increasing human population density are thought to impact coral reef systems (Wilson et al. 2008b; Jackson et al. 2014). An important local factor, the impact of recreational activities on the 3D coral reef structure and therefore fish assemblage is still relatively unexplored. Direct and indirect factors caused by coral reef-related tourism activities are suggested to negatively impact reef health (Eastwood et al. 2017) mainly through e.g. anchor damages, garbage accumulation, sedimentation or diving and snorkelling activities (Dixon et al. 1993; Hawkins et al. 1999; Cope 2003; Hawkins et al. 2005; Lamb et al. 2014). Numerous studies have documented the frequent breakage and damage of corals through divers who collide with the reef (e.g. Harriott, Davis and Banks, 1997; Hawkins et al., 1999; Austin and Tratalos, 2001; Walters and Samways, 2001). The extent of destruction was found to be directly related to the intensity of site use by divers (Dixon et al. 1993; Hawkins et al. 1999; Barker and Roberts 2004; Hawkins et al. 2005). Boat anchoring damage in the British Virgin Islands significantly impacted reef health, as frequently anchored sites were approximately 60% less structurally complex and supported less than half as many fish as rarely anchored sites (Flynn and Forrester 2019). These results are alarming considering the economic importance of tourism, on the one hand, and fish production for livelihoods for millions of humans around the world, on the other hand. Therefore, a good mechanistic understanding of associations between reef fish assemblage and habitat structure and the role local stressors play are required to effectively protect and manage coral reef systems and the valuable services they provide.

Assessing the influence of physical habitat characteristics on fish assemblage in ecologically complex systems, such as coral reefs, can be very challenging (Jennings et al. 1999). However,

size-based approaches that generalize across species but preserve connections to communitylevel characteristics offer potent methods to examine ecological structure and the effects of exploitation or changes of environmental characteristics (Jennings and Dulvy 2005; Nash and Graham 2016). A commonly employed metric of body size distribution is the size spectrum (SS), which describes the distribution of individuals across body sizes regardless of taxonomy (White et al. 2007; Sprules and Barth 2016). Typically, abundance exhibits a negative linear relationship with body size on logarithmic axes, also called a power-law distribution (White et al. 2007). This means that with increasing body size the abundance of individuals decreases geometrically in a community (Rice and Gislason 1996). The size spectrum slope reflects the relative distribution of body sizes in a community where a shallow slope indicates a relatively high number of large relative to small bodied individuals. In marine systems, size spectra parameters were traditionally utilized as indicators for ecosystem-level changes, mainly driven by anthropogenic activities. An example is fishing impacts on fish assemblage (Blanchard et al. 2017) where particularly large-bodied individuals are targeted and their reduction is reflected in a steeper SS slope (Graham et al. 2005). Similarly, lower coral reef structural complexity was often associated with less steep SS slopes, principally a result from a reduced abundance of larger fish (Wilson et al. 2010). In contrast to other size-based metrics, such as mean fish length, SS slope is considered more robust and less sensitive to the number of very large fish.

In this study, we aimed to assess both the habitat structural complexity of five coral reef sites and the SS slope of fish communities; and their relationship among coral reef sites that experience different levels of anthropogenic disturbances. The coral reefs studied span from the north to the south of the coast of Eilat, Israel, in the Gulf of Aqaba, Red Sea. Eilat's relatively small reef area (< 12 km) experiences one of the highest known frequency of recreational diving anywhere in the world (Meshi and Ortal 1995; Wilhelmsson et al. 1998). Two sites in the north are not protected and in closest proximity to the city of Eilat and its harbour. The other three sites further south are protected within the Eilat Coral nature reserve with limited access for visitors. We examined reef structural complexity with five different indices that characterise the reef architectural features from small-to large-scale, including newly described structural complexity indices proven useful in the Red Sea (Lazarus and Belmaker 2021). We hypothesised that differences in habitat structural complexity and fish community SS slope between sites will correspond to the level of anthropogenic disturbances of the sites. The SS-slope complexity relationship will correspond to the site specific level of touristic usage and better protected coral reefs will exhibit a significantly higher structural complexity, reflected by a relatively higher proportion of small relative to large fish, i.e., a steep slope of fish SS.

#### **MATERIALS AND METHODS**

#### Study site and sampling

The study was conducted at five sites along the Israeli coastline in the northern Gulf of Aqaba, in Eilat (see Figure 1) between May and July in both 2018 and 2019. The survey sites span from the north of Israel's coastline to the south, and differ in protection status and the level of anthropogenic disturbances. Generally, the fringing reef along the Israeli coastline is easily accessible from shore for swimmers, snorkelers and divers. Because of the ease of access, Eilat's coral reefs are among the most heavily visited with  $\sim 6$  million tourists annually and >300,000 divers per year along the entire 12 km coastline (Tynyakov et al. 2017). The two survey sites in the north, Dekel and Katza, are more exposed to human activities due to their close proximity to the city of Eilat and commercial ports. The survey sites further south are protected within the Eilat Coral Beach Nature Reserve since 1964 and managed by the local Nature and Parks Authority. The survey sites differ in their level of exposure to touristic activities (e.g. number of divers and snorkelers) along a gradient. Particularly sensitive areas, such as the reef table and the core parts, as at Japanese Gardens, are considered closed with prohibited or restricted access for visitors (Israel Nature Parks Authority 2021). The sites differ in their level of exposure to touristic activities (from best to lowest protection): Japanese Gardens, Katza, IUI, Reserve A and Dekel (see Table 1). Although Katza is not included in the officially designated nature reserve, it can be considered very well protected because it was closed to the public until 2017. This reef requires a boat to reach as it is further away from shore and therefore not often visited in comparison to the other sites.

The surveys along 65 transects (17 transects in 2018 and 48 transects in 2019) within the five sites were done with SCUBA equipment during the day between 9 am and 7 pm. Only continuous reef was sampled. Fish species were identified and their counts and body size (TL, total length) estimates recorded along each 25-m x 5 m belt-transect (Brock 1954) with an upper boundary of approximately 5 m above the bottom. Schooling and cryptic taxa were excluded as they exhibit a greater risk to be over - or underrepresented.





**Table 1:** List and description of studied survey sites inside and outside of the nature reserve in the northern Gulf of Aqaba with an indication of the level of protectiveness from anthropogenic disturbances, such as touristic activities (1-5 = high to low protection status) and the number of surveyed transects on each site

Survey site	Level of Protective	Reserve	Transect No.	Description
Dekel	5	Out	8	<ul> <li>most northern site, closest to the touristic city of Eilat</li> <li>reef has never been protected from human disturbances</li> <li>close proximity to commercial ports and diving centres</li> <li>shallow reef consists of coral knolls on a sandy slope</li> <li>consistent reef starts at 18 m depth</li> </ul>
Katza	2	Out	14	<ul> <li>Some recreational fishing from shore</li> <li>currently inactive pier that was used for pumping oil from tankers</li> <li>open for diving and swimming since 2017</li> <li>relaxed sandy slope with coral knolls</li> <li>dolphin site – touristic activities</li> <li>fringing reef in deeper parts</li> </ul>
Reserve A	3	In	11	<ul> <li>the most northern part of the nature reserve</li> <li>touristic usage</li> <li>fringing reef site with a reef table</li> <li>patchy sandy parts and continuous reef at 15 m depth</li> </ul>
Japanese Gardens	1	In	14	<ul> <li>best-protected site, as parts are restricted to a pre-set number of visitors per day to preserve the reef</li> <li>continuous reef</li> </ul>
Interuniversity Institute for Marine Sciences in Eilat (IUI)	4	In	18	<ul><li> continuous fringing reef site</li><li> most southern site of the nature reserve</li></ul>

Structural complexity of the reefs was quantified using a two-dimensional description of the sea floor, by performing depth measurements along the same 25 m x 5 m belt-transect to create a digitally recorded bottom profile with a water level data logger (Onset HOBO). The collected information was then expressed as five different indices of structural complexity for each transect that characterise the reef architectural features from small-to large-scale, including newly described structural complexity indices proven useful in the Red Sea (Lazarus and Belmaker 2021). The indices included are rugosity, structural richness, structural evenness, vertical relief and free space. These indices describe different aspects of the reef structure and refer to three different resolutions of the transect, including (i) entire transect, for which the complexity is averaged using all measurements along the transect (index: rugosity); (ii) extreme elements, referring to extreme configurations along the transect (indices: vertical relief and free safe space); and (iii) heterogeneity of elements within the transect, referring to complexity generated by physical elements that comprise the transect (indices: structural richness and structural evenness; see Table 2). For two of the 65 transects it was not possible to determine functional richness and functional evenness, as the necessary information was not collected. In other studies examining coral reef structural complexity, often only one or two indices are included. The most frequently employed measure is rugosity, which is defined as the ratio between the length of the reef contour and the linear distance between the bottom profile start and end points. However, this index does not account for the spatial arrangement of complexity-generating elements or the heterogeneity of elements within the transect and extreme measurements of complexity. Therefore, a highly rugged contour may exhibit the exact same rugosity index as a flat contour. Recent evidence suggests that one single index of complexity, such as Rugosity, may not be sufficient to describe reef structural complexity proficiently and explain variance in fish community assemblage (González-Rivero et al. 2017). Instead numerous measures at differing scales are recommended that reflect different aspects of the reef structure affecting the fish community.

Complexity Index	Description	Ecological Implications
Vertical Relief	Depth range	<ul> <li>Vertical relief is a proxy for large-scale depth changes within the profile,</li> <li>large depth range may indicate an area with shelters</li> </ul>
Rugosity	The degree to which the bottom profile is different from a straight line	<ul> <li>high rugosity indicates a heterogeneous profile,</li> <li>strongly affected by extreme values</li> </ul>
Free Safe Space	Amount of concealed area	- high free safe space indicates more concealed area for fish to live in
Structural Richness	Trait range of physical elements	- more heterogeneous physical elements in the bottom profile are suggested to provide a wider range of micro- habitats
Structural Evenness	Regularity of physical elements	<ul> <li>less regular differences among elements within the bottom profile are reflected in lower structural evenness,</li> <li>distinct elements providing more micro-habitat</li> </ul>

**Table. 2.** Descriptions and ecological implications of the five structural complexity indices utilized in this study (Source: content adapted from Lazarus and Belmaker, 2020)

#### **Data treatment and analyses**

The body mass of individual fishes was calculated using the standard species-specific length weight conversion equation (from cm to g), W=aL<sup>b</sup>, where W is mass, L is length (in cm), and a and b are species-specific parameters obtained from FishBase (Froese and Pauly 2000). Only fish above 8 cm total body length were included in the analyses, as for smaller fish the estimates of size are not reliable (Ackerman and Bellwood 2000). SS slopes of coral reef fish communities were calculated by applying maximum likelihood estimation (MLE; Edwards et al., 2017). More specifically, the "MLE method based on binning" was used (Edwards et al. 2020), which is recommended for calculating continuous SS based on 1 cm size classes while accounting for uncertainty in estimated fish mass after converting from body length. Here, a bounded power-law distribution, more precisely the abundance density function, was employed to estimate the SS exponent b (hereafter referred to as SS slope) and the standard error of each slope. A steeper SS slope (i.e., a more negative b), indicates fewer large-bodiedbodied fishes relative to small-bodied fish and/or more small relative to large individuals (e.g. (Daan et al. 2005; Petchey and Belgrano 2010). Size spectra slopes were estimated (Vidondo et al. 1997; Edwards 2008; Edwards et al. 2017) for each transect and the jointed exponents from all 65 transects were tested for homogeneity of variance and normality using Levene's (Levene 1960) and Shapiro Wilk tests, respectively (Shapiro and Wilk 1965). The range of fish counts among the 65 transects included in the analyses was relatively high (n = 11 - 1071).

Exponent b, the five structural complexity indices and average water depth were transformed using a Tukey ladder transformation to fit a normal distribution for further statistical analyses (Tukey 1977). To test if the SS slope and each structural complexity index value differed among the five coral reef sites multiple two-way Analysis of Variance (ANOVA) were used. When a significant difference was found, a pairwise comparison followed to examine for which pairs of sites the SS slope or complexity indices differed. To examine the relationship of the fish SS slope with structural complexity, multiple linear regression analysis was used where the SS slope was the dependent variable and one structural complexity index, average water depth and survey sites the predictors. However, due to the high number of predictors and a relatively low number of transects, we first selected the complexity index best explaining the SS slope. Here each complexity index individually was examined together with the SS slope and the selection was based on the lowest Akaike Information Criterion (AIC) value (Akaike 1974). Therefore, the final multiple linear regression model included only the one complexity index that was found to best describe the variation in SS slope together with average water depth and survey site, as well as the interaction of the complexity index and survey site. Only predictor variables that were not strongly cross-correlated (Pearson correlation coefficient below 0.5, and Variance Inflation Factor (VIF) below 2) were included in the analyses (Belsley et al. 1980), as multicollinearity can result in inflated variance among predictors in the model. The contribution of each index to the linear regressions was weighted using the standard error of each slope (weight =  $(1 / SE^2)$ ) estimated during the MLE to account for uncertainty. Consequently, the estimated slopes that were most robust with the lowest variability had the greatest weight in the regression models. Automatic stepwise backwards selection and the Akaike Information Criterion (AIC) were used to select the variables in the final model by accounting for increasing complexity (as seen in Akaike 1974). The most parsimonious model obtained was the combination of variables that produced the lowest AIC. Besides the examination of the SS Slope, we also aimed to understand if for example a steeper slope is caused by a higher proportion of the smallest or a lower proportion of the largest individuals along the size spectrum. Therefore, the skewness of each SS was identified, which informs if the distribution of body size values is skewed towards smaller sizes (negative skew) or larger sizes (positive-skew). Interaction plots of the best performing complexity index with the (i) SS slope and (ii) skewness for each survey site were plotted and simple slope analysis was employed to examine the significance of the individual slopes displayed. All statistical analyses and plots were conducted with the software R (version 4.0.0; R Core Team 2020). Specifically

the MLE's of fish SS were performed with the provided R code and package (sizeSpectra) from Edwards et al. (2017; 2020).

#### RESULTS

All SS slopes of the coral reef fish community were negative with an overall mean  $\pm$  SD of - 1.56  $\pm$  0.78 (exponent b ranging from -6.14 to -0.50, see Appendix 1). Extreme negative b-values of -6.14 and -3.1 were specifically caused by relative high numbers of small (12 cm TL) *Paracheillinus* spp. individuals and a low overall fish count at Katza on two occasions. The shallowest SS slopes were identified for Japanese Gardens, followed by the other sites inside the nature reserve: Reserve A and IUI, while Dekel and Katza displayed the steepest SS slopes However, the SS slope did not differ significantly among the five sites (F<sub>(4, 60)</sub> = 1.649, p = 0.17; see Figure 2).



**Figure 2:** Boxplot with boxes indicating the range of the central 50% of the data, the central line marking the mean value and the whiskers representing the standard error of size spectrum slope among all five survey sites in 2018 and 2019. The sites Dekel and Katza are outside the nature reserve, while Reserve A, Japanese Gardens and IUI are inside the nature reserve.

Among the structural complexity indices, vertical relief, rugosity and free safe space differed significantly between survey sites (see Table 3). In contrast, functional evenness and functional richness showed no significant difference of index values between sites (see Table 3). Pairwise comparison of the significant complexity indices between sites showed that rugosity was
significantly higher at Katza and Japanese Gardens in comparison to IUI and Reserve A (see Figure 3 a), while vertical relief was significantly higher at Japanese Gardens and higher at Katza in comparison to IUI (see Figure 3 b). Furthermore, the index free safe space was significantly higher at Katza and Japanese Gardens than at IUI (see Figure 3 c and Table 3).



Figure 3: Boxplots with boxes indicating the range of the central 50% of the data, the central line marking the mean value and the whiskers representing the standard error of the mean of each structural complexity index between survey sites for rugosity (a), vertical relief (b), free safe space (c), structural evenness (d) and structural richness (e). Significant (\*) and non-significant (n.s.) differences between sites are indicated in the plot based on pairwise comparisons.

**Table 3.** Results from One-way analysis of variance (ANOVA) of the structural complexity indices rugosity, vertical relief, free safe space, structural evenness and structural richness among the five survey sites Dekel, Katza, Reserve A, Japanese Gardens and IUI and results from pairwise comparisons of significant indices between sites.

Complexity index	ANOVA			Pairwise comparison			
	F	df	p-value	Sites with sign	n. diffe	erences	p-value
Rugosity	2.76	4,60	0.03	Katza	vs.	Reserve A	0.02
				Katza	VS.	IUI	0.01
				Jap. Gardens	VS.	Reserve A	0.03
				Jap. Gardens	vs.	IUI	0.02
Vertical Relief	2.89	4,60	0.03	Katza	VS.	Reserve A	0.04
				Jap. Gardens	VS.	IUI	0.01
Free Safe Space	3.01	4,60	0.02	Katza	VS.	IUI	0.002
				Jap. Gardens	VS.	IUI	0.01
Structural Evenness	0.88	4, 58	0.48	n.a.			
Structural Richness	2.01	4, 58	0.11	n.a.			

The selection of the complexity predictor best explaining the SS slope based on the AIC value revealed rugosity to be superior to the other indices. Therefore, rugosity was the structural complexity predictor included in further models. The final significant model included SS slope as the dependent variable together with rugosity and site as predictors ( $F_{(5,59)} = 2.73$ ,  $R^2 = 0.18$ , p = 0.02). A significant negative relationship of SS slope and rugosity was found. Other predictors, such as average water depth and the interaction between rugosity and site were not included in the final model based on the stepwise backwards selection and the lowest AIC value. Visual inspection of the slopes reflecting the SS-rugosity relationship for each site revealed that their trends were not identical between the five survey sites. The best protected site, Japanese Gardens and the second-best protected site, Katza, exhibited a similar pattern where the SS slope steepens with increasing rugosity index. This indicates that a higher rugosity is associated with a lower relative abundance of large bodied fish and/ or higher abundance of small bodied fish. The other two protected sites, IUI and Reserve A, showed a similar, but weaker trend as found at Japanese Gardens and Katza. In contrast, the most exposed site in the north, Dekel, displayed an opposite trend where the exponent b increased with increasing rugosity index, which would suggest that a higher rugosity is associated with a shallower slope and therefore a higher relative abundance of large bodied fish and/ or lower abundance of small bodied fish. However, simple slope analysis revealed that only the slopes for Katza (p = 0.04) and Japanese Gardens (p = 0.01) were significant. In contrast, the slopes

for IUI (p = 0.78), Reserve A (p = 0.89) and Dekel (p = 0.39) were not significant (see Figure 4 a). Skewness analysis revealed that all fish size distributions are positively skewed, as would be expected for SS. However, the negative relationship between SS Slope and rugosity at Japanese Gardens and Katza is caused by different shifts in fish size distributions in relation to rugosity. At Katza, the proportion of large fish decreases with increasing rugosity index, whereas at Japanese Gardens the proportion of small bodied fish increases with increasing rugosity. The other slopes are not further discussed here as they were not significant (see Figure 4 b).



**Figure 4:** Interaction plots showing the relationship between SS Slope and the complexity index rugosity (a); and the level of positive skewness in relation to the rugosity index (b) for all five survey sites Dekel, Katza, IUI, Japanese Gardens and Reserve A. Significant slopes are indicated with a continuous line whereas insignificant slopes are drawn with a dashed line. All values were transformed using the Tukey ladder transformation.

#### DISCUSSION

Understanding the associations between habitat structural complexity and reef fish assemblages has been a key focus of coral reef ecology for many years (Luckhurst and Luckhurst 1978; Stella et al. 2011; Darling et al. 2017). We assessed structural complexity of the habitat and fish community size structure and their relationship among coral reef sites exposed to different intensities of touristic activities. The two sites, Japanese Gardens and Katza, which are least exposed to disturbances exhibited significantly higher rugosity in comparison to the other sites. However, these sites differed in their mean SS slopes with the overall shallowest slope at Japanese Gardens and the steepest slope at Katza. The SS sloperugosity relationship was negative at Katza and Japanese Gardens. At both sites, the SS slope decreased with increasing rugosity, which implies a steepening of the SS slope with increasing complexity. This would fit with findings from previous studies where higher structural complexity was associated with steeper SS slopes caused by a higher relative abundance of small bodied fish (Graham et al. 2007; Wilson et al. 2010; Alvarez-Filip et al. 2011). However, the change in fish size distributions in relation to rugosity was caused by two opposite shifts of fish abundances along the size spectrum. The proportion of small bodied fish increased with increasing rugosity at Japanese Gardens, whereas at Katza the proportion of large bodied fish increased with increasing rugosity scores. This shift to a higher abundance of large-bodied fish with increasing structural complexity at Katza is contrary to regularly found patterns in previous studies (Graham et al., 2007; Wilson et al., 2010; Rogers, Blanchard and Mumby, 2014). The other sampled coral reef sites revealed no systematic relationship between reef fish SS slope and complexity or a significant influence of the level of anthropogenic disturbances on these parameters. Unexpectedly, Reserve A and IUI, which are included in the nature reserve, were characterised by lower structural complexity scores than the most exposed site, Dekel. Previous studies already proposed that coral reef habitat characteristics, such as reef zonation (Lewis and Wainwright 1985; Bellwood et al. 2018), coral taxonomy and the proportion of live coral cover (Komyakova et al. 2013) also significantly influence the fish assemblage. Our findings indicate that although the level of rugosity shows an effect on the fish community SS slope, a high variability of slopes among transects imply that there is no systematic effect in relation to the level of exposure to touristic activities. Additional factors besides anthropogenic disturbances may influence the fish SS slope and reef structural complexity and their interaction.

Coral reef sites inside the officially designated Eilat nature reserve did not have a significantly higher structural complexity, as one would expect because of their official protection status. In contrast, the unprotected site Katza displayed a significantly higher rugosity than the protected sites IUI and Reserve A. Additionally, free safe space at Katza was higher than at IUI and vertical relief higher than at Reserve A. This could be due to Katza's lower level of daily exposure to recreational activities and its closure to the public until 2017. However, usually one would expect protected sites to display a significantly more complex reef architecture because it is common practise to sufficiently protect pristine and ecologically particularly valuable reef sites from recreational activities and fisheries (ISRS 2004). In the case of Eilat, fisheries are not a factor to consider, as fishing is forbidden except for some recreational angling from shore. Therefore, the close proximity to the shore of sites inside the nature reserve may play an imperative role. Recreational activities are not restricted in the nature reserve, except for particularly sensitive table corals at Japanese Gardens, where the daily number of visitors. These sites are easily accessible from shore and therefore attract numerous snorkelers, swimmers and divers every day. On the contrary, Katza requires a boat drive, making it more difficult to access and therefore less exposed to anthropogenic activities than the protected reefs. Surprisingly, reefs at Dekel, which are closest to the large touristic city of Eilat making it the most exposed site, exhibit no significant difference in the complexity scores to the less exposed sites. Here, one could argue that the lower number of surveyed transects may have statistically influenced the results.

However, our study findings may also indicate that anthropogenic disturbances are not the driver for differences in the physical structure of Eilat's reef. Other habitat characteristics, such as the reef geomorphology and wave exposure have been shown to affect reef complexity (Oakley-Cogan et al. 2020) and fish size distribution (Fulton et al. 2005) respectively. Previous studies have also emphasised the importance of water depth, as deeper reefs are often less structurally diverse than shallower reefs (e.g. Graham et al., 2015). However, average water depth of the transects was included as a predictor in our analyses and showed no effect on the SS slopes. Currently, it is still uncertain how differences of complexity facets among specific reef zones, as well as their interrelationships, affect fish assemblage and distribution. Though, numerous recent studies suggest that complexity metrics differ between reef slope, crest and flat (Oakley-Cogan et al. 2020). It was proposed that coral and fish assemblages can be more distinct among different reef habitats even when they are only separated by 10s of meters in contrast to assemblages of the same habitat on reefs 1000s of kilometres apart (Connolly et al.

2005). Comparably, our results have shown that Japanese Gardens exhibited a significantly higher mean rugosity than the closely located sites Reserve A and IUI. Likewise vertical relief and free safe space were also higher at Japanese Gardens in comparison to IUI. Therefore, these closely located sites may be characterised by distinct habitat zones, which cause the disparities among sites inside the nature reserve rather than the level of exposure to anthropogenic activities.

Rugosity was found to be the structural complexity index best explaining the variance of the SS slope when we utilized Automatic stepwise backwards selection and the lowest Akaike Information Criterion (AIC). This was a surprising result, as it was recently suggested that rugosity lacks a representation of the spatial arrangement of complexity-generating elements and the heterogeneity of elements within the transect, in particular extreme measurements of complexity (Yanovski et al. 2017). Numerous research papers have recently proposed that one single index of complexity, such as the frequently employed rugosity index, may not sufficiently describe reef structural complexity and explain variance in fish community assemblage (González-Rivero et al. 2017). Moreover, the commonly utilized complexity indices were suggested to describe distinctive features of the 3-D reef structure, which affect diverse aspects of the fish community differently. For instance, Lazarus and Belmaker (2021) found that the index free safe space exhibits a positive relationship with fish abundance, while the index vertical relief explained a great amount of variation in fish community biomass and abundance on coral reefs in the Red Sea. This highlights the importance to include numerous different complexity indices at different scales to adequately account for distinct features of the 3D reef structure. Consequently, five different indices that describe different aspects of the reef architecture from small-to large-scale were included in our study.

Overall the coral reef fish community SS slope exhibited no significant difference between the five survey sites. Still, the unprotected sites in the north were found to exhibit much steeper slopes than the sites within the nature reserve. Commonly, steeper SS slopes on unprotected reefs in comparison to protected reefs result from fishing impacts and the removal of the largest individuals of a community (e.g. Wilson et al., 2010; Robinson et al., 2017; Carvalho et al., 2021). However, as earlier mentioned, commercial fisheries are strictly prohibited on the coast of Eilat. The seemingly higher similarity of SS slopes at protected sites in contrast to unprotected sites, and vice versa could be solely due to the proximity of these sites to each other. The protected and unprotected sites are physically not connected, which can cause

differences in the fish communities but would not explain the steeper slopes outside the reserve. The high SS slope variability of the same site show that a clear systematic pattern is missing. The effect of rugosity on the SS slope may be only a facet of the habitat characteristics influencing the relationship between reef structure and fish size distribution. Intriguing is also the SS slope-rugosity relationship at Katza where structurally more complex transects were associated with a higher proportion of large bodied fish. This is contrary to findings of previous studies on tropical coral reefs around the globe, where high-complexity reefs, characterised by numerous caves or overhangs or vertical reliefs, are associated with a relative higher proportion of small-bodied fish (Graham et al. 2007; Wilson et al. 2010; Alvarez-Filip et al. 2011; Rogers et al. 2014). This association of larger fish with higher rugosity cannot be solely explained based on the data available. Food-web models suggest that carnivore and herbivore fish SS slopes are differently affected by structural complexity and benthic resources (Rogers et al. 2014). Most large-bodied fish (> 50 cm TL) recorded at Katza belonged to the taxonomic families Lethrinidae, Epinephelidae, Labridae and Scaridae. It could be suggested that the highly rugged transects at Katza may offer particularly beneficial conditions in regards to feeding opportunities for these taxa. Other environmental characteristics of the coral assemblage, such as individual morphological features and taxonomic identity were also found to contribute to distinct components of the reef fish assemblage. For instance, coral genera richness and functional diversity were recorded to influence total fish biomass and diversity (Komyakova et al. 2013). Overall, the indirect interdependencies between corals and reef fishes are exceptionally complex and in the case of this study, additional information on the habitat characteristics are required to fully grasp the found patterns in the SS slope-complexity relationship.

### CONCLUSIONS

The coast of Eilat offered the great opportunity to examine and compare coral reefs and fish community size distributions among sites experiencing different levels of anthropogenic disturbances without conflicting influences from fishing impacts. Our study revealed a significantly higher structural complexity at the two best protected reefs at Eilat. However, a consistent relationship between fish SS slope and structural complexity among all survey sites in regards to their differing exposure to touristic activities was missing. The findings revealed

the importance to expand the variables describing the habitat characteristics and the limitations of exclusively examining fish community size distributions for a comprehensive understanding of the complex interactions. Structural complexity alone was not able to explain the patterns of fish SS slope and the fish size distribution. Specifically the association of a relative higher proportion of large-bodied fish with increasing rugosity is unusual and taxonomic identification and e.g. consideration of feeding preferences may explain the patterns we found. SS provide insights into factors that shape communities and quantify community-scale changes, which is valuable for conservation and management of threatened ecosystems. The construction of SS for different taxa, not only coral reef fish communities, but terrestrial mammals, soil invertebrates and even trees has proven a promising approach to detect and compare the influence of habitat conditions and different forms of anthropogenic stressors on organisms (Rodriguez and Mullin 1986; Cavender-Bares et al. 2001; Vadruccia et al. 2013; Donadi et al. 2015). Similarly to corals in our study, other foundation species such as kelp are also key determinants of habitat complexity and a higher rugosity of the canopy cover was associated with more negative SS slopes and a higher SS intercept of the fish community (Trebilco et al. 2016). This emphasises the wide applicability of SS and the relationship between community SS and habitat complexity concepts.

#### **Author Contributions**

LMB and YB established the study concept. YB, HB, TG and ML conducted the field surveys, while LMB contributed in data analyses, concept interpretation, manuscript writing and editing. TM and YB revised the manuscript.

# **Chapter 5**

# **General Discussion**

Climate change and numerous other direct and indirect anthropogenic stressors are posing great threats to our natural world, impacting ecosystem functioning and processes (Blois et al. 2013; Comte and Olden 2017; Woolway et al. 2020). Therefore, improving our understanding of these systems for effective management and conservation is crucial. Size-based analyses, such as SS are a promising simple but useful method to increase our knowledge of complex processes particularly in aquatic communities and evaluate their status and health (Petchey and Belgrano 2010; Emmrich et al. 2011; Murry and Farrell 2014). Besides the high regularity of SS across many systems, conflicting conclusions on the key factors driving spectral slopes still exist. In this thesis, I utilized a size-based approach to examine ecological research questions in a temperate lake, as well as tropical coral reefs and to methodologically compare fish sampling methods. More specifically, I investigated trophic interactions and the drivers of a zooplankton community size distribution in the pelagic zone of a lake (chapter 2), compared traditional netting and modern hydroacoustics methods in representing fish community size distributions (chapter 3), and assessed coral reef fish SS slopes and reef structural complexity among sites of differing anthropogenic disturbances (chapter 4). In this final chapter of my thesis, I discuss the findings of chapter 2, 3 and 4 and how these complement the current knowledge on factors influencing SS slopes and the existing understanding of the applicability and limitation of size-based methods in aquatic research.

# Size distribution of zooplankton community not controlled by top-down or bottom effects

Zooplankton are an integral part of aquatic ecosystems, as they link primary producers and higher trophic levels such as fish, while mirroring a balance of food web processes by their body size distribution and taxonomic composition (Mills and Schiavone 1982; Hansson et al. 2007). When I examined trophic interactions in the pelagic area of Lake Stechlin across 13

years of sampling in chapter 2, I utilized seven commonly used parameters to describe the zooplankton community size structure and density. I examined the effect of annual differences in fish size, fish biomass, TP, chlorophyll a and temperature on the zooplankton community size structure. Despite the comprehensive data set analysed, a clear driver of the pelagic zooplankton community size distribution could not be determined. In contrast, numerous previous studies have shown that both bottom-up and top-down factors commonly affect the size distribution of the zooplankton community (Hessen et al. 1995; Pinel-Alloul et al. 1995; Finlay et al. 2007). However, the importance of environmental conditions, such as the limnological characteristics and productivity levels, as essential bottom-up drivers of these dynamics was emphasised before (Finlay et al. 2007). Results in chapter 2 support previous findings that indicate pelagic trophic cascades (top-down drivers) to be particularly weak in lakes with lower productivity (Elser and Goldman 1991; Persson and Diehl 1992; Sarnelle 1992; Mehner et al. 2008). Moreover, Lake Stechlin's increasing productivity levels in the past years may make the determination of one single driver for the zooplankton size distribution community difficult, as the dynamics may change during the sampling period of our long-term dataset. Still, our study demonstrates the usefulness of size-based analyses to gain insights into trophic dynamics. A weak positive effect by TP on zooplankton density (reflected by the intercept of the SS) was recorded, suggesting zooplankton SS to be a sensitive indicator for lake-wide energy availability and transfer efficiency in the food web (Mehner et al. 2018). However, these findings also highlight the limitations of examining key factors driving the SS of a community, when specific taxonomic or functional groups are affected differently. In Lake Stechlin, coregonids feed preferentially upon Bosmina longirostris and B. coregoni (Schulz et al. 2003), whilst these taxa contribute only 9 % to the total zooplankton community biomass. Therefore, even if the zooplankton are eaten and hence controlled by fish, their removal results only in a minimal impact on the entire zooplankton SS community in Lake Stechlin. Additionally, the species- and size selective feeding of certain zooplankton taxa can cause difficulties in determining the mechanistic dynamics between phytoplankton on zooplankton communities when phytoplankton were not identified taxonomically. I utilized chlorophyll a as an indicator of resource availability. However, not all phytoplankton taxa are being eaten by zooplankton. For instance, juvenile daphniids usually avoid green filamentous algae, such as Ulothrix, whereas larger individuals include it in their diet (Chen et al. 2011). Similarly, in the face of global warming, examining trophic interactions by exclusively assessing community body mass distributions will be particularly difficult. Increasing water temperatures are suggested to shift the phytoplankton composition and size, leading to higher biomasses of filamentous cyanobacteria (Selmeczy et al. 2019). This will modify the strength of top-down effects of zooplankton on phytoplankton (Ersoy et al. 2017) and emphasises the need to include taxonomy under certain circumstances when trying to understand trophic interactions.

Overall, size-based approaches clearly have a great potential to answer a range of distinctive questions about complex interactions in aquatic communities. However, trait-based approaches like this one cannot resolve species-specific details, such as species selective feeding common in zooplankton (Chen et al. 2011) and the replacement of nutritious taxa with those of similar size, but with harmful characteristics (Schmidt et al. 2020). Causational confirmation based on stomach content analyses or stable isotopes of fish would allow a better understanding of the strength of trophic links that ultimately affect the size distributions for future studies (Brose 2010; Boukal 2014). Nevertheless, **chapter 2** of my thesis further extends the empirical evidence on the importance of lake level productivity on the strength of trophic cascades and may inspire others with significantly longer datasets to repeat a critical re-consideration of top-down and bottom-up effects on zooplankton size structure in stratified lakes.

### Hydroacoustics reliable to create fish community size spectra

Assessing and proofing the reliability of hydroacoustic techniques to represent fish community size distributions is fundamental to finding an alternative to invasive traditional netting techniques for regular stock assessments. Besides the destructiveness of netting techniques, they are inherently size-selective and were previously suggested to introduce bias in SS analyses (Bonvechio, Pouder and Hale, 2008; Olin, Malinen and Ruuhijärvi, 2009; Prchalová et al. 2011). However the type of echo sounder system utilized and the methods of data processing and analysing were found to affect the size distribution estimates, emphasising the need for standardised methods (de Kerckhove et al. 2016). Findings from chapter 2 of my thesis revealed that exclusively fish biomass based on hydroacoustic estimates showed a negative effect on the zooplankton community but not based on midwater trawling. Therefore, in chapter 3, I aimed to determine whether the estimated SS of the night pelagic fish community in Lake Stechlin differed between net sampling by midwater trawling and two hydroacoustic methods (SEDs and TEGs) across 12 years of sampling. To the best of my knowledge, an attempt to compare freshwater fish size distributions among netting and different acoustic methods was not conducted before. This study showed that acoustic SS are consistent with theory, displaying the negative relationship between abundance and body size

that is predicted (e.g. Kerr and Dickie 2001). Although overall the mean SS slope did not significantly differ between the three methods, the SS slope differed considerably among the three methods in some years, coinciding with higher densities of coregonid juveniles. It was found that the SS obtained by TEGs showed a positive trend over the sampling years, potentially reflecting faster growth of the coregonids in response to recent eutrophication of Lake Stechlin (Braun et al. 2021) as shown in chapter 2. These findings are particularly interesting, as they indicate that the hydroacoustically estimated TEGs may show a higher sensitivity to the effects of eutrophication on fish growth rates. These records may help detect and interpret environmental changes occurring in this lake in the future. The present work extends findings from Wheeland and Rose (2016) in demonstrating that the size composition of freshwater fish communities can be indexed by SS derived from hydroacoustic surveys. In contrast to their exploratory study, we were able to compare the acoustically derived SS with SS from independently collected trawling data. Our results even suggest acoustically derived SS based on TEGs to be superior to the traditionally employed midwater trawling and hence further complement de Kerckhove, Shuter and Milne (2016) conclusions that hydroacoustic methods generate reliable SS, in particular if based on tracking to combine several successive echoes into one trace.

However, hydroacoustics is not a replacement for netting techniques, as it still needs to be complemented by sampling to obtain required information on species composition and individual fish characteristics, including exact body length and weight (Kubečka et al. 2009; DuFour et al. 2019). Furthermore, the biggest challenge when one aims to examine fish SS with hydroacoustics is relating the target strength (TS) to fish length (Simmonds and MacLennan 2008). Therefore, most studies on acoustically derived SS utilize empiricallyderived general TS-length relationships across species (e.g. Yurista et al. 2014; de Kerckhove et al. 2016; Wheeland and Rose 2016). The highest accuracy of TS to body length conversions is attained when an individual species-specific model is established for each species of fish observed due to the influence of the swim bladder morphology on the TS (Foote 1980; McClatchie et al. 1996; Simmonds and MacLennan 2008). However, these specific models do not exist for many species, especially for numerous common taxa in marine systems, making hydroacoustics not necessarily an easily attainable alternative to netting methods in all circumstances. Additionally, not all aquatic systems are as well suited as Lake Stechlin for accurate fish estimates based on hydroacoustics. The occurrence of schooling fishes can negatively affect the ability of hydroacoustics to describe the SS of fish communities, as the

isolation of valid single targets or tracked fishes is commonly not achievable in fish aggregations. The diel vertical migration of fish in Lake Stechlin make the survey and data interpretation more reliable, as the fish strongly disperse spatially, while ascending during the night (Mehner et al. 2007). This makes fish shoals rare at night and the vast majority of fish can be recorded as single echoes. This emphasised also the need of behavioural information on the taxa surveyed when defining the best survey period for hydroacoustics (Girard et al. 2020). Numerous ecosystem-specific parameters need to be considered before. These include the productivity level, which influences the water visibility, and predators present and refuge sites, as they may affect estimations of abundance and biomass (Gliwicz et al. 2006). Besides the numerous information required about the fish taxa in the system surveyed with hydroacoustics, results from my study further support the applicability of acoustically derived fish SS. Accordingly, future acoustics research should aim to expand the existing data on species-specific models across aquatic systems, as well behavioural important aspects to consider for hydroacoustic surveys.

Understanding the usefulness and limitations of data collection methods for monitoring requirements is vital for a appropriate application in ecosystem and fisheries management. Presently, the truthfulness of either fishing or hydroacoustics with respect to their estimations of fish size distribution is not possible, as ground-truthing of fish densities and size distributions is still an unresolved challenge in fish ecology and management (Kubečka et al. 2009). However, **chapter 3** demonstrates the benefits of acoustically derived fish SS estimates in a deep lake and proves the acoustical tracking method to be reliable. Therefore, providing a baseline for future fish assessments in Lake Stechlin, but also for other researchers and fisheries managers when deciding on stock assessment techniques based on hydroacoustics.

# Reef structural complexity and coral reef fish community size structure in relation to touristic activities

Current rates of live coral cover loss and reef degradation are alarming (Hoegh-Guldberg et al. 2017). The level of structural complexity of coral reefs is directly linked to reef fish density and diversity (Graham and Nash 2013). Recreational activities, such as intensive SCUBA diving and snorkelling activities cause breakage and damage, which threatens vulnerable corals (Dixon et al. 1993; Hawkins et al. 1999, 2005; Cope 2003). This emphasises the need for an

improved understanding of the effect of differing levels of anthropogenic stressors on reef structural complexity and fish communities. Previous studies have investigated the effect of anthropogenic disturbances mainly by examining fishing impacts on fish size distribution (Graham et al. 2005) and structural complexity (Robinson et al. 2017). Only few studies examined the fish SS slope and structural complexity on reefs experiencing different exposure to touristic activities without any fishing occurring (Rogers et al. 2014). In chapter 4, I assessed fish SS slope and reef complexity in relation to the intensity of touristic activities and no other major anthropogenic stressors and I examined which of the five tested structural complexity indices best explained the fish SS slope. Most previous studies have employed only one or two indices to describe structural complexity of coral reefs, whereas the features of the reef measured differ among most complexity indices (Lazarus and Belmaker 2021). It was criticised before that a clear definition of what encompasses coral structural complexity is missing and often subjective assumptions are made, making results less comparable (Gratwicke and Speight 2005). Therefore, employing five indices describing the structural complexity of the coral reef from small to large scale, was of high importance in chapter 4 in my opinion. Additionally, I exclusively chose indices that were proven useful in the Red Sea (Lazarus and Belmaker 2021).

Findings of **chapter 4** show that the two best protected reefs, Japanese Gardens and Katza, exhibited significantly higher structural complexity indicated by the index rugosity. This complexity index describes the degree to which the bottom profile is different from a straight line (Lazarus and Belmaker 2021). This result from **chapter 4** fits with previous published results on the level of coral damage among Eilat's diving sites, where Japanese Gardens was found to be significantly less affected by coral skeletal breakage and tissue abrasion than any other site (Zakai and Chadwick-Furman 2002). Contrary to my expectation based on numerous previous studies (Graham et al. 2009, 2015; Wilson et al. 2010; Alvarez-Filip et al. 2011), the higher rugosity at these two best protected sites was not reflected in consistently significantly shallower fish SS slopes. Overall, no consistent association of significantly higher complexity and greater abundance of small bodied fish in relation to the level of protection from touristic activities was found in my study.

Other habitat characteristics such as the habitat zonation on the reef, as well as coral morphological categorization and taxonomic identification may influence the fish community SS slopes. Recent findings by Darling et al. (2017) suggested that besides structural complexity, reef zone significantly affects the fish abundance, biomass, species richness and

trophic structure. The fish assemblage differs drastically between the reef slope, crest and flat (Darling et al. 2017). Survey sites being situated in different reef zones and the associated effect on the fish assemblage may explain the differences in fish SS among sites in my study. Therefore, it can be suggested that including information on the reef zonation should be considered in future studies. Besides the numerous empirical examples of regularities of the relationship between fish assemblage and characteristics of the coral reefs, certain speciesspecific responses to structural complexity are still not clear (Graham and Nash 2013). Previous studies have indicated that different components of fish communities exhibit distinctive responses to structural complexity (Jennings et al. 1996; Öhman and Rajasuriya 1998; Almany 2004). For instance, some fish species may occur in heterogeneous habitats due to feeding, mating or refuge advantages, whilst some species associate with low-complexity habitats (Chabanet et al. 1997; Almany 2004; Bozec et al. 2005). Even associations of certain reef taxa, with specific coral morphologies or genera (Wilson et al. 2008a; Nadler et al. 2014) was previously recorded. Numerous studies have successfully shown that in some cases exclusively employing a body-size approach, such as SS allows to infer an understanding of the association of reef complexity and fish size distribution (Alvarez-Filip et al. 2011; Darling et al. 2017). However, results of chapter 4 are lacking a consistent pattern and more detailed information on habitat condition and potential fish taxa or functional groups are required for a comprehensive and systematic understanding of the found patterns of fish SS slope and structural complexity among survey sites.

The importance of structural complexity for fish communities was also recognised for freshwater systems, such as lakes and rivers (Willis et al. 2005; Sass et al. 2006). Similarly to coral reefs, macrophytes or woody structures for example mediate predator prey interactions and affect fish diversity and density positively (Scheuerell and Schindler 2004; Agostinho et al. 2007). However, especially shallow littoral zone habitats of freshwater systems, which are of great importance to juvenile fish, are threatened by increasing anthropogenic habitat alteration and simplification. This leads to the loss of a diverse range of plants and submerged woody habitat (Christensen et al. 1996; Radomski and Goeman 2001; Sudgen-Newbery 2004) and results in alterations of size-specific fish growth rates and community spatial distributions (Werner et al. 1977; Schindler et al. 2000; Scheuerell and Schindler 2004). Still, research studies on the relationship of habitat structural complexity and fish SS slopes in freshwater systems are rare.

The study in **chapter 4** provides a first step towards a better understanding of the relationship between reef fish SS slope and structural reef complexity on coral reefs experiencing differing levels of exposure to touristic activities. However, a clear consistent association of structural complexity and SS slope across all sites was missing. This study emphasises the need to include topographical features, such as reef habitat zonation in future coral reef studies. Overall, I suggest that an extended understanding of the essential habitat features influencing fish communities may allow the inclusion of habitat complexity aspects as a comparable indicator in monitoring programs and management practices in the future. These features are essential for fish communities in marine but also freshwater systems. Therefore, they should be accounted for and incorporated together with fish SS into research and conservation programs in a manner that is easily attainable and reflective of the complex ecological interactions and interdependencies.

### Limitations of size-based analyses in ecology

Our findings in chapter 2, 3 and 4 revealed a high variation of SS slopes for the zooplankton (-7.4 - -0.7) and for the fish (Lake Stechlin: -1.6 to 0.42; Eilat: -6.14 - 0.5) community. Especially tropical coral reef fish SS exhibited drastic variations in the SS slope due to instances of high counts of small bodied fish on some transects. These discrepancies from the theoretical value of -2 in steady state conditions (Brown et al. 2004; Polishchuk and Blanchard 2019) can be expected, as I exclusively determined the SS slope based on one trophic level. Furthermore, numerous factors, such as environmental gradients and biotic factors (Emmrich et al. 2011; Arranz et al. 2016) are known to influence the estimated SS slope as well. Many studies have emphasised that the greater the range of body sizes and thus trophic levels included in the SS, the closer is the estimated SS slope to the theoretical value (Trebilco et al. 2016; Eddy et al. 2021). Furthermore, a very debated topic that needs mentioning in the context of improved consistency of SS slopes is the fact that an essential group of organisms, the benthic invertebrates, are commonly ignored by most SS studies. In Lake Stechlin, the consistency and robustness of community SS slopes could be potentially be improved by including benthic invertebrates. Relatedly, the frequently relatively high variability in coral reef community SS slopes was found to improve significantly in robustness and consistency when invertebrates were included (Heather et al. 2021). This finding ultimately supported the generality of the biomass equivalence rule for reef communities at the global scale. However, the focus of our

study was the zooplankton community and what effects their size distribution and hence we utilized the SS intercept and slope as indicators. It was not aimed to create a lake-wide community size spectrum. Overall, clearly, size-based approaches such as SS analyses have limitations. They cannot resolve species-specific detail, such as changing distribution patterns or replacement of nutritious taxa with those of similar size, but which are non-nutritious or harmful (Schmidt et al. 2020). or habitat and feeding preferences (Randall and Hartman 1968; Wainwright and Bellwood 2002; Kerry and Bellwood 2012; Sailley et al. 2015; Steneck et al. 2017). However, the major advantage of SS as a tool is that when based on time averaging measurements, and across a sufficiently large range of body mass, it provides a simple instrument to gain insights into key properties and processes of an ecosystem.

## CONCLUSIONS

This thesis demonstrates the wide applicability of size-based approaches, such as SS, to tackle a broad spectrum of research questions from ecological dynamics in a temperate lake and tropical coral reefs to a methodological comparison of fish stock assessment techniques. My thesis findings show that although no clear top-down or bottom-up factor drives zooplankton SS, they may act as an indicator of lake productivity in Lake Stechlin. Results from my thesis also indicate that hydroacoustic methods generate more reliable SS of the fish community in Lake Stechlin than midwater trawling. Finally, I found that a clear systematic pattern of fish SS slope-structural complexity relationship among sites of different levels of anthropogenic disturbances was missing. However, the two best protected reefs were characterised by a significantly higher structural complexity. Conclusions of my thesis have also clearly revealed the limitations when one omits taxonomy and hence species-specific feeding and habitat preferences. Nevertheless, SS give insights into factors that shape communities and quantify community-scale changes, while allowing for simple comparisons between systems or across time. Overall, SS provide the potential for a quantitative index of ecosystem health and resilience, exceptional useful for policy reporting and therefore the conservation of threatened aquatic systems.

# ACKNOWLEDGEMENTS

First, I like to thank my supervisor Thomas Mehner who guided and supported me during my PhD. I am particularly thankful that he was always available, while continuously trying to provide me with all the opportunities possible to make this a great informative learning experience. I am grateful for having had the opportunity to visit the Aquatic ecology research group in Vic, Spain. Especially due to Sandra Brucet and her lab group members who welcomed me warmly and let me be a part of their team for a couple of months and giving me valuable insights into zooplankton and fish ecology. I am also thankful to Sandra Brucet and Renee van Dorst for reviewing my thesis and improving it with their corrections and comments.

I want to thank my friends and colleagues at the IGB, specifically Renee, I am very happy that you became a member of our working group, which definitely enriched my time at the IGB and made it just so much more enjoyable. I am very thankful for our exchange and your feedback, especially in the final phase of my writing process. A specific thanks to Kirsten Pohlman for her engagement and positive energy and all the support throughout my entire time at the IGB.

Moreover, I want to thank the numerous reviewers of my papers whose comments and suggestions upgraded my studies. I also want to thank Andrew Edwards for not only creating the extremely useful R package SizeSpectra, providing the required codes for the analyses, but also for his helpful and detailed explanations to my questions and inquiries. I am thankful to a very long list of people who collected the vast amount of data that I had the opportunity to analyse, which makes up the foundation of this thesis. This includes: Alex Türck, Jan Hallermann, Asja Vogt, Christian Helms, Kathrin Jaeschke, Jeanette Völker and several doctoral students who supported the monitoring of Lake Stechlin fishes over the years, as well as the technical staff of the department Experimental Limnology for taking, analysing and curating the long-term environmental and zooplankton data from Lake Stechlin; and Yoni Belmaker, Mai Lazarus, Hezi Buba, Tal Gavriel from The Belmaker Lab in Tel Aviv, Israel for collecting the coral reef fish and structural complexity data in the Red Sea.

Even if it is many years ago that he was my teacher and personal tutor at Anglia Ruskin University Cambridge, I cannot miss to thank Philip Pugh - the first teacher I had in my academic career. His lessons and interactions, especially his way of simplifying things had a long-lasting effect on my writing and thinking academically. I am very thankful for having met him.

I want to thank my family, who I love so dearly. Especially my grandmother and my aunt for their love and support. My son, Alexander, for motivating me with his curious questions and limitless thirst for answers. I am grateful for my best friend, who is always there for me since over 24 years – our talks and walks were the needed cure in the past years. I am thankful to my grandfather for planting the seeds of an interest in science and the natural world when I was a child. Finally, and most of all, I want to thank my mother for her encouragement and help when I was searching for my path and during my studies, but especially in the past very challenging years. Only your never-ending support and love have made it possible for me to finish this thesis with a child and especially during the pandemic. She is my hero and friend, who never stopped believing in me and the best cheerleader anyone can hope for. As they say, you have to give your child roots, but also wings - you gave me both and lots of wind on top.

# Authors affiliations

Lisa-Marie Braun	Humboldt-University of Berlin, Faculty of Life Sciences, Albrecht Daniel Thaer- Institute of Agricultural and Horticultural Sciences; Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany
Thomas Mehner	Humboldt-University of Berlin, Faculty of Life Sciences, Albrecht Daniel Thaer- Institute of Agricultural and Horticultural Sciences; Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany
Sandra Brucet	University of Vic, Catalonia, Spain, Research Group Aquatic Ecology Group University of Vic

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# Appendices

## Appendix – Chapter 2

Tab. 1 List of zooplankton species names and grouping names utilized for crustacean grouping and analyses

Taxon group name	Order
Diaphanosoma brachyrum	Cladocera
Daphnia hybrid	
Daphnia cucullata	
Ceriodaphnia quadrangula	
Bosmina coregoni	
Bosmina longirostris	
Chydorus sphaericus	
Eudiaptomus gracilis	Calanoida
Eurytemora lacustris	
Mesocyclops leuckarti	Cyclopoida
Thermocyclops oithonoides	
cyclopoide Copepoditstadien	
Cyclops spp.	
Copepodit stages	
Nauplii	Cyclopoida
	Calanoida

**Tab. 2** Example how the rounded weighting factor (WF) for fish abundance (e.g. for 2009) from trawling was calculated from the volume fished by the trawl net in four different water depths. Because the continuous size distribution needs integer data as input, the exact WF was rounded to the nearest integer.

year	Depth (m)	Volume [m <sup>3</sup> ]	WF	Rounded (WF)
2009	14	15167	1	1
2009	20	10500	1.44444444	1
2009	32	5000	3.03333333	3
2009	40	8000	1.89583333	2

**Tab. 3** Zooplankton arithmetic mean ( $\pm$  SD) abundance (Ind m<sup>-3</sup>) and body length (mm) with maximum and minimum values for each taxon group in the upper and lower depth layer of Lake Stechlin during summer months between 2005 and 2018 (excl. 2016). Taxa are listed in order of decreasing abundance for each layer.

		Abundance (Ind m <sup>-3</sup> )			Body len	gth (mm)
Depth						
layer	Zooplankton group	Mean	± SD	Mean	± SD	Range
	Nauplii	20170	$\pm 8915$	0.21	$\pm 0.02$	(0.25 - 0.17)
	Bosmina longirostris	9540	$\pm 9379$	0.29	$\pm 0.02$	(0.34 - 0.24)
	Thermocyclops oithonoides	6179	$\pm 4276$	0.52	$\pm 0.04$	(0.61 - 0.42)
	Daphnia cucullata	4250	$\pm 3744$	0.84	$\pm 0.10$	(1.09 - 0.62)
	Eudiaptomus gracilis	3480	$\pm 2272$	0.61	$\pm 0.07$	(0.83 - 0.46)
Unnor	Diaphanosoma brachyurum	3246	$\pm 3497$	0.53	$\pm 0.04$	(0.63 - 0.43)
Opper	Eurytemora lacustris	2561	$\pm 1745$	0.61	$\pm 0.09$	(0.83 - 0.43)
	Copepodit stages	2487	$\pm 1814$	0.37	$\pm 0.05$	(0.53 - 0.27)
	Chydorus sphaericus	2061	$\pm 1694$	0.25	$\pm 0.02$	(0.29 - 0.21)
	Bosmina coregoni	914	$\pm 809$	0.40	$\pm 0.02$	(0.46 - 0.33)
	Daphnia hybrid	755	$\pm 759$	0.70	$\pm 0.05$	(0.81 - 0.61)
	Cyclops spp.	120	$\pm 68$	0.98	$\pm 0.30$	(1.50 - 0.70)
	Bosmina longirostris	3624	$\pm 3428$	0.31	$\pm 0.01$	(0.37 - 0.23)
	Nauplii	1420	$\pm 1180$	0.20	$\pm 0.03$	(0.27 - 0.15)
	Eurytemora lacustris	1212	$\pm 861$	0.75	$\pm 0.09$	(0.97 - 0.57)
	Thermocyclops oithonoides	323	$\pm 482$	0.51	$\pm 0.03$	(0.57 - 0.42)
	Chydorus sphaericus	310	$\pm 573$	0.25	$\pm 0.01$	(0.27 - 0.23)
Lower	Copepodit stages	199	$\pm 213$	0.42	$\pm 0.06$	(0.51 - 0.31)
Lower	Eudiaptomus gracilis	158	$\pm 198$	0.62	$\pm 0.08$	(0.83 - 0.42)
	Diaphanosoma brachyurum	118	$\pm 223$	0.53	$\pm 0.03$	(0.58 - 0.44)
	Daphnia cucullata	161	$\pm 256$	0.87	$\pm 0.07$	(1.12 - 0.71)
	Cyclops spp.	93	$\pm 87$	1.30	$\pm 0.30$	(2.06 - 0.70)
	Daphnia hybrid	64	$\pm 115$	0.70	$\pm 0.05$	(0.85 - 0.62)
	Bosmina coregoni	60	± 79	0.40	$\pm 0.02$	(0.42 - 0.37)

Year	depth layer	Intercept	Slope	$\mathbb{R}^2$	Adj. R <sup>2</sup>	df	P value
2005	U	13.1923409	-0.3430807	0.09193655	-0.0215714	8	0.39
2006	U	13.4181941	-0.3489039	0.08457283	-0.0462025	7	0.45
2007	U	14.518188	-0.4097235	0.22770088	0.11737244	7	0.19
2008	U	14.0672499	-0.2023091	0.01917979	-0.1442902	6	0.74
2009	U	14.4765566	-1.1078044	0.44073369	0.34752264	6	0.07
2010	U	14.1445737	-0.8872008	0.38863428	0.31221356	8	0.05
2011	U	12.7901514	-0.6968867	0.24901223	0.16556914	9	0.12
2012	U	12.3912447	0.01529357	7.77E-05	-0.1110248	9	0.98
2013	U	14.4977843	-0.3091016	0.05304844	-0.1047768	6	0.58
2014	U	13.6947639	-1.1697316	0.34835916	0.21803099	5	0.16
2015	U	13.5161021	-0.4368444	0.07653589	-0.0553876	7	0.47
2016	U	13.4586904	-0.4625372	0.13246997	0.02402872	8	0.30
2017	U	13.8988973	-0.4834625	0.14250829	0.02000948	7	0.32
2018	U	14.2741469	-1.2140971	0.60928602	0.54416703	6	0.02
2005	L	10.0806443	-0.5356211	0.07551721	-0.0565518	7	0.47
2006	L	11.0819216	-0.2358679	0.03538183	-0.1024208	7	0.63
2007	L	10.3224032	-1.0789338	0.28155424	0.17891913	7	0.14
2008	L	9.70162876	-0.0241799	0.00022872	-0.1247427	8	0.97
2009	L	10.3261908	-0.2472323	0.01816783	-0.1220939	7	0.73
2010	L	10.2783656	-0.8271341	0.37687105	0.3076345	9	0.04
2011	L	10.058896	-0.0574088	0.00205765	-0.1226851	8	0.90
2012	L	10.2260046	-0.3053453	0.07981569	-0.0122027	10	0.37
2013	L	10.6963355	-0.5279735	0.16211323	0.0690147	9	0.22
2014	L	9.82451988	-0.9487234	0.42461586	0.36068429	9	0.03
2015	L	10.366317	-1.0267251	0.42564238	0.35384767	8	0.04
2016	L	10.9112517	-0.8105823	0.31178514	0.24296366	10	0.06
2017	L	11.036579	-0.5214598	0.38708291	0.33136317	11	0.02
2018	L	11.3088757	-0.9102814	0.47283436	0.40693866	8	0.03

**Tab. 4** Results of size spectrum analyses for zooplankton in the upper (U) and lower (L) layer of Lake Stechlin in summer, including spectral slope, intercept,  $R^2$ , adjusted  $R^2$ , denominator degrees of freedom (df) and p value (significant in bold) estimated by ordinary least square linear regression based on binned logarithmic data.



**Fig. 1** – Zooplankton size spectra based on logarithmic binned data of zooplankton mean abundance (Ind m<sup>-3</sup>) within body mass ( $\mu$  g C Ind<sup>-1</sup>) size classes (estimated by OLS) for the upper and lower depth layers from 2005-2008 with annotations of individual spectral slope, intercept and R<sup>2</sup>.



**Fig. 2** – Zooplankton size spectra base d on logarithmic binned data of zooplankton mean abundance (Ind m<sup>-3</sup>) within body mass ( $\mu$  g C Ind<sup>-1</sup>) size cl asses (estimated by OLS) for the upper and lower depth layers from 2009-2012 with annotations of individual spectral slope, intercept and R<sup>2</sup>.



**Fig. 3** – Zooplankton size spectra based on logarithmic binned data of zooplankton mean abundance (Ind m<sup>-3</sup>) within body mass ( $\mu$  g C Ind<sup>-1</sup>) size classes (estimated by OLS) for the upper and lower depth layers from 2013-2017 with annotations of individual spectral slope, intercept and R<sup>2</sup>.



**Fig. 4** – Zooplankton size spectra based on logarithmic binned data of zooplankton mean abundance (Ind m<sup>-3</sup>) within body mass ( $\mu$  g C Ind<sup>-1</sup>) size classes (estimated by OLS) for the upper and lower depth layers for 2018 with annotations of individual spectral slope, intercept and R<sup>2</sup>.



**Fig.5** – Fish size spectra estimated from weighted counts of body wet mass (g) of fish in four trawl hauls fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on trawling surveys for 2005 - 2008.



**Fig. 6** – Fish size spectra estimated from weighted counts of body wet mass (g) of fish in four trawl hauls fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on trawling surveys for 2009 - 2012.



**Fig. 7** – Fish size spectra estimated from weighted counts of body wet mass (g) of fish in four trawl hauls fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on trawling surveys for 2013-2017.



**Fig. 8** – Fish size spectra estimated from weighted counts of body wet mass (g) of fish in four trawl hauls fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on trawling surveys for 2018.

**Tab. 5** – Results from 48 combinations for six response and four different fish predictors (based on trawling \*<sup>1</sup> and hydroacoustics \*<sup>2</sup>) and three environmental predictors (EP) in multiple regression analyses with the best model and AIC value indicated. Statistical results for each significant predictor (in bold) and test statistics for the best model are given. Prey taxa total abundance and median body mass were abbreviated as abu. and b.m. respectively. Size spectra analysed by linear regressions on logarithmic binned data are designated with OLS, while size spectra analysed by maximum likelihood estimates of the coefficient b of continuous size distributions are indicated with MLE.

ar	Predictors				C	Coefficien	ts Statistic	al Results	5			Test S	tatistics	\$
Depth lay	Zooplankton	Fish	EP	Best Model	AIC	Predictors	Estimate	SE	t-value	d	$\mathbb{R}^2$	F	df	d
	SS Slope (OLS)			n.s.										
	SS Intercept (OLS)			Fish	-18.57	Fish	0.62	0.23	2.65	0.02	0.53	5.50	9.00	0.01
				т ТР +		ТР	205.5	53.5	3.84	0.00				
				Chla		Chl a	-0.31	0.14	-2.23	0.05				
U	SS exponent b (MLE)			n.s.										
	Prey taxa total abu.	3)*1		n.s.										
	Prey taxa median b.m.	) (MLF		n.s.										
	Size diversity	nent ł		n.s.										
	SS Slope (OLS)	S expor		n.s.										
	SS Intercept (OLS)	S		n.s.										
L	SS exponent b (MLE)		+ Temp	n.s.										
	Prey taxa total abu.		Chl a ⊣	n.s.										
	Prey taxa median b.m.		TP +	n.s.										
	Size diversity		]	n.s.										
	SS Slope (OLS)			n.s.										
	SS Intercept (OLS)	-3)*1		n.s.										
U	SS exponent b (MLE)	l 000 m		n.s.										
	Prey taxa total abu.	ass (g 1		n.s.										
	Prey taxa median b.m.	n bioma		n.s.										
	Size diversity	n fisl		n.s.										
т	SS Slope (OLS)	Mea		n.s.										
	SS Intercept (OLS)			n.s.										

	SS exponent b (MLE)		n.s.										
	Prey taxa total abu.		n.s.										
	Prey taxa median b.m.		n.s.										
	Size diversity		n.s.										
	SS Slope (OLS)		n.s.										
	SS Intercept (OLS)		n.s.										
U	SS exponent b (MLE)		n.s.										
	Prey taxa total abu.		n.s.										
	Prey taxa median b.m.	; ha)* <sup>2</sup>	Fish	-63.20	Fish	-0.0007	0.0003	-2.21	0.05	0.24	4.88	11.00	0.05
	Size diversity	ss (kg	n.s.										
	SS Slope (OLS)	bioma	n.s.										
	SS Intercept (OLS)	Fish	n.s.										
L	SS exponent b (MLE)		n.s.										
	Prey taxa total abu.		n.s.										
	Prey taxa median b.m.		Fish	-54.28	Fish	-0.0016	0.0004	-3.56	0.004	0.49	12.69	11.00	0.004
	Size diversity		n.s.										
	SS Slope (OLS)		n.s.										
	SS Intercept (OLS)		n.s.										
U	SS exponent b (MLE)		n.s.										
	Prey taxa total abu.	2	n.s.										
	Prey taxa median b.m.	(g)* <sup>2</sup>	n.s.										
	5	3											
	Size diversity	of fish (g	n.s.										
	Size diversity SS Slope (OLS)	mass of fish (g	n.s. n.s.										
	Size diversity SS Slope (OLS) SS Intercept (OLS)	Mean mass of fish (§	n.s. n.s. n.s.										
L	Size diversity SS Slope (OLS) SS Intercept (OLS) SS exponent b (MLE)	Mean mass of fish (	n.s. n.s. n.s. n.s.										
L	Size diversity SS Slope (OLS) SS Intercept (OLS) SS exponent b (MLE) Prey taxa total abu.	Mean mass of fish (	n.s. n.s. n.s. n.s.										
L	Size diversity SS Slope (OLS) SS Intercept (OLS) SS exponent b (MLE) Prey taxa total abu. Prey taxa median b.m.	Mean mass of fish (	n.s. n.s. n.s. n.s. n.s. n.s.										



**Fig. 9** Annual values for independent variables from fish, including biomass (kg ha<sup>-1</sup>) and mean mass (g) from hydroacoustic surveys and exponent b from trawling, as well as environmental predictors, such as mean temperature (°C), Chl a (mg L<sup>-1</sup>) and TP (mg L<sup>-1</sup>) concentration. For water temperature and TP are annual mean values given for the upper (dashed line) and lower (continuous line) layer, all other variables represent data from the entire water column.



**Fig.10** Annual values of zooplankton metrics (dependent variables), including mean spectral intercept and slope (size spectra of log-binned zooplankton masses, linear regressions estimated by ordinary least squares), mean exponent b (size spectra expressed as continuous mass data, exponent b estimated by maximum likelihood), median body mass ( $\mu$ g C) of potential prey taxa for fish and total abundance (Ind m<sup>-3</sup>) of zooplankton and mean size diversity index of zooplankton for the upper (U) and lower (L) depth layers during summer months.

#### Appendix A



**Figure A1.** Fish SS with counts and body wet mass (g) fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on trawling surveys for 2006 – 2010.



**Figure A2.** Fish SS with counts and body wet mass (g) fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on trawling surveys for 2011 – 2014.



**Figure A3.** Fish SS with counts and body wet mass (g) fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on trawling surveys for 2015 – 2018.



**Figure A4.** Fish SS with counts and body wet mass (g) fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on SEDs from hydroacoustic surveys for 2006 – 2010.



**Figure A5.** Fish SS with counts and body wet mass (g) fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on SEDs from hydroacoustic surveys for 2011 – 2014.



**Figure A6.** Fish SS with counts and body wet mass (g) fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on SEDs from hydroacoustic surveys for 2015 – 2019.



**Figure A7.** Fish SS with counts and body wet mass (g) fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on track echo group (TEG) detection from hydroacoustic surveys for 2006 – 2010.



**Figure A8.** Fish SS with counts and body wet mass (g) fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on track echo group (TEG) detection from hydroacoustic surveys for 2011 – 2014.



**Figure A9.** Fish SS with counts and body wet mass (g) fitted using the maximum likelihood estimate of the exponent b with the 95% confidence interval of b based on tracked echo group (TEG) from hydroacoustic surveys for 2015 – 2019.

### Appendix B

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Veer		Exponent b							
rear	TEG (WL)	SED (WL)	TEG (CB)	SED (CB)	Trawl				
2006	-0.56	-0.67	-0.61	-0.71	-1.01				
2008	-0.61	-0.77	-0.69	-0.88	-0.40				
2009	-0.41	-0.55	-0.32	-0.50	-0.60				
2010	-0.42	-0.63	-0.43	-0.65	0.10				
2011	-1.02	-1.25	-1.03	-1.25	-0.68				
2012	-0.58	-0.72	-0.59	-0.72	-1.44				
2013	-0.46	-0.53	-0.45	-0.54	-0.76				
2014	-0.06	-0.14	-0.09	-0.16	0.42				
2015	-0.43	-0.67	-0.45	-0.67	0.04				
2017	-0.24	-0.77	-0.29	-0.73	-2.01				
2018	-0.15	-0.24	-0.15	-0.22	-0.79				
2019	-0.35	-0.56	-0.38	-0.57	0.31				

**Table A1:** Exponent b from maximum likelihood estimation for each method, including hydroacoustics based on single echo detection (SEDs) and tracked echo groups (TEGs) of fish between 1 – 50 g body weight for 2006-2019 (excl. 2007 and 2016) from transects of the whole lake (WL) and the central basin (CB) only

## Appendix – Chapter 4

Appendix 1

**Table 1.** Results from Maximum Likelihood Estimation (MLE) of all fish above 8 cm body length (TL) per transect for each survey sites in Eilat in 2018 and 2019, including the SS slope (exponent b), minimum and maximum confidence interval (CI) and the calculated Standard Error (SE) of each slope

	1	T	T	
Survey Site	Exponent b	Min. CI	Max. CI	SE
Dekel	-1.7621158	-2.0081158	-1.5411158	0.11913265
Dekel	-1.0661655	-1.2321655	-0.9021655	0.08418367
Dekel	-0.81178	-1.31578	-0.29578	0.26020408
Dekel	-1.8183391	-2.0973391	-1.5673391	0.13520408
Dekel	-1.6383551	-2.0033551	-1.3103551	0.17678571
Dekel	-3.0264603	-3.3414603	-2.7384603	0.15382653
Dekel	-1.2900915	-1.4440915	-1.1410915	0.07729592
Dekel	-1.1349294	-1.4199294	-0.8629294	0.14209184
IUI	-1.612402	-1.742402	-1.485402	0.06556122
IUI	-2.1393099	-2.4183099	-1.8943099	0.13367347
IUI	-1.5418455	-1.7318455	-1.3608455	0.09464286
IUI	-1.3503373	-1.4533373	-1.2513373	0.05153061
IUI	-2.1699481	-2.3529481	-2.0019481	0.08954082
IUI	-1.2186818	-1.4616818	-0.9896818	0.12040816
IUI	-1.8120693	-1.9590693	-1.6750693	0.07244898
IUI	-1.4368385	-1.9118385	-1.0188385	0.22780612
IUI	-1.2962036	-1.8072036	-0.8292036	0.2494898
IUI	-0.9759088	-1.3099088	-0.6409088	0.17066327
IUI	-1.1642658	-1.4772658	-0.8622658	0.15688776
IUI	-1.4172963	-1.7512963	-1.1172963	0.16173469
IUI	-0.9581711	-1.2021711	-0.7131711	0.1247449
IUI	-1.3667553	-1.5567553	-1.1867553	0.09438776
IUI	-0.609941	-0.890941	-0.307941	0.14872449
IUI	-1.1334184	-1.5424184	-0.7314184	0.20688776
IUI	-1.3659772	-1.4909772	-1.2439772	0.0630102
IUI	-1.6732308	-1.7942308	-1.5612308	0.05943878
Japanese Gardens	-1.1038426	-1.2838426	-0.9258426	0.09132653
Japanese Gardens	-1.1561218	-1.3571218	-0.9611218	0.10102041
Japanese Gardens	-1.1687948	-1.3197948	-1.0227948	0.07576531
Japanese Gardens	-2.1490521	-2.2310521	-2.0700521	0.04107143
Japanese_Gardens	-1.445888	-1.625888	-1.280888	0.0880102
Japanese_Gardens	-1.3178564	-1.4948564	-1.1488564	0.08826531
Japanese_Gardens	-1.6552258	-1.8212258	-1.5012258	0.08163265
Japanese_Gardens	-1.2979868	-1.5699868	-1.0419868	0.13469388

Japanese_Gardens	-1.2033091	-1.4243091	-0.9913091	0.11045918
Japanese_Gardens	-0.8126792	-0.9986792	-0.6196792	0.09668367
Japanese_Gardens	-1.4426757	-1.7206757	-1.1816757	0.1375
Japanese_Gardens	-1.7171065	-1.9111065	-1.5431065	0.09387755
Japanese_Gardens	-1.6853743	-1.8113743	-1.5653743	0.0627551
Japanese_Gardens	-0.9440254	-1.1950254	-0.6910254	0.12857143
Katza	-3.1725013	-3.7595013	-2.6755013	0.27653061
Katza	-6.1445522	-6.6805522	-5.6475522	0.26352041
Katza	-0.8990563	-1.1280563	-0.6660563	0.11785714
Katza	-2.6732843	-2.8422843	-2.5152843	0.08341837
Katza	-1.0973351	-1.2463351	-0.9503351	0.0755102
Katza	-1.7472511	-1.9882511	-1.5242511	0.11836735
Katza	-2.1406871	-2.2896871	-2.0006871	0.07372449
Katza	-2.6632403	-2.7662403	-2.5642403	0.05153061
Katza	-2.4771643	-2.6141643	-2.3481643	0.06785714
Katza	-1.3843057	-1.5103057	-1.2643057	0.0627551
Katza	-1.0309445	-1.2619445	-0.8009445	0.11760204
Katza	-1.0929942	-1.2549942	-0.9339942	0.08188776
Katza	-1.6576464	-2.4086464	-0.9606464	0.36938776
Katza	-1.5458244	-1.7208244	-1.3858244	0.08545918
Reserve_A	-1.186599	-1.525599	-0.869599	0.16734694
Reserve_A	-1.9433707	-2.2133707	-1.6933707	0.13265306
Reserve_A	-1.2680049	-1.5280049	-1.0180049	0.13010204
Reserve_A	-1.2516743	-1.4366743	-1.0756743	0.09209184
Reserve_A	-0.5018656	-1.1208656	0.18513438	0.33316327
Reserve_A	-1.5710515	-2.1090515	-1.1160515	0.25331633
Reserve_A	-2.3793858	-2.8783858	-1.9303858	0.24183674
Reserve_A	-1.0201694	-1.2221694	-0.8181694	0.10306122
Reserve_A	-1.0371487	-1.2111487	-0.8641487	0.08852041
Reserve_A	-1.4437083	-1.6207083	-1.2757083	0.0880102
Reserve_A	-1.7168922	-1.8928922	-1.5498922	0.0875