

**The body size structure of lake  
fish and its response to biotic  
interactions and environmental  
variation**

**PhD thesis**

**Ignasi Arranz Urgell**



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UNIVERSITAT DE VIC  
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# **The body size structure of lake fish and its response to biotic interactions and environmental variation**

**Dissertation submitted by Ignasi Arranz Urgell to obtain the Ph.D.  
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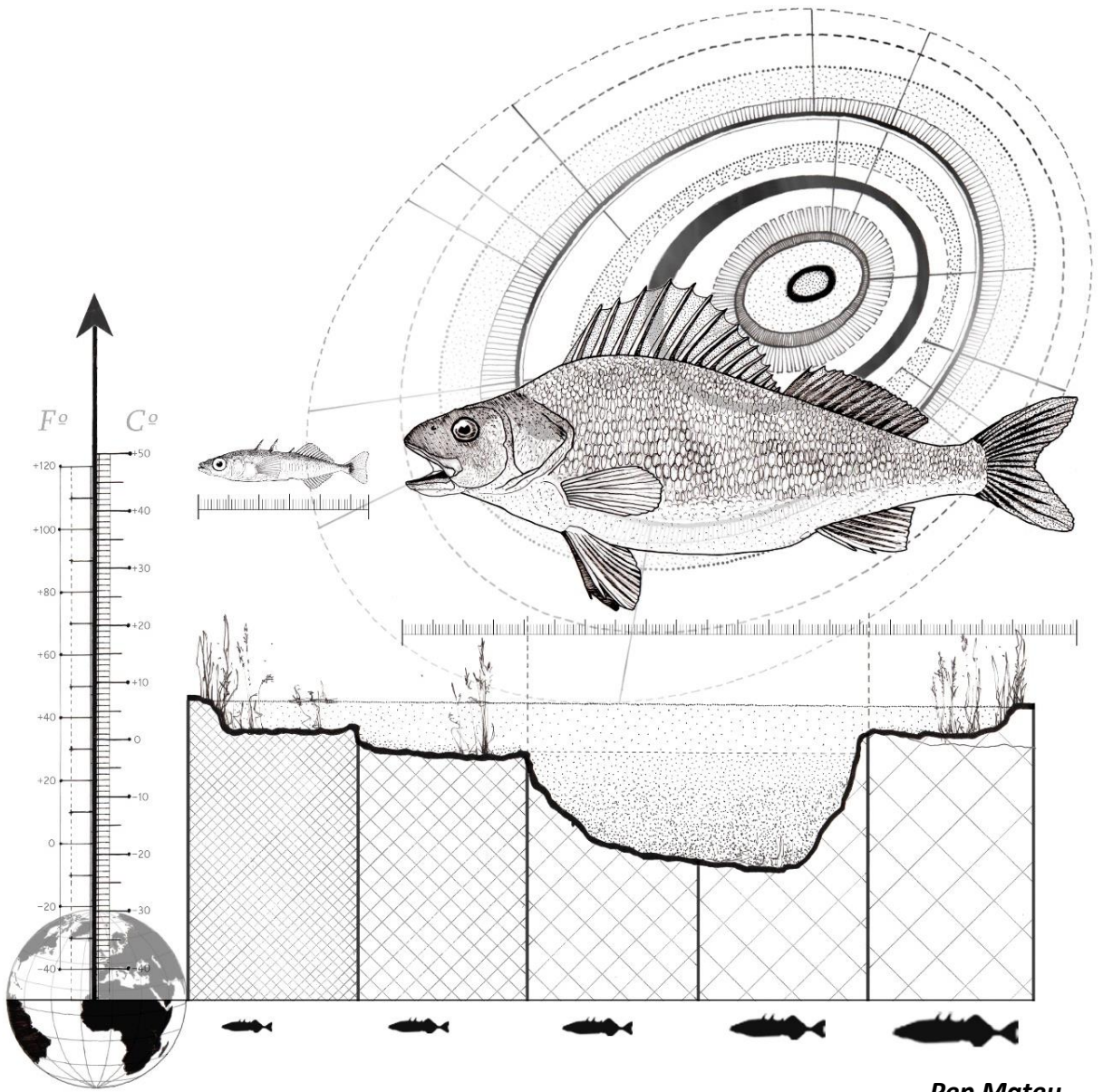
**University of Vic-UCC**



**To my *Tito livio* parents,  
for all constant support in  
everything I do**

Als meus *Tito livio* pares,  
per tot el seu suport  
constant en qualsevol cosa  
que faig





*Pep Mateu*





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## Summary

Finding approaches routinely measured in the field may become a step forward towards mechanistic understanding and prediction in aquatic ecology. Body size is perhaps the simplest metric to quantify in an organism but with a powerful background in the ecological framework. Over the 20th century, an enormous amount of aquatic research has generated intensive debates that relate the body size of organisms to the structure and the functioning of aquatic systems. The widely use of the body size structure is based on the empirical evidence that many of the most important ecological and physiological processes scale with the body size.

The present thesis focuses on the study of body size structure (i.e. the relationship between organisms' body size and abundance) with lake fish as a subject group and at different ecological (both fish populations and communities) and spatial scales (at regional and continental scales). The general objectives were to study the fish size structure to understand the trophic interactions in fish communities and populations as well as the effect of environmental and anthropogenic factors in the lake systems; and to expand the focus on the fish size structure and integrate taxonomic indices as well as other functional approaches that may also influence the fish body size. This was done by compiling several European fish datasets along biotic and abiotic gradients and by using different size-, functional- and taxonomic-based metrics: size spectrum, size diversity, mean body size, fish condition and species diversity.

**The first part of the thesis** investigates the importance of considering the fish size structure when analyzing the trophic interactions such as predation and competition processes in the lakes. Other factors such as environmental heterogeneity, lake morphometry and anthropogenic pressures that may influence the shape of the fish size structure were also included as potential drivers. **The first chapter** examined the size structure of the six most common fish populations in European lakes. We analyzed the response of the size structure of each fish population to density-dependent effects, as surrogates of resource and habitat competition, as well as to environmental variables. We found that density-dependent effects showed a more consistent and stronger response than the environmental variables in the variation of the size structure for all fish populations. That

is, in situations with high fish densities, disproportionately more number of small fish than large fish occupy small size classes resulting in steeper slopes, narrower size diversity and smaller mean body size for most fish populations. This finding suggested that the density-dependent effects are a key driver of the fish body size structure, which is often neglected. **The second chapter** examined systematic deviations from the linear size-abundance relationship of fish communities at a regional scale. We investigated whether the predator-prey interactions as well as human use intensity could give mechanistic explanations to such deviations. According to our results, small predator-prey size ratios and large predator-prey abundance ratios were characteristics of lakes with strong deviations from the linear size-abundance relationship. The low abundance of large predators in lakes with strong deviations likely caused an overrepresentation of small fish in intermediate size classes. In addition, we showed that the deviations were indirectly affected by human use-intensity and lake productivity. This finding suggested that deviated patterns of the size structure may be a sensitive metric to use for the management of fishing or ecological quality, as well as to understand the complexity of the trophic food webs.

**In the second part of the thesis**, we expanded the focus on the fish size structure and we integrated other functional and taxonomic approaches with the aim to further understand the trophic interactions in lake fish. Here we also considered the influence of environmental variations and anthropogenic pressures. **The third chapter** explored the relationship between the size diversity and species diversity with the aim to identify the degree of overlap in size among species and thereby the overlap in niches in a fish community across different spatial scales (both continental and regional scale). The slope of the relationships between the size diversity and species diversity showed different strengths and shapes along the latitudinal gradient, which may be related to the combination of different species richness and life history traits. Results suggested that in lakes located in colder regions (at high latitudes), the fish communities were composed of few species covering large range of sizes. In contrast, in lakes located in warmer regions (at low latitudes), fish species are greater in number but they occupy narrower size ranges which suggests higher niche specialization. This implies that the taxonomic diversity is less informative to evaluate the functionality of the fish community than the size diversity. The study represented a first step towards understanding the link between the species diversity, size structure and community

functioning over large-scale gradients. **The fourth chapter** presented the size structure coupled with other functional approaches in simple food web structures, taking the population structure of Arctic charr (*Salvelinus alpinus*) in Greenland lakes as a case study. These systems are inhabited by only two fish species, Arctic charr and three-spined sticklebacks (*Gasterosteus aculeatus*, sticklebacks). Sticklebacks can be prey for adult charr or competitors for young charr. Furthermore, Greenland lakes span a broad morphometric gradient that may have consequences of the population structure of the fish species. In this sense, we investigated the effects of sticklebacks and lake morphometry on the size structure of Arctic charr in Greenland lakes. We also included age- and weight-based tools to provide a more holistic view of the changes of the Arctic charr population structure. The results showed that larger and longer-lived charr inhabited larger lakes. Furthermore, the size structure of charr was more bimodal in lakes without sticklebacks, or when sticklebacks were few and predominately confined to the littoral zone. We also measured the condition of adult and young charr expressed as a multifunctional measure of individual length-weight relationship. The field evidence also suggested that sticklebacks only affect negatively the condition of young charr, forcing them to move to less favourable habitats. Since climate warming may indirectly impair lake morphology and stickleback density and distribution, this may have consequences for charr population structure.

We concluded that the fish size structure responded to trophic interactions as well as to environmental variables and anthropogenic pressures. Furthermore, the taxonomic-based approaches and other functional traits can be integrated in the study of the fish size structure to increase the accuracy of the understanding of ecological and biogeographic processes. Within the context of the Water Framework Directive, the fish size structure may be used as a bioindicator for the management of freshwater ecosystems, after controlling for trophic interactions and natural variation that may significantly modify the size structure.



## Resum

Trobar aproximacions que es mesurin rutinàriament en el camp pot esdevenir un pas endavant per entendre els mecanismes que regulen la interacció entre el medi ambient i els organismes. La mida corporal és potser la mesura més senzilla per quantificar en un organisme però amb un rerefons potent en el camp de l'ecologia. Al llarg dels segles vint i vint-i-u, una enorme quantitat de recerca en ecologia aquàtica ha generat intensos debats que relacionen la mida corporal dels organismes amb l'estructura i funcionament dels sistemes aquàtics. La utilització de l'estructura de mides corporal està basada en l'evidència empírica que els processos ecològics i fisiològics més importants d'un organisme estan relacionats amb la mida corporal.

La present tesi doctoral es centra en l'estudi de l'estructura de mides corporal (és a dir, la relació entre la mida corporal dels organismes i la seva abundància) amb els peixos del llac com a grup d'estudi i a diferents escales ecològiques (és a dir, a un nivell poblacional i de comunitats de peixos) i espacials (és a dir, a un nivell regional i continental). Els objectius generals són estudiar com l'estructura de mides dels peixos respon a les variacions de les interaccions tròfiques així com integrar altres aproximacions taxonòmiques i funcionals que poden ajudar a entendre aquests canvis. Els factors ambientals i antropogènics també es van tenir en compte ja que poden tenir una influència molt forta en la mida corporal dels peixos. Es va reunir una sèrie de dades de peixos al llarg de gradients biòtics i abiòtics i es van utilitzar diferents aproximacions de mides, funcionals i taxonòmiques: l'espectre de mides, la diversitat de mides, la mida mitjana, la condició del peix i la diversitat d'espècies.

**En la primera part de la tesi** s'investiga la importància de considerar l'estructura de mides dels peixos quan s'analitzen les interaccions tròfiques com ara els processos de depredació i competència en els llacs. Altres factors com ara l'heterogeneïtat ambiental, la morfologia del llac i les pressions antropogèniques que poden influir en la forma de l'estructura de mides dels peixos també es van incloure com a possibles reguladors. **En el primer capítol** s'examina l'estructura de mides de la mida corporal de les sis poblacions de

peixos més comunes en els llacs europeus. Es va analitzar la resposta de la mida corporal de cada població de peix a partir dels efectes densodependents, com a substitut de la competència pel recurs i l'hàbitat, així com les variables ambientals. Es va observar que els efectes densodependents van mostrar una resposta més consistent i forta que les variables ambientals en la variació de l'estructura de mides de les poblacions de peixos. Això indica que en situacions amb una alta densitat de peixos, un elevat nombre d'individus ocupen les classes de mides petites de manera desproporcionada. Aquest resultat implica uns pendents més pronunciats, unes diversitat de mides més baixes i unes mitjanes de mida corporal més petites en la majoria de les poblacions de peixos. Aquesta troballa va suggerir que els efectes densodependents són uns reguladors claus de l'estructura de mides dels peixos malgrat que mai s'hagin tingut en compte. **En el segon capítol** s'examina les desviacions sistemàtiques en la relació entre la mida i l'abundància de les comunitats de peixos a una escala regional. Es va investigar si les interaccions depredador-presa, com també la intensitat antròpica, podrien explicar aquestes desviacions en l'espectre lineal de mides. Segons els nostres resultats, els llacs amb les desviacions més fortes eren aquells llacs que presentaven una elevada ràtio de la mida depredador-presa i una baixa ràtio de l'abundància depredador-presa. La baixa abundància de predadors grans en els llacs amb fortes desviacions probablement causa un excés de peixos petits en les classes de mida intermèdies. A més a més, es va mostrar que les desviacions estaven indirectament afectades per les activitats humanes i la productivitat del llac. Aquests resultats van suggerir que els patrons de desviació de l'estructura de mides poden ser una mesura útil en la gestió de les pesqueries i la qualitat ecològica en llacs, com també per entendre la complexitat de les xarxes tròfiques.

**En la segona part de la tesi**, s'estudia l'estructura de mides dels peixos juntament amb altres aproximacions funcionals i taxonòmiques amb l'objectiu d'entendre millor les interaccions tròfiques dels peixos del llacs. Aquí també es va considerar la influència de les variacions ambientals i les pressions antropogèniques. **En el tercer capítol** s'explora la relació entre la diversitat de mides i la diversitat d'espècies amb l'objectiu d'identificar el grau de solapament de mides entre les espècies de peixos i per tant el solapament dels nínxols en la

comunitat a diferents escales espacials (escala continental i regional). La pendent de la relació entre la diversitat de mides i la diversitat d'espècies va ser diferent al llarg del gradient continental, fet que podria estar relacionat amb les diferències de riquesa de les espècies en la comunitat i les seves característiques de vida. Els resultats van suggerir que en els llacs localitzats a les regions fredes (a elevades latituds), les comunitats de peixos estaven composades per unes poques espècies però que cobrien uns rangs amplis de mida. En canvi, els llacs localitzats en les regions càlides (a baixes latituds), presentaven més espècies de peixos els seus rangs de mides eren més estrets. Aquest fet fa suposar que en baixes latituds hi ha una especialització del nínxol més alta que en les zones de més al nord d'Europa. Això implica que la diversitat taxonòmica és una pitjor indicadora de la funcionalitat de les comunitats de peixos que la diversitat de mides. L'estudi representa un pas endavant per entendre la relació entre la diversitat d'espècies, l'estructura de mides i el funcionament de la comunitat a un gradient continental. **En el quart capítol** es presenta l'estructura de mides juntament amb altres aproximacions funcionals en unes xarxes tròfiques d'estructura simple. Es va tenir en compte l'estructura de poblacions de la truita alpina (*Salvelinus alpinus*) de Groenlàndia com a cas d'estudi. Aquests sistemes estan habitats per només dues espècies, la truita alpina i l'espínós (*Gasterosteus aculeatus*). L'espínós pot ser presa dels adults de la truita alpina o bé competidor dels joves de truita alpina. A més a més, els llacs de Groenlàndia presenten un gradient de morfometria molt ampli que pot tenir conseqüències en l'estructura de poblacions de les espècies de peixos. En aquest sentit, es va investigar els efectes de l'espínós i la morfologia del llac en l'estructura de mides de la truita alpina dels llacs de Groenlàndia. També es va incloure mesures basades en el pes i l'edat per tenir una visió més holística dels canvis en l'estructura de poblacions de la truita alpina. Els resultats van mostrar que les truites alpines més grans de longitud i edat es trobaven en els llacs més grans. A més a més, l'estructura de mides de la truita alpina presentava una forma bimodal en els llacs sense espínós, o quan hi havia poc espínós i predominava a la zona litoral. També es va mesurar la condició dels adults i joves de truita alpina com a una mesura multifuncional de la relació entre la mida i el pes de l'individu. Els nostres resultats van demostrar que



l'espínós només afectava negativament la condició dels joves de truita alpina, forçant-los a moure's cap a hàbitats menys favorables. El fet que el canvi climàtic pot afectar indirectament la morfologia i la densitat i distribució de l'espínós, això fa que tingui conseqüències en l'estructura de poblacions de la truita alpina.

Així concloem que l'estructura de mides dels peixos respon a les variacions de les interaccions tròfiques com també a les variables ambientals i a les pressions antropogèniques. A més a més, les aproximacions basades en la taxonomia i altres trets funcionals poden ajudar en l'estudi de l'estructura de mides dels peixos. Dins el context de la Directiva Marc de l'Aigua, l'estructura de mides dels peixos es pot utilitzar com a una mesura bioindicadora per la gestió dels sistemes aquàtics continentals sempre i quan primer es controli la variació de les interaccions tròfiques i de les variables ambientals que poden influir significativament en ella.

## List of chapters

The four chapters of the present thesis are scientific publications in peer-reviewed journals. The corresponding citation of each chapter and the authorship contribution are stated below:

### Chapter 1

**Arranz, I.**, Mehner, T., Benejam, L., Argillier, C., Holmgren, K., Jeppesen, E., Lauridsen, T.L., Volta, P., Winfield, I.J. and Brucet, S. 2016. Density-dependent effects as key drivers of intraspecific size structure of six abundant fish species in lakes across Europe. *Canadian Journal of Fisheries and Aquatic Sciences*. 72:1-16.

I.A., S.B., L.B. and T.M. developed the idea. I.A. did the analyses. I.A. wrote the first draft of the manuscript. All authors contributed to the critical revision of the manuscript.

### Chapter 2

**Arranz, I.**, Hsieh, C. H., Mehner, T. and Brucet, S. Systematic deviations from linear size-abundance relationships of lake fish communities are correlated with predator-prey interactions and lake-use intensity. *Oikos*. (*Submitted*)

All authors developed the idea. I.A. and T.M. did the analysis. I.A wrote the first draft of the manuscript. All authors contributed to the critical revision of the manuscript.

### Chapter 3

Brucet, S.; **Arranz, I.**; Mehner, T.; Argillier, C.; Beklioglu, M.; Benejam, L.; Boll, T.; Holmgren, K.; Lauridsen, T.; Svenning, J.; Winfield, I.; Jeppesen, E. Size diversity and species diversity relationships in fish assemblages of Western Palaearctic lakes. *Ecography*. (*Submitted*)

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## Chapter 4

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I.A, L.B. and E.J developed the idea. I.A. and L.B. did the analysis. I.A. wrote the first draft of the manuscript. F.L., T.L.L. and E.J. designed the work. T.A.D., N.M., N.V., K.Ö., I.G., J.W., R.F.M. helped with the field campaigns. All authors contributed to the critical revision of the manuscript.

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## GENERAL INTRODUCTION

### The body size structure

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Elton and his textbook *Animal Ecology* (1927) introduced an apparent but unknown ever since perspective of the modern ecology. He was struck by the fact that animal communities vary significantly in body size and abundance with an inverse relationship between the number of organisms and their size. This observation brought a new ecological understanding of the structure of the food webs, physiological processes and trophic interactions that has been studied along decades by many ecologists.

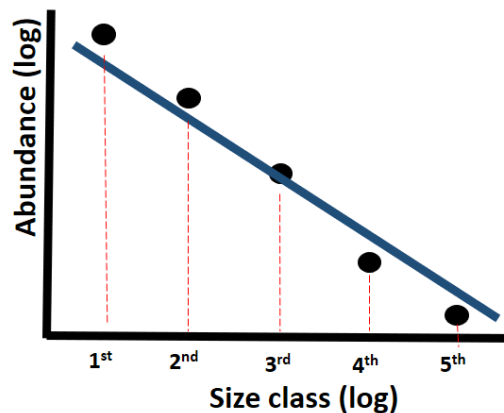
Indeed, the body size is probably the most important trait of organisms since it encapsulates most of their physiological and ecological processes, morphological adaptations and life histories (Huxley 1932; Peters 1983; Brown et al. 2004; Woodward et al. 2005). The body size also determines the metabolic requirements of organisms through allometric scaling relations (Brown et al. 2004; Trebilco et al. 2013). One possibility to represent the body size structure is to show in a two-dimensional graphical form how organisms are organized in biological systems based on single measures of sizes of organisms and their respective abundances.

The abundances and sizes of organisms may also be explained by the Metabolic Theory of Ecology (MTE) under steady-state condition (Brown et al. 2004; Trebilco et al. 2013). MTE links the variation of the size-abundance relationship with the trophic transfer efficiency and predator-prey interactions (Brown et al. 2004). That is, the energy flows in the ecosystem through the metabolic process of energy assimilation between predators (as consumers) and prey (as resources) (Brown et al. 2004; Woodward and Warren 2007). However, part of the energy assimilated by the consumer is lost to cover metabolic requirements such as respiration, reproduction or growth (Brown et al. 2004). Thereby, the size structure is of paramount importance in determining the impact and strength of the trophic interaction.



Apart from its relationship with metabolism, the size structure has also several advantages for understanding ecological patterns of energy transfer through trophic levels. First, it is based on a simple measure of body size regardless the time-consuming effort of species identification. Second, the size structure often shows uniform patterns over geographic gradients and across diverse groups of organisms (Blackburn et al. 2009; Smith 2013). And third, the components of the size structure can be used to predict the variation of biotic and abiotic gradients because they are easily comparable across systems (Gaston and Blackburn 2000).

Pioneered by Sheldon and his colleagues (Sheldon et al. 1972), the Normalized Biomass Size Spectrum (NBSS; a.k.a. size spectrum) is one of the size-based approaches that has been used to simplify explanations of complex trophic interactions and the effects of external factors such climate-related variables, lake morphometry and human activities on aquatic communities. In NBSS, the abundance in each of the body-size classes is scaled to the width of the size class at a log-log scale (Platt and Denmann 1977; Silvert and Platt 1978) (Fig. 1).



**Figure. 1.** Theoretical NBSS with five size classes relating log abundance to log size. Blue line represents the slope of the NBSS. Black dots are the observed log-abundance of organisms in each size class. The logarithmic scale of abundance is divided by the width of the body size intervals.

One of the most important parameters characterizing the NBSS is the slope (blue line in Fig. 1), which quantifies the rate of decrease in abundance of organisms with increasing their body size (Sheldon et al. 1972; Sprules and Munawar 1986; Gaedke 1992). The slope has been found to respond in a consistent way to changes in environmental variations and human impacts across aquatic organisms (Bianchi et al. 2000; Blanchard et al. 2009; Petchey and Belgrano 2010) and predation (e.g. fish predation on the size structure of zooplankton communities, Mazunder et al. 1988; Blumenshine et al. 2000; Zimmer et al. 2001). In contrast, the effect of competitive interactions in the variation of the slope has received little attention. There are other two parameters that can be extracted from the NBSS. First, the intercept, which is a rough surrogate of the food-web capacity or total log-abundance (Rice and Gislason 1996; Daan et al. 2003). And second, the coefficient of determination ( $R^2$ ) from the NBSS, which may be used as a measure of disturbance in the systems that explains to what extent the observations are far from the linear NBSS (Sprules and Goyke 1994). In fact, the structure of aquatic systems were originally characterized by linearly decreasing NBSS but some studies have eventually found considerable residual variation around the NBSS (Vidondo et al. 1997; C3zar et al. 2003; Chang et al. 2014). According to theoretical predictions, the deviations may also emerge due to the variations of predator-prey interactions caused by morphological feeding constraints or efficiencies of predators in handling prey, and indirectly by human activities (Kerr and Dickie 2001; Benoit and Rochet 2004; Law et al. 2009). However, the underlying factors have not been empirically tested yet.

Another size-based approach is the size diversity that indicates how the body sizes and number of individuals are equitably distributed along the size structure, in the same way that the Shannon diversity integrates the species composition and species relative abundances (Brucet et al. 2006; Quintana et al. 2008). In fact, the size diversity may be interpreted as a functional index to evaluate the diversity of life history strategies of aquatic communities (Ye et al. 2013; Garc3a-Comas et al. 2016). The mean body size of individuals is another simple yet general size-based approach to predict environmental and biotic variations (Gardner et al. 2011; G3mez-Canchong et al. 2013). It is computed in many ways, including arithmetic or geometric mean body mass and median body mass. For instance,

mean body size expressed as geometric mean mass is a good metric for assessing environmental gradients in the size structure of fish communities (Bruce et al. 2010; Emmrich et al. 2014).

## **Lake fish and their size structure**

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Lakes represent a very small portion of the total Earth's surface but they, as freshwater storages and biodiversity hotspots, make one of the most valuable freshwater systems (Kalff 2001). Lakes and aquatic systems in general are generally viewed as being strongly size-structured systems owing to the metabolic constraints of aquatic organisms associated with trophic interactions (Kerr and Dickie 2001; Trebilco et al 2013). Fish are the inhabitants best known in the lake because of their visibility, abundance, economic importance and ease of capture and identification. Fish lifespan is longer than any other group of organisms so they can integrate long-term physicochemical and biological records of the lake system. Fish affect the distribution and abundance of other group of organisms (e.g. zooplankton) and can cause cascading changes on the structure of the whole food web (Carpenter et al. 2008; Jeppesen et al. 2010; Cañedo-Argüelles et al. 2016).

The fish body size can span different orders of magnitude because most fish are indeterminate growers. That is, the body size continually increase and never becomes fixed but limited by an asymptotic size trajectory (Andersen and Beyer 2006). The huge variation of fish range size implies that a particular measure of body size typically defines the trophic role of fish in the environment, regardless their taxonomy identity. This is due to the fact that fish undergo ontogenetic niche shifts throughout their life, giving clear evidences that their body size and trophic level are strongly related (Jonsson et al. 2005; Woodward et al. 2005). Put in another words, small-sized fish individuals can exhibit a complete different habitat use and feeding style to their large-sized conspecifics. This contrast with the general theory of single species niche in terrestrial ecosystems in which terrestrial species almost always occupy the same fraction of niche space throughout their lives (White et al. 2007).

## **Trophic interactions and environmental factors influencing fish size structure**

---

Predation and competition play important roles in determining the structure and dynamics of the aquatic food webs (Chase et al. 2002 and references therein). *Feeding and being fed on* has been shown to be the driving force structuring trophic food chains and governing the physiological energetic fluxes (Kerr and Dickie 2001; Chase et al. 2002; Woodward and Warren 2007). In general, the size of fish predators tends to be larger than the size of their fish prey with larger predators feeding on wider size range of prey. Furthermore, fish have to engulf their entire prey item because if only eat pieces of it, the rest of the prey may sink and loss into the bottom of the lake (Brose et al. 2006; Mehner et al. 2016). The predator-prey attributes such as handling time, foraging efficiency or attack rate are all scaled with the size of predators and preys (Woodward and Warren 2007). These may be corresponded to the constraints set by the gape size of predators implying that predators are unable to capture larger-sized prey (Arim et al. 2010; Mehner et al. 2016). The efficiency of predators to obtain their preys due to the size dependent attributes may be translated to variations of the parameters of the size structure.

Competition for food resource or habitat use is the other trophic interaction that may influence the fish size structure but little attention has been paid so far. Low or high competition depends on the number of individual fish to compete for a food resource or occupy a habitat. Variations in the abundance of predators and preys or overall fish density may induce shifts in the fish growth rates triggered by the food resource or habitat availability (Lorenzen and Enberg 2001; Persson and Roos 2007). In situations with low habitat space or resource limitation, fish may inhibit their growth in a certain body size and become determined growers (Ylikarjula et al. 2000; Giacomini et al. 2013). This adaptation is a life history strategy called stunting that is commonly found in both freshwater and marine systems when fish can exhibit either density- or food-dependent growth (Ylikarjula et al. 2000; Persson et al. 2007). If stunted fish is overrepresented in certain sizes (e.g. in small size

classes), the parameters of the size structure will possibly reflect some changes. However, to date, no empirical evidences have demonstrated the effects of stunting on the variations of the size structure.

Apart from the trophic interactions, there are other environmental and anthropogenic factors that can contribute to the shape of the fish size structure. Fish, as being ectothermic animals, rely on external source of heat following the temperature-size and Bergmann's rules (Bergmann 1847; Atkinson 1994). The phenomenon lies on the premise that organisms have much bigger body size at lower temperatures whereas the same organisms at higher temperature have smaller body sizes. Several studies have recently revealed that climate-induced effects on the size structure follow the same patterns of decline of fish body size at warmer lakes (Edeline et al 2013; Brucet et al. 2013; Emmrich et al. 2014). Lake productivity can be another environmental predictor to regulate the fish size structure. This may be due to the shifts in relative abundance of species composition along a productivity gradient. The proportion of percids is generally higher in oligotrophic lakes whereas salmonids or cyprinids dominate in eutrophic lakes (Persson et al. 1991; Jeppesen et al. 2000; Olin et al. 2002). Furthermore, fish density tends to increase with lake productivity (Brucet et al. 2013; Mehner et al. 2016) suggesting an indirect contribution to the stunting growth. Lake morphometry (area, depth and volume) may also be a regulator of the fish size structure because in larger and deeper lakes the number of available niches may be higher than shallower and smaller lakes (Hindar and Jonsson 1983; Riget et al. 2000; Holmgren and Appelberg 2004). Finally, human activities can also directly or indirectly change the abundance and size of fish communities. Fishing, for instance, tends to be size-selective because large fish have higher economic importance (Bianchi et al. 2000; Shin et al. 2005; Gómez-Canchong et al. 2011).

The decline of large individuals in the fish community may be reflected in the shape of the size structure as deviations from the linear size spectrum, as suggested by theoretical models (see first part introduction; Law et al. 2009; Benoit and Rochet 2004). Invasive species based on human introductions can also disrupt the natural patterns of aquatic systems and likely the size structure by causing variations of the predator-prey and strong competition interactions on the native species (Whalter et al. 2002; Comte et al. 2016).

## **The size structure in relation to other functional and taxonomic approaches**

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The body size structure reflects many of the functional aspects of the fish community and populations (White et al. 2007). However, the simultaneous use of taxonomic indices and other functional approaches based on the weight and age of the fish may complement the understanding of the fish trophic interactions and other environmental and anthropogenic gradients. Some research has attempted to partition the relative contributions of the size structure and species composition (Boix et al. 2004; Brucet et al. 2006; Jennings 2005; Yvon-Durocher et al. 2011), but each approach has tended to follow their own trajectories (Belgrano and Reiss 2011). The simultaneous information of functional and taxonomic aspects brings the possibility to know better not only the identity of an organism (as it *is*) but also what it *does* in the environment (as its *functional role*).

Some studies have shown that species diversity is an adequate surrogate for functional diversity of a community (e.g. Stuart-Smith et al. 2009), but this may not always be the case (De Victor et al. 2010; Safi et al. 2011). An example of an incongruence are fish communities dominated by single fish species but with large size range (e.g. Arctic lakes are mostly dominated by only Arctic charr, *Salvelinus alpinus*) (Griffiths 2006). In these lakes, the same fish species can have different food and habitat preferences according to their intraspecific variability in sizes as well as the different ecomorphs. This probably suggest that

taxonomic measures give less information about the functioning of these fish communities than measures based on functional diversity such as the body size.

Size diversity may be a surrogate of the functional diversity since body size is a good proxy of the trophic level (Jennings et al. 2001; Romanuk et al. 2011). The degree of redundancy between species diversity and size diversity will reflect the degree of overlap in size, and likely an overlap in niches, among species in a community (Woodward and Hildrew 2002). Thus, when studying the relationship between size diversity (or functional diversity) and species diversity, one may understand to what extent the fish community is likely to lose functional traits when there is a decline of species diversity. However, the relationship between the size and species diversity has not yet been demonstrated in fish community at large geographical scales.

The fish condition is another metric which may complement the analysis of the fish size structure by providing information about the well-being of fish populations. One can assess fish condition by a variety of physiological (e.g. liver and gonad weights) and biochemical (lipid or protein content criteria) traits (Barton et al. 2002; Lloret et al. 2002). However, other studies have used simple cost-effective measures of the length (mm) and weight (g) of each individual fish (García-Berthou and Moreno-Amich 1993). The length-weight relationship of common fish populations responds to anthropogenic pressures, with a reduced individual fish condition at highly polluted areas (Vila-Gispert and Moreno-Amich 2001; Benejam et al. 2008).

## OBJECTIVES

The general objectives of the thesis were twofold: (1) to study the size structure to understand the trophic interactions in fish communities and populations as well as the effect of environmental and anthropogenic factors in the lake systems; and (2) to expand the focus on the fish size structure and integrate taxonomic indices as well as other functional approaches to get further insight on the mechanisms shaping fish community or population structure.

### Specific objectives

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**The first chapter** analyzed three size metrics (mean body size, size diversity and the slope of linear size spectra) as representatives of the size structure of the six most common freshwater fish species in European lakes. The specific objectives of the chapter were the following:

1<sup>st</sup>) Determine if density dependence, as a rough surrogate of competition (both intra- and interspecific competition), can affect the body size structure of the six fish species.

2<sup>nd</sup>) Determine which environmental variables influenced most the variation in the body size structure of the selected fish species.

The first hypothesis was that the high fish density would contribute to shifts in fish body size structure by decreasing mean body size, size diversity and size spectra slopes (i.e. increasing dominance of small size fish). This is because fish density can modify the availability of food resources, which indirectly affects fish growth rates (Persson and Roos 2007). The second hypothesis was that the changes in the size structure for all fish populations in response to the environmental effects would be consistent with those found



for the community-wide variation in fish size structure (Emmrich et al. 2014). These are a decreased mean body size of fish communities at low temperatures following the temperature-size rule (Atkinson 1994) and an increased mean body size of fish communities in larger and deeper lakes.

**The second chapter** explored the systematic deviations from the linear regression of the size spectrum of the fish communities at a regional scale. The specific objectives of this chapter were:

- 1<sup>st</sup>) Quantify systematic deviations based on size-specific residuals from the slope of the linear size spectra
- 2<sup>nd</sup>) Examine if predator-prey interactions drive these systematic deviations.
- 3<sup>rd</sup>) Examine if human use intensity affects these systematic deviations.

The first hypothesis was that by categorizing the lake systems according to the similarity and dis-similarity of secondary structures, we could develop systematic deviations from linearity of the abundance-size spectrum. The second hypothesis was that the strongest deviations in the size structure would occur in lakes where the predator abundance was low or the predator-prey mass ratio was low, such that a low predation pressure would cause stunted growth in the prey size groups. The third hypothesis was that strong deviations from the fish size structure would occur in lakes of intense human use caused by the depletion of large predatory fish and an over-representation of number of smaller fish (Benoît and Rochet 2004; Law et al. 2009).

**The third chapter** analyzed the relationship between the size diversity and the species diversity in lake fish community across different spatial scales (at continental and regional scale). Size diversity can be an adequate surrogate of the functional diversity in fish community because of the strong link between body size and trophic role. The species and size diversity relationship could give information about the degree of species and size overlap

(i.e. degree of niche overlap) in fish communities. The chapter addressed the following objectives:

1<sup>st</sup>) Investigate the strength of the relationship between species diversity and size diversity across different spatial scales as a measure of the degree of overlap in size among species and thereby the potential overlap in niches in fish community.

2<sup>nd</sup>) To assess whether the size diversity is a good surrogate for species diversity in European lake fish communities.

The first hypothesis was that the relationship between the size diversity and the species diversity would be positively correlated but the slope of the size-species diversity would increase more steeply in warmer regions than in colder regions. This would reflect the higher niche segregation towards the tropics (Vázquez and Stevens 2004). In contrast, fish communities in coldest regions tend to be composed of few species such as Arctic charr or perch (*Perca fluviatilis*) but with large size ranges, thus probably a high size diversity. In this sense, we expected that size diversity would not be a strong surrogate for species diversity, at least in European lakes located in colder regions. We also included climate variables and anthropogenic variables that can influence the size structure of fish communities (Griffiths 2012, Jeppesen et al. 2010, Emmrich et al. 2014) and thus might also affect the size diversity.

**The fourth chapter** analyzed the fish size structure together with other functional approaches related to age and weight of several Arctic charr populations in Greenland lakes. Lakes in Arctic Greenland are good model systems for evaluating trophic interactions because of their low species diversity and simple food web structure. Arctic charr populations were studied in two different areas (i.e. south-west Greenland, Nuuk and north-west Greenland, Ilulissat) with lakes hosting either a solitary population of Arctic charr (i.e. Ilulissat) or occurring with sticklebacks (i.e. Nuuk). In some lakes, sticklebacks are present and constitute an important food item for adult Arctic charr but their diet also overlaps with young Arctic charr (Bergersen 1996). Furthermore, Greenland lakes span a wide range of lake morphometry (areas, depths and volumes).

The specific objectives of this chapter were:

- 1<sup>st</sup>) Investigate the effect of the presence and habitat use of sticklebacks on several populations of Arctic charr in Greenland.
- 2<sup>nd</sup>) Determine if lake morphometry is a key predictor of the population structure of charr.

The first hypothesis was that the presence and habitat use of sticklebacks would modify the size and age structure and the condition of several population of Arctic charr. Sticklebacks may compete with the young Arctic charr forcing to shift their habitat towards less suitable conditions. In contrast, sticklebacks may provide an extra food resource for adult Arctic charr whose condition and growth rates will be better than populations of Arctic charr that inhabit in lakes without sticklebacks. The second hypothesis was to investigate if lake morphometry affected Arctic charr size and age distribution on a given lake, because Arctic charr shows high foraging plasticity and can occupy different habitat niches during ontogeny (Griffiths 1994; Riget et al. 2000).

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# METHODOLOGY

## Study area

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Our study area encompassed a total of 431 lakes and reservoirs from 11 countries along a latitudinal gradient between 36.69°N and 76.62°N and a longitudinal gradient between 54.41°O and 36.16°E. **In the first and third chapters**, data at European continental scale were used. **The second chapter** explored, at a more regional scale, the fish community in German lakes located in the north-eastern range of the country. Finally, **the fourth chapter** focused on lakes from two different regions of the West coast of Greenland: Nuuk, in the southern part, and Illulissat, in the northern part. Information about the geographic position of the study lakes is provided in Figure 2.

Four fish datasets from Western Palearctic and Arctic zones were compiled in the present thesis. All datasets followed the same standardized procedure approved by the European Committee for standardization (CEN 2005) in the context of the Water Framework Directive (2000/60/EC) (WFD). The purpose of the samplings were to characterize the fish community in terms of size, abundance and species composition in each of the lakes and reservoirs. A brief outline of each dataset is given:

❖ *European lake database*

The European Union project WISER (Water bodies in Europe: Integrative Systems to assess Ecological status and Recovery) was approved in 2007 when all European Members face the challenge to collaborate together to apply monitoring programmes with the same continental assessment methods. The large-scale monitoring programme was officially finished with the end of February 2012, and addressed the management and restoration of rivers, lakes, transitional and coastal waters in Europe. The European lake dataset comes from the WISER project and comprises 356 lakes (317 natural lakes and 39 reservoirs) with complete individual-fish body size and limnological information. Following Illies' definition of

ecoregion (Illies 1978), the lakes and reservoirs encompasses nine ecoregions: Boreal Uplands, Fennoscandian Shield, Baltic Province, Central Plains, Great Britain, Western Plains, Western Highlands, Alps and Italy Corsica Malta. The lakes and reservoirs covered eight European countries along a latitudinal gradient between 41.96°N and 69.69°N and a longitudinal gradient between 10.17°E and 31.30°E.

❖ *Iberian reservoirs*

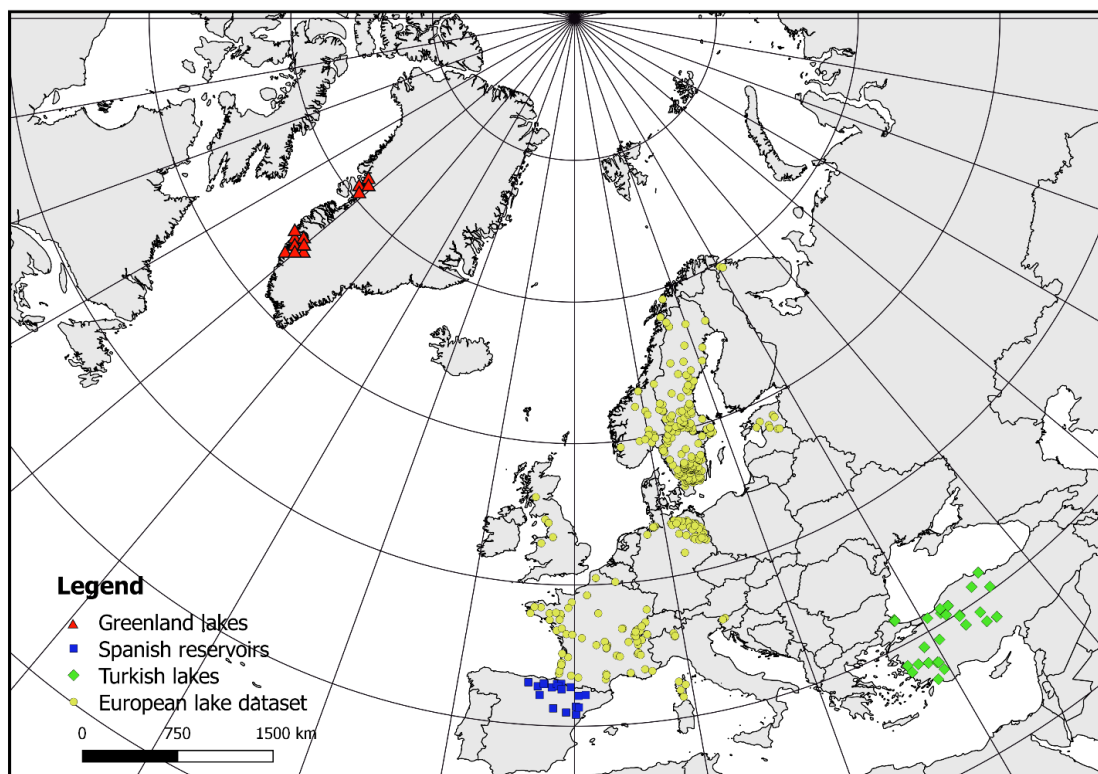
Standardized data from 19 Iberian reservoirs were obtained through the reports from *Confederación Hidrográfica del Ebro* (CHE) during the years 2008-2012. Reservoirs were located in the Ebro basin (North-East part of the Iberian Peninsula) along a latitude coordinates of 42.20°N and 43.00°N and longitudinal coordinates of 3.97°O and 0.95°E. The reservoirs were situated in the ecoregion of the Iberian Peninsula according to Illies (1978).

❖ *Turkish lakes*

We obtained standardized data from 35 Turkish lakes widely distributed across the western half of Turkey and covering a latitudinal gradient between 36.70°N to 41.89°N and a longitudinal gradient between 27.22°E to 36.16°E. The lakes encompassed the ecoregions of Northern Anatolia and Western Anatolia according to Illies (1978). The lakes were sampled once during the period from 2006 to 2012.

❖ *Greenland lakes*

Data from 17 West Greenland lakes in the Nuuk (i.e. Southern part) and the Ilulissat (i.e. Northern part) zones were obtained in late summer 2010-2012. Lakes were located in the Arctic region at the northernmost part of Earth. The study area encompassed a latitudinal gradient between 64.27°N and 76.62°N and a longitudinal gradient between 51.34°O and 54.25°O.

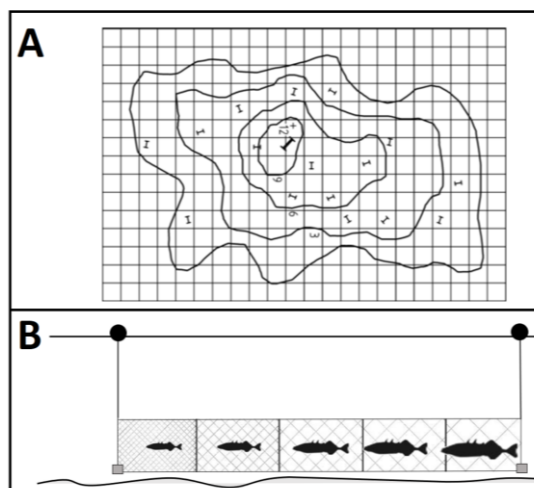


**Figure 2.** Map of the geographic position of the total lakes and reservoirs. Blue squares are the reservoirs from the reports of the CHE of the Iberian Peninsula. Yellow circles are the lakes from the European lake database. Green rhombuses are the lakes from Turkey. Red triangles are the lakes from Greenland. Note that the triangles and circles denominating the position of the lakes in Greenland, Germany, France and Sweden are overlapped.

## Sampling methods

We used one of the largest datasets in freshwater fish covering a large geographic area and ecoregions in the Western Palearctic and Greenland lakes. This dataset was standardized by using multimesh gillnets according to the European standards (CEN 2005) and originally adapted from sampling fish in Sweden (Appelberg et al. 1995). The multimesh gillnets are composed of 12 mesh-size panels of length 2.5 m each ranging between 5 mm to 55 mm (length 30 m, height 1.5 m, knot to knot dimensions following a geometric series: 5, 6.25, 8,

10, 12.5, 16, 19.5, 24, 29, 35, 43, and 55 mm) (Fig. 3A). The sampling design provided reliable representations of the size structure of fish populations and community in lakes, which was in accordance to the main objectives of the present thesis.



**Figure 3.:** Panel A shows the stratified random sampling with a hypothetical lake of 40 ha and 12 m of maximum depth in the central part of the lake. The lake is divided in four parts according to the different levels of depth (3, 6, 9 and 12 m). The number of nets were set according to the area and depth of the lake (figure adapted from CEN 2005). Panel B shows a schematic view of the setting multimesh gillnets and the potential fish size (in black shadows) that may be captured for each panel.

The sampling procedure is based on stratified random sampling in which the lake is divided in depth strata and a random sampling is performed within each depth stratum (Fig. 3B) (CEN 2005). This allow to cover the horizontal distribution of lakes influenced mainly by habitat heterogeneity. The number of nets depends on the deep and area of each lake to receive sufficient netting effort. However, the number of nets in the largest and deepest Greenland lakes were limited due to the extreme conditions and the low fish species diversity in the Arctic region (only represented by one or two fish species). The nets were set for approximately 12 h overnight to include both evening and morning phases of high fish activity. To cope with high between-year variation, the sampling period was carried out in late summer or early fall depending on the lake or ecoregion. This allows to make sampling data between different lakes and years comparable.

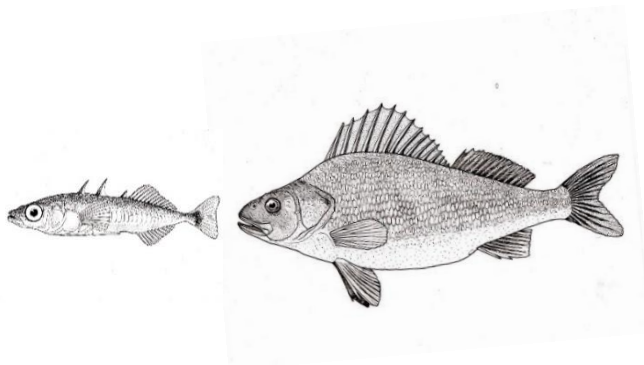
Each individual fish was identified to species level, weighed to the nearest gram and length determined to the nearest centimeter. In the case of the fish caught in Greenland lakes, Arctic charr individuals were aged by counting the annual rings of the otoliths (i.e. small bones in the lateral part of the head of fishes). The relative estimates of fish density in each

lake were calculated by dividing the total number of individual fish caught per the total number of nets and hours. The fish density was expressed as CPUE (Catch per Unit Effort).

Fish behavior and habitat selection may affect the representation of different size classes of fish, particularly to young fish that dwell in the littoral part of the lake to escape from predation (Persson 1987; Lammens et al. 1992). In this case, young individuals of fish species such as perch or roach could also be underrepresented by benthic gillnets. The largest fishes (>60cm) caught in benthic gillnets may also be underrepresented in the dataset (e.g. Fig. 10). As gillnetting is a passive and selective gear, the sample will be dependent on the actual movement of the fish (Lauridsen et al. 2008; Prchalová et al. 2009). This may probably cause that the very large (old) fishes were more inactive than the small (young) fishes. However, in a study comparing different sampling techniques in European lakes, Prchalová et al. (2009) found higher proportions of larger fish in gillnet catches than, for instance, beach seines. Similarly, Emmrich et al. (2011) found that the gillnet catches and vertical hydroacoustically obtained fish biomass estimates were significantly correlated. All in all, multimesh gillnets is probably one of the most efficient techniques in lakes because provides in a cost-effective way a whole-lake estimate for species occurrence and quantitative relative fish abundance and biomass (Appelberg et al. 1995; CEN 2005).







## **PART I**

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# **The influence of biotic interactions on the fish size structure**



## CHAPTER 1

# Density-dependent effects as key drivers of intraspecific size structure of six abundant fish species in lakes across Europe

### Abstract

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We studied fish size structure by using mean size, size diversity, and the slope of linear size spectra of six common European fish species along large-scale environmental gradients. We further analyzed the response of these three size metrics to environmental variables and to density-dependent effects, i.e., relative estimates of abundance (catch per unit effort, CPUE). We found differences in the strength of main predictors of size structure between the six species, but the direction of the response was relatively similar and consistent for most of the size metrics. Mean body size was negatively related to temperature for perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), and ruffe (*Gymnocephalus cernuus*). Lake productivity (expressed as total phosphorus concentration) and lake depth were also predictors of size structure for four out of six species. Moreover, we found a strong density dependence of size structure for all species, resulting in lower mean body size and size diversity and steeper size spectra slopes when density dependence increases. This suggests that density dependence is a key driver of fish size structure.

**Key words:** density-dependent effects, environmental gradients, fish size structure

**The first chapter is the original work of the manuscript:**

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## Resum

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Es va estudiar l'estructura de mides dels peixos utilitzant la mida mitjana, la diversitat de mides i la pendent de l'espectre de mides de sis espècies de peixos europees en un gradient ambiental d'una escala continental. Llavors, es va analitzar la resposta d'aquestes tres mesures de mida en les variables ambientals i els efectes densodependents (és a dir, estimes d'abundància relativa de les espècies de peix en cada llac expressades en captures per unit d'esforç, CPUE). Es van trobar diferències entre les sis espècies en les principals variables predictorres de l'estructura de mides. De totes maneres, la direcció de la resposta va ser relativament similar i consistent en la majoria de les mesures de mides. La mida mitjana va estar negativament relacionada amb la temperatura en el cas de la perca (*Perca fluviatilis*), la madrilleta vera (*Rutilus rutilus*) i el *Gymnocephalus cernuus*. La productivitat del llac (expressada com la concentració total de fòsfor) i la profunditat del llac van ser també unes variables predictorres de les estructures de mides de quatre de les sis espècies. A més a més, es va trobar un fort efecte densodependent en l'estructura de mides de totes les espècies, provocant una disminució de la mida mitjana i la diversitat de mides i uns pendents més pronunciats a mesura que els efectes densodependents augmentaven. Aquest resultat suggereix que la densodependència és un clau regulador de l'estructura de mides dels peixos.

**Paraules clau:** efectes densodependents, estructura de mides dels peixos, gradients ambientals

## Introduction

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Size structure has traditionally been used for elucidating trophic interactions and patterns of energy transfer through trophic levels (Jennings et al. 2002; Woodward et al. 2005; Trebilco et al. 2013). Recent studies have revealed variations in the size structure of fish communities across continental gradients induced by climate-related variables, as well as variations in taxonomic composition (Mims and Olden 2012; Emmrich et al. 2014).

Besides temperature, productivity of local systems also modifies fish community size structure (Jeppesen et al. 2000; Brucet et al. 2013). In northern temperate regions, the shift in fish size structure along the productivity gradient is reflected in part by changes in species composition from nutrient-rich lakes being dominated by cyprinids to more nutrient-poor lakes being dominated by percids or salmonids (Persson et al. 1988; Bergman 1991), but also by intra- and inter-specific competition and perhaps reduced predation by piscivores (Jeppesen et al. 2000; Brucet et al. 2013). Lake morphometry (area and depth) also influences the shape of the size structure of fish communities (Holmgren and Appelberg 2000; Emmrich et al. 2014) due to its strong impact on structural complexity, niche availability, and temperature. The ecosystem size rules predict that the shape of body size distributions will change because of the increase in number of trophic levels (Vander Zanden et al. 1999) and the higher abundance of predatory fish species (Allen et al. 2006). As such, high habitat diversity is more likely to exhibit a higher abundance of large fish and a wider range of size classes (Holmgren and Appelberg 2000; Emmrich et al. 2011).

Variation in the size structure of selected species over large geographical gradients has occasionally been demonstrated (e.g., in Europe (Heibo et al. 2005; Blanck and Lamouroux 2007) or in North America (Knouft 2004)). For example, at the continental scale, Eurasian perch (*Perca fluviatilis*) populations follow the temperature–size rule (Bergmann 1847), with fish body size being smaller in the warmer lakes (Heibo et al. 2005; Jeppesen et al. 2012). This pattern has repeatedly been found for the size structure of entire fish communities (Edeline et al. 2013; Brucet et al. 2013; Emmrich et al. 2014), but it is not universal at the species level (Belk and Houston 2002).

Variations in fish density typically induce substantial changes in the growth rates of individuals, triggered by food resource or habitat availability (Byström and García-Berthou 1999). Dietary shifts are furthermore expected to result from strong sizedependent intraspecific interactions (Persson 1987) and may lead to stunted populations (Ylikarjula et al. 1999). However, most previous work on size structure at the species level has been based on a few lakes or dynamical models, while potential densitydependent effects on the size structure of fish species over largescale gradients have not yet been evaluated.

We analysed the size structure of six common freshwater fish species by measuring mean size, size diversity, and the slope of linear size spectra in several hundred European lakes. Our objective was to assess which environmental variables influenced the variation in size structure of the selected fish species at the continental scale. We hypothesised that the changes in size structure for all species in response to local temperature, productivity, and lake morphometry would be consistent with those found for the community-wide variation in fish size structure (Emmrich et al. 2014). Because fish density modifies the availability of food resources, which affects fish growth rates, we hypothesised that density-dependent effects would also contribute to shifts in species-specific size structures by decreasing mean body size, size diversity, and size spectra slopes when density increases. We therefore included relative estimates of abundance (catch per unit effort, CPUE) as an approximation of density dependence to explore potential modifications in size structure, and hence life history, caused by fish density in the lakes.

## **Materials and methods**

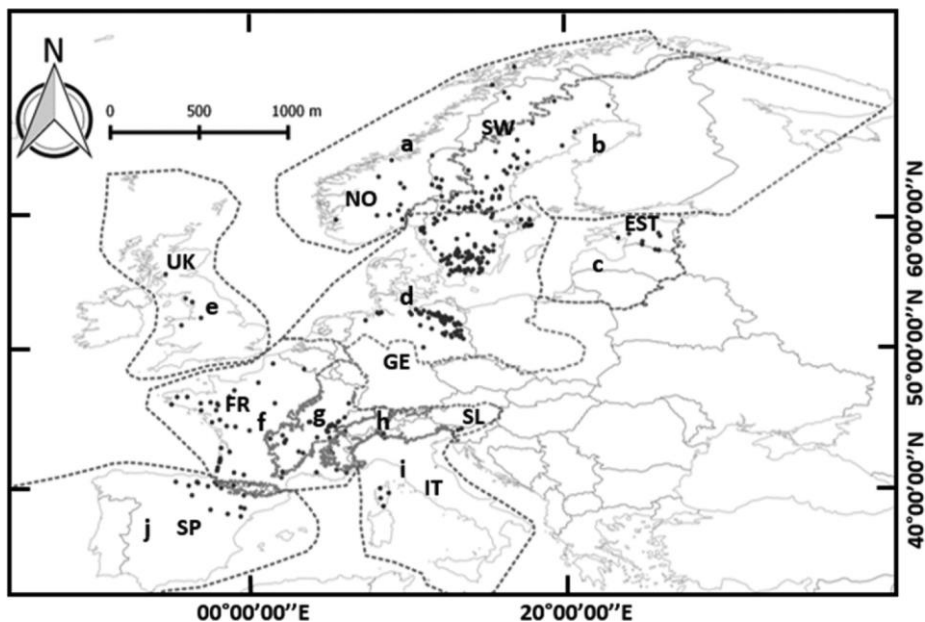
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### **Dataset**

We used the dataset from the EU project WISER (Water bodies in Europe: Integrative Systems to assess Ecological status and Recovery) created during a European intercalibration process with 1632 lakes, considering exclusively, though, the lakes based on the same systematic

approach with complete fish assemblage and limnological information (Brucet et al. 2013). Individual-fish body size information was only available on a subset of 356 lakes (317 natural lakes and 39 reservoirs) covering nine European ecoregions (Illies 1978) and eight countries along a latitudinal gradient between 41.96°N and 69.69°N and a longitudinal gradient between 10.17°E and 31.30°E (Fig. 4).

In cases of multiple sampling years (mainly Swedish lakes), we always selected the data from the most recent sampling campaign. In addition, we obtained corresponding information on 19 reservoirs from the Ebro River basin in Spain, which were sampled following the same standardised procedure (European Committee for Standardization (CEN) 2005; reports from *Confederación Hidrográfica del Ebro* (CHE) 2008–2012); the data were, therefore, comparable with data from the European lakes included in the WISER project. In summary, our dataset encompassed a total of 375 European lakes and reservoirs from nine countries and 10 ecoregions along a latitudinal gradient between 40.81°N and 69.69°N (Fig. 4).



**Figure 4.** Geographical distribution of study lakes across nine European countries: Estonia (EST), France (FR), Italy (IT), Germany (GE), Norway (NO), Slovenia (SL), Spain (SP), Sweden (SW), and UK. Ten ecoregions according to Illies (1978) are separated by dotted lines: (a) Boreal Uplands, (b) Fennoscandian Shield, (c) Baltic Province, (d) Central Plains, (e) Great Britain, (f) Western Plains, (g) Western Highlands, (h) Alps, (i) Italy Corsica Malta, and (j) Iberian Peninsula.



## Sampling

All fish were caught in accordance with European Standard 14757 (CEN 2005) during late summer and early autumn using benthic multimesh gillnets (type NORDEN: length 30 m; height 1.5 m; 12 panels of 2.5 m each with mesh sizes between 5.0 and 55 mm knot to knot in a geometric series). These different mesh sizes allow catching of a wide range of fish sizes and can be used to estimate the size structure of fish populations in a cost-effective way (Appelberg et al. 1995; CEN 2005). The number of nets to be used is determined by lake morphology (area and depth), and these nets were set randomly in all depth strata of the lakes. All nets were left for approximately 12 h overnight because gillnet catching is highly dependent on fish activity (Prchalová et al. 2009). To ensure comparable individual-fish body size measurements and fish densities, the total fishing effort per lake (number of nets) was standardised by lake area and maximum depth according to European Standard 14757 (CEN 2005). Fish catches were expressed as lake-specific CPUE and were standardised by calculating the average number of fish caught per net and night in each lake. We used four lakes sampled for more than 20 years to estimate the interannual variability (and hence uncertainty) of CPUE values (unpublished data). CPUE of the three species found in these lakes (perch, roach (*Rutilus rutilus*), and ruffe (*Gymnocephalus cernuus*)) showed relatively low variability (CPUE means  $\pm$  SD:  $19.71 \pm 14.48$ ,  $8.34 \pm 3.07$ , and  $0.73 \pm 0.32$  for perch, roach, and ruffe, respectively, in the lake with highest variability). The exception was the perch population in the lake at the highest latitude: 1-year-old individuals dominated the catches in 1997. Perch populations in lakes far north at the latitudinal edges of their distribution areas are the most outstanding exceptions from low between year variation (Holmgren 2013). Fish species were identified, counted, and individually measured to determine total length (TL, nearest centimeter) and fresh body mass (FM, nearest gram). For all Swedish lakes, FM was estimated by length–mass relationships from lakes in other countries at the same latitudinal range. For German lakes, the sampling protocol was divided into two different periods: autumn (late August to early October) and the subsequent spring (Mehner et al. 2005). The catches from both periods were summed. For more details, see Brucet et al. (2013).

## Fish species selected

Species selection was hierarchically guided by the following requirements: (i) the species had to be present in a representative number of lakes (minimum 20 lakes; Table 1); and (ii) their presence should encompass a sufficiently widespread area (minimum five ecoregions; Table 1). Accordingly, six species were chosen (Table 1): the percids perch, ruffe, and zander (*Sander lucioperca*) and the cyprinids roach, common bream (*Abramis brama*), and white bream (*Blicca bjoerkna*). Perch and zander are typically piscivorous fish, and both undergo size-related ontogenetic niche shifts. Ruffe, common bream, and white bream feed on cladocerans, copepods, and benthic macroinvertebrates such as midge larvae (Chironomidae) or mussels (Nagelkerke and Sibbing 1996; Volta et al. 2013). Roach is a typical omnivorous feeder, with a diet mainly based on zooplankton, plant material, and detritus (Bergman and Greenberg 1994; García-Berthou 1999). Despite their presence in many lakes, we did not consider typical pelagic species such as bleak (*Alburnus alburnus*) and vendace (*Coregonus albula*) because these are not quantitatively well represented in benthic gillnet catches (Emmrich et al. 2012). To ensure a reliable representation of each selected species, we included only lakes with at least 25 measured individuals, which corresponds to an error in size diversity estimation of approximately 30%.

## Size metrics corresponding to size structure

Three size metrics were calculated from the measurements of individual-fish body size for each population: geometric mean body size and slope of linear size spectrum (both based on fish mass) and size diversity (based on fish length). We combined metrics for fish mass and length to ensure that the response of fish size structure along gradients is adequately captured.

Mean body size expressed as geometric mean mass is a general descriptor for assessing interspecific gradients in the size structure of fish communities (Emmrich et al.

2011, 2014). Size diversity was calculated following the nonparametric methodology of Quintana et al. (2008), which is an analogue of the Shannon diversity index but adapted for continuous variables (herein fish total length). For size diversity, we used fish total lengths because our earlier work showed a significant response of length diversity to environmental gradients (Emmrich et al. 2011). The index was computed using individual-fish size measurements (Bruce et al. 2006; Quintana et al. 2008) for each lake following an integral formula:

$$(1) \quad \mu_2(x) = - \int_0^{\infty} \rho_x(x) \log_2 p_x(x) dx$$

where  $\mu_2$  is the Shannon size diversity index and  $\mu(x)$  is the probability density function (pdf; function that describes the relative likelihood for a random variable to take on a given value) that an organism belongs to a certain size class. The most appropriate approach to calculating the pdf is by using a nonparametric Kernel estimation (Quintana et al. 2008). A kernel estimation is essentially a pdf, usually symmetric, with a dispersion that is controlled by a bandwidth parameter. The estimator is a sum of kernel functions centered at the samples points, which can be applicable for most size distributions. Before computing size diversity, the data are double standardized to (i) make the size data adimensional and (ii) make size data comparable with data from other studies whose samples are measured with different units, e.g., length, weight, or volume, without altering the results (Quintana et al. 2008). Size diversity integrates the range of the size classes and the evenness, that is, the equitability of frequency across the size range, in the same way that the Shannon diversity integrates the species composition and species relative abundances. The single-value index condenses many different aspects of other size metrics into a single comparable value (Bruce et al. 2006, 2010; Emmrich et al. 2011). Furthermore, size diversity is easy to interpret as the concept of diversity has been well established. Low size diversity values imply high accumulation of abundance within a specific size range, whereas high values mean similar proportions of the different sizes along the size distribution. Negative values of size diversity

may be found as the method uses a continuous pdf for the probability estimation and probability densities above one may occur (Quintana et al. 2008).

The linear size spectrum was calculated as the regression between the  $\log_2$  midpoint of size classes (axis  $x$ ) and the  $\log_2$  total numbers per size class (axis  $y$ ). The slope of the linear size spectrum is usually described by a decreasing linear function in fish numbers as midpoint size class increases. Steeper slopes from the linear size spectrum reflect high proportions of small fish, whereas flatter (less negative) slopes indicate a high proportion of large fish (Emmrich et al. 2011). The number of size classes varied between the species (Table 1) but always followed a  $\log_2$  scale (1<sup>st</sup> class:  $2^2 = 4$  g to  $2^3 = 8$  g; 2<sup>nd</sup> class:  $2^3 = 8$  to  $2^4 = 16$  g, etc.).

Multimesh gillnets have been shown to describe well the size structure of populations of perch and roach despite underestimation of the proportion of fish smaller than 6–8 cm TL (Prchalová et al. 2009). Hence, 1 to 4 g fish (i.e., fish in the first year of life) were under-represented in our catches. These small fish easily detect the wall of netting of the smallest mesh size and thus avoid it (Prchalová et al. 2009). In addition, they tend to swim more slowly than larger fish and the probability of catching them is proportional to body length (Rudstam et al. 1984). Accordingly, the few small fishes (<4 g) caught were grouped in the first size class ( $2^2 = 4$  g). Intermediate empty size classes were filled with zeroes. Although there is some debate about the most appropriate way to deal with intermediate empty size classes (Loder et al. 1997; Gómez-Canchong et al. 2013), we considered our approach appropriate for comparison of large-scale patterns in the slope of the linear size spectrum. Furthermore, the frequency of zero infilling for each of the species was less than 5% (less than 20% of the lakes had at least one intermediate empty bin for each species), with the exception of zander for which 17.7% of intermediate classes were filled by zeros (74% of the lakes had at least one intermediate empty size bin). Zander had more empty bins because more size classes were covered (size range of 11 classes; Table 1) than, for instance, for ruffe (size range of five classes; Table 1).

Common name	Total occurrences	Countries	Ecoregions	Mean body size	Size diversity	Slope subset	Slope	Size range
Perch	321	ES,FR,IT,GE,NO,SL,SP,SW,UK	a, b, c, d, e, f, g, h, i	12.05 ± 2.85 (4.83-21.3)	1.56 ± 0.51 (-0.47-2.71)	202	-0.60 ± 0.38 (-1.65-0.81)	9
Roach	282	ES,FR,IT,GE,NO,SL,SP,SW,UK	a, b, c, d, e, f, g, h, i, j	13.58 ± 2.76 (7.05-25)	1.47 ± 0.51 (-0.50-2.52)	91	-0.41 ± 0.54 (-2.16-1.37)	8
Ruffe	115	ES,FR,GE, SW,UK	b, c, d, e, g, h, i, j	8.17 ± 1.34 (5.07-12.45)	0.98 ± 0.48 (-0.67-1.84)	54	-2.16 ± 1.26 (-6.36-0.03)	5
Common bream	83	ES,FR,GE,SW	b, c, d, f, g	17.11 ± 5.76 (6.93-31.29)	1.95 ± 0.59 (0.05-2.90)	20	-0.14 ± 0.36 (-1.19-0.62)	10
White bream	72	ES,FR,GE, SP,SW	b, d f, g, j	13.22 ± 2.83 (8.69-20.75)	1.65 ± 0.44 (0.60-2.61)	30	-0.37 ± 0.50 (-1.69-0.78)	10
Zander	51	FR,IT,GE, SP,SW	d, f, g, h, i	17.62 ± 7.61 (5.13-35.88)	1.89 ± 0.80 (-0.30-3.11)	13	-0.21 ± 0.33 (-0.92-0.60)	11

**Table 1.** Occurrences, countries and ecoregions where the six fish species were sampled. **Note:** Total occurrence represents the lakes with at least 25 individuals per species in the catch. The slope subset is comprised of those lakes for which the significance of the linear regression of size spectra was  $p < 0.1$ . Mean body size (cm), slope of linear spectra and size diversity ( $\mu$ ) ± standard deviation are given in brackets showing minimum and maximum values. Size range: the maximum number of  $\log_2$  size classes. Nine countries: (ES) Estonia, (FR) France, (IT) Italy, (GE) Germany, (NO) Norway, (SL) Slovenia, (SP) Spain, (SW) Sweden, (UK) UK. Ten ecoregions ordered from north to south: (a) Borealic Uplands, (b) Fenno-scandian Shield, (c) Baltic Province, (d) Central Plains, (e) Great Britain, (f) Western Plains, (g) Western Highlands, (h) Alps, (i) Italy Corsica Malta, (j) Iberian Peninsula.

## Predictors of size structure

From a large set of predictors characterising lake geographical position, morphometry, and productivity, we retained six variables but excluded others that were most strongly correlated with the retained predictors (Spearman's rank correlation  $r_s > 0.6$  or  $r_s < -0.6$ ) (Emmrich et al. 2011).

We used four environmental and morphometric predictors (Appendix, Table A1): (1) total phosphorus concentration (hereafter TP,  $\mu\text{g}\cdot\text{L}^{-1}$ ) as a surrogate of lake productivity, (2) maximum depth (m), and (3) lake area (ha) and excluded geographical position and instead used direct local climate data expressed as (4) maximum monthly mean air temperature ( $^{\circ}\text{C}$ ),

which was calculated using the climate Climatic Research Unit (CRU) model proposed by New et al. (2002). This specific model can obtain a spatial resolution of 10° latitude and (or) longitude and takes into account elevational differences between stations (New et al. 2002). Previous studies have successfully used air temperature instead of indirect temperature approximations based on geographical locations (Argillier et al. 2013; Bruçet et al. 2013; Emmrich et al. 2014).

Furthermore, two biotic predictors were included. We used the CPUEs as indicators of fish density to infer their effects on size structure and assumed that high densities are approximations for low individual resource availability and strong competition. However, because resource similarity is usually stronger between individuals of the same species than between species, we split CPUE as a surrogate of density dependence into (5) the intraspecific density-dependent effect (CPUE of the focal species, hereafter, CPUE<sub>intra</sub>) and (6) the interspecific density-dependent effect (sum of CPUE of the other five potentially competing species, hereafter CPUE<sub>inter</sub>). The sum of the six species in each lake was 82.2% ± 29.9% (SD) of total CPUE, and hence intra- and inter-specific CPUE covered a large majority of total fish available and the potential competition effects. No species in our list are strict feeding specialists, and most of them undergo ontogenetic niche and (or) diet shifts (see Persson and Hansson 1999 for perch, common bream, and roach). Accordingly, all species were considered to compete for the same food resources, at least during some part of their life. Finally, we did not consider predation effects on size structure because earlier work in a subset of lakes indicated only limited effect of fish predation on fish prey density and average size (Mehner 2010).

## Statistical analyses

Some fish populations were characterised by unimodal (hump-shaped) or multimodal (two or more distinct peaks) size distributions and hence deviated from linear size spectra. We only included linear slopes with significance  $p < 0.1$ . The two other size metrics (mean size and size diversity) were calculated for all lakes. We graphically represented the cumulative

frequency distribution of sizes for the six species by using the total numbers per size class across all lakes (Appendix, Fig. A1).

General linear models (GLM) were used to identify which predictors were significantly related to the size metrics of the six species. The six predictor variables mentioned above were  $\log_{10}$  transformed to meet assumption of normality. Shapiro–Wilk tests and quartile–quartile plots indicated that the transformed variables closely followed normal distributions. We also included the interaction between density-dependent effects and productivity and lake depth (i.e.,  $\text{CPUE}_{\text{intra}} \times \text{TP}$ ,  $\text{CPUE}_{\text{intra}} \times \text{Depth}$ ,  $\text{CPUE}_{\text{inter}} \times \text{TP}$ , and  $\text{CPUE}_{\text{inter}} \times \text{Depth}$ ) because the latter two variables may influence the density-dependent effects on fish size (i.e., in deeper lakes, the effect of  $\text{CPUE}_{\text{intra}}$  on fish size may be less intense than in shallow lakes because coexistence of all size classes is facilitated by the large pelagic volume). The response variables were mean body size, size diversity, and slope of linear size spectra. The level of significance for GLM was established at 95% (0.05). Using GLM, we searched for the most parsimonious model by an automatic stepwise backward selection of one predictor variable at a time, following the lowest Akaike information criterion (AIC) (Akaike 1974). The most parsimonious model was the combination of variables having the strongest impact on outcomes. To account for moderate robustness of the stepwise selection of variables, we further applied ANOVA to compare the most parsimonious final model (i.e., the one with lowest AIC) with the next best model that included one more predictor. We used standardized regression beta coefficients and percentage of variance explained to compare the relative strength of each significant predictor for each of the size metrics (Table 2). Multicollinearity can inflate the variance among the selected predictors in the model. To identify which predictor was highly correlated with the remaining ones, we examined the variance inflation factor (VIF) values. They were  $<2$  in all analyses, indicating a low degree of multicollinearity (Belsley et al. 1980). We also included a measure of model fitting to explain the deviance in percentage (Table 2). Residual partial plots for each significant variable were then drawn to show the relationship between the predictor and the response variables. All statistical analyses were conducted using package “MASS” (version 7.3; Venables and Ripley 2002), “car” (version 2.0; Fox and

Weisberg 2011), “QuantPsy” (version 1.5; Fletcher 2012), and “BiodiversityR” (version 2.4-4; Kindt and Coe 2005) from the software R (version 3.0.2; R Development Core Team 2008).

## Results

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### General patterns of occurrence and size structure

The temperature range at which fish were found was relatively similar for all species across the European lakes, the widest being recorded for roach and the narrowest for common bream (Appendix, Table A1). The depth of the lakes in which the species were present was also similar, but the TP and lake area ranges differed among species (Appendix, Table A1).

Zander had the highest number of size classes, from the smallest (1<sup>st</sup> class, 4–8 g) to the largest size class (11<sup>th</sup> class, 4096– 8192 g), whereas ruffe sizes covered only five classes (maximum 5<sup>th</sup> class, 64–128 g). The proportion of lakes in which fish populations exhibited linear size spectra was relatively high for perch (62.9%), ruffe (46.9%), and white bream (41.7%). In contrast, nonlinear ( $p > 0.10$ ) size distributions dominated in common bream, zander, and roach populations (non-significant slopes in 76%, 75%, and 68% of the lakes, respectively).

### Size structure predicted by environmental variables

Mean body size of perch, roach, and ruffe significantly decreased with increasing maximum temperatures (Table 2; Appendix, Fig. A2). The slope of linear size spectra for zander was also negatively related to temperature, indicating a relative increase of small sizes in warmer lakes (e.g., Lake Figari from France, 23.1 °C; Table 2; Appendix, Fig. A2). In contrast, the size diversity of white bream and roach showed a positive relationship with temperature,



suggesting that a wider range of size classes occurred at warmer temperatures (Table 2; Appendix, Fig. A4).

Common name	Max. T (°C)	TP ( $\mu\text{g}\cdot\text{L}^{-1}$ )	Area (ha)	Depth (m)	CPUEintra	CPUEinter	Predicted variance (%)
<b>Mean size</b>							
Perch	-0.29*** (15.92)	-0.09* (4.63)		-0.11* (<1)	-0.32*** (13.95)	-0.29*** (14.85)	50.12
Roach	-0.11* (4.45)				-0.54*** (26.38)		30.83
Ruffe	-0.26** (7.19)	0.34*** (7.35)	-0.26* (4.50)			-0.43*** (9.85)	28.89
Common bream		0.30* (3.19)			-0.56*** (18.52)		21.71
White bream		0.45*** (13.54)	0.32* (7.00)		-0.28* (3.63)		24.17
Zander					-0.38*** (26.84)		26.84
<b>Slope</b>							
Perch			-0.14** (4.01)		-0.59*** (38.26)		42.27
Roach					-0.83*** (47.26)	0.2* (7.64)	54.90
Ruffe		0.41** (11.00)				-0.42** (11.00)	22.00
Common bream					-0.88** (43.63)		43.63
White bream		0.58** (13.15)			-0.65*** (27.12)		40.27
Zander	-0.54** (13.75)			0.56** (23.68)		-0.41** (51.51)	88.94
<b>Size diversity</b>							
Perch		-0.17* (2.45)		0.13* (2.69)	-0.33*** (10.27)		15.41
Roach	0.19** (2.40)	-0.18** (3.56)	0.13* (4.72)	0.26*** (8.05)		0.12* (<1)	19.67
Ruffe				0.51*** (27.59)			27.59
Common bream					-0.28*** (8.00)		8.00
White bream	0.28** (10.15)						10.15
Zander					-0.75*** (55.88)		55.88

**Table 2.** Relative strength for each predictor represented by the beta coefficients with their positive or negative trends and the predicted variance (%) (in parentheses for predictors). **Note:** For each species, significant predictors selected by the automatic stepwise model are given. A measure of model fitting is also shown: predicted deviance (%). Max. T, maximum temperature (°C); TP, total phosphorus ( $\mu\text{g}\cdot\text{L}^{-1}$ ); CPUEintra, intraspecific density-dependent effect; CPUEinter, interspecific density-dependent effect. Significance: no asterisk,  $p > 0.05$ ; \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

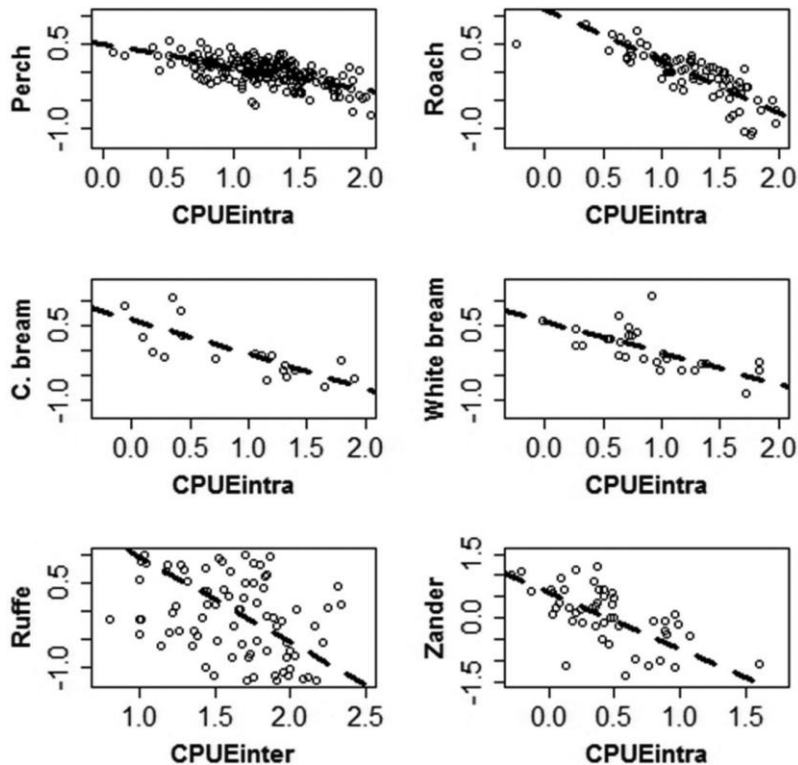
Lake productivity (TP) affected size metrics for five of the six species (Table 2; Appendix, Figs. A2, A3, and A4). The mean size of ruffe, white bream, and common bream, as well as the slope of the linear spectra of ruffe and white bream, increased in highly productive lakes (e.g., Lake Audomarois from France,  $561 \mu\text{g}\cdot\text{L}^{-1}$ ), whereas the mean size of perch decreased with productivity. The size diversity of perch and roach was negatively related to TP, indicating a narrower size range in highly productive lakes.

Size metrics were also influenced by lake depth and lake area. Size diversity increased with lake depth for three species, and the slope of the linear spectra increased with depth for zander, indicating a flatter size spectrum in deeper lakes (Table 2; Appendix, Fig. A3). The slope of the linear spectra for perch became significantly steeper with increasing lake area (Table 2; Fig. A3). There were also some relationships between lake area and mean size, with

smaller sizes being observed for ruffe and larger sizes for white bream in larger lakes (Table 2; Appendix, Fig. A2).

## Size structure predicted by density-dependent effects

There was a strong density-dependent effect on the variation in size structure for all species (Table 2; Fig. 5; Appendix, Figs. A2, A3, and A4). Particularly, lower mean size and steeper slopes (i.e., greater relative abundance of small-sized individuals) occurred at higher CPUE<sub>intra</sub> for five and four, respectively, of the six species (Table 2).



**Figure 5.** Significant partial residual plots selected according to the highest beta coefficients in density-dependent effects: y axes represent size metrics, and x axes represent the density-dependent predictor (i.e., CPUE<sub>intra</sub> and CPUE<sub>inter</sub>). CPUE<sub>intra</sub>, CPUE of the focal species; CPUE<sub>inter</sub>, sum of CPUE of the other five potentially competing species. For perch, roach, white bream, and common bream (c. bream): slope vs CPUE<sub>intra</sub>; for ruffe: mean size vs CPUE<sub>inter</sub>; for zander: size diversity vs CPUE<sub>intra</sub>.

Additionally, a negative response of size diversity to CPUE<sub>intra</sub> was found for three species (Table 2; Fig. 5; Appendix, Fig. A4). In contrast, there was a weaker and less consistent effect for CPUE<sub>inter</sub> (mean beta coefficients for CPUE<sub>intra</sub> and CPUE<sub>inter</sub>: 0.53 and 0.31, respectively). The mean body size of perch and ruffe and the slope of the linear spectra of ruffe and zander responded negatively to CPUE<sub>inter</sub> (Table 2; Appendix, Figs. A2 and A3). In contrast, CPUE<sub>inter</sub> positively affected roach size diversity and the slope of linear size spectra, suggesting a wider size range and flatter slopes at higher abundance of the other five coexisting fish species (Table 2; Appendix, Figs. A3 and A4). Finally, interactions terms were not significant ( $p > 0.05$ ) except CPUE<sub>intra</sub> × TP and CPUE<sub>intra</sub> × Depth for the size diversity of perch ( $p \leq 0.001$  and  $p \leq 0.01$ , respectively).

## Discussion

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Our results showed some differences in main predictors and response strength to continental environmental gradients between the six common fish species in European lakes, but the direction of the response was relatively similar and consistent for most of the size metrics (Table 2). For example, temperature variations across Europe induced the same response for five of the six species, with fish size declining at higher temperatures. Furthermore, productivity and lake depth were predictors of size structure, whereas lake area had little effect on the size metrics. Overall, however, the potential intraspecific density-dependent effect was the strongest and most consistent predictor of the variation in the size structure of fish populations (Table 2).

Temperature affected the size metrics for perch, roach, ruffe, white bream, and zander. These results are in accordance with the Bergmann (1847) and Atkinson (1994) rules explaining that ectothermic animals developing at higher temperature are relatively smaller as adults. However, temperature showed a weaker effect as a predictor of population size structure compared with the effect that it had on the size structure of the whole fish assemblage (Emmrich et al. 2014). Temperature effect is probably masked by the strong

density-dependent effect, which was not considered in the community-wide analyses. Thus, our results suggest that, at least at the species level, it is important to take into account density-dependent effects when studying the influence of temperature on fish size structure. Mean size of roach decreased at higher temperatures, but size diversity increased (Appendix, Figs. A2 and A4). Studies in Swedish lakes have shown that roach populations may attain >20 cm and >100 g already in their fourth growth season in southern Sweden, whereas they often need at least twice as long to reach such size further north (Jeppesen et al. 2010; Holmgren 2013). Likewise, in France, in warmer lakes and reservoirs, high proportions of large roach often occur in the catches. These large roach have reached an antipredation window and are no longer available for most of the carnivorous species such as pike (*Esox lucius*), pikeperch, or perch (Wysujack and Mehner 2002; Schlumberger and Elie 2008).

Lake productivity (TP) mainly affected the size structure of perch, roach, and ruffe and the congeneric species, i.e., common bream and white bream. At the community level, Jeppesen et al. (2000) and Brucet et al. (2013) found a decrease in the mean body size of fish in lakes with increasing TP. Our results at the species level partially contrast these findings: the mean body size of perch decreased, whereas the mean body size of white and common bream and ruffe and the proportion of large individuals of ruffe and white bream increased in highly productive lakes. The differing species responses may be due to their different feeding strategies. Perch is a visual hunter, depending on good light conditions, and hence, perch feeding rates may decrease at higher productivity and algal turbidity. In contrast, the other species are successful predators in turbid waters (Bergman 1991; Lammens et al. 1992). Studies on both bream species (Olin et al. 2002) and on ruffe (Persson et al. 1991) showed that these species dominated the catches at enhanced TP concentrations. There was a negative response of the size diversity of perch and roach to lake productivity as shown by low size diversity in the highly productive Lake Bordeaux (561 TP  $\mu\text{g}\cdot\text{L}^{-1}$ ) and Lake Schwielochsee (260 TP  $\mu\text{g}\cdot\text{L}^{-1}$ ). Roach can be both a prey and a competitor for perch (Persson 1988). Thus, the decrease in mean body size of perch with increasing productivity can be related to competition between small juvenile perch and roach, reducing both juvenile and adult growth and thereby the number of size classes of both species.

Lake morphometry (area and depth) affected the size structure of almost all species, but the strength of the response was relatively weak for all size metrics. Our results demonstrated that lake depth is a better predictor than lake area of the variation in size structure. Size diversity showed a consistent response to lake depth and area, and populations with large fish were found in deeper and larger lakes. However, the morphometric variables seem to be poor predictors of the shifts in slopes of the linear size spectra. A (positive) correlation between lake depth and slope of the linear size spectra was found only for zander, and a negative one was found only for perch. Zander is the largest species in our study, and greater proportions of large individuals were found in larger lakes, probably as a result of higher niche availability, reducing competition and providing habitats to more different age (size) classes (Persson 1983).

Besides abiotic predictors, we found strong density dependence of size structure for almost all species, which corroborates the substantial changes in growth rates when fish compete for food resources (Byström and García-Berthou 1999). However, interspecific density-dependent effects were weaker predictors than the intraspecific density-dependent effects (Table 2). According to our results, disproportionately more small fish than large fish are added at higher population densities, as reflected by lower mean body size, fewer size classes (i.e., lower size diversity), and steeper slopes (i.e., higher proportions of small fish). An exception is the pattern of roach populations in that size diversity and slope of linear spectra responded positively to the interspecific density, indicating wider size distributions and greater proportions of larger individuals when roach coexist with one or more of the other five species. Large roach coexisting with many competitors (i.e., high CPUE<sub>inter</sub>) was found primarily in shallow productive lakes. In these lakes, growth of roach is stimulated by utilization of unique diet components, mainly cyanobacteria and detritus, which cannot be used by other competing species such as perch (Persson and Greenberg 1990; Bergman and Greenberg 1994). Because density and growth rates in fish are usually negatively correlated (Lorenzen and Enberg 2001), the positive correlation between CPUE<sub>inter</sub> and the size metrics of roach may, in turn, suggest a decrease of growth rates and hence recruitment of the competing species that exploit the same resource less efficiently (in our study, reflected by a

reduction in the mean body size of perch and ruffe). Although we do not have the age structure of each population to corroborate recruitment dynamics, our result is similar to those from an empirical experiment with roach, perch, and ruffe (Bergman and Greenberg 1994) showing decreased abundance of perch because they were competitively sandwiched between planktivorous (i.e., roach) and benthivorous (i.e., ruffe) species. Our analysis included only one year of survey in each lake and thus did not capture the interannual recruitment variability that may affect the size structure. Some European studies give examples of high between-year fluctuations of recruitment on perch (Tolonen et al 2003) or roach and other cyprinids (e.g., Mills and Mann 1985; Kahl et al. 2008). In contrast, studies of Swedish lakes from which results of multiple years of sampling are available indicated a relatively low between-year variation in recruitment for perch and roach (Holmgren 2013, 2014). As an example, the mean size of the dominant species perch, roach, and ruffe sampled for more than 20 years in four Swedish lakes shows relatively low variability, which may reflect a relatively constant annual recruitment, except for perch at the highest latitude in the dataset (Lake Jutsajaure; Appendix, Fig. A5). On the other hand, our study expands a large-scale data set and recruitment variability may be integrated in part with the latitudinal gradient.

The increased abundance of small size classes at higher population densities may reflect a decline in growth rates (stunted growth) at high fish densities. Stunted growth of a fish population as a result of density-dependent effects is a common phenomenon (Sandheinrich and Hubert 1984; Ylikarjula et al. 1999), which may contribute to the overall pattern observed in our analysis. This is theoretically included in both the Beverton–Holt (Beverton and Holt 1957) and Ricker (1954) stock recruitment curves predicting lower recruitment when fish reproduction exceeds the carrying capacity of the system. If stunted populations exhibit extremely slow growth and early maturity in lakes with higher fish densities, then a systematic downward shift of slopes is plausible. An example is the temporal study of the vendace population in a Swedish lake (Hamrin and Persson 1986) in which stunting of older age classes was ascribed to competitive superiority of small fish relative to larger conspecifics due to their lower metabolic requirements and foraging energetics.

Alternatively, the density dependence of the slopes of linear size spectra may be considered a mathematical artifact. Normally, there is a negative correlation between the intercept and the slope of linear size spectra (Gómez-Canchong et al. 2013), and the intercept strongly correlates with the total abundance of fish (Sprules and Munawar 1986). Therefore, higher abundances may result in steeper slopes. However, it has to be mentioned that mean size (as based on fish mass) and size diversity (as based on fish length) also showed density-dependent effects, which suggests that steeper slopes at higher densities represent ecological effects.

We found weak but significant interactions between  $CPUE_{intra} \times TP$  and  $CPUE_{intra} \times Depth$  as predictors of size diversity, but only in perch. The interactions suggest that the negative effect of density on size diversity of perch was strongest in shallow lakes at high TP in which perch is outcompeted by the large roach because the availability of benthic diet for perch is low (Persson and Greenberg, 1990). In turn, perch grow better in deep lakes at low TP because availability of benthic macroinvertebrates as preferred diet of perch of intermediate size is high under these conditions (Persson 1983). These results show that lake morphometry, productivity, and fish density and growth can be strongly linked in some species. Nevertheless, significant interactions of CPUE with TP and lake depth were found only for one size metric and one fish species.

The present study is the first to compare congruence in intraspecific variability in the size structure of European fish species along a continental gradient, and our results indicate that density-dependent effects are a key driver of fish size structure. However, more research is needed to unravel the variation in the slope of linear size spectra in relation to density dependence, for example, by studying the temporal evolution of the slope in lakes showing interannual variations in fish densities. In contrast, substantial differences in the size structure of populations between lakes were only marginally affected by environmental variables, except for temperature. Our study indicates that the size structure of the selected species cannot be used as an unequivocal indicator of environmental changes, which contrasts the consistency at the community level found by Emmrich et al. (2014).

Unfortunately, the intraspecific variation in size structure cannot be directly translated into a defined life history strategy along the triangular scheme (Winemiller and Rose 1992), which contrasts the review by Heibo et al. (2005) for perch populations. Therefore, finding approaches that approximate life history from size variables also routinely measured in fish monitoring may be a major step to improving the programmes for managing and monitoring inland waters in the face of the ongoing global climate change.





## CHAPTER 2

# Systematic deviations from linear size-abundance relationships of lake fish communities are correlated with predator-prey interactions and lake-use intensity

### Abstract

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The body size-abundance relationship of organisms at logarithmic scale exhibits a negative linear function; however, substantial deviations from linearity have been found in natural systems. Theoretical studies on size-structured fish communities suggest that predator-prey interactions are the major determinants of the shape of the community-wide size-abundance relationship. Our aim was to find empirical evidence for the association between the intensity of predator-prey interactions among fishes and systematic deviations from linearity in the size-abundance relationships of lake fish communities. We quantified size-specific residuals of the linear regression between the logarithmic fish abundance and the logarithmic mean size in 74 German lakes. Then, we compared species composition, as well as abundances, sizes, and abundance and size ratios of predator and prey fishes among the lake groups. We additionally evaluated human use intensity of lakes to represent anthropogenic effects influencing the predator-prey size and abundance ratios of fishes. Lakes were grouped into three clusters according to similarity of residual patterns. The lakes characterized by strongly linear patterns had low predator abundances and low predator-prey abundance ratios, but high predator-prey size ratios. In contrast, strong deviations from linearity occurred in the lakes with low predator-prey size ratios; these lakes were typically characterized by strong human use intensity and high total phosphorus concentrations. The fish species composition was a poor predictor of deviations from linearity. Our results suggest that predators shape

the size distribution of prey fish and hence the community-wide size-abundance relationship. Specifically, high densities of small predators may cause severe gape-limitation of piscivory, resulting in weak predation effects on prey.

Consequently, density overcompensation of prey creates non-linearity in the size-abundance relationship. The low predator-prey size ratios are caused by stronger human use intensity, especially fishing. We suggest deviations from linearity of size-abundance relationships in lake fish communities may reflect predator-prey interactions and fisheries.

**Key words:** human activities, trophic interactions, secondary structures

**The second chapter is the original work of the manuscript:**

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## Resum

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La relació entre la mida corporal i l'abundància dels organismes a una escala logarítmica sempre presenta una funció lineal negativa (és a dir, a mesura que disminueix l'abundància dels organismes la seva mida augmenta). Malgrat tot, estudis previs han detectat desviacions sistemàtiques en la relació entre la mida i l'abundància en els sistemes naturals. Estudis teòrics en l'estructura de mides de les comunitats de peixos suggereixen que les interaccions depredador-presa són les responsables d'originar aquestes desviacions entre la mida i l'abundància de la comunitat. Es va investigar si les interaccions depredador-presa, com també la intensitat antròpica, podrien explicar aquestes desviacions en l'espectre lineal de mides en les comunitats de peixos d'uns llacs Alemanys. A més a més, es va comparar la composició d'espècies, així com també les abundàncies, mides i les ràtios d'abundància i mida dels depredadors i preses entre els diferents llacs. Els llacs es van agrupar en tres categories segons les seves semblances en els seus patrons residuals. Els llacs que presentaven uns patrons de linealitat molt marcats tenien una abundància baixa de depredadors i una baixa ràtio de l'abundància depredador-presa, però una alta ràtio de mida depredador-presa. Per contra, les desviacions de la linealitat van aparèixer en els llacs amb una baixa ràtio de la mida depredador-presa. A més a més, aquests llacs tenien la característica de presentar una elevada activitat humana i unes concentracions elevades de fòsfor. La composició de les espècies no va influir en les desviacions de la linealitat. Els resultats suggereixen que l'abundància i mida dels depredadors afecta a les distribucions de mida de les preses i per tant la relació entre l'abundància i la mida de les comunitats de peixos. Concretament, unes elevades densitats de depredadors de mida petita poden limitar l'efecte piscívor sobre les preses. Això fa que hi hagi poc efecte de la predació en les preses. Llavors, un excés del nombre de preses fa que apareguin les desviacions de les relacions entre les mides i les abundàncies. A més a més, les baixa ràtio de l'abundància depredador-presa podria ser causada per unes intensitats elevades en les activitats humanes. Els nostres resultats van suggerir que els patrons de desviació de l'estructura de mides poden ser una

mesura útil en la gestió de les pesqueries i la qualitat ecològica en llacs, com també per entendre la complexitat de les xarxes tròfiques.

**Paraules clau:** activitats humanes, estructures secundàries, interaccions tròfiques

## Introduction

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Body size is a fundamental attribute of organisms as many physiological rates, such as respiration, reproduction and growth, are size-dependent (Brown et al. 2004). Furthermore, body size plays a key role in determining ecosystem-level processes, such as population density (Cyr et al. 1997, Brown et al. 2004), species richness and diversity (Brown et al. 2004, Lopez et al. 2016), and the intensity of predator–prey interactions (Woodward and Warren 2007, Hatton et al. 2015). Typically, the number of organisms per unit area or volume decreases with increasing body size (Elton 1927), and this negative relationship reflects loss of energy during transfer from prey (of smaller size) to predators (of larger size) (Kerr and Dickie 2001).

Since the pioneer work of Sheldon and Parsons (1967), scientists have been interested in size-abundance relationships (a.k.a. size spectrum). One common graphical and statistical expression of the size-abundance relationship is to plot the accumulated biomass within logarithmic body size classes against the logarithm of the mean mass per size class (Platt and Denman 1975, 1977). If the total biomass of each body size class is further divided by the width of the size class, the resulting size distribution is called Normalized Biomass Size Spectrum (NBSS) (Platt and Denman 1977, White et al. 2007, Sprules and Barth 2016). Empirically, the NBSS is often linear and the slope of the linear regression through the size distribution is almost always negative (Platt and Denman 1977, Sheldon et al. 1977, Gaedke 1992, Quiñones et al. 2003).

The negative linear relationship between log abundance and log size may be explained by the Metabolic Theory of Ecology (MTE) (Brown et al. 2004, Trebilco et al. 2013). According to MTE, the NBSS slope is constrained by trophic transfer efficiency (TTE) between adjacent trophic levels and predator-prey mass ratio (PPMR) as calculated from diet inspections of predators (Brown et al. 2004, Trebilco et al. 2013). If one assumes some typical values ( $TTE=10^{-1}$  and  $PPMR=10^4$ ), the NBSS slope is predicted to be close to -1 for communities composed of several coupled trophic levels (Brown et al. 2004). While this

prediction has been confirmed in some aquatic ecosystems (Platt and Denman 1977, Sheldon et al. 1977, Gaedke 1992, Quiñones et al. 2003), studies in many other aquatic systems have shown that size spectra can more appropriately be characterized by non-linear size-abundance relationships in log-log plots (Vidondo et al. 1997, Cózar et al. 2003, Bruce et al. 2005, 2010, Chang et al. 2014). These deviations from linearity have been called secondary structures in some studies, and have been observed for example in the pelagic food webs of North American Great Lakes (Sprules and Goyke 1994, Yurista et al. 2014).

Various hypotheses have been proposed to explain mechanisms underlying secondary structures. Results from theoretical models demonstrate that secondary structures can appear if morphological feeding constraints of gape-limited predators or low efficiencies of predators in handling prey change the effective PPMR (Thiebaut and Dickie 1992, 1993; Kerr and Dickie 2001; Sprules and Goyke 1994). Based on a community model, Law et al. (2009) predicted that the secondary structures were more likely to appear when predators are strongly specialized on a narrow range of prey sizes much smaller than the size of the predators. These examples suggest that the sizes of predator and prey and the resulting PPMR may be important predictors of deviations from linearity of the size-abundance relationships.

Apart from the sizes of predator and prey, their respective abundances and the abundance ratio of predator and prey may cause deviations from linearity. We have recently demonstrated that the density of fish populations is a strong predictor of the size structure of the respective populations in lakes (Arranz et al. 2016). High densities caused lower mean sizes and steeper slopes of size-abundance relationships. High fish densities increase competition for resources, and thus growth of fish may decrease or even stop (De Roos and Persson 2002, Ohlberger et al. 2011). This phenomenon that fish stop growing at a certain body size is called stunting (Ylikarjula et al. 2000, Giacomini et al. 2013). Our previous analyses have shown that fish density increased with lake productivity (Bruce et al. 2013, Mehner et al. 2016), and hence higher concentrations of total phosphorus as a proxy of lake productivity may indirectly contribute to stunted growth. Although not yet empirically

tested, it may be plausible that negative density-dependence and stunted growth in fish populations may be manifested as deviations from linearity in the size-abundance relationship of the entire fish community.

Fishing is one of the major human activities, which change abundances and size structure of fish communities. Modeling studies have shown that overfishing on large predator fish may cause shifts in the intensity of predator-prey interactions, ultimately resulting in changes in the shape of size spectrum (Rice and Gislason 1996, Shin et al. 2005, Gómez-Canchong et al. 2011). Furthermore, Benoît and Rochet (2004) simulated the effects of fishing-induced depletion of large predator fish, which caused an accumulation of smaller prey fish due to release from predation. Relaxed predation pressure can lead to biomass overcompensation of prey fish (Schröder et al. 2009), and the resulting size-abundance relationships are non-linear and mirror secondary structures (Benoît and Rochet 2004). The interplay between predator removal by fishing and changes in the size spectrum suggests that certain combinations of predator and prey abundances and sizes may cause deviations from linearity, for example, the secondary structures in the size spectrum. However, empirical studies exploring non-linear size-abundance relationships in fish communities have not been conducted so far.

The objective of this study was to explore deviations from linearity in the size-abundance relationships of fish communities in 74 German lakes from the European Central Plains and identify potential correlates of non-linearity across the lakes. Specifically, we tested whether groups of lakes with similar systematic deviations from linearity had correspondingly similar fish species composition, abundance and average sizes of predator and prey fish. Furthermore, we included total phosphorus concentration and human use intensity of lakes as potential indirect predictors of abundance and size structure of lake fish communities. We hypothesized that the strongest deviations from linearity in the size-abundance relationships would occur in lakes where the predator abundance is low, overcompensation of prey has occurred, and hence the ratio between predator and prey abundance is low. Predator depletion was assumed to occur more often in lakes exposed to



high human use intensity, in particular induced by fishing and angling. Furthermore, deviations from linearity may occur also in those lakes, in which the average size of prey is high relative to the average size of predators, which may cause a size refuge of larger prey from gape-limited predators (Mehner et al. 2016). Finally, since different fish species vary in their metabolic requirements (e.g. for growth or reproduction; Jennings et al. 1998) and trophic roles (Persson et al. 2000), we also explored if the species composition can explain the deviations from linearity.

## **Material and methods**

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### **Fish sampling and data**

Seventy-four German lowland lakes (<100 m a.s.l.) were sampled once during the summer periods of 2001 through 2003. These lakes are situated in northern Germany (latitude: 51.49°N-53.88°N and longitude: 8.02°E-14.21°E) within the Central Plains ecoregion (Illies 1978). These lakes are a subset of 1922 lakes in the European Water Framework Directive Intercalibration program (Argillier et al. 2013, Bruce et al. 2013), which have been sampled in a standardized procedure according to the European Committee for Standardization (CEN 14757 2005). Environmental and morphometric information of sampled lakes are included in Table A2 (Appendix).

Fishes were caught using benthic Nordic multi-mesh gillnets (length 30 m, height 1.5 m, 12 mesh-size panels of 2.5 m length each, knot to knot dimensions in a geometric scale: 5, 6.25, 8, 10, 12.5, 16, 19.5, 24, 29, 35, 43, and 55 mm). These multi-mesh gillnets were designed to catch lake fish communities in a representative way with respect to fish abundance, fish species composition and size distributions (Appelberg et al. 1995; CEN 14757 2005). The total number of nets per lake and their distribution across the depth zones

followed the European standard (CEN 14757 2005). The nets were set for approximately 12 h overnight to include both evening and morning phases of high fish activity. Two fishing campaigns were conducted in each lake, one sampling during autumn (August to early October) and another during the subsequent spring (May to early July). The catches from both periods were summed. Each individual fish was identified to species level, weighed to the nearest gram and length determined to the nearest centimeter. Lake-specific catch per unit effort (CPUE) was calculated as total number of caught fish divided by the number of nets per lake, and was used as a relative index of fish abundance (Emmrich et al. 2012).

In total, 167,131 individual fishes were caught. The number of fishes caught per lake ranged between 13,251 (Lake Müritzt) and 183 (Lake Buckowsee). The fish communities encompassed a total of 32 fish species, but were dominated by the cyprinids roach (*Rutilus rutilus*), common and white bream (*Abramis brama* and *Blicca bjoerkna*), and the percids perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernuus*), and zander (*Sander lucioperca*). The remaining 26 fish species represented only about 6% of the total number. Perch and zander were the dominant predator species, representing 97% of the predators. More information on the lake fish communities can be found in (Mehner et al. 2005, 2007).

## **Abundances and sizes of predators and prey**

Piscivorous fishes exhibit ontogenetic diet shifts; that is, juveniles are often omnivorous, whereas adults switch to feeding on prey fishes (Persson et al. 2000). Therefore, we considered only individuals > 32 g (=25 g, equivalent to about 15 cm total length) of asp (*Aspius aspius*), burbot (*Lota lota*), catfish (*Silurus glanis*), perch (*Perca fluviatilis*), pike (*Esox lucius*), rainbow trout (*Oncorhynchus mykiss*), and zander (*Sander lucioperca*) as predators (feeding on fish prey), but classified smaller individuals (i.e.  $\leq 32$  g) of these species as prey (Mehner et al. 2016). All other fish species were considered as prey of the predators.

Based on the aforementioned definition of predators and prey, we calculated separately the total CPUE of predators and prey for each lake. The ratio of predator and prey abundance is subsequently termed logarithmic predator-prey ratio (hereafter, logPPR). This ratio is a numerical reflection of the potential feeding strength of predators on prey (Woodward et al. 2005), and we hypothesized that low PPR would correlate with deviations from linearity. In addition, we estimated the average body size of predators as the geometric mean of all predator individuals in each lake, and likewise for prey. The logarithm of the ratio of average body size of predators and prey is called the predator-prey mass ratio (hereafter, logPPMR). This ratio represents the potential morphological constraints of gape-limited predators relative to the community-wide available prey, in contrast to the PPMR as based on the realized prey sizes per individual predators (Brose et al. 2006). We hypothesized that a low PPMR would correlate with deviations from linearity, because strong gape limitation of predators will relax prey from predation, and hence may cause overcompensation and stunted prey growth.

## **Anthropogenic lake descriptors**

We calculated two lake descriptors representing the potential anthropogenic pressure and use intensity in the German lakes. Human use intensity per lake was estimated as the sum of three different anthropogenic effects as considered similarly by Bruçet et al. (2013): (1) shoreline bank modification, which is the amount of shoreline changed by human activity (e.g. bathing places, sheet piles, rip-rap habitats), on a ranked scale from 1 (no modification) to 5 (highly modified); (2) fish exploitation by commercial and recreational fisheries classified from 1 (low fishing activity) to 3 (high fishing activity); and (3) human activities such as bathing and boating and overall water-use activities (coded 1-3 with increasing activity). Hence, the final descriptor ranged from 3 (minimum disturbance) to 11 (maximum disturbance), and we expected that high human use intensity induces low PPR and low PPMR

due to the preferential removal of large predators. Accordingly, human use intensity can be hypothesized to correlate positively with deviations from linearity. Furthermore, we used information on total phosphorus concentration (TP,  $\text{mg}\cdot\text{m}^{-3}$ ) per lake (average of a minimum of four samples from the growing season), which likewise reflects variability in anthropogenic influence on the lakes. Fish density increases with TP in lakes, and hence we hypothesized that high TP causes deviations from linearity by stunted growth.

## Calculation of size spectrum and size-specific residuals

We grouped individual fish according to their mass (g) into 22 size classes along a  $\log_2$  scale, with each  $\log_2$  size class further divided into two halves (i.e.  $\log_2/2$ ; 1<sup>st</sup> class:  $21/2 = 1.41$  g to  $22/2 = 2$  g; 2<sup>nd</sup> class:  $22/2 = 2$  g to  $23/2 = 2.83$  g, etc., and 22<sup>nd</sup> class:  $>2048$  g). Very small fish ( $< 6$  g) and very large fish ( $> 2048$  g) were underrepresented (Mehner et al. 2016); hence, we omitted the size classes 1, 2, 3, 4 and 22 such that the linear spectra ultimately covered 17 size classes with fish in the mass range between 6 g and 2048 g (total  $n=44,385$  fish). No empty intermediate size class was found in any lake.

For each lake, we calculated the slope of the linear size spectrum using least-squares linear regression of  $\log_2$  abundance (CPUE) versus  $\log_2/2$  size class. Then, we calculated the explained variance (hereafter,  $R^2$ ) of the linear model. We used  $1-R^2$  as the common measure of non-linearity, which gives an overall idea of to what extent the observations deviate from the fitted line.

Size-specific residuals were quantified as the difference between the observed abundance per size class and the predicted abundance according to the regression line of the abundance spectrum for each lake. Positive residuals indicate over-representation of fish in a specific size class, whereas negative residuals indicated under-representation. Collectively, we obtained a matrix of 17 size-specific residuals x 74 lakes. We used the size-specific

residuals to determine whether there are systematic patterns in secondary structure of fish communities among lakes.

## Statistical analyses

To detect similarity of secondary structures among the lakes, we applied K-means clustering (MacQueen 1967) on the 17 residuals x 74 lakes matrix. The optimum number of clusters was based on the lowest value of the Akaike Information Criterion (AIC, Akaike 1974). For each lake cluster, we calculated the geometric mean and standard deviation of size-specific residuals for each size class across all lakes from this cluster (Fig. 6). Then, we conducted one-sample t-tests to examine whether the mean residuals per size class deviated significantly from zero (at  $\alpha < 0.05$ ), indicating significant deviations from linearity for that size class per lake cluster (Fig. 6). Subsequently, we calculated two metrics to describe each cluster. The first metric was the number of size classes whose residual means significantly deviated from zero (Figs. 6a-b-c). The second metric was the sum of absolute residual variation from all size classes, representing the total degree of residual variation for each cluster.

Subsequently, we tested for potential correlates of systematic residual patterns in the lake clusters. To detect whether significant differences exist in species composition among the clusters, we used Discriminant Correspondence analysis (DCA) (Legendre and Legendre 1998). Many rare fish species were present in only few lakes and this may lead to statistical problems due to a zero-inflated species x lakes presence/absence matrix. Therefore, we limited the DCA to fish species that occurred in at least 50% of the lakes. The DCA was done using log CPUE of bleak (*Alburnus alburnus*), common bream, predator (>32 g) perch, prey (< 32 g) perch, predator pike (*Esox lucius*), roach, rudd (*Scardinius erythrophthalmus*), ruffe, tench (*Tinca tinca*), and white bream. We used the standardized discriminant functions from the predictors (i.e. species abundances approximated by species-specific CPUE) to assess their relative contributions (Legendre and Legendre 1998). The

percentage of cases correctly classified reflects the degree to which the samples yield consistent information based on the cross-validation method (Miller and Miller 2010).

Furthermore, we tested whether the anthropogenic descriptors (human use intensity and TP concentration), predator and prey abundances and sizes, and ratios of predators and prey (logPPR and logPPMR) differed between lake clusters. Significant differences in these variables between lake clusters would suggest that the respective variables may explain systematic deviations in size-specific residuals. Due to non-normal distributions of variables, we carried out non-parametric Kruskal-Wallis tests, followed by pairwise Wilcoxon post-hoc tests ( $\alpha < 0.05$ ). In addition, we tested whether  $1-R^2$  of the linear size-abundance relationships differed among the lake clusters, in order to examine whether there is correspondence between  $1-R^2$  and the residual patterns.

To individually link the residuals per size class with the predictor variables, we used Partial Least-Squares (PLS) analysis, which is a latent variable regression method based on covariance between the predictors and the responses (Wold et al. 2001). This analysis exchanges predictor and response variables, but avoids the necessity to test the strongly correlated residuals per each size class individually against all predictors. Hence, PLS is particularly useful to detect the correspondence between residuals in single size classes and predictors, because it avoids the dimension reduction as for example applied by Principal Component Regression or redundancy analysis. We used the 17 size-class residuals as predictors. The  $1-R^2$ , human use intensity and TP, and the predator and prey abundances, sizes, and PPR and PPMR in the lakes were treated as response variables. Therefore, we evaluated whether the residual x lake matrix predicted the gradients of trophic interactions and anthropogenic pressure. All variables were normalized to zero mean and unit variance prior to analysis. The quality of the PLS was evaluated based on permutation tests (1000 times) with respect to the variance of the response variable predicted by the full model (R2Y) and the predictive performance of the model estimated by cross validation (Q2Y). For variables significantly predicted by the residual matrix, we calculated the loadings to the 17 size classes.

All analyses were carried out using R (version 3.0.2; R Development Core Team 2008), with PLS conducted using the package "ropls" (Thévenot et al. 2015).

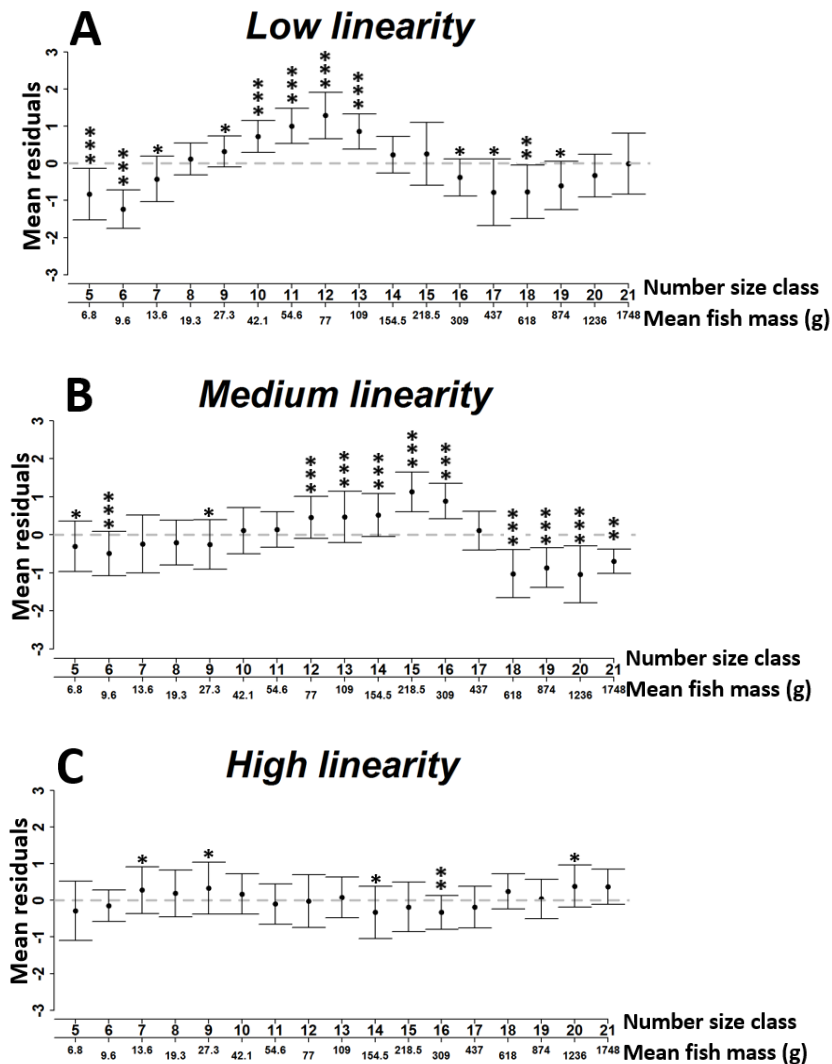
## Results

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### Deviations from linear size-abundance relationship

Substantial deviations from the linear size-abundance relationship were found in many of the German lakes. The measured  $1-R^2$  ranged from 0.02 to 0.61 across the lakes (arithmetic mean  $\pm$  SD,  $0.16 \pm 0.13$ ), albeit the slope of the size-abundance relationship was significant for all lakes ( $P < 0.05$ ).

According to  $K$ -mean clustering based on the similarity of the residual patterns across the lakes, the optimum cluster number characterized by the smallest AIC was three (AIC<sub>k<sub>2</sub></sub> = 527.4; AIC<sub>k<sub>3</sub></sub> = 513.4; AIC<sub>k<sub>4</sub></sub> = 514.9; AIC<sub>k<sub>5</sub></sub> = 530.2;  $k_n$  = number of clusters). Subsequently, we refer to the three clusters as *High*, *Medium* and *Low linearity* lake groups (Figs. 6a-b-c), according to the number of size class whose residual means deviated significantly from zero as well as the total sum of absolute residual variation. Spectra from lakes in the *High linearity* cluster did not show obvious secondary structures and the residual means were all close to zero across the entire body size range (only 5 out of 17 residuals weakly deviated from zero,  $t$ -test with  $\alpha < 0.05$ ; total sum of absolute residuals = 2.09, Fig. 6c).

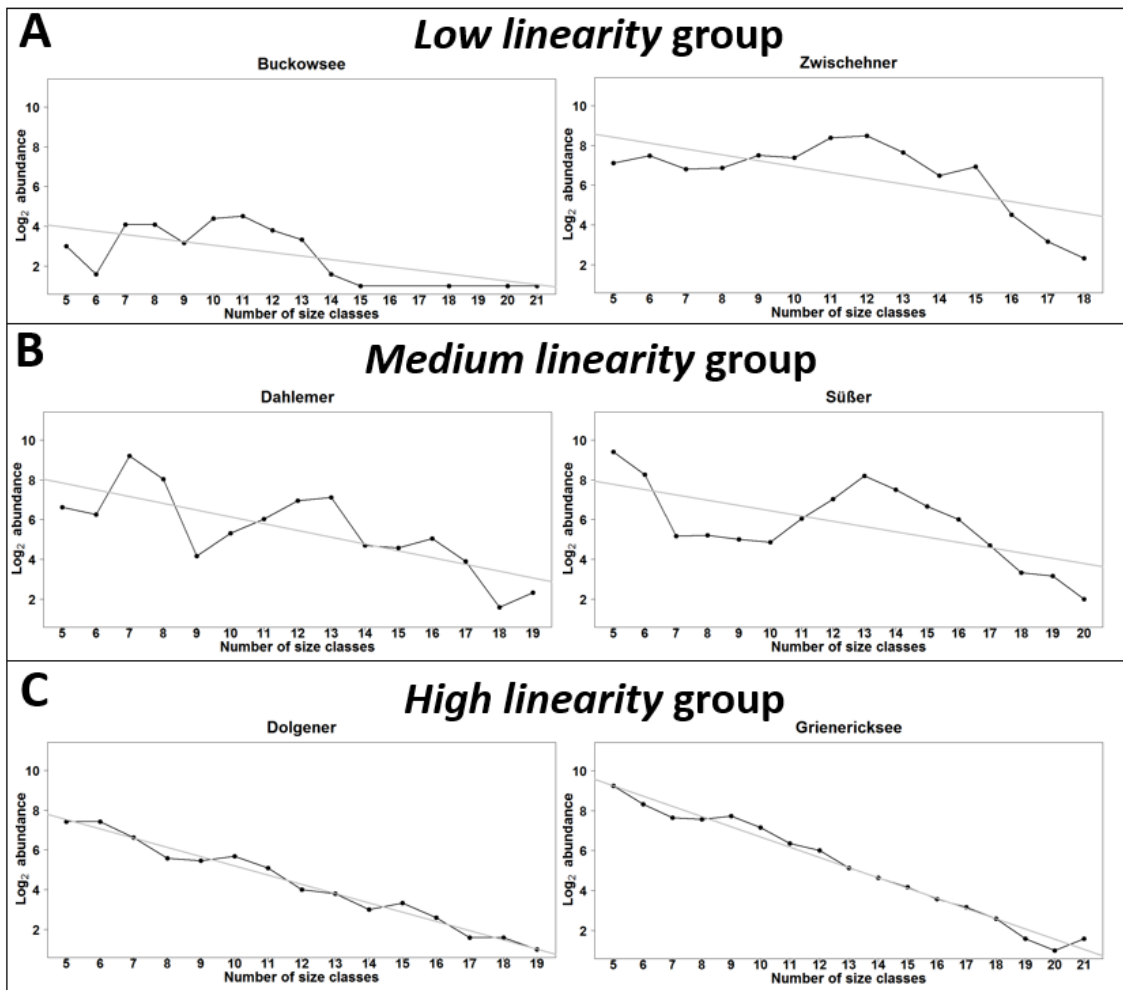


**Figure 6.** Patterns of residuals (i.e. deviations from the linear size-abundance relationship at log scale) for the three lake groups categorized according to *K*-means clustering: (panel A) *Low linearity* (13 lakes), (panel B) *Medium linearity* (33 lakes) and (panel C) *High linearity* (28 lakes). The first X-axis represents the number of size classes in the  $\log_2/2$  scale. The second x-axis shows the mean mass (g) for each size class. Y-axis summarises the residuals (shown as mean  $\pm$  standard deviation) for each cluster. Asterisks (\*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; \*,  $P < 0.05$ ) highlight the result of Student's t-test for deviations of the mean residuals from zero.

In contrast, clear secondary structures were found in the other two clusters (i.e. *Medium* and *Low Linearity*), with 12 out of 17 size classes exhibiting residuals significantly deviating from zero (Figs. 6a-b). The total sum of absolute residual variation was 3.83 in the



*Medium linearity* cluster, and 4.81 in the *Low linearity* cluster. The spectra from the *Low linearity* cluster were characterized by the highest positive residual around the 11<sup>th</sup> size class and negative residuals for size classes 4 and 5 (Fig. 6a). In contrast, the *Medium linearity* spectra showed positive residuals around the 14<sup>th</sup> size class and negative residuals in the largest size classes (Fig. 6b). We graphically represented the size spectra using two lakes per lake cluster group to illustrate the systematic deviations from linearity (Figs. 7a-b-c).



**Figure 7.** Size-abundance relationships in two example lakes per cluster group. X-axis represents the size classes in the  $\log_2/2$  scale; Y-axis shows the  $\log_2$  abundance in each size class.

## Comparison of fish species composition among lake clusters

Fish species composition showed a strong overlap among the three clusters, indicating that many fish species occurred in all lake groups. Discriminant analysis based on abundance composition of the dominant species correctly classified only 62% of lakes (Appendix, Fig. A6), suggesting that the fish community composition is a relatively poor predictor for the residual variation. The first discriminant function explained most of the between-cluster variance (78%), whereas the second discriminant function was not significant (Table 3). The abundances of predator perch (i.e. perch > 15 cm length, positive loadings) and roach (negative loadings) contributed strongly to the first function (Table 4). Predator perch were overall more abundant in lakes of the *Medium* and *Low linearity* clusters, whereas roach were primarily present in lakes of the *High Linearity* cluster (Table 4 and Fig. A1).

	Eigenvalue	Percentage of variance (%)	Wilk's Lambda	Chi- square	d.f.	<i>P value</i>
Function 1	0.88	78.2	0.43	56.50	20	<0.0001
Function 2	0.24	21.8	0.80	14.56	9	0.104

**Table 3.** Results of Discriminant Correspondence Analysis (DCA) of dominant fish species in the communities of 74 German lakes between three lake groups split by *k*-means clustering, based on similarity of residual patterns.

	Function 1
Bleak	0.17
Common bream	-0.03
Predator perch	0.26
Predator pike	0.02
Prey perch	0.07
Roach	-0.35
Rudd	0.17
Ruffe	0.21
Tench	0.22
White bream	0.00

**Table 4.** Relative contribution of the most representative species to the first discriminant function of the DCA. Perch and pike were split into prey and predators according to the 32 g size threshold.

## Comparison of descriptors among lake clusters

The  $1-R^2$  and many of the anthropogenic and trophic descriptors showed significant differences among the three clusters (Kruskal-Wallis tests with Wilcoxon post-hoc tests; Table 5). Specifically,  $1-R^2$  was significantly lower (and hence  $R^2$  higher) in the *High linearity* cluster than in the clusters *Low* and *Medium linearity* (Table 5). Human use intensity was lowest in the lakes of the cluster *High linearity*, whereas there was no difference in TP between the clusters (Table 5). CPUE of predators and logPPR were highest in the *Low linearity* cluster (Table 5). In contrast, predator body size and logPPMR were highest in the *High linearity* cluster (Table 5). These patterns indicate that strong deviations from linearity

(high residuals) were correlated with high abundances but low sizes of predator fishes. CPUE of prey fish did not differ among the clusters.

The PLS analyses indicated that the same predictors, which exhibited significant difference between the lake groups, were also significantly predicted by the residual variation between the lakes. The CPUE of predators, the PPR and the PPMR were significant response variables (Table 6). Both anthropogenic descriptors (human use intensity and TP) were also significant response variables (Table 6). In contrast, the measure of non-linearity ( $1-R^2$ ) was not predicted by the residual variation, suggesting that the size specific residuals represent a more nuanced reflection of the non-linearity of size-abundance relationships than  $1-R^2$ .

	Kruskal-Wallis Test		Mean values per cluster (Pairwise Wilcoxon post-hoc test)		
	$\chi^2$	<i>P</i> -value	<i>Low linearity</i>	<i>Medium linearity</i>	<i>High linearity</i>
<b>Measure of non-linearity</b>					
$1-R^2$		0.001	0.21 <sup>a</sup>	0.18 <sup>a</sup>	0.10 <sup>b</sup>
<b>Anthropogenic descriptors</b>					
Human use intensity	8.44	0.01	5.53	5.39 <sup>a</sup>	4.15 <sup>b</sup>
Total phosphorus (mg·m <sup>-3</sup> )	3.90	0.14			
<b>Trophic descriptors</b>					
CPUE of prey (ind net <sup>-1</sup> night <sup>-1</sup> )	0.27	0.87			
CPUE of predators (ind net <sup>-1</sup> night <sup>-1</sup> )	19.01	<0.001	7.75 <sup>a</sup>	5.32 <sup>a</sup>	2.62 <sup>b</sup>
Mean body size of prey (g)	6.29	0.04	14.5	9.6	9.3
Mean body size of predator (g)	7.11	0.03	75.3 <sup>a</sup>	99.4	108.4 <sup>b</sup>
Predator Prey mass ratio (PPMR)	14.03	<0.001	6.37 <sup>a</sup>	12.23	12.69 <sup>b</sup>
Predator prey abundance ratio (PPR)	18.81	<0.001	0.15 <sup>a</sup>	0.09 <sup>a</sup>	0.04 <sup>b</sup>

**Table 5.** Results of Kruskal-Wallis analyses testing whether significant differences exist between the three lake clusters for each variable. When significant ( $P$ -value < 0.05), Wilcoxon post-hoc tests with Bonferroni correction were used for pairwise comparisons. The arithmetic mean of the variables per cluster group is shown. Different letters on the means indicate significant difference at 95% confidence level ( $P < 0.05$ ), as based on Wilcoxon tests of log-transformed values. Ind net-1 night-1: total individuals of fish caught per net and night.

	R <sup>2</sup> X				
	(cum)	R <sup>2</sup> Y (cum)	Q <sup>2</sup> Y (cum)	<i>P</i> -value R <sup>2</sup> Y	<i>P</i> -value Q <sup>2</sup> Y
<b>Measure of non-linearity</b>					
<i>1-R</i> <sup>2</sup>	0.238	0.195	-0.047	0.052	0.275
<b>Anthropogenic descriptors</b>					
Human use intensity	0.246	0.264	0.149	<b>0.005</b>	<b>0.002</b>
Total phosphorus (mg·m <sup>-3</sup> )	0.202	0.382	0.155	<b>0.001</b>	<b>0.002</b>
<b>Trophic descriptors</b>					
CPUE prey (ind net <sup>-1</sup> night <sup>-1</sup> )	0.161	0.179	-0.014	0.150	0.100
CPUE predators (ind net <sup>-1</sup> night <sup>-1</sup> )	0.242	0.228	0.111	<b>0.026</b>	<b>0.003</b>
Mean body size prey (g)	0.196	0.282	0.009	0.050	0.250
Mean body size predator (g)	0.191	0.178	-0.113	0.100	0.700
Predator Prey mass ratio (logPPMR)	0.182	0.195	0.057	0.086	<b>0.012</b>
Predator prey ratio (logPPR)	0.204	0.324	0.144	<b>0.001</b>	<b>0.002</b>

**Table 6.** Results of the Partial Least-Squares (PLS) testing whether the size-specific residuals predicted the variability of the lake variables. The measure of non-linearity, anthropogenic descriptors and trophic descriptors were treated as response variables (first column). R<sup>2</sup>X (respectively R<sup>2</sup>Y): percentage of predictor (respectively response) variance explained by the full model. Q<sup>2</sup>Y: predictive performance of the model estimated by cross validation. Significant response variables in bold (*P*-value < 0.05). Ind net<sup>-1</sup> night<sup>-1</sup>: total individuals of fish caught per net and night.

The loadings of the five significant response variables to the 17 size classes of the size-abundance relationships in the PLS indicated that CPUE of predators, PPR, human use intensity, and TP concentrations were all positively correlated with the residuals in intermediate size classes (numbers 11-17, Table 7). In contrast, the PPMR loadings were negative for these intermediate size classes, but positive for the smallest (5-6) and the larger (16-19) size classes (Table 7). These results also indicate that strong positive residuals for intermediate-sized fish are associated with high abundances, but small sizes of predator fish. Note that these occurred primarily in the lakes of high use intensity and high nutrient (TP) concentration.

Size-specific residuals	Human use intensity	Total		Predator	
		phosphorus (mg·m <sup>-3</sup> )	CPUE predators (ind net <sup>-1</sup> night <sup>-1</sup> )	Prey mass ratio (logPPMR)	Predator prey ratio (logPPR)
r5	0.026	0.040	-0.123	<b>0.358</b>	-0.254
r6	-0.095	-0.032	-0.276	<b>0.406</b>	<b>-0.405</b>
r7	-0.299	-0.011	-0.287	0.176	-0.253
r8	-0.291	-0.159	-0.183	-0.078	-0.098
r9	-0.187	<b>-0.493</b>	-0.100	-0.059	0.054
r10	-0.018	<b>-0.336</b>	0.126	-0.204	<b>0.323</b>
r11	0.117	-0.011	0.291	<b>-0.362</b>	<b>0.407</b>
r12	0.235	0.275	<b>0.375</b>	<b>-0.499</b>	<b>0.394</b>
r13	0.232	<b>0.418</b>	<b>0.300</b>	<b>-0.375</b>	0.233
r14	<b>0.344</b>	0.242	<b>0.308</b>	-0.260	0.213
r15	<b>0.376</b>	<b>0.332</b>	0.259	-0.067	0.150
r16	<b>0.312</b>	<b>0.372</b>	0.182	0.107	0.085
r17	0.192	0.165	0.058	0.211	0.014
r18	-0.286	<b>-0.354</b>	<b>-0.312</b>	0.282	-0.261
r19	<b>-0.382</b>	<b>-0.303</b>	<b>-0.384</b>	0.290	-0.359
r20	<b>-0.330</b>	-0.268	-0.251	0.034	-0.188
r21	-0.255	-0.149	-0.143	-0.021	-0.126

**Table 7.** Loadings of the five significant predictors in PLS for the residuals from linearity in the 17 size classes (r5 to r21) of fish communities. Loadings  $>|0.30|$  are indicated in bold. Ind net<sup>-1</sup> night<sup>-1</sup>: total individuals of fish caught per net and night.

## Discussion

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Our results showed that the size spectra of fish communities differed substantially across the 74 lakes. The size-abundance relationship was almost linear in some lakes (Fig. 7c), similar to what has been found in several other aquatic ecosystems (Gaedke 1992; Jennings and Mackinson 2003; Quiñones et al. 2003). Worth noting, systematic deviations from linearity were found in other lakes (Fig. 7a-b) whose fish communities differed in their ratios of predator and prey abundances and sizes as well as human use intensity. Thus, our results provide empirical evidence, supporting predictions from community models (Kerr and Dickie 2001; Benoît and Rochet 2004; Law et al. 2009) that deviations from linearity (a.k.a. secondary structures of the size spectrum) may be directly caused by predator-prey interactions and indirectly by anthropogenic pressures.

In our study, the strongest deviations from linearity of the size-abundance relationships were found in the lakes characterized by a high abundance of predators relative to the abundance of their prey (i.e. at high PPR). Our result is in contrast to the expectation that a low abundance of predators relative to their prey (i.e., low PPR) may cause non-linearity of the size spectrum as predicted by some community models (Kerr and Dickie 2001; Benoît and Rochet 2004; Law et al. 2009). These opposite results suggest that a high abundance of predators alone is not sufficient to explain the secondary structure of fish community. Instead, in the lakes of the Medium and Low linearity where the predator abundance was high, abundances of fish in the intermediate size classes (classes 10-16, 33 to 362 g) (Figs. 7a-b) were still over-represented.

Then, what may explain the nonlinear structure of the size-abundance relationships? We found that secondary structures mainly appear in fish communities dominated by predators that are small relative to their prey (i.e. low PPMR). In fact, the same lakes, which were characterized by a high PPR, were also characterized by a low PPMR. These results suggest that the gape limitation of the predator is functionally a stronger predictor of the deviations from linearity of the size spectrum than the abundance of predators. Specifically,



the size spectra in the lakes of Low and Medium linearity were characterized by negative residuals for the larger size classes (classes 16-21, 257 to 2048 g) (Figs. 7a-b), indicating the lack of large-sized predators in the lakes of these clusters. In addition, we found an accumulation of intermediate-sized fish in these lakes (Figs. 7a-b). These findings suggest that the abundant, but small, predators cannot regulate the densities of fish of intermediate size (classes 10-16, 33 to 362 g) (Figs. 7a-b) and this may cause an over-representation in these intermediate size classes. Thus, the strongly positive residuals in size classes 10 to 16 in the lakes of the Low and Medium linearity (Figs. 6a-b) may reflect the fact that many prey fish were no longer accessible by the smaller predators (i.e. achieved a size refuge) and the resulting high density caused stunted growth (see Mehner et al. 2016).

The gape limitation of small fish predators may cause the surprising effect that a low abundance of large predators seems to have a stronger predation effect on prey abundances and sizes than a high abundance of small predators. In our study, the majority of the predators in the lakes with strong deviations from linearity were perch, as suggested by Discriminant Correspondence Analysis. Earlier studies in lakes with cannibalistic perch populations have shown that the size structure of the predators determines the density and growth of the cannibalistic victims (Persson et al. 2000, Claessen and Dieckmann 2002). Obviously, the size structure of the perch population is also one of the major determinants of the community size-abundance relationship, because density-dependent competition strength and predation interact. In addition, predators such as perch may also face stunted growth when occurring at high densities. Then the smaller average size of predators caused by retarded growth at high densities intensifies the effect of gape limitation.

Fishing pressure may contribute to the deviating patterns of the size-abundance relationship because fishing targets primarily the largest fishes (preferably predators), causing the prey numbers to increase due to decreased predation (Benoît and Rochet 2004, Shin et al. 2005, Andersen and Pedersen 2009). Thus, fishing may be one of potential reasons for the low abundance of large predators in some lakes (i.e. in the clusters of Low and Medium linearity) (Table 5). In our study, we used a metric of human use intensity that

integrated several anthropogenic effects in addition to fishing activity, such as bathing places or boating activities, which might be additionally important for the depletion of large predators and the appearance of secondary structures. Our results support that human use intensity was correlated with predator and prey fish abundances and sizes, and hence may be considered an indirect predictor for the non-linear size abundance relationships in some lakes.

Our analysis goes beyond the traditional focus on the slope of size-abundance relationships as the primary response variable to over-harvesting of large predator fishes (Sheldon et al. 1972, Platt and Denman 1977, White et al. 2007, Sprules and Barth 2016), and explores the size-specific deviations from linearity. It is commonly assumed that when large predators are removed from a system, the resulting size spectrum without large predators is often still strictly linear, but with a steeper slope than that of the original spectrum (Jennings and Mackinson 2003, Jennings et al. 2007, Blanchard et al. 2009). However, our results demonstrate that this is not necessarily the unique response of the size-abundance relationship under disturbance. Rather, we show a different kind of response; that is, a decreased abundance of large predators (perhaps due to anthropogenic impacts) may result in an accumulation of intermediate-sized fishes and thus causes nonlinear size-abundance relationships. The positive and negative size-specific residuals deviating from the best-fit linear size-abundance relationship shown in this study may reflect the inefficiency of predation (e.g. the gape size-limited feeding process) and community dynamics (e.g. overcompensation and stunted growth) as structuring forces for the size-abundance relationships of fish communities.

To our knowledge, systematic deviations from linearity have rarely been used to explore abiotic or biotic effects on the size-abundance relationship of fish communities. In freshwater systems, the effect of anthropogenic pressures has been analyzed by using the slope or intercept of linear spectra (Holmgren and Appelberg 2000, Emmrich et al. 2011, Benejam et al. 2016). Some studies have simply used the predicted variance ( $R^2$ ) of linear regressions to show deviations of the spectrum among lakes across large productivity

gradients (Sprules and Munawar 1986, Sprules and Barth 2016). In this sense, progressive departures from the steady-state conditions and declining  $R^2$  have been found with increasing productivity (Sprules and Munawar 1986) because eutrophication tends to raise the biomass levels at the lower end of the size spectrum (Minns et al. 1987, Emmrich et al. 2011) and probably leads to changes in predator-prey ratios. Similarly to our study, Chang et al. (2014) fitted a polynomial function to the residuals from a phytoplankton-zooplankton size spectrum to quantify nonlinear structures. These authors found that the deviating patterns can be explained by the nonlinear size-trophic level relationship which arose due to zooplankton omnivory and trophic interactions in microbial food webs. Accordingly, the results of these studies as well as our results suggest that the non-linearity of the size spectra is an important reflection of the complex predator-prey interactions. Non-linearity may be caused by size-constrained predator-prey interactions within the spectrum, as in our study, or by subsidized predator-prey interactions, where predators are additionally subsidized by prey not included in the community-wide size-abundance relationship (Chang et al. 2014). All in all, systematically deviating patterns from linearity within the size spectrum may become a sensitive metric to support the management of fisheries or aquatic ecosystems, as well as to understand the complexity of the trophic food web.



## **PART II**

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# **The fish size structure in relation to other functional and taxonomic approaches**



## CHAPTER 3

# Size diversity and species diversity relationships in fish assemblages of Western Palearctic lakes

### Abstract

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Body size, coupled with abundance and taxonomy, may help to understand the mechanisms shaping community structure. Since the body size of fish is closely related to their trophic niche, size diversity (based on individual body size) of fish communities may capture intraspecific variations in fish trophic niches that are not detected by species diversity. Thus, the relationship between size diversity and species diversity may help to integrate variation at both intraspecific and interspecific levels. We studied the relationship between species diversity and size diversity as a measure of the degree of overlap in size among species and thereby the potential overlap in niches in a community. We hypothesized that the relationship between size diversity and species would be different across the continent due to different levels of size overlap in fish communities. The data were derived from samplings of fish communities using standardized benthic gill nets in 363 lakes across Europe. At the continental scale, size diversity increased with species diversity; at the ecoregion scale, the slope of the relation changed across the continent, with the greatest mismatch occurring in northern Europe where communities comprised only one or a few species, but each of which exhibited a great range in size. There was an increase in slope towards the south with significant relations for four out of six ecoregions. The steeper size diversity-species diversity slope at lower latitudes suggests lower overlap in size and thus likely finer niche separation. Our results also suggest that size diversity is not a strong surrogate for species diversity in European lake fish communities. Thus, particularly in fish communities composed of few

species, measuring size diversity may help to detect potential functional variation which may be neglected by measuring species diversity alone.

**Key words:** niche overlap, size diversity, species diversity

**The third chapter is the original work of the manuscript:**

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## Resum

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La mida corporal, juntament amb l'abundància i la taxonomia, poden ajudar a entendre els mecanismes que formen les estructures de les comunitats. El fet que la mida corporal dels peixos estigui estretament relacionada amb el nínxol tròfic, la diversitat de mides de les comunitats dels peixos poden explicar les variacions intraspecífiques dels nínxols tròfics en els peixos i que no són detectades per la diversitat d'espècies. Per tant, la relació entre la diversitat de mides i la diversitat d'espècies pot ajudar a entendre la variació tant a un nivell intraspecífic com a un nivell interespecífic. Es va estudiar la relació entre la diversitat d'espècies i la diversitat de mides com a mesura del grau de solapament de les mides entre les espècies, i per tant el possible solapament dels nínxols en les comunitats. Es va suposar que la relació entre la diversitat de mides i la diversitat d'espècies seria diferent al llarg del continent degut a les diferències del nivell de solapament de mides en les comunitats de peixos. Les dades de les comunitats de peixos provenien de 363 llacs d'Europa amb el mateix mètode de mostreig. En una escala continental, la diversitat de mides es va incrementar amb la diversitat d'espècies. En una escala regional, la pendent de la relació canviava al llarg del continent. En el nord d'Europa, les comunitats estaven composades per només una o unes poques espècies, però cada una tenia un rang de mides molt ampli. Per contra, en el sud d'Europa, els pendents entre la diversitat de mides i la diversitat d'espècies era més pronunciat. Aquests pendents indiquen un solapament més baix de mides i per tant una separació dels nínxols més marcada en latituds baixes. Els resultats també suggereixen que la diversitat taxonòmica és una pitjor indicador de la funcionalitat de les comunitats de peixos que la diversitat de mides. Per tant, en les comunitats de peixos composades per unes poques espècies, les diversitats de mides poden ajudar a detectar possibles variacions funcionals i que no són detectades utilitzant només les diversitats d'espècies.

**Paraules clau:** diversitat d'espècies, diversitat de mides, solapament de nínxol



## Introduction

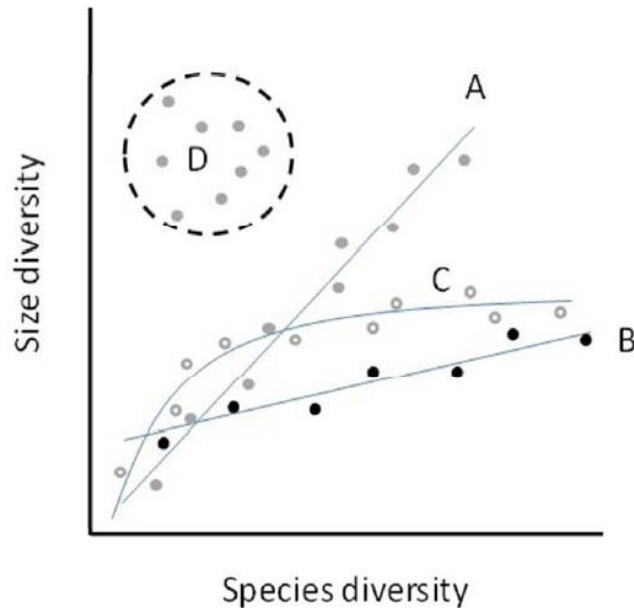
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Biodiversity has a multifaceted nature since it embraces biological variation of taxonomic, functional, and genetic components (Diaz and Cabido 2001, Hooper et al. 2005). Taxonomic diversity is the most considered component of biodiversity and has been the main basis of most biogeographical studies (Violle et al. 2014). Functional diversity quantifies the diversity of traits in a community (Hooper et al. 2005, Cadotte et al. 2011). Based on niche theory, it contributes to our of the processes related to community functioning and assembly rules (Cadotte et al. 2011, Safi et al. 2011, Schleuter et al. 2012). While some studies at large-scale gradients have shown strong relationships between the different diversity measures (e.g. Stuart Smith et al. 2013), others have revealed mismatches, which may challenge their interchangeable use (de Victor et al. 2010, Safi et al. 2011).

Body size is one of the most important animal traits because it affects physiology and determines competitive and predator–prey interactions (Peters 1983, Cohen et al. 1993, De Roos, et al. 2003, Woodward et al. 2005); furthermore, it is easy to measure. Additionally, body size is a key trait for defining ecological niches, especially so in aquatic ecosystems where organisms that are comparable in size often occupy similar niches (Woodward and Hildrew 2002, Jennings et al. 2001). Body size has been used as a trait in several functional diversity indices, but usually it refers to just one estimate of the size of the adult per species. A simple and intuitive way to assess variation in the individual body size structure of a community is to use its size diversity (Brucet et al. 2006, 2010, Quintana et al. 2008, Ye et al. 2013, Garcia-Comas et al. 2016). Size diversity, based on the Shannon diversity index (Pielou 1969), integrates the amplitude of the size range and evenness in the same way as the Shannon species diversity index integrates the number of species and their relative abundance. Since body size aggregates multiple traits influencing community functioning (e.g. Woodward et al. 2005), the size diversity index based on individual body size facilitates studying the functional diversity of a community expressed as the size variation within the community. Empirical studies in fresh waters and marine systems have shown that size

diversity represents an index of functional diversity that links community structure and trophic dynamics (Ye et al. 2013, Quintana et al. 2015, Garcia-Comas et al. 2016, Mindel et al. 2016). Size diversity based on individual body size may also capture intraspecific variability, the importance of which is being increasingly recognized for many ecological evolutionary processes (Violle et al. 2012).

The relationship between species diversity and size diversity will depend on the extent to which different species in a community exhibit similar body sizes. If the species differ strongly in adult and/or maximum size (e.g. they have different sizes at sexual maturity), the addition of new species to a community will likely increase body size diversity, resulting in a linear positive relationship between species and size diversity (Micheli and Halpern 2005, Guillemot et al. 2011; Fig. 8, A and B). The slope of this function indicates the rate of increasing new body sizes: a steep slope means that the diversity of body sizes increases rapidly with species diversity (Fig. 8, A), whereas a shallower slope implies an increasing overlap in size while species accumulate (Fig. 8, B). Size diversity may also increase at declining rates with increased species diversity and reach an asymptote at high diversity (Fig. 8, C). A weak relationship between species and size diversity will occur in a community composed of a single or of few species with a wide size range and thus high size diversity (Fig. 8, D). Hence, the strength and the shape of the relationship reflect the overlap in size, and likely an overlap of niches, among species in a community. A low overlap in size may imply that size-related traits are lost from a system as species diversity declines, resulting in changes of the functioning of the community, as has been found in studies relating species diversity and functional diversity (Micheli and Halpern 2005, Guillemot et al. 2011). A relationship between species and size diversity has not yet been demonstrated at large geographical scales, while varying patterns have been observed in local-scale studies (Brucet et al. 2006, Gascón et al. 2009).



**Figure 8.** Hypothetical relationships between species diversity and size diversity (modified from Micheli and Halpern (2005) and Guillemot et al. (2011) showing the relationship between taxonomic and functional –including several traits – diversity). (A) The two types of diversity increase at a similar rate and the relationship is strongest (grey dots); (B) linear relationship with slope  $\ll 1$  (black dots); (C) size diversity increases fast at low species diversity but subsequently increases at declining rates (open circles); (D) no relationship between size diversity and species diversity: example of communities composed of a single or a few species with high size diversity.

Fish are well-suited for studying the relationship between species diversity and size diversity because they are of key importance for functions and services of aquatic ecosystems in numerous ways. Thus, they are, for instance, important for the transfer of energy and cycling of nutrients and they also supply food and recreational activities (Holmlund and Hammer, 1999). Furthermore, intraspecific size variation within fish species strongly affects the dynamics and structure of lake communities even at low species diversity (Jansson et al. 2007, Lemmens et al. 2017). Since the body size of fish is closely related to their trophic niche (Jennings et al. 2001, Romanuk et al. 2011), size diversity of fish communities may capture intraspecific variations in fish trophic niches that are not detected by taxonomic approaches.

We used data from Western Palearctic lakes to assess the relationship between size diversity and species diversity in freshwater fish communities. We hypothesized that the relationship between size diversity and species diversity would reflect ecological and

biogeographical processes that typically lead to an increased niche specialization (i.e. species become better adapted, by natural selection, to the specific characteristics of a particular habitat) in lower latitudes (Gaston 2000, Griffiths 2006, Mittelbach et al. 2007, Mason et al. 2008). Thus, since body size is a good proxy of niche separation and niche segregation tends to be higher toward the tropics (latitude–niche breadth hypothesis; MacArthur 1972, Vazquez and Stevens 2004), particularly in freshwater food webs (Cirtwill et al. 2015), we hypothesised that the slope of the size diversity and species diversity relationship would be steeper in low latitude than in high latitude regions (i.e. the diversity of body sizes will increase more rapidly with species diversity in warmer lakes). This would mean that there is lower overlap in fish body size in southern regions compared with northern regions. In the models, we also included climate variables and features of the lake basins because they have been found to influence the size structure of fish communities (Griffiths 2012, Jeppesen et al. 2010, Emmrich et al. 2014) and thus also affect the size diversity. In this sense, temperature was found to be a main driver negatively affecting fish body size across large-scale gradients (Emmrich et al. 2014). Thus, we hypothesised a decrease to occur in size diversity in warmer lakes due to higher dominance of small sized fish. Fish body size can also be influenced by human activities such as fish species introductions or stockings and intensive removal fisheries (Blanchet et al. 2010). Consequently, we tested for a potential bias caused by human intervention in our analyses.

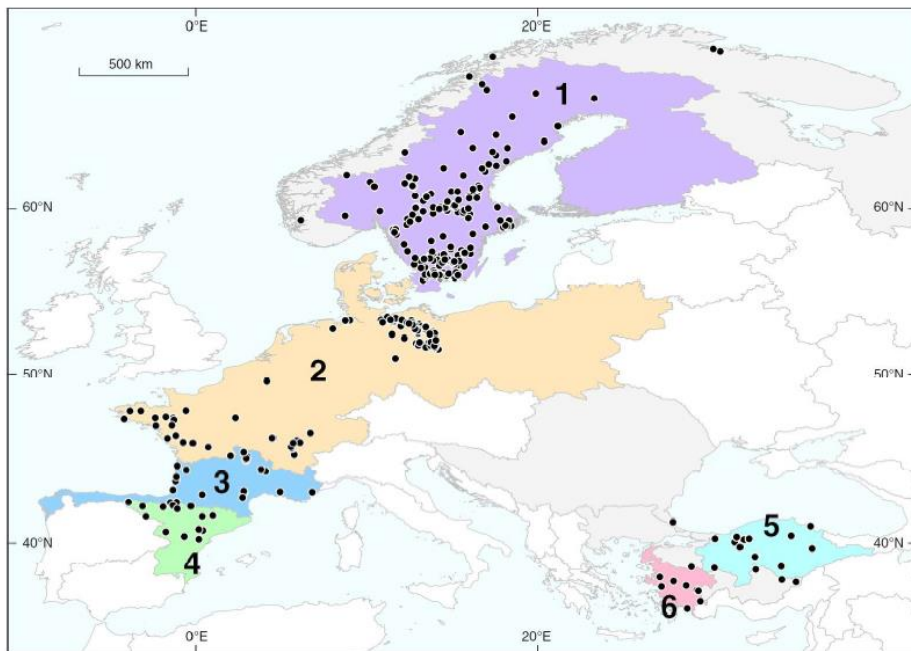
## **Materials and methods**

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### **Data set**

We used a fish database including 363 Western Palearctic lakes located in eleven countries (mostly in Europe) and covering latitudes between 69°69'N to 36°69'N (Fig. 9). The lakes were sampled once between 1993 and 2012 using stratified random sampling with benthic

multi-mesh gillnets (type NORDIC: length 30 m; height 1.5 m; 12 panels of 2.5 m each with bar mesh sizes between 5 and 55 140 mm knot to knot). The database was created to facilitate implementation of the European Union Water Framework Directive 2000/60/EC (for details see Bruçet et al. 2013) and was supplemented with additional data from the authors. Samplings were undertaken during late summer and early autumn with a pre-defined number of nets per lake set randomly in each depth stratum depending on lake area and depth in accordance with a European standard protocol (Appelberg et al. 1995; CEN 14757 2005). Captured fish were identified to species level and measured (total length rounded to the nearest cm). For more details on the samplings and lake environmental characteristics, see Bruçet et al. (2013) and Emmrich et al. (2014).



**Figure 9.** Geographical distribution of 363 lakes. Freshwater ecoregions (coloured) are defined according to Abell et al (2008): (1) Northern Baltic Drainages, (2) Central and Western Europe, (3) Cantabric Coast- Languedoc, (4) Eastern Iberia, (5) Northern Anatolia and (6) Western Anatolia. Lakes in grey ecoregions were not considered because there were too few to allow statistical analysis.

Four abiotic variables known to influence fish species diversity and size structure (Bruce et al. 2013, Emmrich et al. 2014) were used (Table 8): maximum lake depth (m), lake area (ha), total phosphorus concentration (TP, mg m<sup>-3</sup>), longitude and maximum air temperature at the geographic location of the lake (obtained from the Climate Research Unit (CRU) climate model and based on the maximum monthly mean temperature). Maximum air temperature was used as an approximation to maximum lake temperature because previous studies have shown that it is a reliable surrogate for epilimnetic lake temperature (Livingstone and Lotter, 1998) and because fish diversity and size structure are more sensitive to maximum than to average local temperatures (Bruce et al. 2013, Emmrich et al. 2014). We did not include lake area because it was correlated with lake depth, nor latitude as it was strongly correlated with maximum temperature (Pearson correlation 0.44 and -0.87, respectively,  $P < 0.001$ ). We log<sub>10</sub>-transformed all variables in order to achieve normally distributed variables.

	N	Minimum	Maximum	Mean
Lake area (km <sup>2</sup> )	363	0.001	113.0	3.08
Maximum depth (m)	363	0.550	115.7	17.63
Total phosphorus (mg m <sup>-3</sup> )	363	1.000	401.9	35.74
Maximum temperature (°C)	363	7.400	33.2	17.30

**Table 8.** Environmental variables analysed (minima, maxima, and means) and the number of lakes.

The 363 lakes were situated in 11 freshwater ecoregions (Abell et al. 2008; 159 Fig. 9). However, freshwater ecoregions that had less than five lakes were removed from the analysis (Barents Sea Drainages, Norwegian Sea Drainages, Dniester–Lower Danube, Thrace, Central Anatolia). Thus, a total of 346 lakes was used for the analysis and the number of lakes per freshwater ecoregion is presented in Table 3. In Eastern Iberia, the dataset was composed

only of reservoirs, and in Cantabric Coast-Languedoc and Central and Western Europe there were 7 and 22 reservoirs, respectively. The remaining water bodies sampled were natural lakes.

In order to test for a potential bias in our analyses caused by fish introduction (i.e. introduction of small or big fish that may change that natural patterns of size diversity), we calculated the percentage of non-native individuals out of the total number of individuals in each water body. We considered non-native species to be those that had been introduced or translocated. The native/translocated/introduced status of each fish species was defined to at least a lake basin specific level according to the literature (Filipsson 1994, Tammi et al. 2003, Kottelat and Freyhof 2007, Brosse et al. 2013, Dias et al. 2014, Tarkan et al. 2015, Boll et al. 2016). For some ecoregions (Northern and Western Anatolia and Northern Baltic Drainages) information was available for each individual study lake.

## **Species diversity and size diversity calculations**

Species richness was calculated as the total number of fish species sampled in a lake. Shannon diversity ( $H$ ) was calculated according to Shannon and Wiener (Pielou 1969) using catch per unit effort (CPUE, number of fish net<sup>-1</sup> night<sup>-1</sup>). We calculated size diversity for each fish community in each lake by using individual length measurements (total length) as the measure of size (Brucet et al. 2006, Quintana et al. 2008) and the methodology proposed in Quintana et al. (2008), applying the open source software “diversity08” available at [www.limnolam.org](http://www.limnolam.org). The size diversity index ( $\mu$ ) is computed based on the Shannon diversity expression adapted for a continuous variable, such as body size. This measure takes the form of an integral involving the probability density function (pdf; i.e. a function that describes the relative likelihood for a random variable to take on 185 a given value) of the size of the individuals described by the following equation:

$$(1) \quad \mu_2(x) = - \int_0^{\infty} \rho_x(x) \log_2 p_x(x) dx$$

where  $p_x(x)$  is the pdf of size  $x$ . The non-parametric kernel estimation was used as a pdf, which is to any type of size distribution. A kernel function is essentially a pdf, usually symmetric, whose dispersion is controlled by a bandwidth parameter. The estimator is a sum of kernel functions centered at the sample points (Quintana et al. 2008). Before computing size diversity, data are standardised by division of each size value by the geometric mean of the size distribution (Quintana et al. 2008). This standardisation allows comparison with data from other studies whose samples are measured with different units, such as length, weight or volume, while it does not alter the results. The size diversity index ( $\mu$ ) is the continuous analogue of the Shannon diversity index and it produces values in a similar range to those of the Shannon species diversity index (Quintana et al. 2008). The use of size diversity for analysis of the shape of size distribution has the advantages that (1) it is a single-value metric that simplifies comparisons between samples (Brucet et al. 2010); (2) its meaning is easy to interpret since the concept of diversity is well established: high size diversity means a wide size range and similar proportions of the different sizes along the size distribution (i.e. Emmrich et al. 2011). All lakes had more than 50 measured, which corresponds to a size diversity error estimation lower than 10%.

## Statistical analysis

To evaluate species diversity and size diversity relationships across the environmental gradient and ecoregions, we ran a Linear Mixed-Effects Model (LMM) with size diversity as dependent variable. As independent variables we included species diversity, ecoregion, interaction between species diversity and ecoregion, lake depth, TP, longitude, maximum temperature and percentage of non-natives.



Lakes were used as a nested random factor within the ecoregion. We searched 209 for the most parsimonious model by an automatic stepwise backward selection of one predictor variable at a time by minimising the Akaike information criterion (AIC) (Akaike 1974). The most parsimonious model was the combination of variables having the strongest impact on outcomes. Since the AIC between the full and final model was  $<2$ , we further applied ANOVA to compare the most parsimonious final model (i.e. the one with lowest AIC) with the next best model that included one more predictor. Spatial autocorrelation of the residuals of the best model was examined using Moran's  $I$  (Legendre and Legendre 1998).

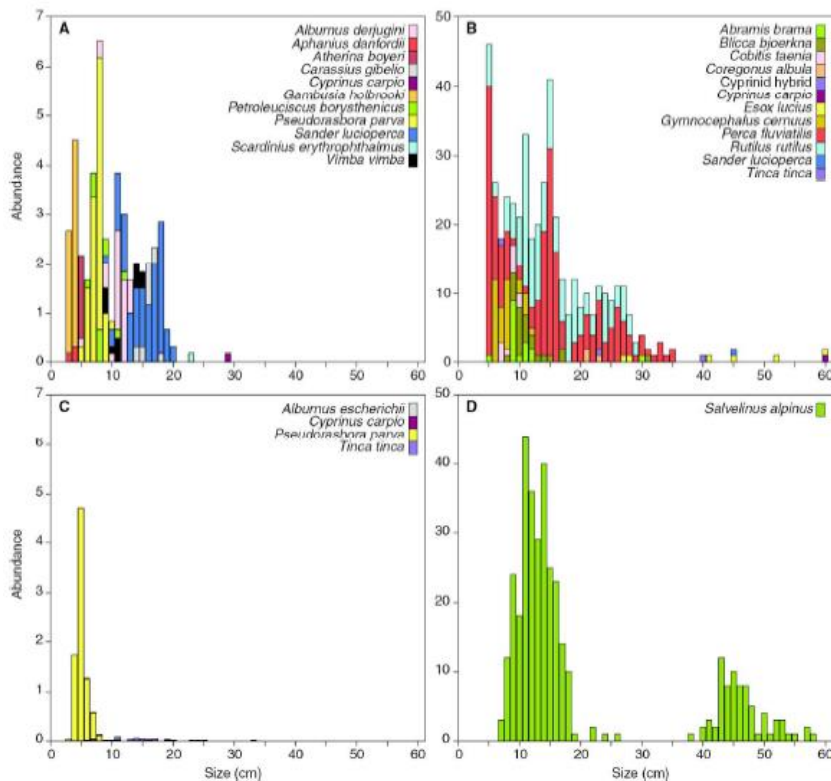
The same LMM analysis was repeated using species richness instead of species diversity as an independent variable. Similar results were obtained, but with less variation of fish size diversity explained than when using species diversity. For this reason, and because both size diversity and species diversity use Shannon diversity formulae and have similar range of values, we do not present the results for species richness here. We also tested whether species and size diversity relationships provided better fits by applying an asymptotic model (Fig. 8C), but this model was not superior to the linear models.

We tested for the effects of reservoirs, where human intervention is expected to be highest, by redoing LMM and Moran  $I$  spatial autocorrelation on a subset of water bodies only including lakes. We also used an ANOVA on a subset of lakes for which fisheries intensity data was available ( $n=175$ ) to compare the size diversity in lakes having reported high fisheries intensity with lakes with no or low fisheries intensity. The size diversity of fish communities did not differ between the two sets of lakes (ANOVA,  $p > 0.05$ ); thus, we did not consider this aspect any further.

For all analyses, we checked that assumptions of normal distribution of residuals and were not violated. We inspected the variance inflation factor (VIF) to assure that there was no multicollinearity among predictors in the final set used for the analyses. Analyses were performed in 'R' version 2.9.1 (Development Core Team 2009) using "nlme" (Pinheiro et al. 2011), "ape", (Paradis et al. 2004) and "MuMIn" (Bartoń 2009).

## Results

Size diversity ( $\mu$ ) and species diversity ranged between minima of 0.65 and 0 and maxima of 3.34 and 2.55, respectively. Three different combinations of species and size diversity of fish communities were observed: high species and high size diversity (Fig. 10, A and B), low species and low size diversity (Fig. 10, C) and low species diversity and high size diversity (Fig. 10, D). No significant relationship was found between size diversity and the total number of measured fish suggesting that the increase in size diversity was not a consequence of measuring more fish.



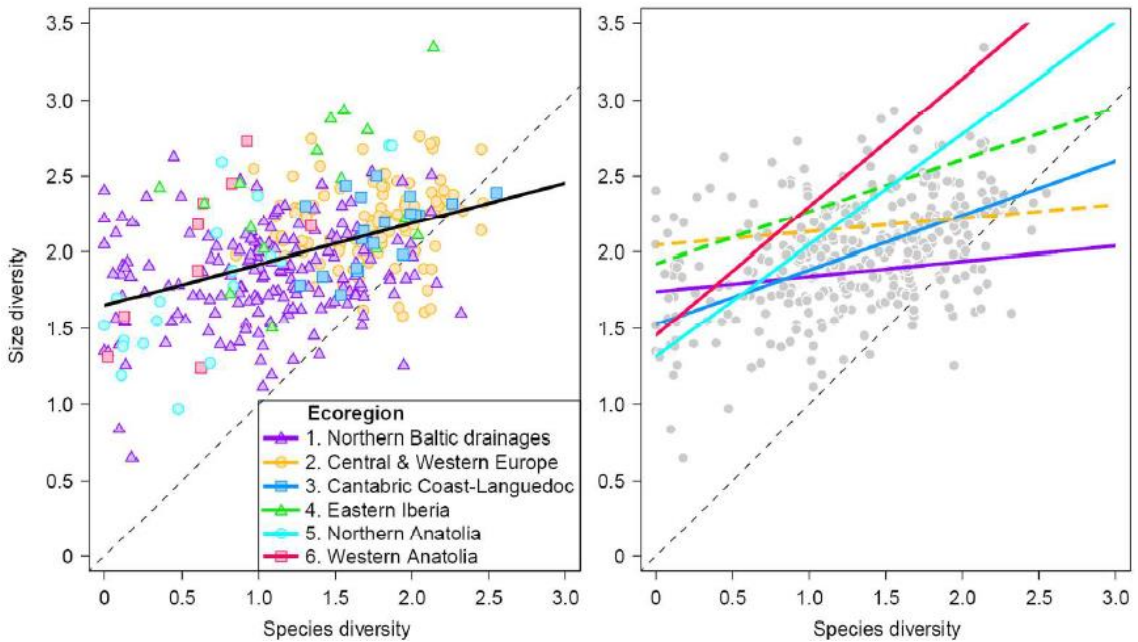
**Figure 10.** Examples of size distributions (abundance in CPUE (fish net<sup>-1</sup> night<sup>-1</sup>) as a function of size classes in cm) and species composition of a fish community in different lakes: (A) high species diversity ( $H = 1.9$ ) and size diversity ( $\mu = 2.7$ ) in a community composed of fish species of relatively different sizes in a lake from Northern Anatolia; (B) high species diversity ( $H = 2.1$ ) and size diversity ( $\mu = 2.8$ ) in a community composed of species growing over large size ranges in a lake in Central and Western Europe; (C) low species diversity ( $H = 0.3$ ) and size diversity ( $\mu = 1.4$ ) in a lake in Turkey and (D) low species diversity ( $H = 0$ ) and high size diversity ( $\mu = 2.4$ ) in a lake in the Northern Baltic Drainages.

Ecoregion	slope	R <sup>2</sup>	<i>p</i>	N
Northern Baltic Drainages	0.097	0.028	0.03	179
Central & Western Europe	0.089	0.016	0.20	103
Cantabric Coast-Languedoc	0.363	0.241	<0.001	20
Eastern Iberia	0.342	0.146	0.15	16
Northern Anatolia	0.730	0.624	<0.001	19
Western Anatolia	0.846	0.417	0.06	9

**Table 9.** Slope (size diversity divided by species diversity), R<sup>2</sup>, significance (*p*) and number of lakes (N) for the linear relationship between size diversity and species diversity within each ecoregion.

LMM results (Table 10) showed that fish species diversity, lake maximum depth, maximum temperature, ecoregion and the interaction between species diversity and ecoregion were significant predictors of the variation of fish size diversity. The best model excluded longitude, and this model was not significantly different from the second best model including longitude (ANOVA,  $P > 0.05$ ). Hence, we excluded longitude from the final model (Table 10). Size diversity was influenced positively by both species diversity and lake depth and negatively by temperature. Altogether, the model explained 36.6% of the variation of fish size diversity at the continental scale. No significant relationships were found between size diversity and TP, longitude and percentage of non-natives. The slope of the relationship between size and species diversity was 0.12 ( $\pm 0.04$  SE) and size diversity was higher at low species diversity but quantitatively more similar at higher species diversity (Fig. 11).

The LMM analysis was performed on a subset of water bodies ( $n = 301$  lakes) excluding reservoirs and the significant predictors of the variation of fish size diversity were the same as for the whole dataset (Appendix, Table A3). The model explained 32.8% of the variation of fish size diversity. No significant spatial dependence was shown (Moran's  $I$ ,  $p > 0.05$ ) in the whole dataset or in the subset excluding reservoirs, which is in agreement with previous studies using the same (Trochine et al. submitted).



**Figure 11.** Relationship between species diversity and size diversity for all lakes (left) and for different ecoregions (right). In both panels stippled black lines indicate the 1:1 relationship for comparison purposes. In the right panel, the non-significant relationships are represented by discontinuous lines.

The significant interaction between species diversity and ecoregion indicated that the slope between fish size diversity and species diversity differed among the ecoregions (Table 9 and 10; Fig. 11). Notably, the relationship between size diversity and species diversity had the steepest slope in Northern and Western Anatolia, an intermediate slope in Iberia and Cantabric Coast-Languedoc, and shallowest slope in Central and Western Europe and the Northern Baltic Drainages (Table 9; Fig. 11).

The strongest relationships (highest  $R^2$ ) between size and species diversity were also found in Northern and Western Anatolia, followed by Cantabric Coast-Languedoc (Table 9; Fig. 11). In Central and Western Europe and Eastern Iberia, size diversity and species diversity followed a similar trend, but the slope was not significant. This may to some extent reflect that the number of water bodies available was low for Eastern Iberia.

	AIC	Estimate	Std. Error	d.f.	t-value	p-value
<b>Full model</b>	<b>161.87</b>					
(Intercept)		2.35	0.35	329	6.69	<0.001 ***
Species diversity		0.10	0.04	329	2.80	<0.01 **
Maximum depth (m)		0.12	0.04	329	2.26	0.02*
Maximum temperature (°C)		-0.52	0.32	329	-1.62	0.10
Total phosphorus (mg . m <sup>-3</sup> )		-0.04	0.05	329	-0.84	0.40
Longitude (°)		-0.01	0.003	329	-1.67	0.09
Non-natives species (%)		-0.11	0.09	329	-1.27	0.20
<b>Full model:</b>						
Size diversity ~ species diversity + maximum depth + maximum temperature + total phosphorus + longitude + non-native species + species diversity x ecoregion						
<b>Stepwise selection</b>						
<b>Model 1 = Full model except total phosphorus</b>	<b>160.59</b>					
<b>Model 2 = Model 1 except non-natives species</b>	<b>160.53</b>					
<b>Best model = Model 2 except longitude</b>	<b>160.47</b>					
(Intercept)		2.62	0.32	332	8.00	<0.001***
Species diversity		0.11	0.04	332	2.99	<0.001***
Maximum depth (m)		0.14	0.04	332	3.05	<0.01**
Maximum temperature (°C)		-0.89	0.26	332	-3.41	<0.001***
<b>Best model:</b>						
Size diversity ~ species diversity + maximum depth + maximum temperature + species diversity x ecoregion						

**Table 10.** Results for the Linear Mixed Model for fish size diversity. Note that the models include the interaction between species diversity and the factor ecoregion (species diversity x ecoregion)

Particularly in the Northern Baltic Drainages, several lakes held fish communities with low species diversity and high size diversity (29 lakes from this region had communities composed of  $\leq 3$  species and a size diversity  $\geq 2$ ). This was the case, for example, for lake fish communities composed of a single species, such as Arctic charr (*Salvelinus alpinus*) (Fig. 10, D) or brown trout (*Salmo trutta*), covering a wide size range and thus having high size diversity (average size diversity 2.2 and 1.8 for fish communities composed of only *Salvelinus alpinus* or *Salmo trutta*, respectively).

## Discussion

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The size diversity of lake fish communities at the continental scale was overall positively related to the species diversity. This means that addition of species results in an increase in size diversity in fish communities at the continental scale, a result corroborating those of previous studies using multiple functional traits (e.g. trophic breadth, trophic group, body depth, eye position, etc.; Micheli and Halpern 2005, Safi et al. 2011, Stuart Smith et al. 2013). The shallow slope ( $\ll 1$ ) of the size diversity – species diversity relationship at a continental scale suggests that an increase in species diversity leads to a greater overlap in size among species and hence likely in a greater overlap of their niches well. This may reflect the fact that many fish species grow over large body size ranges and change during ontogeny (Fig. 10, B and D). In fact, several lake fish communities showed low species diversity but high size diversity which suggests that fish communities with low species diversity may potentially be functionally diverse. However, results at the ecoregion level showed that the slope of size diversity and species diversity relationship increased towards warmer low-latitude ecoregions (Table 9, Fig. 11), though the regression was significant only for four out of six tested ecoregions. At the extreme of this gradient, lakes from Northern and Western Anatolia showed the steepest slopes and the strongest relationship between the two diversity measures. Therefore, towards low latitudes, size diversity increases almost at the same rate as species diversity. This suggests that fish species have less overlap in their individual body sizes in warmer lakes, maybe reflecting that biogeographical differences and ecological processes (e.g. higher interspecific competition) at local or evolutionary scales lead to increased niche specialisation towards low latitudes, as has been found in several previous studies (Reyjol et al. 2007, Tedesco et al. 2012, Schleuter et al. 2012).

Lake depth also positively contributed to the variation of size diversity, probably because deep lakes provide larger space and habitat heterogeneity to a wider range of fish sizes, in accordance with the Habitat Diversity Hypothesis which states that diversity is controlled by the availability of different habitat types (Williams 1943). This contribution was

also significant when reservoirs were excluded from the analysis. Total phosphorus concentration and longitude did not influence size diversity at the continental scale.

In accordance with the temperature–size rule (Atkinson 1994) and empirical observations (Emmrich et al. 2014, Arranz et al. 2016), the average body size of fish tended to decrease with increasing temperature ( $r^2=0.37$ ,  $p<0.001$ ; results not shown), which may explain the decrease in size diversity with temperature. This is also shown by the fact that for some widely distributed species, the smallest body sizes occurred in the warmest ecoregion (Appendix Table A4). Our results agree with observed variations in life-history traits with latitude and temperature, showing small body size, early maturation, continuous spawning and short-lived species in low latitude warm lakes (Blanck and Lamouroux 2007).

The higher slope of the size diversity to species diversity relationship towards lower latitude regions suggests that fish communities are composed of species which are less similar in size (Fig. 8, A; Fig. 10, A) and probably in their niches and functional roles, which is in accordance with the “niche packing” theories that predict that species should have narrower niches in species-rich communities (MacArthur 1972). A similarly strong coupling between species and functional diversity (measured from several traits) was observed in the highly diverse marine fish communities of coral reefs (Micheli and Halpern 2005, Guillemot et al. 2011) and the Galapagos Archipelago (Stuart-Smith et al. 2013) and was explained by the high partitioning of resources among species and the relatively low overlap in their niches.

The patterns found at the latitudinal extremes of our study may also reflect biogeographic differences. Due to the lack of widespread major glaciations (except for the mountain areas during the Quaternary period), fish communities in Northern and Western Anatolian lakes may have had longer time for speciation and colonization, which may have resulted in a less body size overlap. Furthermore, Anatolian lakes and some lakes from Cantabric Coast-Languedoc belong to basins that have historically been isolated for longer periods than most of the remaining lakes and thus display higher levels of endemism and beta diversity (Dias et al. 2014). Dispersal limitation, caused by the rise of the Anatolian Plateau whose average height is 1100 m with mountains forming barriers between the river

basins, may also have promoted speciation in Anatolian lakes along with a lack of major glaciation (Kosswig 1955, Boll et al. 2016). In contrast, in central and northern European ecoregions, the fish fauna is impoverished as a result of climatic changes caused by periods of glaciations (Dynesius and Jansson 2000, Griffiths 2006, Leveque et al. 2008). These climatic changes and the resulting cycles of range expansion and contractions have favoured the dominance of ecological generalist species, capable of exploiting a variety of ecological niches (Robinson and Schluter 2000, Griffiths 2006).

The greatest mismatch between species and size diversity was found in lakes in the northern ecoregions, particularly in some lakes in the Northern Baltic Drainages where fish communities were composed of a single or a few species, but had high size diversity (Fig. 8, C; Fig. 10, D). In these northern and previously glaciated lakes, the depauperate fish fauna shows high levels of intraspecific variability related to resource polymorphism (Griffiths 2006, Robinson and Schluter 2000), and these eco-morphs mimic the co-occurrence of several species. Fish species in these lakes have a relatively large size range and change their trophic niche as they grow (e.g. *Salvelinus alpinus*; Fig. 10, D; Griffiths 2006). As a result, overall these lakes have higher fish size diversity relative to species diversity than lakes further south in Europe. Consequently, the concept of species diversity is misleading in this context because it prevents detecting the potentially much higher size or functional diversity in these communities.

Human actions like introductions and fishing are not size-independent phenomena. Some fish species are introduced as juveniles or adults, particularly in reservoirs. This may disrupt the natural patterns of size diversity by causing changes in the relative abundance of size classes and because the introduced species may predate on the native ones. However, we did not find a significant influence of human intervention on the overall patterns of size diversity. For some ecoregions such as the Northern Baltic Drainages, the reason may be that reported introductions did not result in established populations as revealed by the low numbers of non-native individuals even many years later (Trochine et al. 2017). Although some of the data were compiled for monitoring rather than research purposes and were based on a single sampling over some years only, we believe that the magnitude of the data



set (one of the most comprehensive and large scale data set for lakes; Bruce et al. 2013) and the fact that sampling was highly standardised give strength to the results.

We are also aware that we only studied one fish trait. However, indices of functional diversity integrating multiple traits (e.g. morphological traits related to diet and habitat niche) very often do not include intraspecific variability but rather use average trait values for species (Cianciaruso et al. 2009). The size-based approach as applied here overcomes this issue because body size is easily measured for all individuals in a population and hence helps to detect the potential intraspecific functional trait variation, which may have large effects on the dynamics and structure of aquatic (Jansson et al. 2007, Persson and De Roos 2013, Norkko et al. 2013).

Given the fact that body size is a key trait for defining ecological niches and the strong relationship between organism body size and several ecological traits (e.g. Woodward et al. 2005), it might be possible to draw links between the variations in size diversity and changes in the structure and functioning of communities (Ye et al. 2013). For example, according to the Niche Diversification Hypothesis (Connell 1978), which suggests that systems of higher diversity could take greater advantage of the niche opportunities in an environment, a highly size-diverse community may be able to capture a greater proportion of resources relative to a less size-diverse one. Thus, size diversity may indicate diet niche partitioning, as has already been reported for zooplankton and invertebrate communities (Bruce et al. 2006, Rudolf 2012, Ye et al. 2013). In this sense, the high fish size diversity in species poor communities of northern lakes would indicate trophic niche partitioning among different sizes of the same species. We assumed, with many precedents from the literature, that for European fish, trophic function changes with body size (Romanuk et al. 2011). Therefore, since large fish are more predatory than small ones, increased size diversity may also reflect higher chances for between- and within-guild predation (Jennings et al. 2001).

In warmer low latitude lakes, the potentially lower overlap of fish sizes (Fig. 8, A; Fig. 10, A) may render these communities more vulnerable to extinctions compared with the communities in colder lakes (Fig. 8, B; Fig. 10, B) (except for lakes with only one species) in that the removal of one species could result in loss of a size-related trait. An exception would

be when the existing species is able to expand its niche and occupy the new available niche. It is also important to take into account that, in some ecosystems, size niche may be decoupled from functional niche, and niche specialisation may become manifest along morphological traits in similar-sized species (e.g. cichlids in ancient and highly productive African lakes, Steele and Lopez-Fernandez 2014). In this case, loss of a species may mean loss of a function even if species have the same body size.

In conclusion, at a continental scale, the size diversity of lake fish communities is similarly high for different levels of species diversity, suggesting that most fish species show relatively similar size distributions and thus may potentially cover similar trophic niches, instead of forming distinct size groups. However, the slope of the size-species diversity regression changed across the continent, suggesting different levels of size overlap, with increasing overlap toward higher latitude. Our results also suggest that size diversity is not a strong surrogate for species diversity in European lake fish. The main reason for this discrepancy is that there are fish communities composed of one or a few species but with high size diversity. In this case, species diversity is less informative of the functional role than the size diversity and, thus, the use of species diversity alone as a measure of biodiversity may compromise our ability to understand the fish community functioning. This study represents a step towards understanding the link between species diversity and size diversity and community functioning over large-scale gradients. More research is needed to measure individual size overlap in fish communities and to understand how the different levels of size overlap at the scale affect their vulnerability to environmental change and its implications for conservation ecology.



## CHAPTER 4

# Impact of lake morphometry and sticklebacks on the population structure of Arctic charr (*Salvelinus alpinus*) in West Greenland lakes

### Abstract

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We studied 17 lakes in West Greenland hosting either Arctic charr (*Salvelinus alpinus*, charr) only or both charr and three-spined sticklebacks (*Gasterosteus aculeatus*, sticklebacks). The collected data provided a unique opportunity to assess the influence of sticklebacks on the different developmental stages of charr (i.e., young and adults). We also analysed morphometric effects on two sympatric morphotypes of charr (i.e., dwarf and normal charr). The lakes were separated into three categories according to presence/absence of sticklebacks and their trophic habitat use: (1) lakes without sticklebacks, (2) lakes with sticklebacks caught in the limnetic zone and (3) lakes with sticklebacks predominantly caught in the littoral zone. Our results showed that the size and age of normal morph of charr varied significantly with lake morphometry. Furthermore, the results showed that the best fish condition of young charr was in systems without sticklebacks. The field evidence suggests that sticklebacks may trigger an ontogenetic habitat shift in young charr, forcing them to move to less favourable habitats. Since climate warming may indirectly impair lake

morphology and stickleback density and distribution, this may have consequences for Arctic charr population structure.

**Key words:** trophic interactions, fish condition, habitat shifts, Arctic region

**The fourth chapter is the original work of the manuscript:**

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## Resum

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Es van estudiar 17 llacs de la part oest de Groenlàndia: uns presentaven només truita alpina (*Salvelinus alpinus*, truita) mentre que uns altres hi havia truita alpina i espinós (*Gasterosteus aculeatus*, espinós). Les dades recol·lectades van permetre tenir una oportunitat única per avaluar la influència de l'espínós en els diferents estadis de desenvolupament de la truita (és a dir, truites joves i adultes). També vam analitzar l'efecte de la morfologia del llac en dos morfotips simpàtrics de truita (és a dir, truites nans i normals). Els llacs van ser separats segons tres categories segons la presència/absència del peix espinós i l'ús del seu hàbitat: (1) llacs sense espinós, (2) llacs amb espinós capturats en la zona limnètica i (3) llacs amb espinós majoritàriament capturats en la zona litoral. Els resultats van mostrar que la mida i l'edat de la morfologia normal de la truita variava significativament amb la morfologia del llac. A més a més, els resultats van mostrar que la millor condició física de les truites joves va ser en els sistemes on no hi havia espinós. Les dades indicaven que l'espínós pot causar un canvi d'hàbitat ontogenètic en les truites joves, forçant-los a moure's cap a hàbitats menys favorables. El fet que el canvi climàtic pot afectar indirectament la morfologia i la densitat i distribució de l'espínós, això fa que tingui conseqüències en l'estructura de poblacions de la truita alpina.

**Paraules clau:** interaccions tròfiques, condició del peix, canvi d'hàbitats, regions àrtiques

## Introduction

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Lakes in Arctic Greenland are relevant model systems for evaluating fish population structure because of their relatively low species diversity and simple food web structure (Jeppesen et al., 2001; Christoffersen et al., 2008). Few studies have, however, focused on the population structure of Arctic charr (*Salvelinus alpinus*, charr) in Greenland (Sparholt, 1985; Riget et al., 2000) in comparison with, for example, Norway (Jonsson and Hindar, 1982; Svenning and Borgstrøm, 1995; Knudsen et al., 2006) or Iceland (Jonsson et al. 1988; Sandlund et al., 1992).

Charr in Norwegian lakes occur in sympatry with other *Salmo* species (brown trout, *Salmo trutta*, and/or Atlantic salmon, *Salmo salar*) (L'Abée-Lund et al., 1992; Amundsen and Knudsen, 2009) and here charr may undergo habitat shifts to more profundal zones with poorer habitat conditions where they feed mainly on benthic crustaceans (Halvorsen et al., 1997). Charr can have up to four sympatric morphs, including a dwarf form (Klemetsen et al., 1997; Jonsson and Jonsson, 2001). When co-occurring with different morphotypes, the dwarf form usually inhabits deep zones where the risk of predation from large-sized morphs is reduced, but where food conditions are poorer than in other habitats (Hegge et al., 1989; Klemetsen et al., 1989). Such intraspecific habitat segregation may lead to more genetically isolated morphotypes (Klemetsen et al., 2002; Knudsen et al., 2006). Anadromous charr (i.e., individuals migrating from salt water to freshwater) may also appear when lakes are connected to the sea, and these may exhibit higher growth rates than landlocked specimens (Rikardsen et al., 2000).

In Greenland, the distribution of the small planktivorous fish three-spined sticklebacks (*Gasterosteus aculeatus*, sticklebacks) is limited to both the eastern and western coastlines up to about 70°N (Wootton 1985). When present, they inhabit in all kinds of lake habitats but they also migrate to sea through the streams (Lucas et al. 2001). Charr undergo ontogenetic diet shift. Adult charr prey on sticklebacks, when present, but cannibalism among charr also occurs (L'Abée-Lund et al., 1992; Halvorsen et al., 1997; Klemetsen et al., 2002). In contrast, young charr have a clear preference for invertebrate food items such as

small insect larvae or crustaceans and may thus have resource requirements overlapping with those of sticklebacks (Jørgensen and Klemetsen, 1995). Comparable observations are found in Faroese lakes, Brodersen et al. (2012) found that when sticklebacks were living in sympatry with brown trout, the salmonid was forced to shift their niche preferences towards the pelagic zone. In an enclosure experiment, O'Neill (1986) showed that sticklebacks compete with sockeye salmon by reducing the amount of food items. In fact, interspecific competition between sticklebacks and other young salmonids (e.g. sockeye salmon, *Oncorhynchus nerka*, and/or brown trout) has been reported (Wootton, 1985; Brodersen et al., 2012), whereas evidence of stickleback interactions with charr is scarce.

Besides trophic interactions, lake morphometry (depth, area and volume) affects charr distribution in a given lake as charr show high foraging plasticity and can occupy different niches (Adams and Huntingford, 2002; Klemetsen et al., 2003). In fact, the charr size population structure seems to be more dependent on lake size and volume (Riget et al., 2000; Murdoch and Power, 2013) than is the case for other salmonids (e.g. brown trout, Brodersen et al. 2012). In a compiled data set of charr populations in approx. one hundred lakes, Griffiths (1994) found that bimodal size distributions of charr increased in large and deep lakes. The distinct modes may be attributed to development of morphotypes occupying different ecological niches as lake morphometry is a key regulator of the size structure. Moreover, empirical studies related to other freshwater fishes have revealed an important influence of lake morphometry on population structure, with high proportions of larger individuals in larger and deeper lakes (Emmrich et al. 2011; Arranz et al. 2016).

In the present study, we investigated the charr populations of seventeen lakes in West Greenland hosting either a solitary population of charr or co-occurring charr and stickleback (Fig. 1). Therefore, the study lakes in West Greenland provide a unique opportunity to assess the role of sticklebacks in the different developmental stages of charr (i.e., adults and young). Accordingly, in our study, we explored charr age and size distributions, fish condition (total length-weight relationship) and potential habitat shifts based on the presence/absence of sticklebacks and their trophic habitat use. Furthermore,



as the study lakes covered a wide range of areas, depths and volumes (Table 1), we investigated the correlation between lake morphometry and the body size and age of two sympatric morphotypes of charr (i.e., dwarf and normal charr). We hypothesised that the interactions with sticklebacks, lake morphometry and possible intraspecific interactions with anadromous charr would contribute to shape the population structure of charr in Greenland lakes.

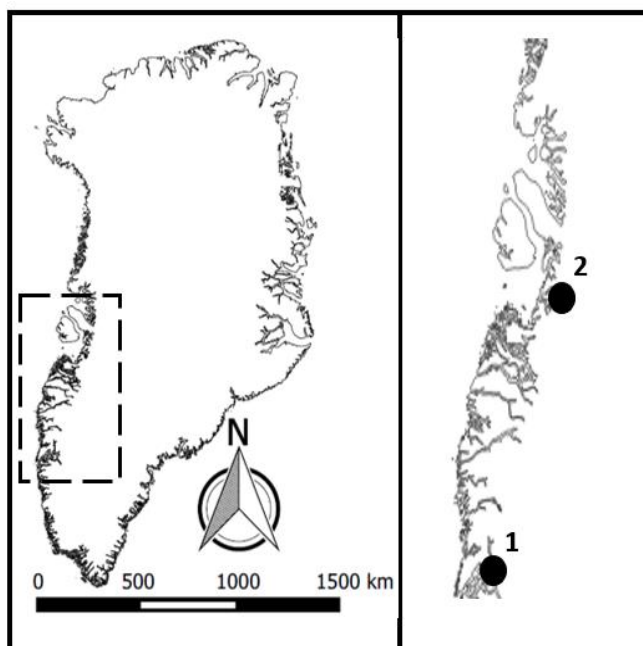
## Materials and methods

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### Study site

Charr populations were studied in West Greenland lakes in the Nuuk and the Ilulissat regions in late summer 2010-2012 (Fig. 12). In total, 17 unnamed lakes were sampled to obtain a set of physical and chemical variables (Table 11). All lakes were considered oligotrophic (chlorophyll a <2 µg/l) with similar values of water surface temperature, ranging between 9.4 and 14 °C (average ± SD 11.8 ± 1.2 °C). Water quality was measured by using a YSI probe multiparametric equipment. Lake area, depth and volume ranged from 0.4 to 380 ha (43.9 ± 98.7 ha), 1.7 to 152 m (32.5 ± 40.7 m) and 3.4x10<sup>2</sup> to 28.9x10<sup>5</sup> m<sup>3</sup> (24.2x10<sup>4</sup> ± 76.5x10<sup>4</sup> m<sup>3</sup>), respectively (Table 11). The lakes were either isolated or had an indirect hydrologic connection with the sea through streams (i.e., sea connection; Table 11). In the Ilulissat region (i.e., Northern part), charr was the only fish species present, whereas charr and sticklebacks mostly co-occurred in the Nuuk region (i.e., the Southern study area) (Fig. 12). Accordingly, we classified the lakes into three categories based on the presence/absence of sticklebacks and their trophic habitat use (Table 12): (1) lakes without sticklebacks (four lakes in the Ilulissat region and one lake in the Nuuk region), (2) lakes with sticklebacks caught at least in the limnetic zone (seven lakes in the Nuuk region) and (3) lakes with sticklebacks only caught in the littoral zone (five lakes in the Nuuk region) (Table 12). In the latter category, the possibility of occurrence of sticklebacks in the limnetic zone cannot be fully excluded due

to the limited effort. However, this does not change the fact that their abundance in the limnetic parts of the given lakes was low and thus of minor importance than in lakes where sticklebacks were caught throughout the lake.



**Figure 12.** Map of Greenland showing the (1) Nuuk and (2) Ilulissat sampling areas. Sticklebacks were only caught in the Nuuk region (1), while charr was the only fish species present in the Ilulissat region (2).

## Sampling

Fish were caught by multimesh gillnets as they provide a good representation of the size distribution of fish populations (Emmrich et al. 2011; Arranz et al. 2016). Each gillnet was 42 m wide and 1.5 m deep and divided into 14 sections with a mesh size ranging from 6 to 75 mm (knot to knot following a geometric series: 6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60 and 75 mm). The smaller sticklebacks (< 50 mm) were underrepresented in the catches since they were only caught by coincidence in the smallest mesh size (6.25 mm).

The gillnets were set in three different zones: (1) the near-shore zone (hereafter termed the 'littoral zone'), (2) the profundal zone in shallow lakes and (3) in deep lakes also in the pelagic zone at half the depth (Table 13). For further analysis, we pooled the fish catch from the profundal and pelagic zones (hereafter termed the 'limnetic zone'). Nets were placed in the afternoon and left overnight to maximize the catchability of the fish (Prchalová et al. 2009). Depending on the size of the lake, the number of nets varied from one to eight throughout the zones (i.e., ca. two gillnets in each zone), but the deep and large Lake 16 from Ilulissat was sampled only in the littoral zone (Table 1). In contrast, Lake 4 from the Nuuk region and Lake 17 from the Ilulissat region were only sampled in the littoral zone due to their small size and shallow water (Table 13). As three out of five lakes without sticklebacks were only sampled in the littoral part (Lakes 4, 16 and 17; Table 13), we analysed the dataset both with and without these three lakes.

Water temperature was measured at the lake surface in each lake. We estimated lake volume as half the lake area times maximum depth (Riget et al., 2000) (Table 11). A composite sample was collected with a 5 L Heart valve sampler at 0.5-3 m intervals (depending on the depth of the lakes) from the surface to 1 m above the bottom in the deepest part of the lakes and mixed. For chlorophyll a, a duplicate 1 litre sample was sub-sampled from the pooled sample, filtered on a GF/C filter (Whatman) and frozen until analysis. Chlorophyll a was determined spectrophotometrically after ethanol extraction (Jespersen and Christoffersen, 1987).

Region	Sampling year	Lake	Latitude	Longitude	Sea connection	Lake category	No. of morphs	Altitude (m)	Area (ha)	Max. depth (m)	Volume (m <sup>3</sup> )*	Water temp. (°C)	Chla (µg/l)	Cond. (mS/m)
Nuuk	2010	Lake 1	64°27'20.53"	51°35'08.40"	Yes	2	2	12	4.7	12.6	2.96x10 <sup>3</sup>	-	1.1	4.6
		Lake 2	64°27'52.1"	51°34'44.2"	No	2	1	44	3.2	3.6	5.76x10 <sup>2</sup>	-	1.6	4.0
		Lake 3	64°27'54.6"	51°34'15.8"	No	1	1	40	0.4	1.7	3.40x10	11	0.8	4.3
		Lake 4	64°27'49.5"	51°33'51.1"	No	2	2	27	2.2	8.9	97.90x10	13.5	1.4	5.4
		Lake 5	64°28'49.68"	51°32'56.1"	Yes	2	2	70	25	13.4	16.75x10 <sup>3</sup>	12	1.1	4.3
		Lake 6	64°29'15.74"	51°33'03.20"	No	2	2	82	3.7	8.5	15.72x10 <sup>2</sup>	12.5	1	4.0
		Lake 7	64°29'10.56"	51°32'50.88"	No	3	2	86	2.6	11.5	14.95x10 <sup>2</sup>	14	0.5	3.5
		Lake 8	64°29'35.58"	51°32'59.4"	No	3	2	96	9	37	16.65x10 <sup>3</sup>	13	0.6	3.9
		Lake 9	64°29'48.0"	51°34'42.6"	No	3	2	98	75	85	31.87x10 <sup>4</sup>	12	0.5	6.5
		Lake 10	64°29'40.70"	51°35'07.20"	No	2	2	97	380	152	28.88x10 <sup>5</sup>	12	0.6	5.1
Nuuk	2011	Lake 11	71°81'81.0"	53°09'18.0"	Yes	2	2	177	15.6	9.5	74.10x10 <sup>2</sup>	11.97	0.80	2.17
		Lake 12	71°83'49.4"	53°16'46.0"	Yes	3	2	190	17.3	12.0	10.38x10 <sup>3</sup>	-	0.66	-
		Lake 13	71°82'88.5"	54°18'78.0"	Yes	3	1	120	10	10.5	52.50x10 <sup>2</sup>	11.23	0.96	2.45
Ilulissat	2012	Lake 14	76°61'25.4"	54°32'49.0"	No	1	2	290	39.8	29.4	58.51x10 <sup>3</sup>	11.47	0.4	9.6
		Lake 15	76°61'37.0"	54°36'09.0"	No	1	2	289	14	20.4	14.28x10 <sup>3</sup>	11.44	0.5	17.8
		Lake 16	76°62'11.6"	54°41'05.0"	No	1	2	280	24.3	49.7	60.38x10 <sup>3</sup>	10.35	1.2	3.4
		Lake 17	76°61'49.9"	54°25'14.0"	No	1	2	298	1.3	5.3	34.45x10	9.42	0.9	10.1

**Table 11.** Location and morphological and environmental data on the studied Greenland lakes. Blank spaces indicate that no data was available. Lakes were classified into three categories: (1) lakes without sticklebacks, (2) lakes with sticklebacks caught in the limnetic zone and (3) lakes with sticklebacks predominantly caught in the littoral zone. In column N<sup>o</sup> of morphs: 1 refers to lakes with only normal morphs and 2 refers to lakes with normal and dwarf morphs. \*Lake volume was estimated as half the lake area times the maximum depth.

Lake category	No. lakes	Total normal	Total dwarfs	Area (ha)	Max. depth (m)	Volume (m <sup>3</sup> )	Surface water temp. (°C)	Chla (µg/l)	Conductivity (mS/m)
No stick. (1)	5	176	65	15.9 ± 16.6	21.3 ± 19.4	26.7x10 <sup>3</sup> ± 30.4x10 <sup>3</sup>	10.7 ± 0.9	0.8 ± 0.3	9.0 ± 5.7
Stick. lim. lit (2)	7	264	38	62.1 ± 140.4	29.8 ± 53.0	41.7x10 <sup>4</sup> ± 10.9x10 <sup>5</sup>	12.4 ± 6.1	1.1 ± 0.3	4.2 ± 1.0
Stick. lit. (3)	5	98	38	22.9 ± 29.6	31 ± 32.1	70.5x10 <sup>3</sup> ± 13.9x10 <sup>4</sup>	12.6 ± 5.7	0.6 ± 0.2	4.1 ± 2.3

**Table 12** The three lake categories based on stickleback presence/absence and their trophic habitat use: (1) lakes without sticklebacks, (2) lakes with sticklebacks caught in the limnetic zone and (3) lakes with sticklebacks predominantly caught in the littoral zone. Total numbers of normal and dwarf individuals in each lake category are shown as is the mean ± SD for each morphometric and environmental variable.

## Fish information

Gillnet catch per unit effort (hereafter CPUE) was expressed as the number of fish caught per net (Table 13). CPUEs were calculated for each habitat and species (Table 13). Charr were measured (fork length) to the nearest millimeter and weighed to the nearest gram. We further accounted for the total charr weight-length relationship as an estimation of fish condition. One may argue that the development of the gametes overestimated the fish condition, but sampling was undertaken in the most commonly spawning season of charr, i.e. in autumn (Klemetsen et al. 2003). Age determination of charr was performed by counting the annual opaque zones of the otoliths. The otoliths were immersed in glycerol and polished to enhance the annular ring structure. To ensure consistent readings, blind tests and multiple readings were performed for each pair of otoliths. Roughly 8% of the charr caught could not be age determined because of poor otolith condition.

Charr individuals were sexed and classified as mature if they carried distinct eggs and ripening sperm. Following Riget et al. (2000), we distinguished between normal or dwarf charr morphs based on body size and sexual maturity. Accordingly, individuals reaching sexual maturity at small body sizes (80-150 mm) were categorised as dwarf morphs, and charr with larger body sizes (>150 mm) or no sexual maturity at lower sizes were categorised as normal morphs. Normal charr were further separated into individuals < 200 mm (young charr) and individuals ≥ 200 mm (adult charr). This length has been used in several studies as

the threshold of smoltifying charr (e.g. Kristoffersen et al. 1994; Halvorsen and Jørgensen 1996). Due to the lack of microchemical analysis, information regarding whether or not the lakes were connected to the sea (Table 11) could give an overall idea of the potential occurrence of anadromous charr.

Region	Sampling year	Lake number	Dwarfs (%)	Net type (n° nets) *	CPUE charr			CPUE stickleback	
					Littoral	Limnetic**	Total	Littoral	Limnetic**
Nuuk	2010	Lake 1	19.35	li,pr,pe (4)	10.5 (21)	5 (10)	15.5 (31)	8.5 (17)	8 (16)
		Lake 2	0	li,pr (4)	7 (14)	4.5 (9)	11.5 (23)	10 (20)	31.5 (63)
		Lake 3	0	li (1)	1 (1)	-	1 (1)	-	-
		Lake 4	8.89	li,pr (4)	16.5 (33)	6 (12)	24.5 (45)	12.5 (25)	28 (56)
		Lake 5	25.49	li,pr (4)	15.5 (31)	11 (22)	26.5 (53)	0.5 (1)	2.5 (5)
		Lake 6	20	li,pr (2)	4.5 (9)	3 (6)	7.5 (15)	1 (1)	1 (1)
		Lake 7	88	li,pr (2)	11 (11)	14 (14)	25 (25)	5 (5)	-
		Lake 8	63.64	li,pr (4)	3 (6)	2.5 (5)	5.5 (11)	6 (12)	-
		Lake 9	14.29	li,pr (4)	18.5 (37)	6 (12)	23.5 (49)	13.5 (27)	-
		Lake 10	33.33	li,pr,pe (8)	8 (24)	5 (15)	13 (39)	-	<1 (1)
	2011	Lake 11	2.63	li,pr,pe (6)	13 (26)	35 (70)	48 (96)	10 (20)	160.5 (321)
		Lake 12	5.41	li,pr,pe (6)	20 (20)	8.5 (17)	12.3 (37)	6 (12)	-
		Lake 13	0	li,pr (3)	1 (1)	6.5 (13)	7.5 (14)	4 (4)	-
Ilulissat	2012	Lake 14	32.61	li,pr,pe (6)	13.5 (27)	9.5 (19)	23 (46)	-	-
		Lake 15	11.38	li,pr,pe (6)	29.5 (59)	16 (64)	45.5 (123)	-	-

**Table 13** CPUEs of charr and sticklebacks in each lake and their habitat use. In brackets are given the total number of captures of charr and sticklebacks. \*Net type refers to littoral (lit) and profundal shallow lakes (pr) or pelagic deep lakes (pe). \*\*Pelagic nets and profundal nets in shallow lakes were pooled (limnetic zone).

## Statistical analyses

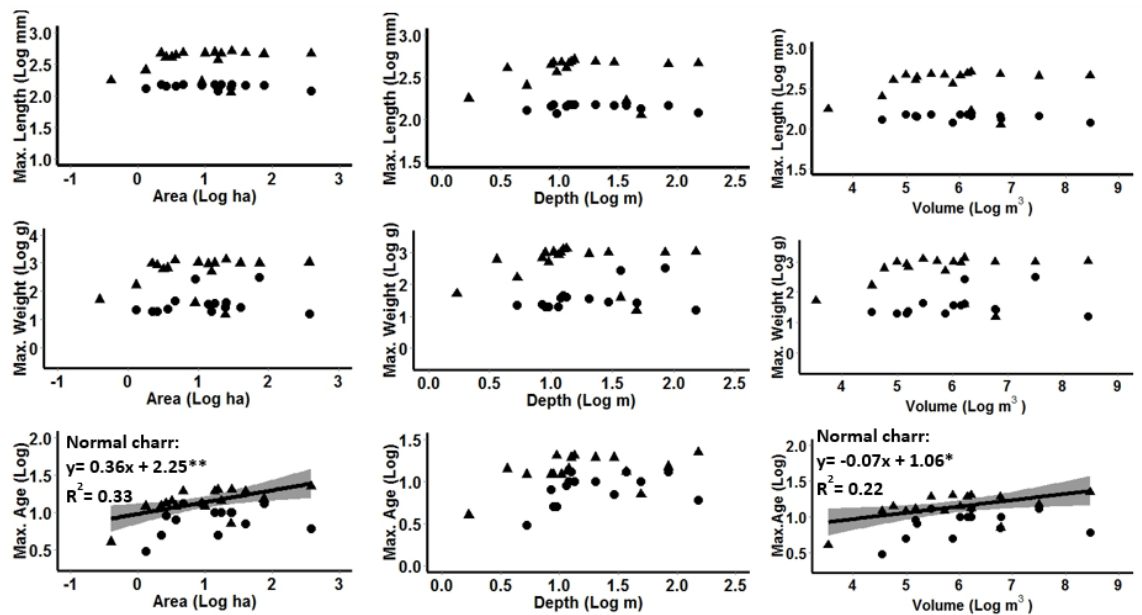
We performed linear regressions to detect whether lake morphometry (depth, area and volume) was related to maximum fish body size (length and weight) and otolith age of the two charr morph populations (i.e., dwarf and normal morphs). We graphically illustrated the length frequency distribution of normal charr relative to the lake categories (mean  $\pm$  SD) for each study lake. Linear Mixed Models (LMM) were used to test the influence of fish condition

(total weight-length relationships) between the different developmental stages of charr (i.e., adults and young) and the presence/absence of sticklebacks and their habitat use. We used fish weight as a dependent variable. Fish length was treated as covariate because it is less vulnerable to environmental changes and physiological conditions than weight (García-Berthou and Moreno-Amich, 1993). The predicted mean weights from the total weight-length relationship were interpreted as fish condition. We included sea connection and lake category as fixed effects as well as their interaction because the potential presence of anadromous charr may influence the fish condition (sea-run charr may exhibit higher growth rates than lake-dwelling charr; Rikardsen et al. 2000). The total number of charr individuals in the study lakes was treated as a random factor to eliminate fish density as an influence on the total weight-length relationship. We excluded all dwarf individuals (i.e., charr reaching sexual maturity at small body size, 80-150 mm) to ensure comparable weight means among lake categories. To test for possible effects of environmental variables (area, depth, volume, conductivity, altitude, temperature and chlorophyll a) on the fish condition of char in all lakes, we separately used multiple analysis of variance (MANCOVA, Wilks Lambda) (Brodersen et al 2012). The proportional abundances (% CPUE) of normal young and adult charr in each zone (littoral and limnetic) were calculated to explore potential habitat shifts among lakes categories. To test the habitat shift of normal young and adult charr, we used Generalised Linear Models (GLMs) with binomial error distribution and logit link function for the proportional abundance (% CPUEs) at each developmental stage. GLMs provide a more appropriate error structure for data such as counts and proportions. Lake 3, Lake 16 and Lake 17 were not included in the GLMs analysis since only the littoral zone was sampled. Finally, we graphically illustrated the age frequency distribution of normal charr relative to lake category and trophic habitat use (mean  $\pm$  SD). All variables were previously assessed for normality using the Shapiro-Wilk test and when deviations from normality occurred ( $P$ -value $<0.005$ ), they were  $\log_{10}$ -transformed. All statistical analyses were performed with SPSS 21.00 (SPSS 21.0, Armonk, NY, U.S.A.).

## Results

A total of 679 charr and 609 sticklebacks were caught across all West Greenland lakes. Maximum charr length-weights recorded were 505 mm and 1355 g in Lake 5 (2010) and maximum age, 22 years, was recorded in Lake 10 (2010). The number of normal charr morphs registered was 538, and individuals with dwarf morphs constituted approximately a fourth of the total charr catch.

The linear regressions demonstrated a significant morphometric variation in normal charr morph, but not for dwarf morph (Fig. 13). Only maximum age of normal charr was positively related to lake area and volume (Fig. 13), indicating that longer-living normal charr inhabited larger lakes. The results were similar when excluding the three lakes only sampled in the littoral part (Appendix, Fig. A7).

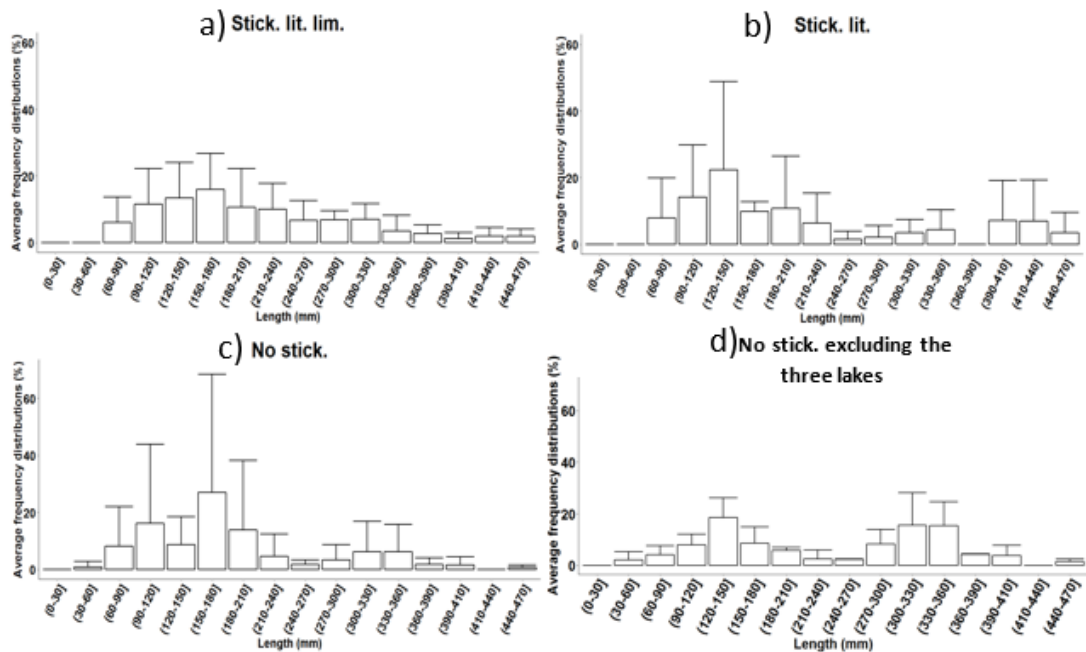


**Figure 13.** The relationships between the  $\log_{10}$  morphometric variables area, depth and volume (ha, m and  $\text{m}^3$  in X axes) and maximum  $\log_{10}$  charr weight (g), length (mm) and age (Y axes). When significant, the corresponding regression line and formula are given for each charr morph. Circles denote dwarf charr and triangles normal charr populations. The grey shadows indicate the 95% confidence limits. Significant differences are indicated by asterisks: \*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; \*,  $P < 0.05$ . Note the different Y axes scales.



The length frequency distributions of normal charr showed that in lakes where sticklebacks were confined to the littoral zone and in lakes without sticklebacks, both categories had bimodal size distributions when adding an upper mode to the higher size classes (Figs. 14b, 14c and 14d). In contrast, in lakes where sticklebacks occupied both the limnetic and littoral zones, charr length distribution was clearly unimodal, peaking in size classes 150-180 mm (Fig. 14a). However, for some size classes we found some intra-variability (i.e., large error bars) within the size classes for all lake categories (Fig. 14).

The fish condition of charr in the lakes was not related to any of the environmental variables, (MANCOVA; Wilks Lambda;  $p > 0.05$  for all). Instead, LMM analysis showed significant differences in fish condition (i.e., total weight-length relationships) but only for young charr (Table 14; Fig. 15; Appendix, table A5).

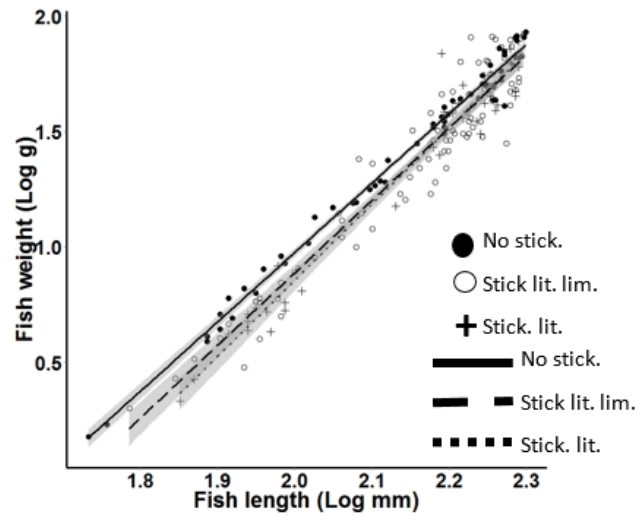


**Figure 14.** Average  $\pm$  SD frequency distribution of charr according to the presence and absence of sticklebacks and the trophic habitat use of sticklebacks. X axes represent charr size classes in mm and Y axes the frequency distribution (%) of the mean  $\pm$  SD of all lakes in each category. Sticklebacks at least in the limnetic zone (a, stick. lit. lim.), sticklebacks predominantly caught in the littoral zone (b, Stick. lit.), lakes without sticklebacks (c, No stick.) and lakes without sticklebacks but excluding the three lakes only sampled in the littoral zone (d, No stick. excluding the three lakes).

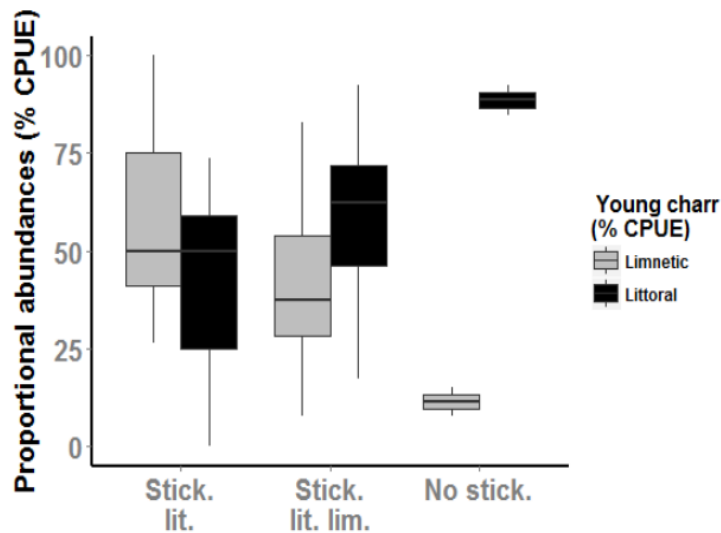
The condition of young charr was significantly better in lakes without sticklebacks (fish condition,  $FC=1.436 \pm 0.02$ ) than in lakes with sticklebacks inhabiting the littoral zone ( $FC=1.385 \pm 0.03$ ) and in lakes with sticklebacks distributed in both the littoral and limnetic zone ( $FC= 1.380 \pm 0.02$ ) (Fig. 15). Moreover, the fish condition of young charr was significantly better in lakes connected to the sea than in lakes not connected to the sea:  $FC=1.446 \pm 0.03$  and  $FC=1.356 \pm 0.02$ , respectively (Table 14). Yet, the interaction term (i.e., sea connection\*lake category) did not show any significant effect for either young or adult normal charr (Table 14). However, when excluding the lakes with only littoral sampling LMM revealed that the condition of young charr was only significantly better in lakes connected to the sea than in lakes not connected to the sea ( $FC= 1.442 \pm 0.03$  and  $FC= 1.34 \pm 0.02$ , respectively) (Appendix, Table A5).

<b>Developmental stage</b>		<b>d.f.</b>	<b>F</b>	<b>P value</b>
<b>Adult charr</b>	Fish length	1	3387.68	<0.0005
	Lake category	2	1.46	0.29
	Sea connection	1	1.53	0.25
	Sea connection*Lake category	1	0.001	0.98
<b>Young charr</b>	Fish length	1	4599.94	<0.0005
	Lake category	2	6.50	0.01
	Sea connection	1	14.12	<0.005
	Sea connection*Lake category	1	0.62	0.45

**Table 14** LMM results for the different developmental stages (i.e., young and adult normal charr). The predicted mean weights from the total weight-length relationships were interpreted as fish condition.



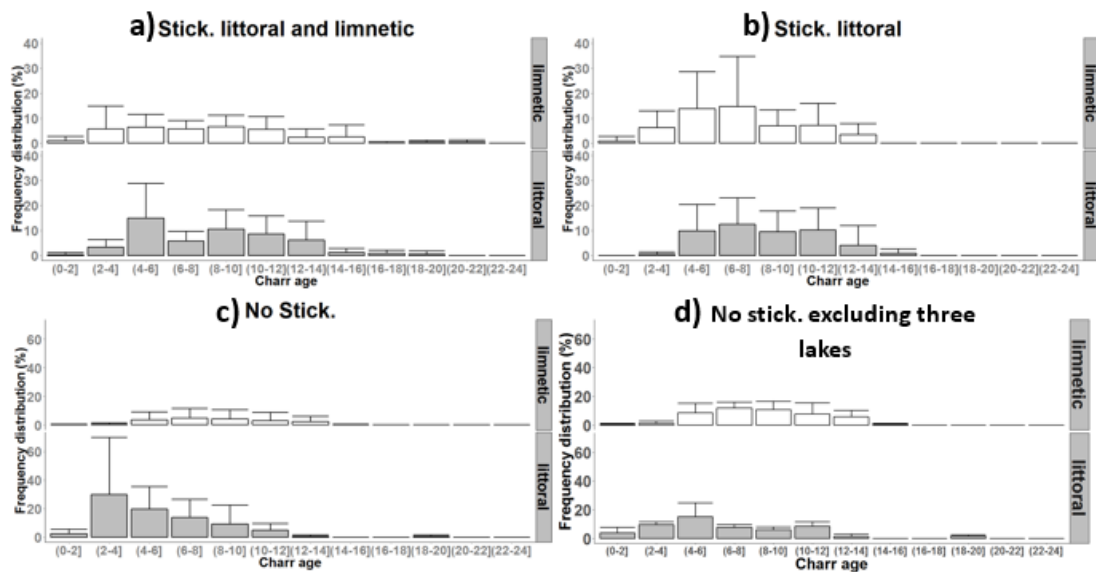
**Figure 15.** Total length-weight relationships of young normal charr relative to lake category. The different lines represent categories: (—) lakes without sticklebacks, (---) lakes with high abundance of sticklebacks throughout the lake and (····) lakes with sticklebacks in the littoral zone. No Stick.= No sticklebacks; Stick. lit. lim.= Sticklebacks at least in the limnetic zone; Stick. lit.= Sticklebacks in the littoral.



**Figure 16.** Proportional abundances (%) of young charr in each lake category. The number of lakes in each category was 7 (Stick. lit.), 5 (Stick. lit. lim.) and 2 (No stick.). Lake 3, Lake 16 and Lake 17 were not included since only the littoral zone was sampled. Stick. lit.= Sticklebacks littoral; Stick. lit. lim.= Sticklebacks at least in the limnetic zone; No Stick.= No sticklebacks.

GLM detected significant differences in the proportional abundances (% CPUE) of habitat shifts in young charr relative to lake category ( $P$ -value  $< 0.0005$ ), suggesting that young charr display habitat shifts towards the limnetic zone when sticklebacks are present (Fig. 16).

Finally, the age frequency distributions of charr showed that, when sticklebacks occurred in both the littoral and the limnetic zone, charr ages were equally distributed in the lakes (Fig. 17a). In lakes where sticklebacks predominantly inhabited the littoral zone (Fig. 17b), the older age classes 8-10 and 10-12 were found both in the limnetic and littoral zones, whereas the younger age classes (0-2 and 2-4) were mostly confined to the limnetic zone. In contrast, in lakes without sticklebacks, the youngest age classes, 2-4 and 4-6, were mainly confined to the littoral zone (Fig. 17c and 17d).



**Figure 17.** Age frequency distributions of charr populations relative to lake category and trophic habitat use. X axis represents charr age class and Y axis the mean  $\pm$  SD frequency (%) of the total number of lakes in each age class and category. Sticklebacks at least in the limnetic zone (a, Stick. lit. lim.), sticklebacks predominantly in the littoral zone (b, Stick. lit.), lakes without sticklebacks (c, No stick.) and lakes without sticklebacks but excluding the three lakes only sampled in the littoral zone (d, No stick. excluding three lakes). White bins represent the limnetic zone and grey bins all Arctic charr caught in the littoral zone.

## Discussion

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The field evidence supported the key role played by lake morphology in the population structure of charr. The maximum age from normal charr populations increases with volume and area whereas no morphometric variation was found in the dwarf charr populations. Larger and longer-living normal charr inhabited the larger lakes. The modality of the length frequency distribution differed among the lakes, but a clear unimodal size distribution was found in lakes with high stickleback densities. Moreover, the presence of sticklebacks negatively correlated with the condition of young charr, likely due to habitat shifts from the littoral to the less favourable limnetic zones. Furthermore, the results confirmed that the condition of young charr was better in lakes connected to the sea than in landlocked lakes.

In agreement with the results of our study, Riget et al. (2000), exploring other Greenland lakes, found that differences in charr lengths were related to lake depth and volume gradients. The pattern fits well with the general theory that larger lakes hold more available niches (MacArthur and Wilson, 1963), thereby providing more microhabitats acting as a refuge and reducing the predation risk (Holt, 1984; Byström et al., 2003), as well as favouring higher longevity. For the dwarf morph, however, we found no morphometric variation. In contrast, others studies have found that the main habitat niche of the chiefly landlocked dwarf charr is deep-benthic areas (e.g. Jonsson and Hindar 1982; Klemetsen et al. 2002; Klemetsen et al. 2003).

We found bimodality in charr populations in some of the lakes. In our study lakes, absence of sticklebacks, or when sticklebacks were few and predominately confined to the littoral zone, bimodal size distribution was generated. However, the underlying mechanisms causing bimodality in charr populations are subject to debate (Griffiths, 1994; Guiguer, 2002). By simulating growth trajectories in charr populations from gillnet samples, Finstad et al. (2003) concluded that the bimodal size distributions of charr were an artifact of biased sampling. Likewise, Borgstrøm et al. (2015) mainly attributed the bimodality to sampling bias by the use of gillnets but found that also stagnation in old charr within a restricted length

range played a role. In another biotic effect instead of sampling bias, Hammar (2000) stated that cannibalism contributes to bimodality by providing adult charr with an extra food resource (i.e., young charr), raising their survival. Our results also indicate that in lakes with absence or few sticklebacks, adult charr undergo a cannibalistic behavior to feed on their conspecifics resulting in bimodal size distributions.

The total weight-length relationship, as an indicator of fish condition, is a useful index for estimating the well-being of fish subjected to anthropogenic, environmental and morphometric stressors (García-Berthou and Moreno-Amich, 1993; Benejam et al., 2008, 2010). However, so far, the viability of using total charr weight to evaluate the effect of interspecific competitions, in our case with sticklebacks, has not been documented. Our results showed that the high variability of the characteristics of the lakes systems did not modify the condition of charr. Instead, the condition of young individuals of charr was independently affected by connection with the sea, presence/absence and trophic habitat use of sticklebacks. The lack of significant effect of the trophic habitat use of sticklebacks in the LMM when excluding the three lakes where sampling only was conducted in the littoral zone (Appendix, table A5) likely reflect low number of lakes as the pattern with and without these lakes apparently were rather similar (Figs. 13-17; Appendix, Fig. A7). It is well known that salmonid migration to the sea is considered a beneficial life history strategy for multifunctional traits such as growth rates and reproduction investment (Rikardsen et al., 2000). In our study, sticklebacks apparently negatively influenced the condition of young but not of adult charr. We focus on the group of young charr because of too few data for old charr (Fig. 14). In the absence of sticklebacks, young charr were mostly confined to the littoral zone, which is the most favourable zone for foraging and with the lowest risk of predation (Nieminen, 2012; Eloranta, 2013). In contrast, when sticklebacks were predominantly present in the littoral zone, strong interspecific competition occurred, and young charr exhibited a habitat shift by migrating to the (less favourable) limnetic zone. This pattern was reflected in a low condition factor of young charr and relatively high proportions of small and young age classes in the limnetic zone (Figs 16 and 17b). Competition is generally considered a key factor in structuring the interactions between fish species (Simberloff, 1982) and in

agreement with this competition from sticklebacks was observed to modify the habitat preferences of young charr, as has been reported in similar studies (Wootton, 1985; Brodersen et al., 2012). In fact, the competition for food resources in the littoral zone is presumed to be the main cause of habitat shifts.

Studies on charr population structure in Greenland are scarce (but see Riget et al. 2000) in comparison to other charr populations in the sub-Arctic regions (e.g. Norway or Iceland). We encourage further research including more lakes to study the effect on sticklebacks on the variations in charr size distributions since charr may be impacted by global warming in various ways. The ongoing increase in global temperatures may indirectly impair lake morphology, and consequently charr population structure by increasing evaporation and drainage due to longer ice-free periods in the region (Vincent et al., 2013). The persistence of connections to the sea through Arctic streams varies between years and some anadromous fish are unable to reach the upstream due to low water flow in the summer (Klemetsen et al. 2002). More recently, however, the increase of the snowmelt by the retreat of glaciers may facilitate the connection between lakes and the sea due to higher runoff in Arctic streams. This may allow a decrease of the mortality in anadromous populations when migrating upstream (Svenning and Gullestad 2002). Consequently, some fish-free lakes will have better possibilities to be colonized by charr (Bennike et al. 2008) and in particular in the northern Greenland lakes (in our study the Ilulissat region) also by sticklebacks. Anadromous migrations by sticklebacks will have more opportunities to extend their range distribution towards the north (e.g. the Ilulissat region) where charr today is the only fish species present. Potential stickleback colonization in regions where charr currently is the only fish species present may increase the interspecific competition for habitat, with sticklebacks being competitively superior to young salmonids. The species spread to new areas in Arctic lakes may increase trophic interactions by triggering habitats shifts, which in turn may have strong cascading effects on the whole food web structure (Carpenter et al. 2008; ACIA, 2005). The development of size- and age-based analysis approaches may be valuable in the prediction of responses to climate warming by key fish species in the Arctic, such as charr.

## **GENERAL DISCUSSION**

The present thesis revealed consistent patterns on the lake fish size structure across different levels of biological organizations (fish community in Chapters 2 and 3; and fish populations in Chapters 1 and 4) and spatial scales (at regional scale in Chapters 2 and 4; and at continental scale in Chapters 1 and 3). The results suggested that, overall, trophic interactions can be considered as one of the most important key predictors of the variation in the fish size structure in lakes, whereas environmental and anthropogenic factors also contributed but to a less extent. The taxonomic composition of fish communities also contributed to the variation of the size structure of fish communities at a continental scale. The fish size structure coupled with other functional approaches and taxonomic indices also provided valuable insights for the understanding of ecological patterns related to niche overlap among species and body sizes, and interspecific interactions for habitat and food resource in aquatic food webs.

### **Trophic interactions and the variations of the size structure**

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This PhD thesis shows the importance of considering the size structure to understand the trophic interactions in fish across different biological organizations and spatial scales. This agrees with the general theory that the trophic interactions are to a large extent dictated by the functional traits, such as body size (Cohen et al. 1993; Rossberg et al. 2010).

According to the results, the variations in the trophic interactions modified the distributions of abundances and sizes of lake fish. Previous studies that attempted to find predictable key regulators of the fish size structure in lakes typically did not assess the effects of trophic interactions (Emmrich et al. 2011; Bruce et al. 2013; Chu et al. 2015). Emmrich et al. (2014), for instance, studied the geographical patterns in the size structure of European lake fish assemblages along large abiotic and biotic gradients. They found a consistent



temperature effect on the fish size structure but they did not estimate the effect of competitive or predator-prey interactions. Our results provided evidence that, at least at population scale, there is a strong density-dependent effect on the size structure of fish populations that should be taken into account to properly understand the variation on the size structure. Overall, we found a decline in several size-structured metrics (i.e. low mean sizes, low sizes diversities and steeper slopes of linear size spectra) of the most common European fish species at high fish densities.

In contrast to competitive interactions, predation seems to have a weaker influence on fish size structure in European lakes (Mehner et al. 2016). These authors searched for the relationship between the slope of the linear size spectra of predator and prey fish along a large-scale continental scale. Surprisingly, they did not find evidence of predation effects of piscivores fish on the slope of linear size spectra of prey fish. In contrast, they found a positive relationship between the density of fish prey and predators. This is probably due to the gape-size limitation of predators in some European lakes, where prey reach sizes large enough that are not accessible by their predators (Mehner et al. 2016). The low abundance of large fish predators, as shown by Mehner et al (2016), may explain the patterns observed in this thesis: (1) an over-representation in intermediate size classes of fish community that reflected deviations from the linear size spectra in some German lakes; and (2) a strong influence of density-dependent effects on the three size metrics of fish populations which lead to a relative increase in smaller size class fish (Fig. 18, box A).

The results in Chapter 2 expanded the classical view of the slope of the size spectra, which has been evaluated in Chapter 1 and in other previous studies (Sheldon et al. 1972; Sprules and Munawar 1986; Gaedke 1992). Predator-prey interactions have been postulated as major forces of the theory of the size structure (Kerr and Dickie 2001) but so far they had not been evaluated empirically through the deviations from the linear size spectra. Here we showed that the residual variation of each size class could provide a picture of the predator-prey interactions in fish communities. In marine systems, it is commonly assumed that when large predators are removed from the system, the slope of the size spectra continues to be linear but more steeply than the ones in the original systems (Jennings et al. 2007; Blanchard

et al. 2009). However, our results showed that the decline of abundances of large predators may also cause an accumulation of similar-sized fishes from intermediate size classes and the appearance of non-linear size structures.

Beyond the classical trophic interactions models (e.g. Lotka-Volterra, Lotka 1925; Volterra 1926) and based on the results in Chapters 1 and 2, the size-based metrics may provide new insights to test empirical predictions about the strength and impact for both density-dependent and predation effects. That is, the slope of linear size spectra, mean size and size diversity responded uniformly to the variations of the fish density, whereas the deviations from the linear size spectra were related the shifts of the size and abundance of predators and prey. Our findings support the idea that the fish size structure could give mechanistic understandings of the efficiencies of predators in controlling prey density (i.e. gape limitation; Brose et al. 2006; Arim et al. 2010); the decrease of fish growth rates in situations with high fish density (i.e. stunting; Ylikarjula et al. 2000); or the ability of prey to reach a size refuge from predation (Wysujack and Mehner 2005; Mehner et al. 2016).

## **The size structure coupled with other taxonomic and functional approaches**

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Studies on biogeography have typically focused on taxonomic approaches but recently there is a growing interest to use functional traits to predict the consequences of species loss or invasions at biogeographical scale (Olden et al. 2006; Safi et al. 2011; Brose et al. 2016). We combined the Shannon diversity index and the size diversity to evaluate the size overlap (as a proxy to niche overlap) of lake fish community across both continental and regional scales. The size diversity was estimated as a measure of functional diversity, which is similar to other works that used several other functional traits (e.g. Safi et al. 2011; Stuart Smith et al. 2013). However, it is important to note that size diversity does not capture the entire functional diversity in communities. This is the case of other works that used a suite of traits related to different ecological function (e.g. in fish, locomotion and food acquisition) to assess

functional diversity in fish communities (Goldstein and Meador 2004). In our results, the slope of the relationship between species diversity and size diversity was used to understand the vulnerability of fish communities to loss of functional traits such as the body size.

The results showed that species diversity and size diversity were positively related but the slope of the relationship was shallow at a continental scale (slope  $\ll 1$ ) (Fig. 18, box D). This shallowness of the slopes suggested that the increase of fish species lead to an overlap of size among species. When we calculated the slope at a regional scale, we found different responses of size overlap across the continent (i.e. increasing size overlap toward higher latitude). Our results suggest that size diversity is not a strong surrogate for species diversity in European lake fish communities. A low correspondence between species and size diversity occurs particularly in some fish communities (i.e. colder high-latitude regions) where there is a low number of fish species but they have large size ranges and may display ontogenetic diet and habitat shifts (e.g. Arctic charr, Knudsen et al. 2006; or perch, Byström et al. 2012) (Fig. 18, box D). In this sense, the fish community is functionally diverse despite having only one or few species. This implies that the measure of taxonomic diversity in fish communities in lakes in cold regions is less informative to evaluate the functioning of the system than size diversity. Several other studies have also confirmed that functional diversity, rather than species diversity *per se*, may be key to understand the functioning and structure of freshwater fish communities (Mason et al. 2008; Olden et al. 2010; Comte et al. 2016). For instance, Comte et al. 2016 found that the niche partitioning was the primary force underlying the functional diversity of several freshwater fish communities around the world. All in all, the use of functional metrics may be more useful than the traditional approaches for assessing ecosystem functioning on both large and regional scales in freshwater systems (Mouillot et al. 2006). In this sense, the understanding of functional diversity could give insights about their vulnerability to environmental change and their implications for conservation ecology.

Worth noting, not only the taxonomic approaches but also the combination of several functional aspects of organisms can complement the analysis of the fish size structure. In the present thesis, we used the relationship between the length (mm) and

weight (g) of the fish individuals of Arctic charr in Greenland lakes to calculate the fish condition. The index integrates two aspects (length and weight) at the individual level and it is widely used to estimate the well-being of fish populations to anthropogenic, environmental and morphometric stressors (García-Berthou and Moreno-Amich, 1993; Benejam et al. 2008; 2010). It is known that the use of multiple aspects of organisms can help explaining more accurately the complex trophic interactions (Eklöf et al. 2013; Brose et al. 2016) but so far fish condition had not been used to evaluate trophic interactions such as interspecific competitions.

We found that fish condition could explain the negative effects of sticklebacks presence on young Arctic charr (Fig. 18, box A). In contrast, the condition of the adult charr was not affected by the sticklebacks as a food resource (Fig. 18, box A). Sticklebacks may probably cause habitats shifts from the littoral to the less favorable limnetic zones that were reflected by the low fish condition of young charr in Greenland. This result is similar to other studies that found a dominance of the habitat preference of sticklebacks to other young salmonids (e.g. sockeye salmon and/or brown trout, Wootton 1985; Brodersen et al. 2012). Furthermore, the young charr exhibited a better fish condition in lakes connected to the sea than lakes with landlocked populations. Salmonid migration to the sea is considered a beneficial life history strategy for functional traits such as growth rates and reproduction investment (Gulseth and Nilssen 2001; Rikardsen et al. 2008; Sæther et al. 2015). Since fish condition may be strongly related to the metabolic requirements (García-Berthou and Moreno-Amic 1993), the anadromous charr may have better conditions than non-anadromous charr. All in all, fish condition, here evaluated as a case study of arctic charr populations in Greenland, can significantly contribute to the understanding of the trophic interactions.

## The variation of the fish size structure across environmental gradients

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Environmental variables affected the fish size structure at both population and community level and across regional and continental scales. The response of the fish size structure community to climate-related variables is in accordance with the well supported Bergmann' rule and temperature-size rule (Bergmann 1847; Atkinson 1994). Since environmental temperature tends to decline with latitude, the mean size of fish community were generally smaller at southern latitudes than fish communities located in northern regions (Fig. 18, box B). The same consistent response was found by previously other freshwater studies at fish community level (Emmrich et al. 2014; Chu et al. 2015).

Nevertheless, temperature showed inconsistency and different direction of response among the three size metrics representing the size structure of the six European fish populations (Fig. 18, box B). The mean body sizes of perch, roach and ruffe were influenced by temperature whereas temperature only affected the slope of linear size spectra of zander and the size diversity of roach and white bream. This suggest that the mean body size showed in part a stronger response to the variations of temperature than the slope of linear size spectra and the size diversity. This is in agreement with other population studies that showed small body size of several European freshwater fish species in low latitude warm lakes (Blanck and Lamouroux 2007; Ohlberger et al. 2013). The size diversity of roach and white bream increased in warm lakes whereas the other two size metrics decreased. This may be due to the fact that some cyprinids (e.g. roach) at low latitudes can reach a size large enough to avoid being feed for some piscivores (Wysujack and Mehner 2002; Schlumberger and Élie 2008). This increase of size may be reflected to a higher number of size classes and thus higher size diversity.

Even if temperature is perhaps the most important variable influencing life-history traits (Angilletta et al. 2004), we found a relatively weak role of temperature as a predictor of the size structure of the six European fish species compared to the strong density

dependent effect. Furthermore, we tested if the three size metrics induced some trends predicted by the life-history theory (Reznick et al. 1990; Mims and Olden 2012). Nevertheless, our results suggested that the three size metrics are not sufficiently consistent to classify the fish populations according to particular life-history strategies (Winemiller and Rose 1992). This contrast with other studies that used several other traits (e.g. maturation, fecundity) to identify life-history patterns among European freshwater fish species along latitudinal gradients (Vila-Gispert and Moreno-Amich 2002; Heibo et al. 2005). In these studies, however, they did not assess density dependent effects in the life-history models, which probably would mask the environmental temperature effects on the life-history patterns.

Primary productivity, as a measure of the energy available at the bottom of the trophic web, is strongly related to the TP concentration in lakes. According to our results, TP did not influence size diversity of fish community at the continental scale when species diversity was also taken into account. This contrast with other European studies that found an overall decrease of fish mean size at highly productive lakes (Jeppesen et al. 2000; Brucet et al. 2013). However, Brucet et al. (2013) found that productivity effect on the fish size was stronger at smaller geographical and morphometric scales than at larger (i.e. continental) scales. Similar to our results, the weak response of the size diversity of fish community to productivity may be because trophic status depends on the wide variation of depth and temperature in the studied lakes. In general, shallow and warm lakes are typically more nutrient rich than deep and cool lakes (Nöges, 2009). Thus, productivity effects may be covered by temperature and lake depth variations.

We also found that the three size metrics representing the fish size structure responded differently among species along productivity gradient. This is probably due to the different feeding strategies of fish species in lakes (Persson et al. 1991; Bergman 1991). In general, cyprinids tend to adapt successfully in turbid waters whereas percids need good light conditions to feed (Lammens et al. 1992; Olin et al. 2002). This is similar to our results at population level: the mean body size and the size diversity of perch decreased with increasing lake productivity but the mean body size and the slope of linear size spectra of the cyprinids white and common bream and ruffe increase in highly productive lakes (Fig. 18, box B).

Among lake morphometric variables, lake depth had the strongest effect of the variation in fish size structure. In this sense, it contributed more to the variation of size structure of zander, perch, roach and ruffe than the lake area (Fig. 18, box B). Furthermore, lake depth was also positively related to the size diversity of lake fish community at the continental scale when the effect of species diversity was controlled for (Fig. 18, box B). Lake depth is strongly correlated to habitat complexity (Hakanson 2005) that probably provides more space and habitat heterogeneity to a wider range of fish size. Thus, an increase of lake depth may represent an increase in the number of size classes (i.e. high size diversity) that would occupy different habitats. This result agrees with the Habitat Diversity Hypothesis which stated that diversity is controlled by the availability of different habitat types (Williams 1943).

The other size metrics (i.e. the slope of linear size spectra and the mean body size) showed a weak and inconsistent response to lake morphometric variables compared to the size diversity. Only few exceptions showed significant results between the slope of linear size spectra and the mean body size and the morphometric variables. This was the case of zander that showed greater proportions of large individuals (i.e. shallow slopes of linear size spectra) in deeper lakes. This contrast with other European studies that have revealed consistent effects of lake morphometry on fish assemblage composition (Dieckman et al. 2005; Mehner et al. 2007). They found that in deepest and largest lakes, fish species composition were dominated by vendace, pike and perch whereas in shallow and small lakes were mainly dominated by the cyprinid roach.

In the case study of Arctic charr populations in Greenland, the size and age structure of Arctic charr responded positively to increasing lake area and volume. That is, larger and longer-living normal charr inhabited the larger lakes (Fig. 18, box B). Since Arctic charr may exhibit high morphological variation (Snorrason et al. 1994; Klemetsen et al. 2003), it was plausible to assume a key role of lake morphometry in Arctic charr populations in Greenland lakes. Furthermore, it is known that the different morphotypes of Arctic charr populations can occupy different lake habitats (Klemetsen et al. 2002; Knudsen et al 2006). For instance, dwarf form usually inhabits benthic parts of the lakes where the risk of predation of other

large-sized morphs is reduced (Hegge et al. 1989). This high niche specialization can result in completely isolated morphotypes and thus may be independent of the total fish density.

Low or high efficiencies in catching size-specific classes could shift the shape of the slope of linear size spectra or other size-based approaches. The efficiency of catchability of fish species may depend upon several factors such as the lake trophic state or lake depth that vary among lakes (Deceliere-Vergès et al. 2009). That is, for instance, the multimesh gillnets may have high fish density in productive and shallow lakes. In our analysis, we considered the interaction term between the productivity and lake depth and the relative estimates of fish populations as predictors of the size structure of fish populations. The results showed that only the size diversity of perch was slightly higher (more size classes) in more productive and deeper lakes than in less productive and shallower lakes.

## **Anthropogenic pressures in relation to the variation of the fish size structure**

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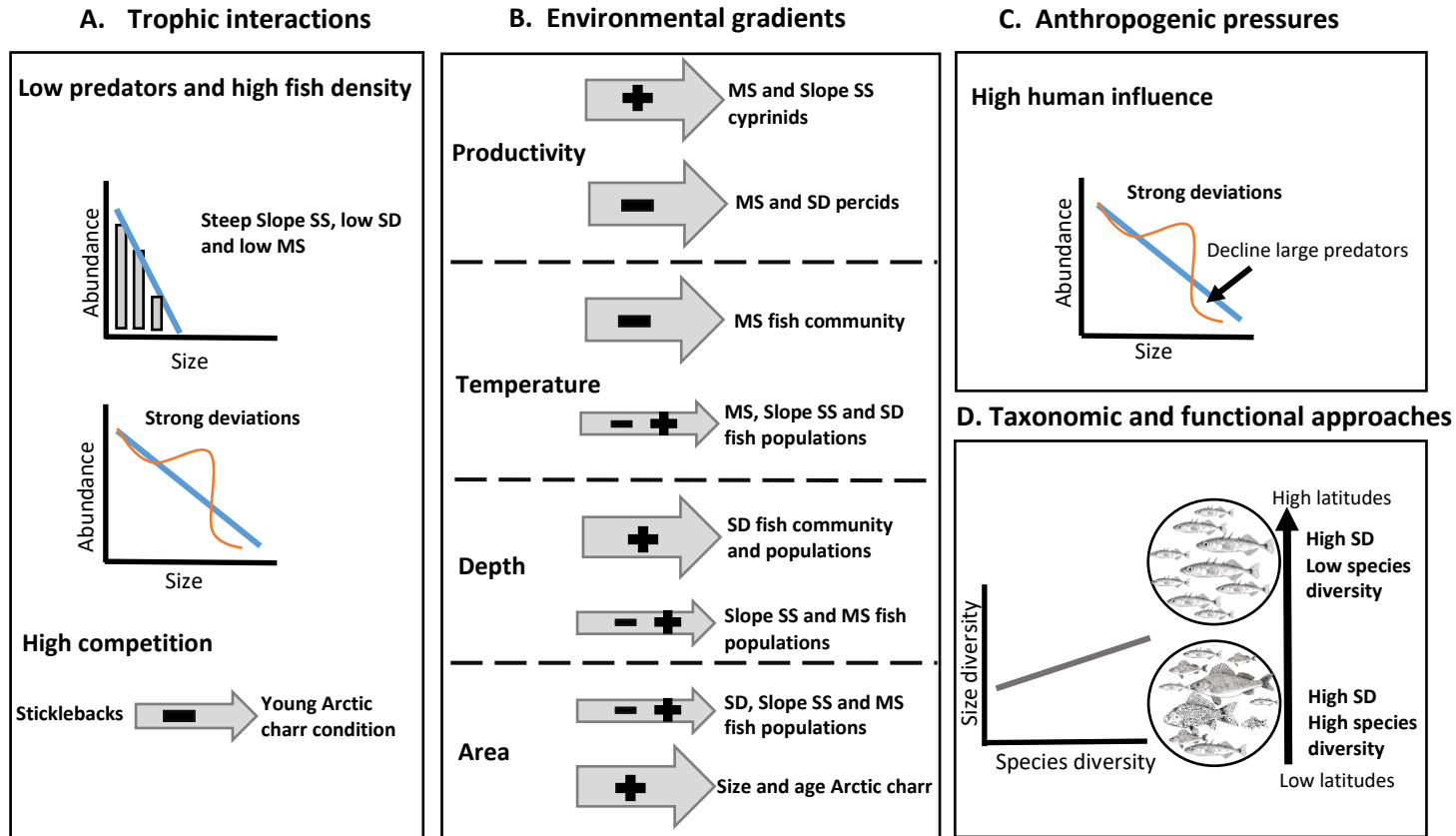
Anthropogenic pressures such as fisheries activity, human modifications, exotic species introductions and lake eutrophication are known to have severe impacts on fish species diversity and their trophic interactions (Jennings et al. 1999; Schindler and Scheuerell 2002; Dieckmann et. al. 2005). The present thesis considered several of them that could affect the size structure of freshwater fish communities at both regional and continental scales. In Chapter 2, for instance, we considered (1) human activities, as measures of fisheries activity and shoreline modifications, and (2) total phosphorus, as a rough surrogate of lake eutrophication and hence an anthropogenic influence on the lakes. We found that both anthropogenic pressures affected indirectly the deviations from the linear size spectra of fish communities in German lakes. That is, in situations with high human activities and total phosphorus, the abundance of large predators was low and this would probably explained the overaccumulation of abundance of small fishes in intermediate size classes and the appearance of deviations from the linear size spectra (Fig. 18, box C). A similar response was



observed in fishery models that predicted the overfishing effects on the marine fish size structure (Benoit and Rochet 2004; Law et al. 2009; Jacobsen et al. 2014). They found deviations from the linear size spectra in situations with intensive fishing which was related to deviations from the linear size spectra.

The exotic species introductions and the fact of inhabiting artificial lakes or reservoirs may also alter the natural patterns of fish communities (Carol et al. 2006; Villegger et al. 2012). We considered both effects when analyzing the size diversity of fish community at a continental scale. However, neither the percentage of non-native species in each lake nor the number of reservoirs from the data showed a response to the overall patterns of size diversity of community. This may be due to by the fact that reported introductions at least in some cases were not established populations as indicated by the low numbers of fish individuals (Trochine et al. 2017). Probably we did not find an effect of the reservoirs on the fish size structure because the fish populations in these systems are already established since several years ago and thus reservoirs are acting similarly to natural systems.

# FISH SIZE STRUCTURE



**Figure 18.** Schematic representation with the main results found in the present thesis. Boxes A, B and C represent the group of predictors that they have been analyzed through the four chapters. Box D represent the combination of the fish size structure and other taxonomic and functional approaches. Positive and negative signs represent the direction of the response. The size of the grey arrows was proportional to the strength of the response. SD: size diversity; Slope SS: slope of linear size spectra; and MS: mean size. Blue line is the Slope SS.

## Synthesis

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The present thesis analyzed the fish size structure as a set of several size-based metrics with the further integration of other functional and taxonomic approaches. Since nearly all characteristics at the level of individual organism scale with body size (Brown et al. 2004; Woodward et al. 2005), studying the size structure may help to understand the structure and dynamics of aquatic communities in a more comprehensive and integrative way. The results provided the empirical evidence that the size structure of lake fish responds to trophic interactions, the taxonomic composition of the communities, as well as to environmental variables and anthropogenic pressures.

The analysis of fish size structure in lakes and freshwater systems is in general scarce with some recent attempts to predict the variations of the size structure along environmental and anthropogenic gradients (DeLeeuw et al., 2003; Emmrich et al., 2011; Chu et al. 2015). In fact, most of the research in the fish size structure is done in marine systems and tends to quantify the impacts of fishing exploitation on the size structure (Gislason and Rice 1998; Bianchi et al. 2000; Jennings et al. 2001). This contrast with the demands made by the monitoring programmes from the Water Framework Directive (2000/60/CE) that require a good ecological status of freshwater systems based upon physicochemical, hydro-morphological, chemical and biological criteria such as fish size structure.

The present thesis may become a basis to use the size structure as an ecological indicator of lake systems, even across large geographical ranges and multiple scales of organization. Indicators describing the structure and dynamics of lake fish such as the slopes of the size spectra and size diversity could be promising tools because of their theoretical foundation and because they respond to environmental variation. The size-metrics variables could overcome the problems of (1) the lack of consensus to develop indices based on fish species assemblages (Belpaire et al. 2000; Baker et al. 2005) and (2) having sufficient metrics to detect anthropogenic impacts (Moyle and Marchetti 1999; Benejam et al. 2008). Nevertheless, the effects of trophic interactions and natural variation have to be taken into

account before developing biological indices. Other size metrics such as the slope of the size spectra or the intercept have also been found to respond to the anthropogenic pressure in freshwater systems (Holmgren and Appelberg 2002; Emmrich et al. 2014; Benejam et al. 2016). As such, the size-based approaches may help to develop complementary metrics at the population or community level and formulate reliable indices such as a Fish Index of Biotic Integrity. This would help to detect anthropogenic effects on the fish community or population structure, particularly in lakes where the number of species is low and taxonomic measures are not enough strong to detect variations in fish community or populations.

The novel approach based on the deviations from the linear size spectra could be also a useful sensitive metric in the management of fisheries and the understanding of trophic interactions. However, more work is needed to evaluate the anthropogenic effects on the deviations from the linear size spectra in lake fish. Furthermore, the taxonomic-based approaches and other functional traits can be integrated in the study of the fish size structure. Thereby, they may be able to increase the accuracy of the understanding of ecological and biogeographic processes as well as predict the consequences of climate warming by using key fish species in the Arctic, such as charr. Nevertheless, further investigation of the influence of environmental and anthropogenic factors on the slope of the size-species diversity relationship and fish condition is needed in order to complement the theory of the size structure.

## GENERAL CONCLUSIONS

The conclusions of the present thesis are as follow:

- ❖ Density-dependent effects are key drivers of the variation of the size structure of the most abundant fish species in European lakes. In lakes with high fish density, there was an overall decrease of the mean size, size diversity and the slope of the linear size spectra of the most representatives European fish populations. This is probably due to changes in the growth rates in situations of high competition (e.g. stunting).
- ❖ Variations of the size and abundance of fish predators and prey are reflected in the deviations from the linear size spectra in fish community in German lakes. The results suggest that the deviations appear when small fish predators are large in number and cannot regulate the abundances of their preys.
- ❖ Size-based and taxonomic approaches are complementary measures to understand the ecological and biogeographical processes in large-scale studies. Our results suggest that species diversity is not a strong surrogate of size diversity in European lake fish communities, particularly in cold regions where only few species occur but encompassing large size ranges and thus having high size diversity. This implies that the measure of taxonomic diversity in fish communities in lakes in cool regions is less informative of the trophic niches than size diversity (or functional diversity).
- ❖ The combination of several functional aspects of organisms can complement the information provided by the size structure. The results suggested that the fish condition could explain the interspecific interactions between sticklebacks and young Arctic charr. Furthermore, fish condition of young charr was better in lakes connected to the sea than lakes with landlocked populations.

- ❖ The response to temperature was different between the size structure of fish at community and population level. It is generally assumed that the mean size of fish community is smaller at southern latitudes than those located in northern regions. In contrast, not all fish species analyzed in this Thesis showed a smaller body size with increasing temperature. Furthermore, a different direction of response between the three size metrics representing the size structure of the six European fish populations was observed. Mean body size showed a stronger response to the variations of temperature than the slope of linear size spectra and the size diversity.
  
- ❖ The weak role of temperature as a predictor of the size structure of the six European fish species may be due to the strong density dependent effect. The results suggest that the size metrics cannot be sufficiently consistent to classify the fish populations according to particular life-history strategies.
  
- ❖ Lake TP did not significantly explain the variability in size diversity of lake fish community. Productivity effects on the size diversity of lake fish community may be covered by the wide temperature and lake depth variations. In contrast, lake TP affected the three size metrics representing the size structure of fish populations but the direction of the response was different among species along productivity gradient. This is probably due to the different feeding strategies of fish species in lakes.
  
- ❖ Lake depth was the most important morphometric variable explaining the variation in fish size structure at community and population level. The case study in Chapter 4 supported the key role of lake morphology on the population structure of Arctic charr.
  
- ❖ Human activity and total phosphorus affected indirectly the deviations from the linear size spectra of fish communities in German lakes. Lakes with strong deviations

were those with high levels of TP and high human activity. However, size diversity did not respond to the percentage of non-native species in each lake and it was similar in lakes and reservoirs.

- ❖ Linking size structure with trophic dynamics may become an area of increasing interest because body size is an easily measured trait. Size diversity may help to detect the potential intraspecific functional trait variation, which may have large effects on the dynamics and structure of aquatic communities. However, some size based approaches such as the analysis of deviated patterns in the fish size spectrum are still quite unexplored and there are still questions and issues to be resolved (e.g., to what extent fish populations can cause the appearance of the deviated patterns of linear size spectrum?; how the environmental conditions can affect the deviated patterns at different time and spatial scales?).
  
- ❖ The taxonomic-based approaches and other functional traits can be integrated in the study of the fish size structure and may help detecting anthropogenic effects on the fish community or population structure as well as forecasting their vulnerability to environmental change and its implications for conservation ecology.

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# Appendix

## List of tables and figures

Common name	Max.T (°C)	TP ( $\mu\text{g}\cdot\text{L}^{-1}$ )	Area (ha)	Depth (m)
Perch	11.1–23.1 (16.15)	1–330 (25.72)	0.02–113 (3.11)	1–190 (20.53)
Roach	12.1–24.6 (16.5)	1–561 (33.27)	0.06–6478 (35.71)	1–135 (18.88)
Ruffe	13.3–21.2 (17.03)	2–330 (44.39)	0.06–113 (5.57)	1.2–190 (23.12)
Common bream	14.2–21.9 (17.59)	3–330 (64.09)	0.24–113 (5.24)	1.2–100 (14.48)
White bream	14.6–23.1 (17.83)	2–561 (76.17)	0.36–927 (31.53)	1.2–69.5 (16.01)
Zander	14.5–24.6 (18.76)	6–330 (82.8)	0.44–6478 (199.02)	1.2–100 (16.99)

**Table A1.** Minimum, maximum and arithmetic mean (in brackets) of all environmental predictors for each species. **Note.** Max.T. is maximum temperature (°C) and TP is total phosphorus ( $\mu\text{g L}^{-1}$ ).

Environmental information	
Max. Temp. (°C)	16.6-18.6 (17.44)
Total phosphorus ( $\text{mg}\cdot\text{m}^{-3}$ )	10-402 (69.13)
pH	7.5-9.3 (8.4)
Morphometric information	
Depth (m)	1.2- 72.3 (18.57)
Area ( $\text{km}^2$ )	0.5-113 (4.70)
Elevation (m)	1-98 (46.62)

**Table A2.** Minimum, maximum, and arithmetic mean (in parentheses) of the environmental and morphometric information for the German lakes

	AIC	Estimate	Std. Error	<i>d.f.</i>	t-value	<i>p</i> -value
<b>Full model</b>	<b>127.14</b>					
(Intercept)		2.53	0.37	286	6.84	<0.001 ***
Species diversity		0.10	0.04	286	2.80	<0.01**
Maximum depth (m)		0.11	0.06	286	1.90	0.06
Maximum temperature (°C)		-0.67	0.35	286	-1.93	0.05
Total phosphorus (mg . m <sup>-3</sup> )		-0.04	0.05	286	-0.75	0.45
Longitude (°)		-0.01	0.01	286	-0.85	0.38
Non-natives species (%)		0.10	0.14	286	-0.81	0.49
<b>Full model:</b>						
Size diversity ~ species diversity + maximum depth + maximum temperature + total phosphorus + longitude + non-native species + species diversity x ecoregion						
<b>Stepwise selection</b>						
<b>Model 1 = Full model except total phosphorus</b>	<b>125.64</b>					
<b>Model 2 = Model 1 except non-natives species</b>	<b>124.22</b>					
<b>Best model = Model 2 except longitude</b>	<b>123.45</b>					
(Intercept)		2.74	0.34	289	8.12	<0.001***
Species diversity		0.11	0.04	289	3.07	<0.01**
Maximum depth (m)		0.13	0.05	289	2.64	<0.01**
Maximum temperature (°C)		-0.99	0.27	289	-3.69	<0.001***
<b>Best model:</b>						
Size diversity ~ species diversity + maximum depth + maximum temperature + species diversity x ecoregion						

**Table A3.** Results for the best and most parsimonious Linear Mixed Model for fish size diversity excluding the reservoirs (n=301). Species diversity x Ecoregion shows the interaction between species diversity and ecoregion.

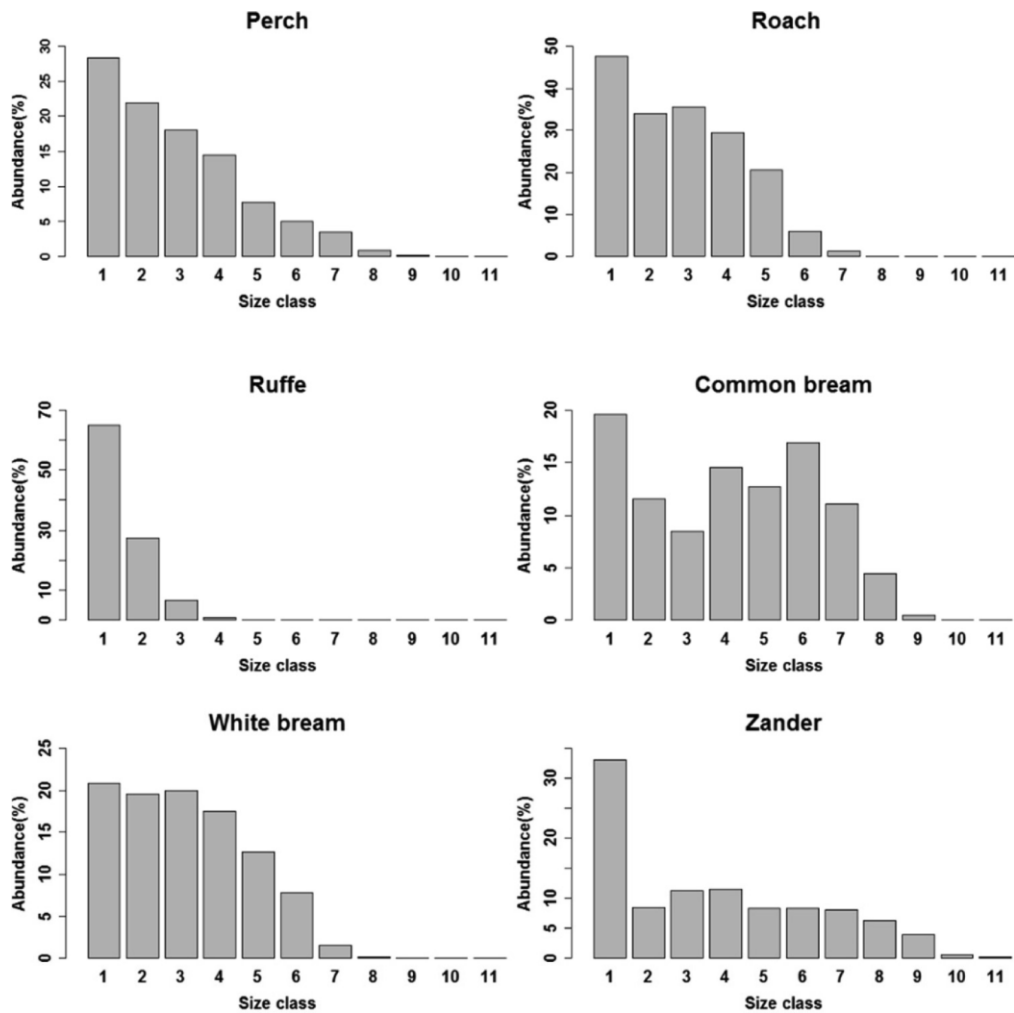


	Mean size (cm)		Max. of mean size (cm)	
	Turkey	Rest of lakes	Turkey	Rest of lakes
<i>Abramis brama</i>	9.5	18.6	10.1	32.3
<i>Alburnus alburnus</i>	9.7	12.1	11.9	15.5
<i>Perca fluviatilis</i>	9.3	12.8	17.5	21.6
<i>Sander lucioperca</i>	16.5	19.9	17.1	40.7
<i>Scardinius erythrophthalmus</i>	9.1	17.7	23.0	29.7

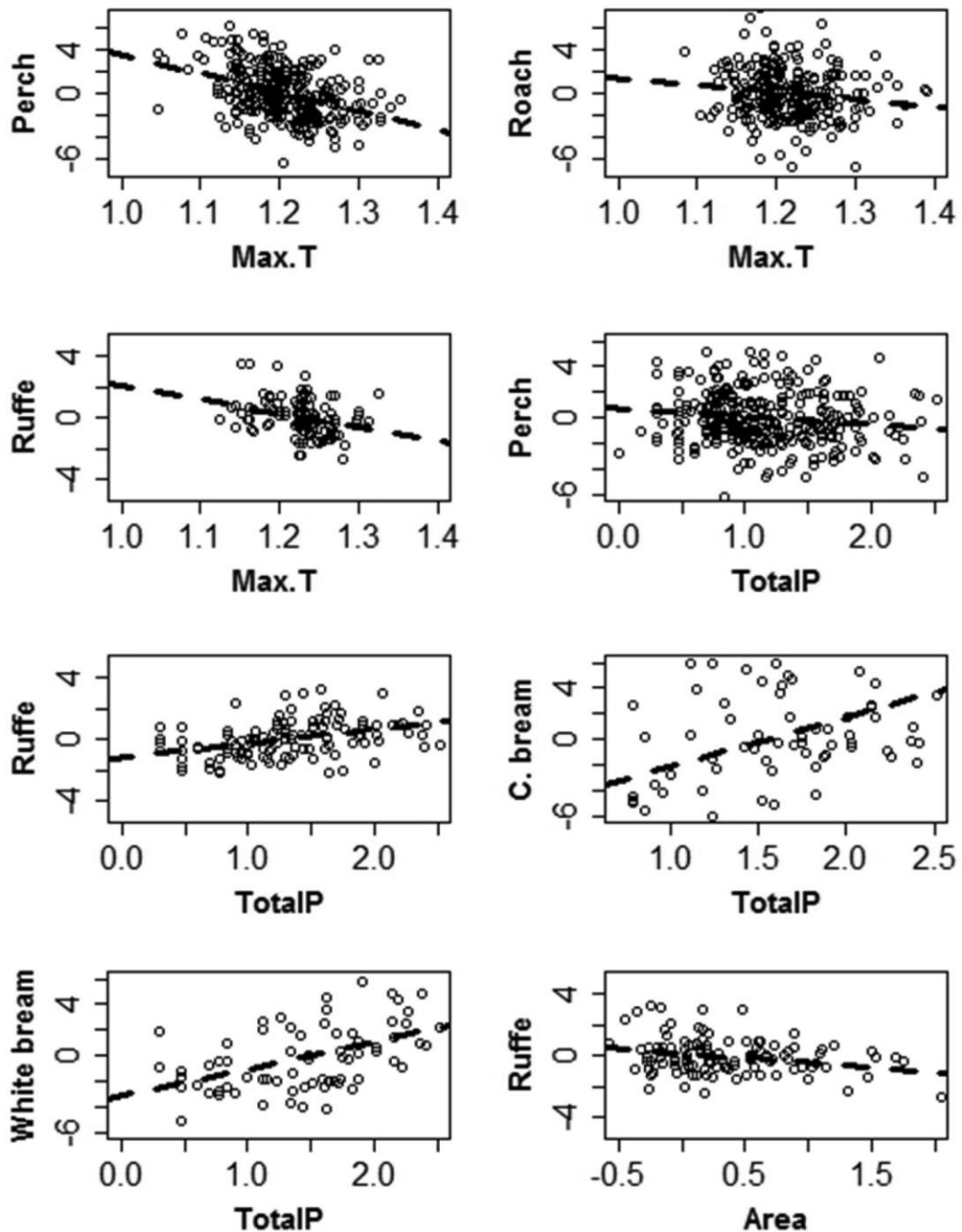
**Table A4.** Comparison of mean body size (cm) for some widely distributed species between Turkey (Northern Anatolia and Western Anatolia ecoregions) and the European ecoregions.

Developmental stage		d.f.	F	P value
<b>Adult charr</b>	Fish length	1	3249.74	<0.0005
	Lake category	2	0.73	0.52
	Sea connection	1	1.30	0.29
	Sea connection*Lake category	1	0.00	0.99
<b>Young charr</b>	Fish length	1	4034.16	<0.0005
	Lake category	2	2.15	0.17
	Sea connection	1	11.83	0.01
	Sea connection*Lake category	1	0.51	0.49

**Table A5.** Idem to caption of Table 4 but excluding the three lakes only sampled in the littoral zone.



**Figure A1.** Frequency distributions based on all individuals for each species for all lakes accumulated together: x axis, fresh mass by a log2 scale; y axis, relative frequencies (%) for each size class. Note the different scales on the y axis.



**Figure A2.** Partial residual plots for each species between the size metric mean body size (y axis) and the climatic, morphometric, productivity, and density-dependent predictors (x axis) included in the final model. Max.T, maximum temperature ( $^{\circ}\text{C}$ ); TotalP, total phosphorus concentration ( $\mu\text{g}\cdot\text{L}^{-1}$ ); Area, lake area (ha); Depth, maximum lake depth (m); CPUE<sub>intra</sub>, catch per unit effort of the focal species; CPUE<sub>inter</sub>, sum of CPUE of the other five potentially competing species; c. bream, common bream. (Fig. A2 is concluded on the next page.)

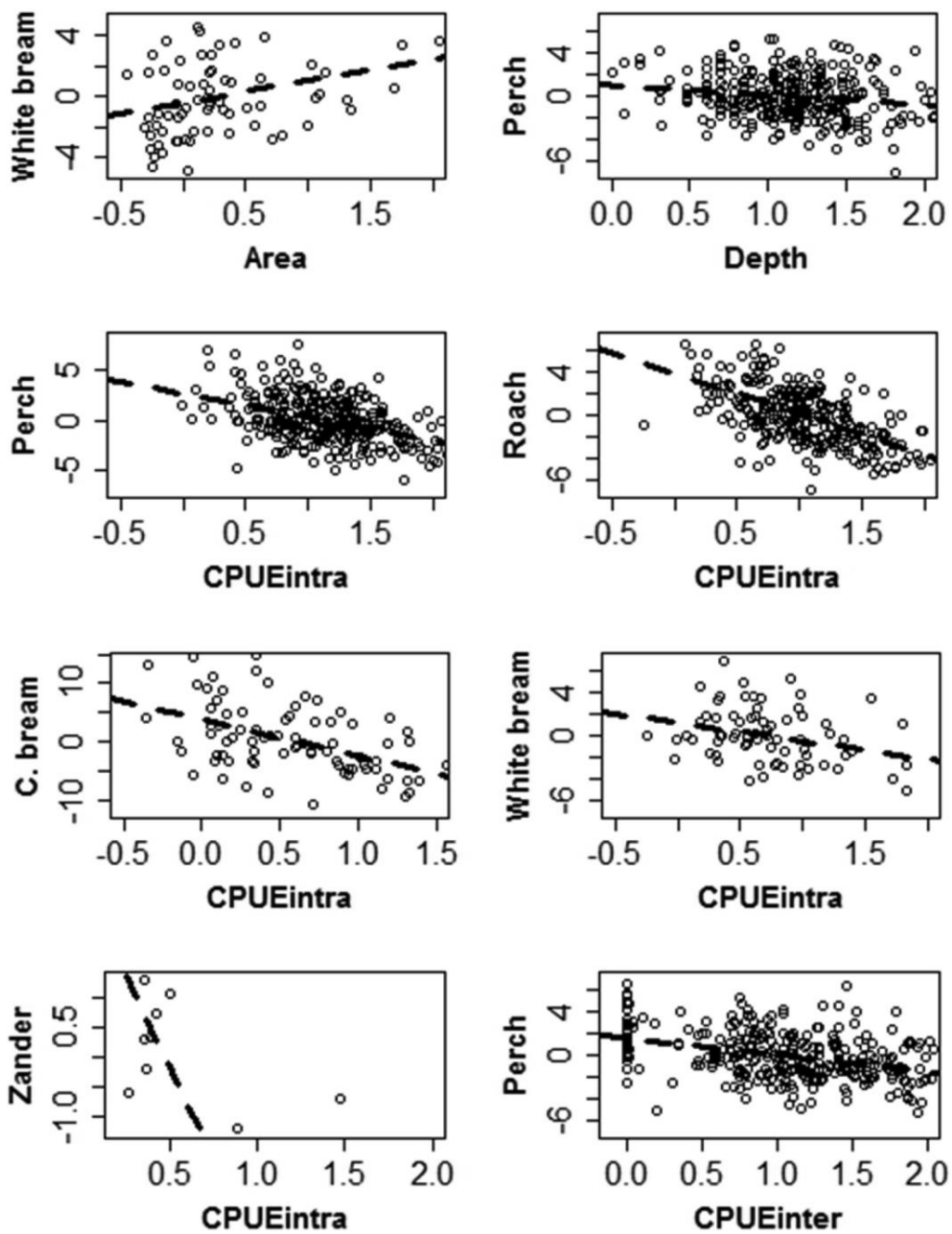
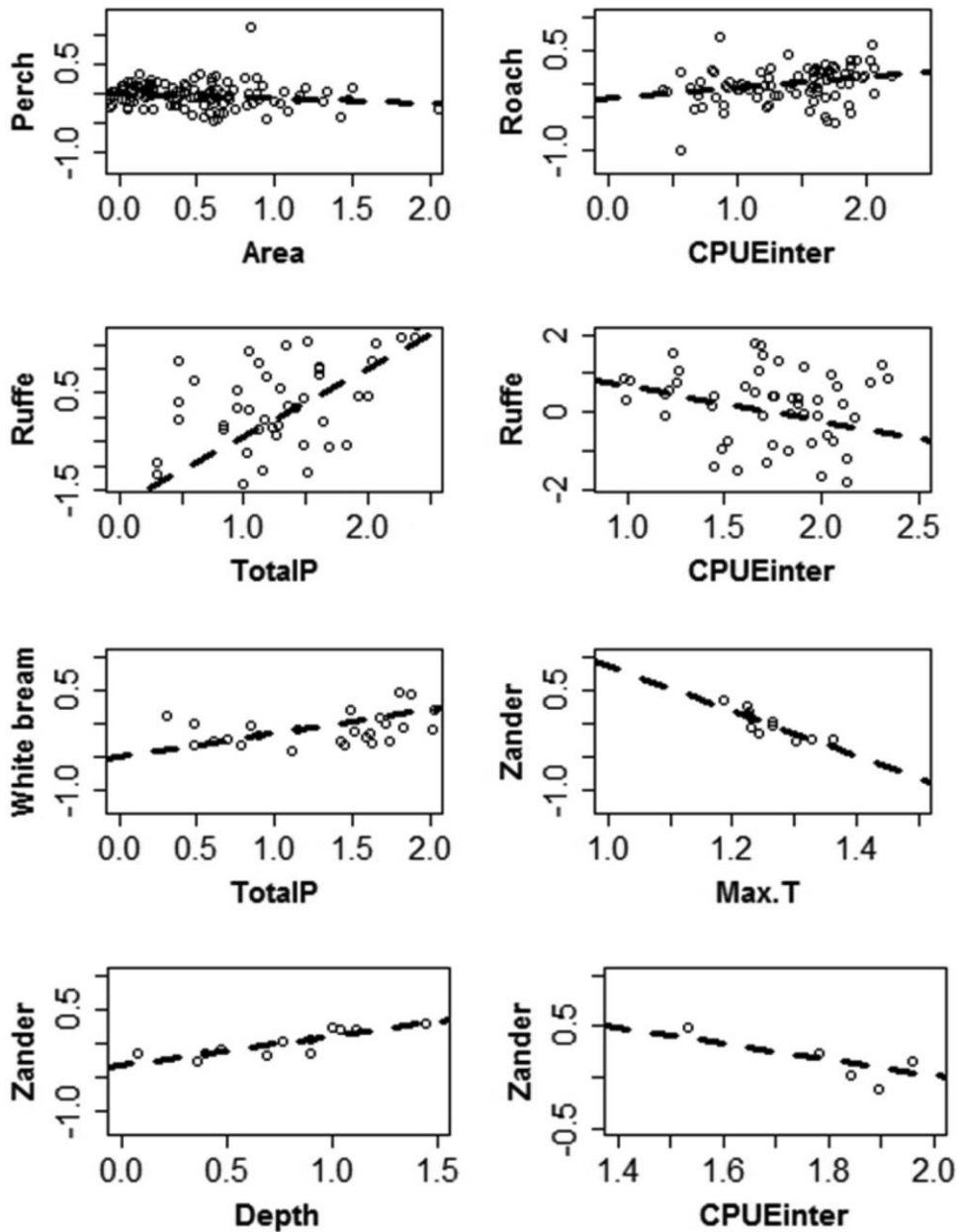
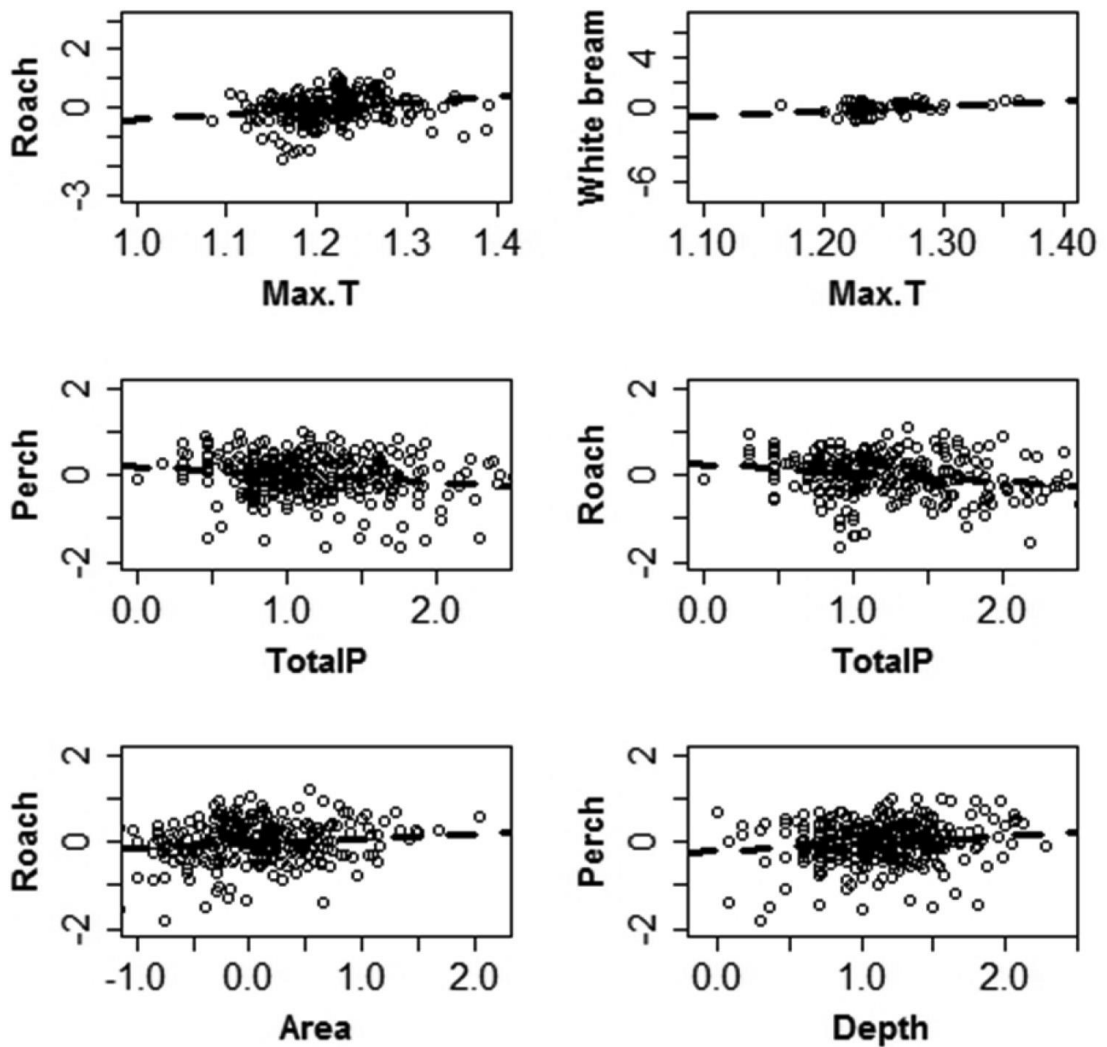


Figure A2 (concluded).



**Figure A3.** Partial residual plots for each species between the size metric slope (y axis) and the climatic, morphometric, productivity, and density-dependent predictors (x axis) included in the final model. See caption of Fig. A2 for explanation of predictor abbreviations.



**Figure A4.** Partial residual plots for each species between the size metric diversity ( $y$  axis) and the climatic, morphometric, productivity, and density-dependent predictors ( $x$  axis) included in the final model. See caption of Fig. A2 for explanation of predictor abbreviations. (Fig. A4 is concluded on the next page.).

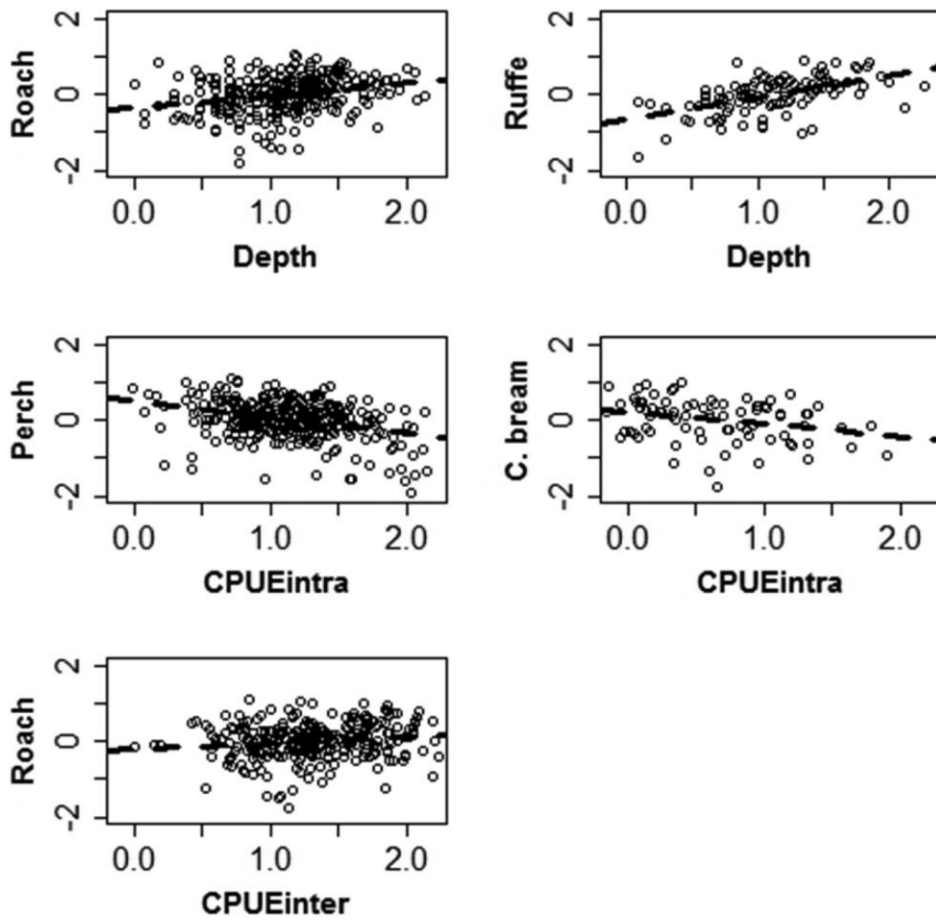
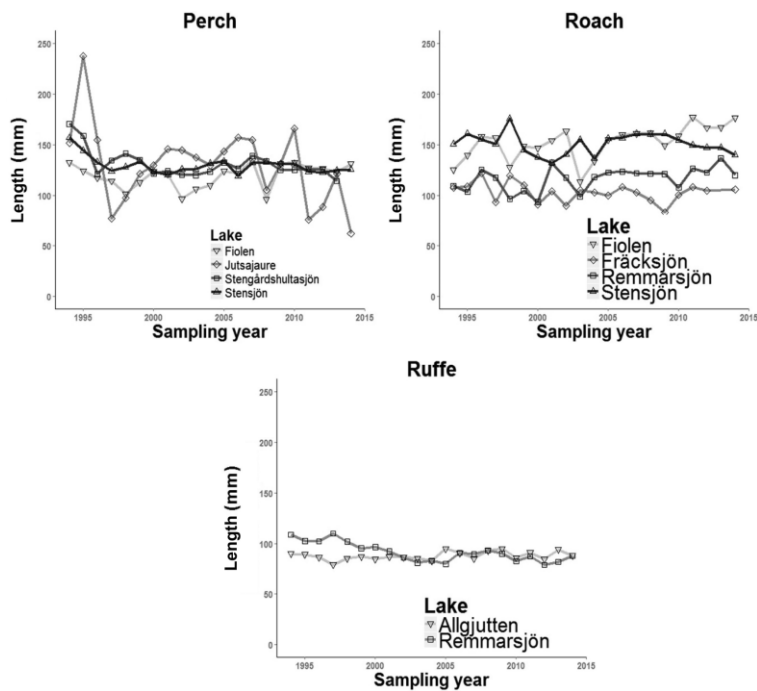
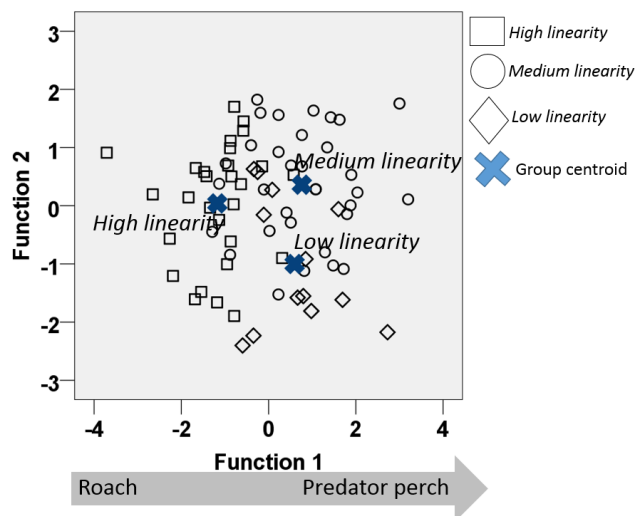


Figure A4 (concluded).



**Figure A5.** Between-year variation of the geometric mean length for perch, roach, and ruffe in some Swedish lakes: x axis, mean length (expressed in mm); y axis, sampling year.



**Figure A6.** Discriminant Correspondence Analysis (DCA) of the CPUE of the most common fish species in 74 German lakes. Symbols indicate the three cluster groups determined by *k*-means clustering, based on the similarity of the residual patterns. For the significant function 1, the dominant species are indicated below. Predator perch = perch >32 g.



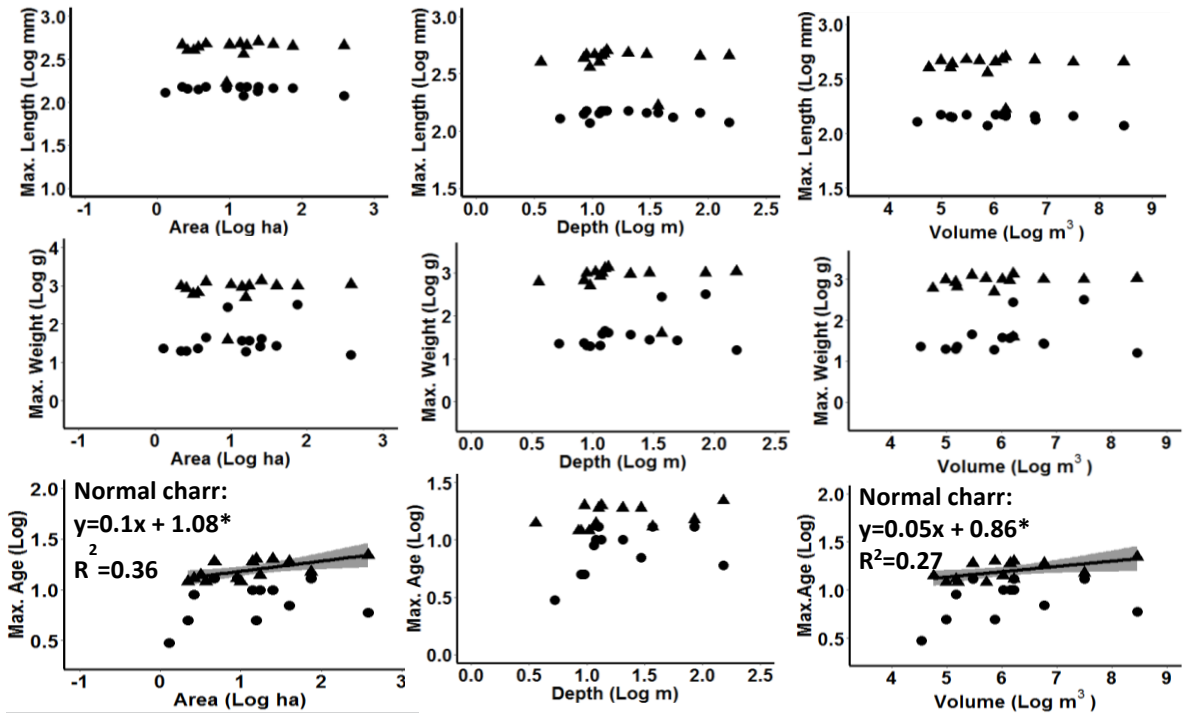


Figure A7. Idem to caption of Fig. 2 but excluding the three lakes only sampled in the littoral zone.

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## Other related publications by the author

Ersoy, Z., Jeppesen, E., Sgarzi, S., **Arranz, I.**, Cañedo-Argüelles, M., Quintana, X.D., Landkildehus, F., Lauridsen, T.L., Bartrons, M., Brucet, S. 2017. Do size-based interactions determine top-down and bottom-up controls in planktonic food web of Lake Mývatn? *Freshwater Biology* (*Submitted*)

Trochine, C., Brucet, S., Argillier, C., **Arranz, I.**, Beklioglu, M., Benejam, L., Ferreira, T., Hesthagen, T., Kerstin, H., Jeppesen, E., Kelly, F., Krause, T. Rask, M., Volta, P., Winfield, I.J. and Mehner, T. 2017 Catch-based local records of non-native fish occurrence and biomass in Western Palearctic lakes and reservoirs and their abiotic and biotic correlates. *Ecosystems*.

Cañedo-Argüelles, M.; Sgarzi, S.; **Arranz, I.**; Quintana, X. D.; Ersoy, Z.; Landkildehus, F.; Lauridsen, T.; Jeppesen, E.; Brucet, S. 2016. Role of predation in biological communities in naturally eutrophic subarctic Lake Mývatn, Iceland. *Hydrobiologia*. 790(1): 213-223.

## Participations in conferences as presenting author

### Association for the Sciences of Limnology and Oceanography (ASLO)

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### International Society of Limnology (SIL)

**Arranz, I.**; Benejam, L.; Brucet, S.; Landkildehus, F.; Lauridsen, T. L.; Davidson, T. A.; Mazzeo, N.; Vidal, N.; Özkan, K.; Gallego, I.; Wischniewski, J.; Menezes, R. F.; Jeppesen, E. Impact of lake morphometry and sticklebacks on the population structure of Arctic charr (*Salvelinus alpinus*) in West Greenland lakes. August 2016. Torino. Oral presentation.

### Iberian Society of Limnology (AIL)

**Arranz, I.**, Hsieh, C. H., Mehner, T. and Brucet, S. Deviated patterns in fish size structure reflect predator-prey interactions in lakes. July 2016. Tortosa. Oral presentatio





