Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change

Marine ecosystems are exposed to a range of environmental and anthropogenic stressors, including climate change and overexploitation. A promising way towards understanding the impacts of such stressors on community composition is by considering species traits rather than species identity. Here, we describe the spatio-temporal dynamics in fish community traits using >30 yr of species abundance data from the North Sea combined with trait information on body size, life history, growth rate, reproduction and trophic level for demersal fish species in the area. We assessed whether the derived patterns and trends in community-weighted mean traits could be explained by a range of environmental stressors and fishing. Our results revealed strong spatial structuring and long-term changes in the trait composition of North Sea fish, with temporal changes not being uniformly distributed in space. Among the environmental drivers investigated, depth was one of the best predictors, primarily explaining the spatial variation in lifespan, growth rate, trophic level and fecundity. This can be explained by variables that co-vary with depth, e.g. temperature, seasonality, salinity and productivity. Finally, we found only weak relationships between fishing and the spatial variation of traits, suggesting that the spatial trait composition of the community is mostly determined by the environment. Yet, long-term changes in trait composition, primarily in body size, have previously been shown to be affected by size-selective fishing. Our study exemplifies how traits can be used to summarize complex community dynamics and responses to environmental and anthropogenic stressors as well as their usefulness for ecosystem-based management.
Spatial distribution of life-history traits and their response to environmental gradients across multiple marine taxa

Trait-based approaches enable comparison of community composition across multiple organism groups. Yet, little is known about the degree to which empirical trait responses found for one taxonomic group can be generalized across organisms. In this study, we investigated the spatial variability of marine community-weighted mean traits and compared their environmental responses across multiple taxa and habitats, including pelagic zooplankton (copepods), demersal fish, and benthic infaunal invertebrates. We used extensive, spatially explicit datasets collected from scientific surveys in the North Sea and examined community composition of these groups using a trait-based approach. In order to cover the key biological characteristics of an organism, we considered three life-history traits (adult size, offspring size, and fecundity) and taxon-specific feeding traits. While many of the traits co-varied in space and notably demonstrated a south–north gradient, none of the traits showed a consistent spatial distribution across all groups. However, traits are often correlated as a result of trade-offs. When studying spatial patterns of multiple traits variability in fish and copepods, we showed a high spatial correlation. This also applied to a lesser extent to fish and benthic infauna, whereas no correlation was found between benthic infauna and copepods. The result suggested a decoupling in the community traits between strictly benthic and strictly pelagic species. The strongest drivers of spatial variability for many community traits are the gradients in temperature seasonality, primary productivity, fishing effort, and depth. Spatial variability in benthic traits also co-varied with descriptors of the seabed habitat. Overall, results showed that trait responses to environmental...
gradients cannot be generalized across organism groups, pointing toward potential complex responses of multi-taxon communities to environmental changes and highlighting the need for cross-habitat multi-trait analyses to foresee how environmental change will affect community structure and biodiversity at large.

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Using ecological traits of marine fish to detect responses to environmental change: which traits to choose?

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A trait-based approach to understanding marine communities composition, assembly and diversity
A species occurs and thrives in a community thanks to its capacity to grow, reproduce and feed in its surrounding environment. Understanding how and why some species thrive in particular areas has often been touched upon by
studying the species composition of communities. Traditionally, communities are characterised by their taxonomic diversity, such as their species richness or the evenness in their abundances. However, there is growing evidence that it is not the taxonomic identity of the species per se that control its presence and abundance in a given environment but its characteristics. Species traits refer to quantitatively or qualitatively measurable characteristics of a species. Characterizing species by their key traits can permit an understanding of general mechanisms and unravel the processes affecting coexistence in communities. The aim of this thesis was to apply the trait-based approach to study the composition of marine communities located in the European Seas and relate their spatial patterns to environmental and anthropogenic pressures.

The species composition of communities can be constrained by several processes, such as competition and the environment. Using a trait-based approach, we studied the diversity and the processes influencing the composition of demersal fish communities in the Baltic Sea. While species richness was sharply decreasing from the saline Kattegat to the brackish Gdansk Bay, trait richness tended to decrease at a lower rate. We found that the species co-occurring in the Eastern Baltic Sea were in general more ecologically similar, in terms of their traits, than expected by random chance alone with a strong influence of the environment and notably the salinity gradient on the distribution and trait composition of the communities. While traits are increasingly used in community ecology, they are often selected and used without a consistent framework. We made use of a theoretical framework that defines life history strategies as a combination of key traits and their trade-offs to investigate large-scale patterns and drivers of fish community composition across European Seas. We assembled an extensive number of surveys in the European seas and collected reproductive traits for more than 300 fish species present in these surveys. Based on their traits, fish species could be categorized into three strategies that reflect the evolutionary and environmental constraints acting on the species. The strategies' prevalence exhibited strong geographical patterns which could be explained by spatial variability in annual sea surface temperature, temperature seasonality, depth and fishing intensity. Due to their tight coupling to the environment, not only temperature and fishing, life history strategies could be a suitable tool to monitor and understand community changes in response to natural and anthropogenic stressors, including climate change. Spatial patterns of community mean traits and their relationship with the environment are generally assessed on a single taxonomic group. As a result, it is still unclear whether the relationship found for one taxonomic group can be generalised to other taxonomic groups that compose the ecosystem. Yet, understanding the responses of these different groups to environmental pressures is a prerequisite to conserve and manage ecosystems. We studied the spatial pattern of community traits of three key taxonomic groups in the North Sea: copepods, benthos, and fish. We extracted the community composition of these groups from three scientific surveys covering the entire North Sea and combined them with key life history traits common to all three groups: adult size, offspring size and fecundity. While many of the traits co-varied in space and notably demonstrated a latitudinal gradient, none of the traits had a consistent, either positive or negative, relationship across all taxa. The spatial trait-variability could be explained by taxa-specific habitat condition. Thus, trait responses to environmental gradient cannot be generalized across these marine taxonomic groups, pointing toward potential complex responses of multi-taxa communities to environmental changes.

This thesis highlights the value of using traits to understand why communities are composed of a specific set of species and how the mean traits of these communities varies along environmental and anthropogenic gradient. This thesis stresses the utility of the trait-based approach, due to its generality, to compare communities at different scales, from different regions as well as communities composed of different taxonomic entities. The trait-based approach still has a lot to offer to unravel the processes controlling the composition of communities and species distribution, and its use in marine ecology has yet to be extended to other domains, such as understanding the impacts of functional traits composition on the ecosystem functioning in the marine realm.
Temporal and spatial differences between taxonomic and trait biodiversity in a large marine ecosystem: Causes and consequences

Biodiversity is a multifaceted concept, yet most biodiversity studies have taken a taxonomic approach, implying that all species are equally important. However, species do not contribute equally to ecosystem processes and differ markedly in their responses to changing environments. This recognition has led to the exploration of other components of biodiversity, notably the diversity of ecologically important traits. Recent studies taking into account both taxonomic and trait diversity have revealed that the two biodiversity components may exhibit pronounced temporal and spatial differences. These apparent incongruences indicate that the two components may respond differently to environmental drivers and that changes in one component might not affect the other. Such incongruences may provide insight into the structuring of communities through community assembly processes, and the resilience of ecosystems to change. Here we examine temporal and spatial patterns and drivers of multiple marine biodiversity indicators using the North Sea fish community as a case study. Based on long-term spatially resolved survey data on fish species occurrences and biomasses from 1983 to 2014 and an extensive trait dataset we: (i) investigate temporal and spatial incongruences between taxonomy and trait-based indicators of both richness and evenness; (ii) examine the underlying environmental drivers and, (iii) interpret the results in the context of assembly rules acting on community composition. Our study shows that taxonomy and trait-based biodiversity indicators differ in time and space and that these differences are correlated to natural and anthropogenic drivers, notably temperature, depth and substrate richness. Our findings show that trait-based biodiversity indicators add information regarding community composition and ecosystem structure compared to and in conjunction with taxonomy-
based indicators. These results emphasize the importance of examining and monitoring multiple indicators of biodiversity in ecological studies as well as for conservation and ecosystem-based management purposes.

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From traits to life history strategies: deconstructing fish community composition across European Seas

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**Patterns and drivers of fish community assembly in a large marine ecosystem**
The presence and survival of the species in a community depend on their abilities to maximize fitness in a given environment. The study of the processes that control survival and co-existence, termed ‘assembly rules’, follows various mechanisms, primarily related to biotic or abiotic factors. To determine assembly rules, ecological similarities of co-occurring species are often investigated. This can be evaluated using trait-based indices summarizing the species’ niches in a given community. In order to investigate the underlying processes shaping community assembly in marine ecosystems, we investigated the patterns and drivers of fish community composition in the Baltic Sea, a semi-enclosed sea characterized by a pronounced environmental gradient. Our results showed a marked decline in species- and functional richness, largely explained by decreasing salinities. In addition, habitat complexity and oxygen were found to be significant drivers. Furthermore, we showed that the trait composition of the fish community in the western Baltic Sea is more similar than expected by random chance alone. This implies that environmental filtering, acting along the salinity gradient, is the dominant factor shaping community composition. However, community composition in the eastern part, an area beyond the steep decline in salinity, was characterized by fewer species with largely different trait characteristics, indicating that community assembly is also affected by biotic interactions. Our results add to the knowledge base of key abiotic drivers impacting marine fish communities and their vulnerability to environmental changes, a key concern for fisheries and marine ecosystem management.
Reproductive traits (Fecundity, egg diameter, parental care) of marine European fish

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Spatial structuration of life history traits: congruence between multiple taxa and environmental drivers in the North Sea

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Environmental filtering drives functional diversity of fish assemblages in a temperate system.

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Impacts of the local environment on recruitment – a comparative study of North Sea and Baltic Sea fish stocks

Impacts of the local environment on recruitment: a comparative study of North Sea and Baltic Sea fish stocks

While the impact of environmental forcing on recruitment variability in marine populations remains largely elusive, studies spanning large spatial areas and many stocks are able to identify patterns common to different regions and species. In this study, we investigate the effects of the environment on the residuals of a Ricker stock-recruitment (SR) model, used as a proxy of prerecruits’ survival, of 18 assessed stocks in the Baltic and North Seas. A probabilistic principal components (PCs) analysis permits the identification of groups of stocks with shared variability in the prerecruits’ survival, most notably a group of pelagics in the Baltic Sea and a group composed of gadoids and herring in the North Sea. The first two PCs generally grouped the stocks according to their localizations: the North Sea, the Kattegat-Western Baltic, and the Baltic Sea. This suggests the importance of the local environmental variability on the recruitment strength. Hence, the prerecruits’ survival variability is studied according to geographically disaggregated and potentially impacting abiotic or biotic variables. Time series (1990-2009) of nine environmental variables consistent with the spawning locations and season for each stock were extracted from a physical-biogeochemical model to evaluate their ability to explain the survival of prerecruits. Environmental variables explained >70% of the survival variability for eight stocks. The variables water current, salinity, temperature, and biomass of other fish stocks are regularly significant in the models. This study shows the importance of the local environment on the dynamics of SR. The results provide evidence of the necessity of including environmental variables in stock assessment for a realistic and efficient management of fisheries.
Long–term functional trends in Baltic Sea coastal macrofauna and fish

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A trait-based approach towards understanding benthic-pelagic pathways in marine ecosystems
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