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3.2.1 The impact of climate variability on aquatic ecosystems: Match and mismatch resulting from shifts in seasonality and distribution – The concept of AQUASHIFT

Klimafolgeeffekte auf physikalischer und biologischer Ebene in aquatischen Ökosystemen. – Das Konzept AQUASHIFT

Key words: DFG-Focus programme AQUASHIFT, match-mismatch of interactions

General focus of the 'DFG- Schwerpunktprogramm' AQUASHIFT

The Schwerpunktprogramm (SPP, Focus programme) AQUASHIFT focuses on a fundamental understanding of the impact of climate variability on aquatic ecosystems. Its main goal is to improve our ability to predict future ecosystem states under a changed climate. The SPP encompasses marine, lake, and running water ecosystems. It is motivated by the conspicuous gap which currently exists between the ability to forecast future climatic conditions on a global scale, and the lack of forecast of future states for individual ecosystems. While some biological responses to the recent warming trend have already been noticed, it is not clear to which extent they have led to new, stable ecosystem states. There is currently no solid basis for the assessment of the stability of current ecosystem states against further climate change exceeding the limits of contemporary variability.

Aquatic species of temperate zones are already adapted to the seasonal and inter-annual variability of their physical environment, and most of them are likely to survive further change. Nevertheless, even subtle changes in fitness, and in the timing of seasonal activity/growth patterns could tilt the balance of power in inter-specific interactions (e.g. competition, predator-prey) and lead to far-reaching ecosystem-wide consequences. Many key processes in ecosystems depend on a tight temporal and spatial coupling ("match"), e.g. the supply of suitable food organisms has to coincide with the seasonal start of feeding by consumer organisms. Meteorologically driven shifts in seasonal activity patterns or in geographic distribution might lead to a decoupling ("mismatch") of such processes, because different biological processes respond differently to light, temperature, vertical mixing and food availability. Physiological and genetic variability as well as microevolution, (new genotypes or positive selection of hitherto rare genotypes), might act as an insurance against this mismatch, but the strength of the insurance effect is generally unknown.

In AQUASFIFT we combine studies at different hierarchical levels, beginning with the analysis of long-term change and geographic patterns of species abundance and distribution, through experimental studies on the mechanisms of biotic interactions and ecosystem processes, to the physiological and evolutionary response of species and their molecular basis. In addition, we will develop and employ models to investigate the influence of possible changes in the environmental conditions on the interactions between species in numerical experiments, and to identify the processes and the components of the ecosystem most sensitive to changes in the external forcing (Fig. 1).

Three projects from the IGB are part of AQUASHIFT- a summary of each now follows:

The DFG- Focus programme AQUASHIFT

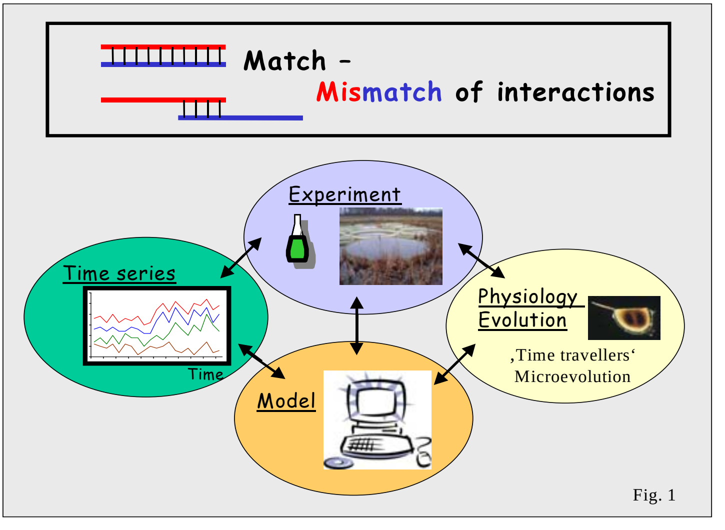

Fig. 1: The concept of AQUASHIFT. In AQUASHIFT we combine studies at different hierarchical levels: time series analysis, experiments, physiological and evolutionary responses of species and their molecular basis, and modelling.

Das DFG-Schwerpunktprogramm AQUASHIFT ist ausgerichtet auf Studien der Einflüsse klimatischer Variabilität auf aquatische Ökosysteme- wie marine Systeme, Seen und Flussökosysteme. Das Programm ist im Kontext der Prognosen globaler klimatischer Veränderungen einerseits und der Vorhersagbarkeit des Antwortverhaltens aquatischer System andererseits, angesiedelt. Obgleich eine Reihe klimainduzierter Veränderungen auf biologischer Ebene bereits bekannt sind, sind Auswirkungen auf gesamt-ökosystemarer Ebene nicht verstanden.

Aquatische Organismen der gemäßigten Zone sind bereits an jahreszeitliche und interannuelle Schwankungen ihrer physikalischen Umgebung angepasst. Man kann daher davon ausgehen, dass die meisten Organismen den Bereich prognostizierter Erwärmungen überleben werden.

Es hat sich jedoch gezeigt, dass selbst kleine Veränderungen in der Fittness oder dem zeitlichen Auftreten von Spezies zu Komplikationen in den Interaktionen (z. B. Konkurrenz, Räuber-Beute) führen können. Viele Prozesse in Ökosystemen unterliegen einer engen zeitlichen und räumlichen Verknüfpung (‚match') wie bspw. das gleichzeitige Auftreten einer Beute und eines Räubers. Wetter bzw. klimainduzierte Veränderungen dieser saisonalen Muster können zu einer Entkopplung (‚mismatch') dieser Verknüpfungen führen. Physiologische und genetische Variabilität von Spezies als auch der Prozess der Mikroevolution könnten dieser Entkopplung entgegenwirken. Die Bedeutung dessen ist jedoch nicht verstanden. Im Schwerpunkt sollen darüber hinaus Modelle entwickelt und angewandt werden, die zu einer Identifikation sensibler Ebenen innerhalb aquatischer Nahrungsnetze gegenüber klimatischen Veränderungen beitragen (Fig. 1).

Das IGB ist mit drei Projekten in AQUASHIFT vertreten. Eine kurze Zusammenfassung der Inhalte dieser Projekte ist in Folge gegeben.

3.2.1.1 Phase shifts within lake plankton communities in response toward climate warming: Implications for the match/mismatch of species interactions (Adrian, Gerten)

Long term studies suggest that seasonal succession in aquatic ecosystems is currently advancing in temperate latitudes (MÜLLER-NAVARRA et al. 1997, GERTEN & ADRIAN 2000, STRAILE & ADRIAN 2000). Those changes are likely to generate complex, and possibly time-lagged responses, leading to a decoupling (mismatch) of so far tightly coupled (matched) processes (CUSHING 1995). Previous studies have basically focussed on individual species' responses to warming, while neglecting inter-specific interactions. Within AQUASHIFT, we aim to identify past phase shifts and time-lagged responses in phyto- and zooplankton communities, and subsequent changes in species interaction induced by observed and projected climate warming. Our methodological approach is focussed on statistical data exploration, time series analysis, and modelling, based upon long-term records (>24 years) of plankton, physical and chemical data from shallow, polymictic, eutrophic Müggelsee (Berlin). We anticipate to separate direct, temperature driven responses, from indirect responses, through changes in thermal regime and species interaction. A stochastic and/or deterministic model will be created to describe the linkage between winter and spring meteorological conditions and vernal phytoplankton development in Müggelsee. Model development builds on previous statistical analysis and will be complemented by stochastic terms resulting from the parallel time series analysis. The model will be coupled to an existing lake physics model. This offline–coupled model system will be used to project changes in the timing and intensity of the phytoplankton spring blooms under a range of climate change scenarios.

This project is part of the cluster: "Climate impact on physical and biological levels in shallow polymictic lakes: a case study of Müggelsee (Berlin)", which includes the project by Kirillin and Behrendt (see 1.2, Fig. 2).

In this cluster we will study climate-induced changes within lake plankton communities with emphasis on changes in the phenology (annually reoccurring events such as the timing of occurence, or the timing when population maxima are reached) of species, as coupled to thermal properties.

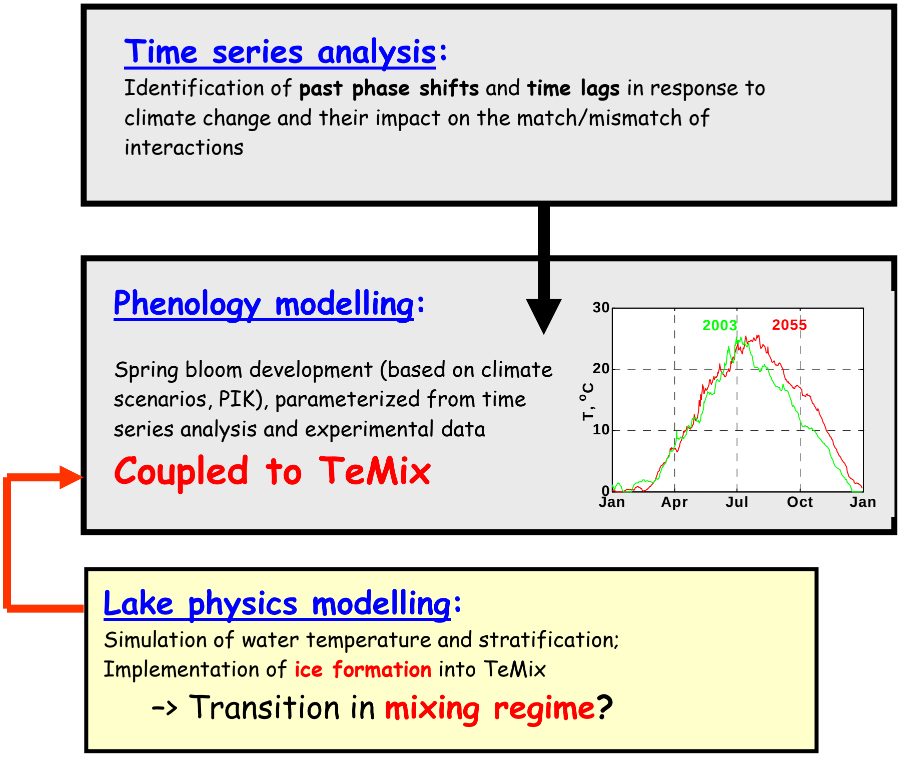

Fig. 2: Cluster: Climate impact on physical and biological levels in shallow polymictic lakes: The case study of Müggelsee (Adrian & Gerten, upper two boxes / Kirillin & Behrendt, lower box). TeMix stands for a lakes physics model.

3.2.1.2 Climate impact on temperature and mixing regime of polymictic lakes and its consequences for lake ecosystems (Kirillin/Behrendt)

The most pronounced link between climate and lakes are the fluxes of heat, momentum, and light *at the air-lake interface*. These fluxes directly affect the physical parameters of lakes, viz. the heat content and the vertical density stratification, thus determining, to a great extent, subsequent ecological response. Therefore, estimation of anticipated changes in thermal and mixing regimes associated with the current climatic trends is one of the primary tasks of climate impact studies on lakes.

The AQUASHIFT-project „Climate and Polymixis“ is dedicated to the investigation of the climatic impact on seasonal temperature pattern, vertical mixing regime, and ice conditions, with emphasis on shallow polymictic lakes, where the physical response to climatic variabiliy is more pronounced than in deep water bodies. Each of the three above-mentioned physical factors is of primary importance for chemical and biological processes in lakes. The research strategy therefore includes, in addition to qualitative estimation of climate-driven physical changes, uncovering the physical-chemical and physical-biological links, such as the nutrients and oxygen exchange between the water column and lake sediments in relation to the summer mixing conditions, and the role of the mixing and ice regimes in plankton succession. The latter task is carried out in close co-operation with the AQUASHIFT-project Adrian & Gerten (see above, Fig. 2). In both projects –Müggelsee– as a typical polymictic lake – is chosen the primary research site. The lake has been studied in great detail at the IGB during recent decades. The multi-decadal database on the long-term physical and biological parameters in the lake offers a reliable background for the climate impact studies. In addition, the regional climatic scenarios for 2005-2055 are used for the estimation of the anticipated changes in the near future.

The 1-D lake model TEMIX/FLAKE (KIRILLIN 2002, MIRONOV et al. 2003) is used as the main research and analysis tool in the project. An essential distinction of the TEMIX/FLAKE model from the variety of other 1-D lake modeling systems are the original algorithms for calculation of the heat transfer across the lake sediments and across the ice cover – the crucial factors determining long-term trends in the temperature regime of lakes.

Research on the impact of climatic changes on *seasonal temperature pattern* includes the determination of biologically relevant climate-driven shifts in thermal regime characteristics, such as occurrence and duration of spring and autumn convective periods (overturns) and the surface temperature regime during the summer heating period. *Vertical mixing regime* of temperate lakes demonstrate a pronounced tendency to stronger summer stratification during the last decades. An apparent conclusion can be made that polymictic lakes with certain morphometry could switch their mixing regime to the dimictic one in the near future, even at the presently observed climatic trends. Such switching would imply transition of the ecosystem to another, completely different steady state. The determination of the conditions necessary for such a transition is one of the primary project's tasks. The *ice conditions* play an essential role in the heat budget and mixing in early spring, and by that determine the plankton production in the starting phase of the vegetation period. Because the warming tendency in the current climate is most pronounced in winter temperatures, one can expect remarkable changes in the ice regime in the near future, the consequences of which are to be estimated.

As was mentioned above, the lake sediments play an essential role in the heat budget of polymictic lakes. In particular, the internal nutrients loading and the oxygen regime are strongly affected by the water-sediment heat exchange. In addition to the well-known Mortimer mechanism of the hypolimnetic iron oxidation, which appears in stably stratified conditions, the viscous density convection in the upper sediments, described by GOLOSOV &

IGNATIEVA (1999), becomes of great importance here, when the heat flux across the water-bottom interface is directed upward. Clarifying the role of the sediments in the climatic aspect as a link between shallow lake physics and its ecological state is considered to be the next step in the project. The TEMIX/FLAKE model in combination with currently developed sub-models of oxygen and nutrients dynamics provide us with the necessary tools for this investigation.

3.2.1.3 The impact of climate variability on recruitment, life history, and physiology of sympatric pairs of ciscoes (Teleostei: *Coregonus* spp.) in lakes (Mehner/Freyhof)

Recently, it has been speculated that global warming trends may favor spring-spawning rather than autumn-spawning fish species. There was evidence for an increase in year-class strength of the spring-spawning smelt (*Osmerus eperlanus*) and pikeperch (*Sander lucioperca*) after years with warm spring temperatures, whereas the catches of ciscoes (*Coregonus albula*) were high after years with late ice-break and slow spring warming (NYBERG et al. 2001). The underlying mechanisms were assumed to be a differential timing of the larval hatching and the spring peak of the zooplankton as food for the small fish, and a variable recruitment due to temperature-sensitive adaptations of the life cycle. These general patterns of differential timing of larval hatch and spring zooplankton blooms may become more dramatic if global warming results in warmer winter temperatures in lakes, later mixing events, or earlier ice break ups in spring. However, since the species studied by NYBERG et al. (2001) belong to different orders of fish, the predicted match/mismatch dependent upon spring warming may also have been influenced by species-specific differences in the potential to adapt physiologically to changing temperatures. Therefore, the link between shifts in species abundance and an assumed decoupled timing of larval occurrence and zooplankton blooms due to global warming is weak.

Our knowledge could be improved substantially if physiologically very similar species, ideally only differentiated by spawning time, could be used as model organisms. Such a pair of very similar species within one ecosystem give the unique opportunity to study the effect of different spawning times on the response of year-class formation to the changing environment. Very young sympatric species pairs of fishes may be as close as possible to this optimal attempt. Therefore, we compare the timing of hatch and early recruitment of a sympatric species pair of ciscoes in the deep Lake Stechlin (Brandenburg) where the normal Baltic cisco (*Coregonus albula*) spawns in autumn, and the endemic deepwater Fontane cisco (*Coregonus fontanae*) spawns in spring (SCHULZ & FREYHOF 2003). In Lake Stechlin, speciation and divergence of both species have occurred during the last 10,000 years. The ecological, behavioural and physiological differences between both species (except for the spawning time) are assumed to be low, whereas a significant genetic difference and restricted gene flow between the populations were determined (SCHULZ et al. submitted). By following the growth, feeding, distribution and physiological performance of the early life stages of both species, we will test whether the spring-spawning species is indeed better adapted to the anticipated earlier ice break and higher spring water temperatures due to global warming. Furthermore, the predation risk posed by piscivorous fish, principally the adult perch (*Perca fluviatilis*), is estimated for both cisco species by inspecting the stomach contents of littoral predatory fish. In the future, the physiological adaptation of both species, and potential hybrids, to cold and warm temperatures will also be analysed.

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