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Alfred-Wegener Institute for Polar and Marine Research,
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**Adaptations of Marine Organisms
and Problems
of Global Climate Changes**

ABSTRACTS

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Salinity Adaptations and Osmoregulatory Capacities of Hydrobionts from the Sea of Azov

N.V. Aladin, N.A. Lemeshko, I.S. Plotnikov

Zoological Institute RAS, St. Petersburg, Russia

Among marine and continental waters often there are water areas with changing salinity, often at that salinity is the limitative factor for hydrobionts spreading. It is necessary to find out types of hydrobionts internal medium attitude to the external medium, to determine experimentally limits of salinity tolerance ranges, to analyze information about salinity limits of spreading in the nature. These three aspects, being a primary basis in the studies of hydrobionts' osmoregulatory capacities, are studied enough, but unfortunately only in the small number of aquatic animals from different types and classes.

We shall try to apply the mentioned approach to the inhabitants of the Sea of Azov. In our opinion, in this water body there are prevailing hydrobionts capable to active osmoregulation or to wide isoosmoticity. In the Sea of Azov the following groups of hydrobionts are widespread:

- euryhaline marine hydrobionts (osmoconformers-III);
- widely euryhaline marine hydrobionts (confohyperosmotics-I);
- brackish water hydrobionts of marine origin (confohyperosmotics-II);
- freshwater hydrobionts from estuaries of Azov rivers (hyperosmotics-I);
- brackish water hydrobionts of freshwater origin (hyperosmotics-II or secondary confohyperosmotics);
- some Caspian brackish water hydrobionts (amphiosmot-

- ics-I) that invaded Sea of Azov;
- euryhaline hydrobionts of freshwater origin (amphiosmotics-III);
 - widely euryhaline hydrobionts of freshwater origin (amphiosmotics-IV);
 - euryhaline marine hydrobionts of freshwater origin (hypoosmotics).

As is obvious from afore given data, the Sea of Azov is very rich in hydrobionts with various types of osmoregulation. In fact only stenohaline marine hydrobionts of freshwater origin (osmoconformers-I, II) and also euryhaline Australian hydrobionts of freshwater origin (amphiosmotics-II) are absent.

As a result it is possible to find in the Sea of Azov practically all barrier salinities. Barrier salinities of lower salinity range are expressed in the estuaries of Azov rivers, and those of the higher one are expressed in Sivash Sea and in poly- and hyperhaline shallows.

Global Change in Antarctic Pelagic Ecosystems: Effects of Bottom-up Regulation (Iron Fertilisation) and Top-down Control (Krill–Salp Interactions) on Plankton Biomass

U. Bathmann

***Alfred-Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany***

Several experiments have demonstrated that iron supply leads to enhanced primary production in the Southern Ocean as in other high-nutrient-low chlorophyll (HNLC) open ocean areas. But in all *in situ* experiments to determine processes that follow such iron supply, the long-term fate of the carbon fixed additionally remained unknown. Contrary to the com-

mon assumption that zooplankter play a minor role in plankton productivity of Southern Ocean HNLC areas, zooplankter structure and influence phytoplankton development and thus alter carbon flux, as we will show from results of two iron fertilization experiments EisenEx and EIFEx in the Atlantic sector of the Southern Ocean. As EIFEx was successful of stimulating a phytoplankton bloom in an closed oceanic eddy located in the Antarctic Polar Front, we also could follow the fate of the accumulated carbon into the ocean interior and to the deep-sea sediments between January and April 2004.

In areas of the Southern Ocean that are subject to iron (natural or man-made) fertilization, and in some other HNLC regions, Antarctic krill *Euphausia superba* dominates the pelagic biota. The life cycle of this species is well adapted to the Antarctic sea ice and the hydrographic feature of some regions in the Southern Ocean. In recent times it became more evident that global change might also effect this species as salps became more abundant in areas previously known as krill grounds. Consequences of these two scenarios for future ecosystem structure and carbon sequestration in the Southern Ocean will be discussed.

Mechanisms of Salinity Adaptation of Osmoconformers

V. Ya. Berger,* A.D. Kharazova**

***Zoological Institute RAS, St. Petersburg, Russia**

****St-Petersburg State University, St. Petersburg, Russia**

Osmoconformers lack capacity of osmotic regulation on the level of the organism. Nevertheless many of them can tolerate significant changes in salinity thus substantially contributing to the fauna composition of estuary, littoral and other biotopes with fluctuating salinity. Euryhalinity of os-

moconformers is provided by a complex of molecular, cellular, organism and population mechanisms of adaptation. These mechanisms form differently depending on animal species and play different role in water basins with different salinity regime.

Original and literature data on mechanisms of salinity adaptation are discussed, including biosynthetic activity of cells, their non-specific and specific resistance, changes in electrophoretic pattern of proteins, intracellular isoosmotic and volume regulation, pseudoosmoregulation (short-term osmotic regulation according to Davenport, 1979) on the level of the organism, population mechanisms of adaptation, etc.

The role of mechanisms of salinity adaptation in the evolution of osmoconformers and in the formation of fauna of water basins with different salinity regime is analyzed.

We also speculate on the possible interrelationship between the defense (immune) reactions of the organism caused by antigen and processes of salinity adaptation.

Performance Studies of *Arenicola marina* in a Latitudinal Cline

C. Bock, A. Wittmann, M. Schröer, H.-O. Pörtner

***Alfred-Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany***

Climate change affects individual organisms and their performance capacity, thereby eliciting drastic changes in the composition and function of ecosystems. Based on the observation that the thermal tolerance of individuals and their populations vary depending on latitude and associated temperature means and variability, knowledge of the physiological mechanisms underlying thermal tolerance in organisms

from different populations will support predictions of the effect of climate change on organismic up to ecosystem levels. Previous studies on different lugworm populations (*Arenicola marina*) have shown that oxygen supply versus demand are most crucial in thermal adaptation and limitation.

In this talk data from previous studies of the oxygen limitation of thermal tolerance in lugworm populations from a wide latitudinal regime ranging from the Atlantic, North Sea up to a sub-polar population of the White Sea will be presented. In addition, studies of the temperature dependence of ventilatory peristalsis, of oxygen consumption, energy metabolism as well as growth performance have shown a clear dependence of performance parameters of *A. marina* on seasonal and latitudinal conditions. Currently, studies of the dependence of performance capacity of different *A. marina* populations on temperature dependent oxygen supply are underway. The implications of these results for the different populations in the context of climate change will be discussed.

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Immune Reactions in Marine Invertebrates

T. C. G. Bosch

Zoological Institute, Christian-Albrechts-University, Kiel, Germany,

Many components of the innate immune system in vertebrates can be reliably traced to urochordates and successful strategies for the detection and elimination of pathogens are present at that level of animal evolution, but the issue of where and how the adaptive immune system emerged is still obscure. There is a paucity of evidence for a gradual transition from the innate immune system of invertebrates to the

recombinatorial immune system of higher vertebrates. None of the classical elements of MHC based transplantation immunity (MHC, TCR) or humoral immunity (Ig) have been found in urochordates. This remarkable paradox raises a number of questions. How do these ancestral chordates discriminate between the constituents of the external world and the constituents of “self”? Are these strategies universal within the animal kingdom and among chordates, or are different strategies used by representatives of the different taxonomic groups? The current state of our knowledge indicates that the immune system of lower chordates is very different from that of cartilaginous fishes. Pure homology hunting for vertebrate-specific immuno-relevant molecules in invertebrates is therefore of limited value. A more promising approach may involve unbiased functional screening methods. We discuss here the outcome of two such approaches. First, to gain insight into the molecular changes associated with allorecognition in *Botryllus*, we carried out a comparative analysis of gene expression profiles between naive and rejecting colonies. And second, based on the fact that a prerequisite for any histocompatibility system is the presence of highly variable molecules which should vary between individuals, we compared the somatic transcriptomes of several *Ciona* individuals with the goal to identify cDNAs which are variable between these individuals. We show that these comparative studies shed light on the evolution of the innate immune system in deuterostomes, the emergence of adaptive immunity, and the mechanisms of allorecognition.

Local Effects of Global Change: High Resolution Reconstruction of Mollusk Life and Environmental History

T. Brey

***Alfred-Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany***

Lifetime growing carbonate skeletons can serve as archives of environmental and living conditions during the organism's life, as they record proxies in form of growth increments, stable isotope ratios and trace element concentrations. Long lived organisms offer the opportunity to establish decadal or even longer time series of such parameters which can be analysed for long term changes and oscillations coupled to large scale climate phenomena such as ENSO or AO/NAO. In boreal and polar waters research concentrates on long lived molluscs such as the bivalve *Arctica islandica*. So far, the focus of such investigations is the reconstruction of past environmental conditions, i.e. we use the organism to learn about the past environment, preferably at larger scales. Here, we will explore whether and how those proxy time series may be used to reconstruct ecological history: How developed the performance of the organism, the population, and maybe the community at local and at larger scales?

Transmission Adaptations of Parasite Life Cycles in Northern Coastal Ecosystems and the Climate Change Perspective

K.V. Galaktionov

Zoological Institute RAS, St. Petersburg, Russia

Parasitism is now widely recognized as a factor that influences the composition and structure of natural animal communities. As applied to marine realm the coastal ecosystems turn out to be most influenced by parasites. The rich and abundant fauna of animals associated with intertidal and upper subtidal zones promotes transmission of complex parasite life cycles involving coastal invertebrates, fish and birds as intermediate and final hosts. Taking into account the global climate change perspective we analyzed a complex of adaptations of parasite life cycles to transmission in coastal ecosystems of Arctic and sub-Arctic. We focused mostly on trematodes as the most abundant parasites in coastal communities. It has been shown that parasites with two-host life cycles devoid of free-living larvae predominate in the Arctic regions. If climate in Arctic becomes milder distribution areas of parasites with more complicated life cycles (majority of parasitic worms) may extend to the north. Long-term studies on trematodes in intertidal communities show that all aspects of larval trematode development and activity associated with their first intermediate hosts (molluscs) display regular seasonal variations that are ultimately temperature dependant. In the cold season, structure of sporocyst/redia infrapopulations inside molluscan hosts is modified in such a way that production of dispersive larvae (cercariae) stops. In spring, the infrapopulations of sporocysts and rediae resort to their functional mode and cercarial production resumes. Cercarial release from molluscan hosts often displays daily

rhythms and longer periodic patterns of increased release that are temperature related. In addition, total cercarial production (over the entire transmission period) correlates positively with water temperature. The same applies to cercarial infectivity for second intermediate hosts. It is clear that trematode transmission from the first intermediate host to the second one only occurs in a temperature above critical. An increase in water temperature due to global warming would therefore widen the window for larval trematode transmission and result in an increase of marine animal parasitism in northern coastal ecosystems.

Investigating Ecological and Physiological Consequences of Environmental Change

O. Heilmayer, T. Brey

***Alfred-Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany***

There is an urgent need to increase our understanding of mechanisms by which animals respond to their environment, especially for organisms that occur in stressful habitats or at the edge of their range. This is becoming increasingly important to predict changes in the structure of ecological communities as a consequence of anthropogenic climate change.

Temperature is one of the most significant abiotic factors in marine ecosystems. It affects almost all facets of organismal physiology, from the basic structures of macromolecules to the turnover rates of complex physiological systems. Hence, adaptation to environmental temperature has been recognized for a long time as one of the major challenges in evolutionary adaptation and is thought to be dependent, to a large extent, on the organism's ability to undergo metabolic reorganization on both short-term and evolutionary time-

scales.

This talk will give an overview about recent developments of our research using biochemical indicators (RNA/DNA, Hsp70 and so on) concomitantly with organismal and ecological measures of responses to climate change (i.e. growth rates, growth performance, metabolic rate, survival and so on) to gain a better insight into the adaptation of marine invertebrates (i.e. scallops and oysters) to extreme environmental conditions.

Long-term Changes in the Communities Associated with Dense Assemblages of Blue Mussels: Old Theories and New Data

V.M. Khaitov,* A.D. Naumov, A.V. Artemyeva,***
M.V. Fokin,** E.L. Yakovis*****

****St. Petersburg Palace of Youth Creativity,
St. Petersburg, Russia***

*****Zoological Institute RAS, St. Petersburg, Russia***

******St. Petersburg State University, St. Petersburg, Russia***

Communities with obvious keystone species are convenient objects for research of long-term processes. Dense assemblages of mussels are favourite such an object in the White Sea. During the investigations that were carried out by Lukanin, Naumov and Fedyakov, the model of autocyclic long-term changes of dense settlement of mussels (LNF-model) has been developed. According to this model, a mussel bed should demonstrate alternation of periods of mass mussel perishing and periods of prosperity of mussel population. This model is based on negative influence of adult mussels on larvae and juveniles. The cycles predicted by LNF-model have been shown on many natural settlements of mussels in different parts of the White Sea. At the same time, the

long-term dynamics of populations of other species inhabiting mussels' assemblages is practically not investigated. During long-term investigations of several natural mussel settlements in the Kandalaksha and Onega Bays of the White Sea it has been shown, that cyclic changes in settlements of mussels was associated with changes in populations of other members of community. The complex of opportunistic species (Capitellidae and Spionidae polychaetes, several species of amphipods) starts to dominate on a mussel bed during periods of old mussels perishing. Various predators (nemertins, polychaets, priapulids) are numerous also during this period. During periods of prosperity of mussel population a mussel bed is inhabited by species lacking in pelagic development stages (oligochaetes, several species of gastropods) or by adult mobile forms (*Macoma balthica*, *Hydrobia ulvae*). In addition, it has been shown, that during certain periods on mussel banks filamentous algae (*Cladophora*, *Enteromorpha*) start to grow intensively. It is possible, that this process is caused by inflow of nitrates and phosphates caused by mussels' activity. At the same time, filamentous objects are favourite substrates for mussel plantigrades. These data allows to modify LNF-model. According to modified LNF-model absence of juveniles in mussel assemblages is a consequence of absence of substrates for larvae settlement. Periodic blooms of filamentous algae stimulate inflow of juveniles. After settlement, young mussels press a layer of algae to bottom that lead to perishing of algae and old mussels (because of low oxygen concentration) whereupon young molluscs form new population.

Ecological Similarities and Differences: Species Characters in the North Sea and the White Sea

R. Knust

***Alfred-Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany***

A number of key species of the Wadden Sea Area in the southern North Sea show a boreal distribution and are also inhabitants of the shallow waters in the White Sea. Fishes like cod (*Gadus morhua*), eelpout (*Zoarces viviparus*), butterfish (*Pholus gunnelus*), sea scorpion (*Myoxocephalus scorpius*) and invertebrates like *Crangon crangon*, *Arenicola marina* and *Mytilus edulis* are prominent examples. Although this overlap of species could be found, both areas are significantly different in their climate regime. Key eco-physiological processes which determine population structure and dynamics of a species are reproduction, growth and mortality. These parameters are strongly related to the climate regime and the main driving force is temperature. In the light of current and future climate change, a deeper understanding of the mechanisms behind the relationships between water temperature regimes and biological responses is necessary to understand the changes in species distribution and biodiversity. To deepen our understanding comparative investigation of species living in different climate regimes is a promising tool. The talk will present results from bilateral research in the 1990-s and will propose possible future projects in the North and White Seas.

Microscale Evolution in Cod (*Gadus morhua*) along a Latitudinal Cline: Mitochondrial Capacities and Gene Expression

M. Lucassen, N. Koschnick, H.-O. Pörtner

***Alfred-Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany***

Mitochondrial functions and their alterations with temperature are proposed to be key processes in seasonal as well as evolutionary temperature adaptations of ectotherms. Molecular approaches are necessary for an understanding of the genetic basis and the regulatory networks involved in temperature adaptation. To examine whether gene expression mechanisms contribute to different settings of aerobic capacities in populations of cod (*Gadus morhua*) along a latitudinal cline, maximum activities of key enzymes of mitochondrial metabolism and their respective mRNA levels were compared in white muscle and liver of cold and warm acclimated individuals from populations of the North Sea (NSC) and the Barents Sea (NEAC), respectively. Differences between populations at the functional levels became evident mostly at cold temperature with higher capacities in the sub-Arctic population. Evidently, the sub-Arctic NEAC was more capable of cold acclimation than the population of NSC. In the case of muscle citrate synthase, the increments in enzyme activity were accompanied by elevated transcript levels and indicated transcriptional control, whereas such a strong correlation was absent for cytochrome-*c* oxidase. Overall, the comparison of functional levels and transcript levels may reflect genetic differentiation at functional sites between the two populations. By differentiation into genetically and functionally distinct populations Eastern Atlantic cod may extend its distribution over a larger latitudinal range than would be possible for one genetically uniform population. Very likely,

the genetic differences reflected in our present data are only representative of a larger array of genetic differences, which underlie the observed functional patterns. Therefore, the second part of the talk will focus on genomic approaches to identify such differentially expressed genes within the latitudinal cline and new candidate genes with so far unknown functions, which contribute to thermal plasticity.

Long-term Monitoring as a Methodological Approach in Studies of Bivalve Mollusks in the White Sea

N.V. Maximovich, A.V. Gerasimova

St. Petersburg State University, St. Petersburg, Russia

Our monitoring of populations of common species of bivalve mollusks in the White Sea includes about 20 populations of more than 10 species, inhabiting 12 different habitats from mid-intertidal zone to a depth of 40 m. Studies are carried out in 1-3 years interval in June-July. The main aim of long-term monitoring is to study and model the principles of spatial-temporal organization of molluscs populations. During a study period mollusc populations showed different stability patterns. One of the typical features was the absence of stability in age structure of populations. Recurrence in age structure reflected extremely instable annual recruitment patterns. If relatively regular annual recruitment is maintained populations are formed that can be viewed as stationary.

Long-term Dynamics of Abundance in the Eelgrass *Zostera marina* in the Chupa Inlet (White Sea, Kandalaksha Bay)

A.D. Naumov

Zoological Institute RAS, St. Petersburg, Russia

Both long-term and seasonal dynamics in *Zostera marina* and associating flora and fauna (more than 100 of animal and algae species) were studied during 19 years (1987–2006) every hydrological season at two sites on the Chupa Inlet intertidal (75 sampling periods, 578 benthic stations, 1614 benthic samples). Besides clearly expressed seasonal dynamics, an approximately 10-years-long periodic trend of the sea-grass biomass changes was found at one of the sites. It explains a small part of total dispersion however. Moreover, cyclic biomass oscillations of about 5-years-long duration were discovered at both sites. This trend together with the seasonal one explains the most part of the total eelgrass biomass dispersion.

The 10-years-long trend mentioned above fits the cycle of solar activity with a lag of around 2 years, but this relationship cannot be considered as significant due to low level of explained dispersion. No association between 5-years-long cycle and salinity changes was found out. At one of the sites investigated, a weak link with ice melting conditions can be followed. A significant correlation (0.710 ± 0.137) between this cycle and array of average summer seawater temperature shifted by 3 years backward was found at the same site. Extracting time variables from averaged summer temperature time-series shows a statistically significant 5-years-long trend. It correlates with corresponding trends of eelgrass biomass oscillation at both sites ($r = 0.939 \pm 0.033$ and 0.666 ± 0.154) on the assumption of 3-years-long lag. Inves-

tigation of relationship between trends mentioned above and shifted for 3 year backward AOI showed only correlation with oscillations in June ($r = 0.948 \pm 0.028$ and 0.783 ± 0.107).

The direct comparison of observed biomass with temperature changes and AOI does not show any correlation.

Thus, the straight impact of main abiotic factors cannot be considered as a proved one. They affect only some tendencies in *Zostera marina* biomass oscillations, which can be only seen in filtered time variables. The main changes of biomass in *Zostera marina* most probably can be explained by influence of intraspecific and interspecific biotic factors.

Longevity in *Arctica islandica* – Environmental Constraints and Evolutionary Adaptation

E. Philipp, T. Brey, D. Abele

***Alfred-Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany***

The ocean quahog *A. islandica* is among the longest-lived and slowest growing of marine bivalves with maximum ages > 300 years (e.g. Schöne et al. 2003, 2004). The animals exhibit a unique behaviour of self-induced metabolic reduction, by seemingly at random burrowing under to anoxic sediment layers (Taylor 1976). The time burrowed represents a period of deliberate metabolic reduction with heart rates suppressed to 10% of normoxic levels (Taylor 1976). Living at a much “slower” pace increases individual life span (Yoon et al. 2002) and therewith the chances to participate in yet more reproduction events. However, in mammals, chronic intermittent hypoxia increases oxidative stress (Peng & Prabhakar 2003) and, both, hypoxia and oxidative stress cause functional and biochemical changes (Chi & Karliner 2004). We

conjecture that chronic anoxic/oxic exposure fosters the extreme stress resistance in *A. islandica*. The Ocean quahog is the only animal known to deliberately induce a torpor-like state that does not serve to escape adverse conditions (like hibernation in snails and frogs) but, presumably, to prolong individual life span. This behaviour speaks for a unique level of stress competence (Diaz & Rosenberg 1995, Storey 1996, Abele 2002), presumably based on unique physiological and genetical features.

Investigations of quality and plasticity of the hypoxia response and of the biochemical cue for surfacing in young and aged individuals from different populations with distinct maximum life span (Baltic, White Sea, Mid Atlantic) will provide insight into physiological and genetic mechanisms of the extraordinary stress hardiness in *Arctica islandica*.

Physiological Constraints Involved in Setting Limits to Biogeography and Biodiversity?

H.-O. Pörtner

***Alfred-Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany***

Through functional analyses, integrative physiology is able to link molecular biology with ecology as well as evolutionary biology and is, thereby, expected to provide access to an integrative understanding of the patterns of evolution and ecology. This task is challenging especially at the highest levels of functional complexity found, in animals and plants. By identifying the tradeoffs and constraints involved in environmental adaptation the principle reasons should become accessible that limit each species to specific habitats. Such an approach will also give access to the mechanistic bases of organismic responses to environmental alterations, including

climate change.

Accordingly, our physiological studies at molecular, cellular and organismic levels currently aim to clarify the mechanistic basis of bio-geographical patterns on large scales, i.e. in a latitudinal cline, as they are determined by various climate regimes and associated abiotic factors like temperature, oxygen or CO₂. Key elements of previous data have been elaborated in collaboration with colleagues from the Russian Academy of Sciences, St. Petersburg, in various phyla across a latitudinal cline, including the White Sea. Some mechanisms as well as constraints and tradeoffs involved in thermal adaptation and in the setting of tolerance windows of ectothermic animals have been identified and led to the concept of oxygen and capacity limited thermal tolerance. Current hypotheses address the bio-energetic consequences of thermal adaptation with important implications at the ecosystem level. Associated modifications in energy budgets require investigation, as well as their consequences for growth, reproductive output, capacity for motor performance, lifestyle strategies including aging and possibly, even biodiversity. In this context, an integrated view of gene functions at various complexity levels up to the whole organism is required for an identification of mechanistic links between environment, evolutionary history and the organism's survival and success.

Long-term Observations of Macrozoobenthos Populations and Communities in the North Sea Compared with Results from the Barents Sea

E. Rachor

***Alfred-Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany***

Macrozoobenthos has been annually studied at 4 stations in the offshore waters of the German Bight by the AWI and its predecessor since the second half of the 1960s. In addition, survey data of the whole area are available from 1923, 1965, 1975 and 2000. These data show changes related to eutrophication and intensive demersal fisheries as well as some alterations that can be interpreted as driven by warming. The results are compared to changes known from the Barents Sea.

The Invasion of the Pacific Mussel *Mytilus trossulus* into the Barents and White Seas

P. Strelkov,* H. Bufalova,* M. Katolikova,* A. Sukhotin,
R. Vainola*****

****St. Petersburg State University, St. Petersburg, Russia***

**** *Zoological Institute RAS, St. Petersburg, Russia,***

***** *Finnish Museum of Natural History, Helsinki, Finland***

Originally, our study questioned the peculiarities of the blue mussel *Mytilus edulis* population dynamics in the SW Barents Sea, in particular collapse of mussel stocks in late 1960th. However in the frame of the study taxonomical integrity of the Barents Sea mussel was questioned. In our presentation, we summarise data on the long-term *Mytilus* spp. dynamics in the Barents Sea and examine its probable link

with climate; prove the presence of the so-called Pacific mussel *M. trossulus* in the Barents and also White Seas and present data on *M. edulis* and *M. trossulus* mutual distribution; question the obstacles of *M. trossulus* invasion into the region. It is concluded that mussel populations in the Barents Sea are unstable; their dynamics is temperature-dependent. *M. trossulus* dominates in the regions of several harbors and was possibly recently introduced there with ships from West Atlantic populations. However substituted data indicates that in early Holocene the Pacific mussel was widely distributed in Northern Europe, and we are faced with the specie re-colonization of its historical area.

Longevity, Size and Growth of Aquatic Poikilotherms in Latitudinal Temperature Gradients

A.A. Sukhotin

Zoological Institute RAS, St.-Petersburg, Russia

Variation in longevity, maximal size and growth rate which are functionally interrelated in continuously growing animals is discussed for aquatic poikilotherms within latitudinal (climatic) gradients. Maximal longevity depends on the maximal size which can be attained by the species in a certain habitat and on the growth rate at which this maximal size is approached. The present data on growth variability in *Mytilus edulis* L. in North-European seas show that basic growth characteristics depend mostly on local conditions in specific habitats rather than on climatic/temperature clines. Similarity of maximal lifespans of mussels from latitudinally separated populations can be explained by similar metabolic rates at ambient temperatures due to metabolic compensation in cold adapted animals. Several methods of growth comparison are

discussed. An analytical method that allows comparing growth performance in a certain population in different years irrespective of age and generation of animals is suggested. The method implies a statistical analysis of size-specific age-corrected annual growth increments of animals in a sample, which makes possible also to compare growth success of different generations in one of several populations. Long-term (1983-2003) reconstruction of growth performance in *Mytilus* in the White and the Barents Seas is presented and discussed along with the sea water temperature changes in the respective areas.

Flexibility of Zooplankton Community to the Hydrological Environmental Changes in the White Sea

N.V. Usov, D.M. Martynova, I.M. Primakov

Zoological Institute RAS, St. Petersburg, Russia

It is well known that seasonal changes of temperature and salinity are rather wide in some Arctic seas and in the White Sea, as well. The temperature and salinity amplitude may reach up to 16°C and 6 PSU in the surface water layers, respectively (Babkov, 1998). The dependence of zooplankton community structure to such parameters in the White Sea was first shown by Babkov, Prygunkova and Golikov (1989).

Careful analysis of more than 36-year hydrological and plankton time-series data permits us to reveal the subtle differences of zooplankton abundance due to the environmental changes. The differences in seasonal hydrological parameters are usually unique to every year of observation and are exposed to the environment factors of previous year. The breeding periods both of arctic and boreal species are strongly depend on temperature, e.g. on the temperature op-

timum of the each species. The aggregate trend of hydrological environment causes the reportioning of zooplankton species impact to the community structure. The temperature factor impact is major as to the total zooplankton abundance so to the population parameters of the different species. Nevertheless, the population abundance tends to reach annual average even after the strong deviations.

The long-term observations also possess to exploit the potentialities of cyclability and long duration climatic trends. The analysis of such data shows the slight rise in total annual temperature in the White Sea during the last forty years. Nevertheless, the annual average zooplankton abundance, species impact and vertical community structure seem to have no any reliability changes. Thus, we state that zooplankton community in the White Sea is rather stable for the hydrological (climatic) changes in the observation period.

Plurality of Steady States of Fouling Communities as an Adaptation of Benthic Organisms to Specific Environmental Conditions

V.V. Khalaman

Zoological Institute RAS, St. Petersburg, Russia

Succession nature of development of marine fouling communities has been repeatedly disputed. The reasons of these debates are significant stochastic component in development of fouling assemblages, presence of several stable terminal stages, and a significant role of seasonality in fouling formation. However, the studies having led to these conclusions were based on relatively short time of observations and dealt only with the initial succession stages, which are indeed very variable. In fact, successions in bottom communities last for tens of years, which is comparable with succes-

sions in terrestrial ecosystems. At closer examination, multiple stable stages appear to reflect micro-differences in abiotic environmental conditions, while seasonal changes are smoothed at longer exposures. Regardless to all the diversity of specific ways of fouling communities' development, in an absence of external catastrophic impacts the main characteristic is replacement of *r*-strategists by *K*-strategists. Any type of fouling community has its analog among benthic assemblages, while the whole course of fouling development is directed to formation of community that maximally corresponds to the natural community typical for the specific environments.

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