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# Ecology of host-parasite relationships in the brackish SW Baltic Sea, with special regard of small-size fish – a review

## Ökologie der Wirt-Parasit-Beziehungen in der brackigen SW-Ostsee unter besonderer Berücksichtigung von Kleinfischen – ein Rückblick

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**Summary:** This review examines the relationships of parasites to hosts and host communities in a brackish water environment. After six local parasite communities have been investigated at the SW coast of the Baltic, the existence of a regional parasite fauna became evident. Density of parasites and hosts were examined by analysis of supra-populations. The investigation of supra-communities revealed the existence of core and satellite species, which vary between single hosts. Specifity of several parasite species became obvious by comparison of several host species of a guild. The numbers of specialist and generalist parasites within guild communities may be used as indicator for the quality of the environment. Prevalence, which reveals the range of microhabitats occupied by parasites in diverse hosts, is a characteristic measure of component populations. Component communities describe the diversity of parasites in host populations, which also allows conclusions on the quality of the environment. The calculation of the intensity of infra-populations may indicate zero, normal or massive parasite infections; the last case may be caused either by high infection of the intermediate hosts, accumulation or special host-parasite-relationships. The infra-community is a measure for parasite capacity and richness in a single host. The calculation of an infra-community index makes affinities and competition between parasites evident. The combined results are the basis of a model, in which colonizing parasites were filtered by genetic, phylogenetic and ecological distances. The respective strengths of two environmental stressors in the Baltic Sea, brackish water and eutrophication, can influence colonization of parasites and parasite composition in different localities.

**Key words**: Level concept, colonization of hosts, salinity, eutrophication

**Zusammenfassung:** Diese Rückschau behandelt die Beziehungen zwischen Parasiten und ihren Wirten und Wirtsgemeinschaften in einem Brackgewässer. Nach Untersuchung von sechs lokalen Parasitengemeinschaften der südwestlichen Ostsee wird die Existenz einer regionalen Parasitenfauna in diesem Areal wahrscheinlich. Die Dichte von Parasiten und Wirten wird durch die Analyse von Supra-Populationen offenbart (Abb. 1). Die Untersuchung aller Parasit-Wirtsbeziehungen (Supra-Gemeinschaften) enthüllt die Verteilung von Kern- und Satellitenarten, die sich jeweilig zwischen den einzelnen Wirtsarten unterscheidet. Beim Vergleich verschiedener Arten einer Wirtsgilde kann die Spezifität von Parasitenarten erkannt werden. Die Anzahl von Generalisten und Spezialisten innerhalb einer Gildengemeinschaft wird als Indikator für die Qualität der Umwelt verwendet. Die Prävalenz als Kennzeichen der Befallstärke einer Wirtspopulation ist ein typisches Maß für die Komponentenpopulation. Komponentengemeinschaften beschreiben die Diversität der Parasitengemeinschaften in den einzelnen Wirtspopulationen und geben ebenfalls Hinweise auf die Qualität der Lebensräume. Die Berechnung der Intensitäten einzelner Parasitenarten in Wirtsindividuen (Infrapopulationen) kann geringen, normalen oder massiven Befall anzeigen, im letzteren Fall wird als Grund entweder ein hoher Befall des Zwischenwirtes, Anreicherung von Parasiten über die Nahrung oder spezielle Wirt-Parasitenbeziehungen angenommen. Die Infragemeinschaft ist Maß für Kapazität und Artenreichtum von Parasiten in einem Wirtsindividuum. Mit Hilfe eines Parasitengemeinschaften-Indexes werden Toleranz oder Konkurrenz innerhalb einer Parasitengemeinschaft aufgedeckt. Diese Ergebnisse sind kombiniert miteinander die Grundlage eines Modells, in dem Parasiten bei ihrer Infektion von Wirten durch

genetische, physiologische und ökologische Distanzen mehr oder weniger gehindert werden. Zusätzlich können zwei Stressoren im Ostseewasser, verringerter Salzgehalt und Eutrophierung, die Kolonisation von Parasiten und Parasitengemeinschaften in verschiedenen Standorten beeinflussen.

**Schlüsselwörter**: Stufenkonzept, Besiedlung von Wirten, Salzgehalt, Eutrophierung

## 1. Introduction

Ecological investigations focus on the analysis of structure and dynamic of which the two important components are habitat and biocenosis (Krebs 1994). These influence each other by several relationships. Whereas most habitats of free living organisms are characterized by abiotic factors, the habitats of parasites are living hosts which, together with other parasites, can establish a more or less extent community. Esch et al. (1975) presented a "level concept" of host-parasite systems, which had been successfully used in the parasitological literature (Bush et al. 1997). These levels regard communities and populations of parasites, and communities, populations and single individuals of hosts. Later on, the guild, a group of related species, was added as a further host level (Zander 1998a, 2001). The combination of host levels with the levels of parasites results in establishing eight categories (fig. 1.), which can be analyzed within a single locality and is presented by the local parasite fauna. Such an analysis includes several important parameters like intensity (level infra population) and prevalence (level component population) as well as ecological niche (level infra community) and diversity (level component community). The level of the guild population is used to reveal specifity of parasites, that of

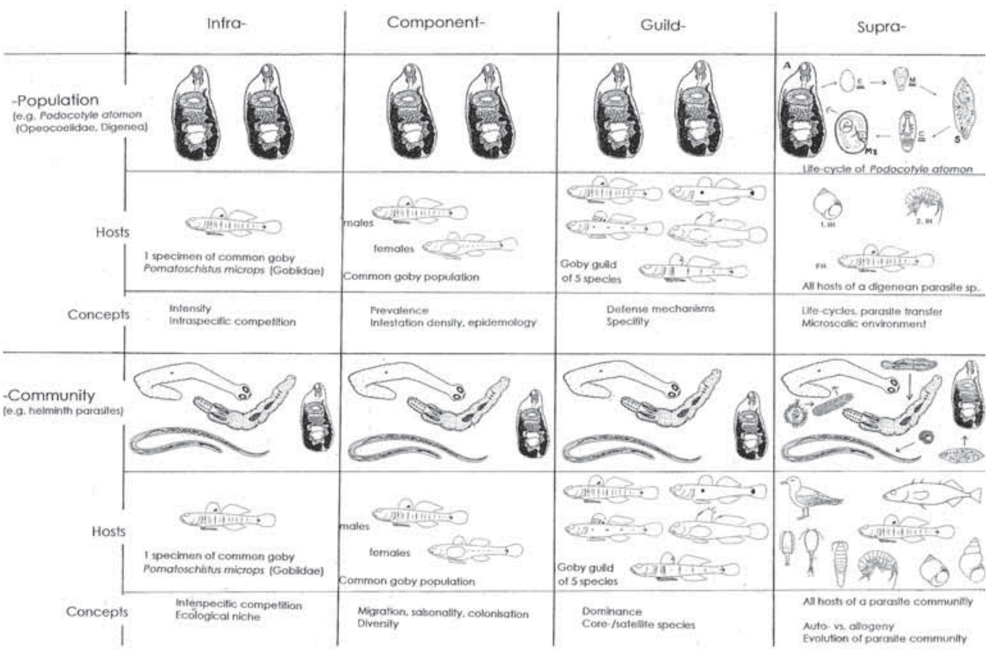



**Fig. 1:** Model of levels in the ecological parasitology, in which four levels of hosts (individual, population, guild, community and two levels of parasites (population, community) are distinguished. Each level is provided with concepts important in parasite ecology (from Zander 2001).

**Abb. 1:** Stufenmodell in der ökologischen Parasitologie. Vier Stufen der Wirte (Individuum, Population, Gilde, Gemeinschaft) werden mit zwei Stufen der Parasiten (Population, Gemeinschaft) kombiniert. Jede Stufe ist mit Konzepten ausgestattet, die in der ökologischen Parasitologie von Bedeutung sind (aus Zander 2001).

the guild community dominances of generalists and specialists. The supra population describes the transfer and cycle of a parasite species, whereas the supra community comprises all hosts and parasites of an ecosystem (fig. 1). The reservoir for local faunas of a greater area is the regional fauna, the sum of all local faunas (Holmes 1990).

The Baltic Sea presents a brackish environment and comprises a west-east gradient of salinity from the marine Kattegat until limnetic waters of the Bothnian and Finnish Bays (Matthäus 1996). The ecological investigations on parasites in the western Baltic Sea began 1989 in the locality Dahmeshöved / Ostholstein (Northern Germany) and were extended in the following time to the Danish border and western Mecklenburg which comprises an air line distance of 150 km. In this area not only a decrease of salinity is found but also a local variability of ± 3-4 ‰ dependant to the prevailing currents. In this review we prove whether the single local faunas can be distinguished from each other under the strong differences of this abiotic factor or is a regional fauna present which comprises several local faunas. Generally, brackish waters can be viewed as an extreme environment between the marine and limnetic milieu and excludes the existence of several organisms (Remane 1958).

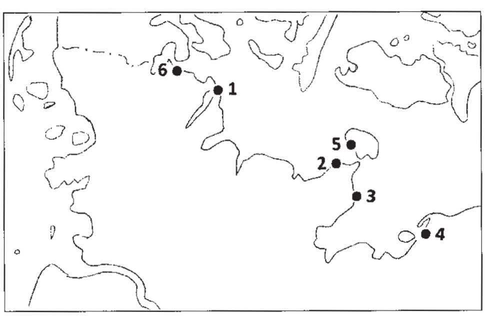



**Fig. 2:** Map of Schleswig-Holstein and NW Mecklenburg, northern Germany showing the site of the six localities investigated: 1 = Schlei, 2 = Blank Eck, 3 = Dahmeshöved, 4 = Salzhaff, 5 = West Fehmarn, 6 = Flensburg Fjord (from Zander 2009).

**Abb. 2:** Karte von Schleswig-Holstein und NW-Mecklenburg, Nord-Deutschland, mit der Lage der sechs Untersuchungsstellen. 1 = Schlei, 2 = Blank Eck, 3 = Dahmeshöved, 4 = Salzhaff, 5 = West Fehmarn, 6 = Flensburg Förde (aus Zander 2009).

Our investigations were concentrated on four localities in Kiel Bight and two localities in the joining Mecklenburg Bight (fig. 2). The salinity of these spots ranges between 19 and 8 ‰. Host objects were benthic and planktonic crustaceans, bivalves, snails, and small-size-fish, especially gobiids of which five species are distributed in the Baltic: *Gobius niger, Gobiusculus flavescens, Pomatoschistus minutus, Pomatoschistus pictus and Pomatoschistus microps.* The aim of the present review is to give an overview on the structure of host-parasite relationships beginning with the regional parasite fauna as a preliminary unit and ending on the level of the parasite infra population, which includes also the one host-one parasite relationship as the last unit of these interspecific relationships.

## 2. Regional parasite fauna

The regional parasite fauna is considered here as the sum of the parasite faunas of all six localities. These attain only partially the species numbers of the regional fauna and are only partially congruent with faunas of other localities (Zander 2009). As much as 83 parasite species were found in this region, but only eight (9 %) were found in all localities. Thus, three groups with a third of parasite species can be distinguished: species in one host only, species in two and three hosts, and species in four to six hosts. Also the parts of total numbers and the main parasite groups differed in the investigated localities. In Flensburg fjord, Dahmeshöved and Salzhaff more than 50 % of the regional parasite fauna was present, whereas Blank Eck attained the lowest value of 21 % (fig. 3). Digenea were the largest group in all localities, of lesser importance were Nematoda. Species identity was greatest between Flensburg fjord and four other localities, as it was also valid between Schlei and West Fehmarn and Dahmeshöved (high probability values of > 0.6). The numbers of parasite species in the single localities (18-49) correspond also with the numbers of joint parasite species which

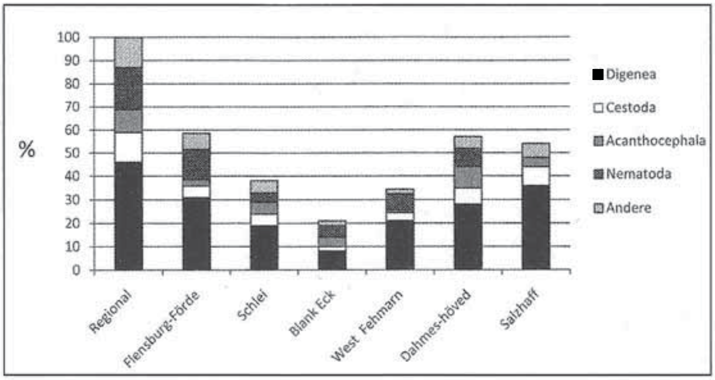



**Fig. 3:** Percentage of parasite guilds from six localities correlated to the regional parasite fauna of the SW Baltic (from ZANDER 2009).
**Abb. 3:** Anteile der Parasitengilden aus sechs Fundstellen mit ihrer Korrelation zur regionalen Parasitenfauna der SW-Ostsee (aus ZANDER 2009).

**Tab. 1:** Importance of parasites from Salzhaff, expressed as abundances by the core/satellite species model. XXX = core species, XX = secundary species, X = satellite species, o = rare species. Disregarded are parasites which were rare in all hosts (from ZANDER et al. 2000).
**Tab. 1: Die** Bedeutung von Parasiten des Salzhaffs, ausgedrückt durch das Kern-/Satelliten-Art-Modell in Form der Abundanzen. XXX = Kernarten, XX = Sekundärarten, X = Satelliten Arten, o = seltene Arten (aus ZANDER et al. 2000).

| Parasites / Hosts | *Gobius niger* | *Gobiusculus flavescens* | *Pomatoschistus minutus* | *P. microps* | *Gasterosteus aculeatus* | *Pungitius pungitius* | *Spinachia spinachia* | *Syngnathus typhle* | *Nerophis ophidion* | *Zoarces viviparus* |
|---|---|---|---|---|---|---|---|---|---|---|
| **Digenea** | | | | | | | | | | |
| *Podocotyle atomon* | o | X | X | o | XXX | o | XXX | o | X | XXX |
| *Brachyphallus crenatus* | | | | | X | X | | | | |
| *Asymphylodora demeli* | o | o | X | o | | | | | | |
| *Magnibursatus caudofilimentosa* | | | | | XXX | o | | | | |
| *Aphalloides timmi* | | | o | XXX | | | | | | |
| *Acanthostomum balthicum* | | | | o | o | o | | XXX | | o |
| *Apatemon gracilis* | | o | | XX | | | | | | |
| *Bunocotyle cingulata* | | o | | | | XX | | | | |
| *Cryptocotyle lingua* | XXX | o | o | X | o | | | | | |
| *Cryptocotyle concavum* | XXX | XX | XX | XXX | X | o | o | XXX | o | X |
| *Tylodelphis sp.* | | | | | XX | o | | | | |
| *Diplostomum spathaceum* | o | | | | X | o | o | o | o | XXX |
| *Cardiocephalus longicollis* | o | | | | XX | o | | | | X |
| **Cestoda** | | | | | | | | | | |
| *Proteocephalus filicollis* | | | | | X | o | | | | |
| **Acanthocephala** | | | | | | | | | | |
| *Pomphorhynchus laevis* | | | | o | | | | | o | X |
| **Nematoda** | | | | | | | | | | |
| *Anguillicola crassus* | | | | | | | | X | | |
| *Hysterothylacium sp.* | o | o | o | o | o | o | | | o | XX |
| *Ascarophis arctica* | | | | o | X | | | | | o |
| **Copepoda** | | | | | | | | | | |
| *Thersitina gasterostei* | | | | | XXX | o | X | o | | |

attain nine to 36. Such combinations were highest if values of Salzhaff and lowest if those of Blank Eck were regarded.

The differences between the six investigated localities may be explained by decreasing salinity and changing eutrophication. As already mentioned above, within an air line distance of 150 km between Flensburg fjord and Salzhaff salinities decrease from 19 to 8 ‰. Nevertheless much accordance was found and, thus, the existence of a regional fauna in the SW Baltic appeared very probable. The localities presented many significant accordance of species identities and percentages of infection with major parasite groups, especially Digenea (ZANDER 2009). This is especially obvious, if Flensburg fjord and Salzhaff are compared, the localities which are separated by the farthest distance. The factor salinity is not very decisive, because the organisms have adapted to fluctuating values since many thousand years (REMANE 1958). In contrast, the factor eutrophication is a phenomenon which appeared especially since the last decades after 1950 (Gerlach 1995).

The question how far the distribution of the regional parasite fauna of the SW Baltic is restricted, may be responded by the existence of the shallow Bank of Darß which can be an eastern limit with only 6 ‰ salinity (Reimer 1970). A comparison of the regional parasite faunas of the SW Baltic with that of Helgoland (North Sea) revealed extreme differences, though both lie in the boreal climate zone and are connected by the straits of Skagerrak (Zander 2005b). The reasons lie mostly on the special adaptation of hosts to the marine milieu (fig. 4). If only one host in the life cycle of a parasite is sensitive to alterations of salinity, the parasite cannot exist. The same influence has the factor eutrophication to which also many species may be sensitive. Finally, habitats may not be suited in every case to meet a host with parasite larvae and the next host in the cycle (fig. 4). For example, the snail *Littorina saxatilis*, which is first intermediate host of the digenean *Podocotyle atomon* lives in the North Sea in the intertidal zone, but in the brackish Baltic in deeper layers.

## 3. Supra community and supra population

A supra population comprises all stages of a parasite and includes also the host changes during its development. If only one stage is specialized to a certain host, the cycle of the parasite is interrupted in the case this host is not present. Such specializations are characteristic for the first stages of digeneans, but may also be valid for adults in final hosts. The digenean *Cryptocotyle concavum* is a parasite living in brackish water, which settles in the kidney of its optimal second intermediate host, the goby *Pomatoschistus microps*, which organ is a new microhabitat (Zander 2011) (fig. 5). In other fish it colonizes the skin as does generally its relative *Cryptocotyle lingua*.

The host and parasite density are positively correlated in the locality Dahmeshöved (see fig. 2). Among the parasites, which were pursued on their way from intermediate hosts to final hosts, *Hydrobia*-snails and gammarid crustaceans attained high population and also high infection density (fig. 6) (Zander 1998b). In contrast, the situation in the digenean *C. lingua* and *Podocotyle atomon* is reverse because their first intermediate host, the periwinkle, *Littorina saxatilis*, is larger than *Hydrobia* spp and, therefore, its population

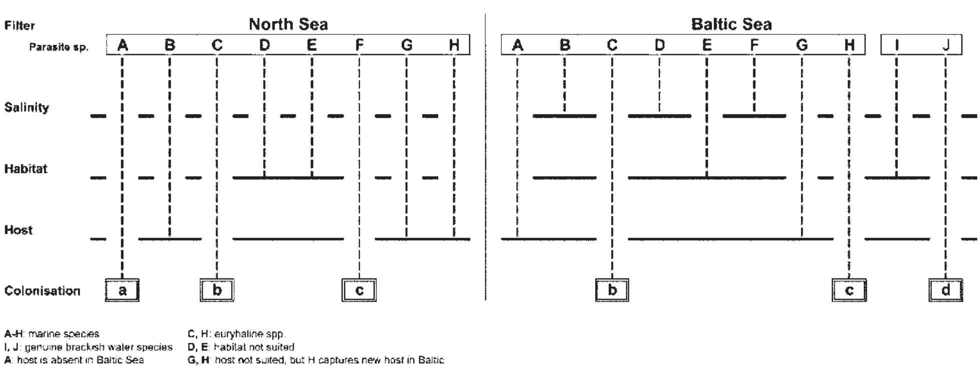



**Fig. 4:** Model of the effect of several filters for the colonization of hosts by parasites in North and Baltic Sea. **A-J** Parasite species of which I and J occur only in the Baltic; **a-d** host species. Solid lines = filters, which are partly open, dashed line = course of parasites onto their hosts. On the left side some of the most important filters are seen (from Zander 2005b).

**Abb. 4:** Modell der Wirkung verschiedener Filter in Nord- und Ostsee beim Befall von Wirten durch Parasiten. **A-J** Parasitenarten, von denen I und J nur in der Ostsee vorkommen**;** **a-d** Wirtsarten. Durchgezogene Linien = Filter, die nur z.T. offen sind, unterbrochene Linien = Wege der Parasiten zu ihren Wirten (aus Zander 2005b).

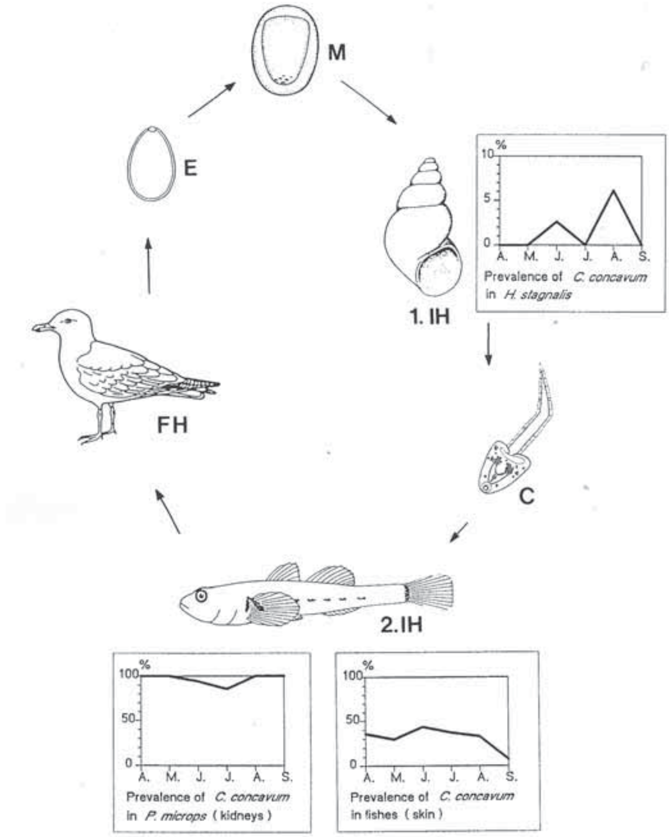



**Fig. 5:** Life cycle of the digenean *Cryptocotyle concavum*. Free living and parasitic stages and the most frequent hosts (from KESTING et al. 1996). IH = intermediate hosts.
**Abb. 5:** Lebenszyklus des Digenen *Cryptocotyle concavum*. Freie und parasitische Stadien in den häufigsten Wirten (aus KESTING et al. 1996). IH = Zwischenwirte.

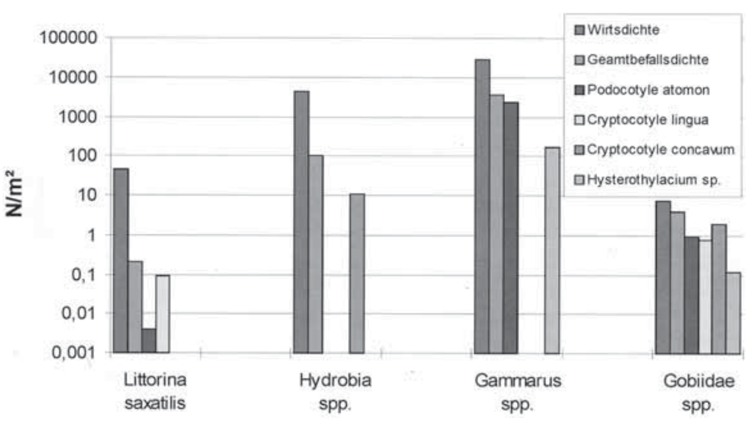



**Fig. 6:** Density of hosts (the snails *Littorina saxatilis* and *Hydrobia* spp.), benthic crustaceans (*Gammarus* spp.) and fish (Gobiidae) and their parasites (from ZANDER 1998b).
**Abb. 6:** Populationsdichte von Wirten (die Schnecken *Littorina saxatilis* und *Hydrobia* spp.), benthischen Krebsen (*Gammarus* spp.) und Grundeln (Gobiidae) und deren Parasiten (aus ZANDER 1998b).

is of lower abundance than of mud snails. This disadvantage is compensated by an extreme high production of cercariae larvae within the snails by parthenogeny. In gobiid fish, which were second intermediate or final hosts, the infection density is in order of 1-2 magnitudes lower than in the first intermediate hosts (fig. 6). That means a great loss of parasite larvae.

The structure of parasite supra communities can be described by the dominance of parasites, by the way of life of final hosts and the environment in which they live. Core species are parasites with more than 60 % prevalence and high intensity, satellite species are below 5 % prevalence; the intermediate values characterize secondary species (Holmes & Price 1986, Zander 1998a). I improved these terms by use of the abundance as the product of prevalence and intensity: where values of > 2 are core species, of 0.6-2 are secondary species, of 0.2-0.6 satellite species and < 0.2 are rare species (tab. 1). In the combination of ten fish species and 19 parasites from Salzhaff the numbers of core species attained ten, of secondary species seven and of satellite species 14. Many core species are specialists, which rarely infect other, mostly related hosts. The highest found abundance value (101) was attained by *Cryptocotyle concavum* in *Pomatoschistus microps*. Beside the parasites, which were compiled in table 3, additionally, 16 parasites on the rare species level were present in Salzhaff fish. Some of them are also host specialists (below). Obviously, every fish host can be characterized by its own core or satellite parasite species (tab. 2). In total 49 parasites species were found in snails, crustaceans and fish host from Salzhaff.

The concept of Esch et al. (1988) distinguishes parasites, which remain during its whole developmental cycle in the same ecosystem (autogenic parasites) or change the ecosystem (allogenic parasites). Examples of allogenic cycles are hosts, which remain in the aquatic habitat, but perform like sea mammals wide migrations or live like sea birds above the water level, but prey on water organisms. The eggs of parasites are shed by the birds into the water, where their developmental cycle begins (Reimer 2002). The investigations in the brackish waters of the SW Baltic Sea led to divide the autogenic parasites into two categories, i.e. in those using host either as final or intermediate hosts (Zander 2011). Mostly, autogenic parasites prevail in localities of the North and Baltic Sea within five goby species and infect these fish especially as final hosts (fig. 7). The ratio of allogenic parasites is obviously high in *P. minutus*. The relationship of auto- and allogenic parasites can indicate to what grade waters are polluted because low fish density as in oligotrophic waters is not attractive for fish predators. In contrast, eutrophic waters present an exuberant food supply, which cause increased fish density by high production of invertebrates and attract, therefore, predators (Esch et al. 1988).

**Tab. 2:** Prevalence of some parasite specialists (and generalists) in goby, stickleback and pipefish hosts from Salzhaff (from Zander et al. 2000).

**Tab. 2:** Prävalenzen ausgewählter Spezialisten (und Generalisten) unter den Parasiten von Grundeln, Stichlingen und Seenadeln aus dem Salzhaff (aus Zander et al. 2000).

| **Specialized parasites** Hosts | *Gobius niger* | *Gobiusculus flavescens* | *Pomatoschistus minutus* | *Pomatoschistus microps* | *Gasterosteus aculeatus* | *Pungitius pungitius* | *Spinachia spinachia* | *Syngnathus typhle* | *Nerophis ophidion* | Specifity index |
|---|---|---|---|---|---|---|---|---|---|---|
| *Apatemon gracilis* | | 2 | | 35 | | | | | | 0.973 |
| *Aphalloides timmi* | | | 7 | 52 | | | | | | 0.941 |
| *Acanthostomum balthicum* | | | | 0.6 | 8 | | 7 | 59 | | 0.877 |
| *Bunocotyle cingulatum* | | 2 | | | | 26 | | | | 0.864 |
| *Magnibursatus caudofilamentosa* | | | | | 38 | 1 | | | | 0.987 |
| *Schistocephalus solidus* | | | | | 3 | | | | | 1 |
| *Schistocephalus pungitii* | | | | | | 12 | | | | 1 |
| *Thersitina gasterostei* | | | | | 71 | 8 | 10 | 1 | | 0.502 |
| **Unspecialized parasites** | | | | | | | | | | |
| *Cryptocotyle concavum* | 94 | 26 | 32 | 100 | 15 | 7 | 6 | 87 | | 0.518 |
| *Podocotyle atomon* | 1 | 21 | 15 | 3 | 57 | 19 | 57 | | 83 | 0.566 |

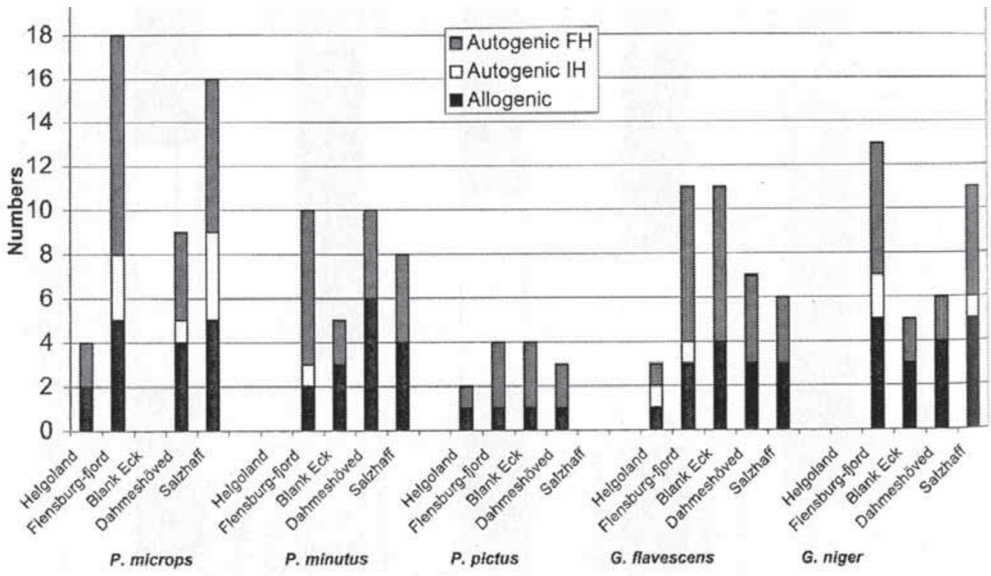



**Fig. 7:** Numbers of parasite species in five goby hosts arranged in three categories of different life cycles (from ZANDER 1998b, 2005b; JOSTEN et al. 2008).
**Abb. 7:** Anzahl der Parasitenarten bei fünf Grundelwirten, geordnet in drei Kategorien unterschiedlicher Lebenszyklen (aus ZANDER 1998b, 2005b; JOSTEN et al. 2008).

## 4. Guild population and community

A guild comprises a group of related species, which also possess much conformity of their ways of life (ROOT 1967). The parasite guild population and community can reveal, similarly as the supra community, the specifity of parasites to distinct hosts. ZANDER et al. (2000) compared related species of the fish guilds gobies (four species), sticklebacks (three species) and pipefish (two species) in the locality Salzhaff. Here, a selection of combination of single parasites and hosts presented such with high prevalence but also several others with low prevalence of the same parasite (tab. 3). Such divergences appeared also among relatives (e.g. goby, stickleback or pipefish spp.) and may be caused by the stress of the brackish environment, which may weaken the immune system of fish against parasites in different ways (tab. 4). In contrast to two species of generalists the specifity index of ROHDE (1982) is in all cases high (tab. 2).

The host numbers of a parasite species is also the basis for a way to judge about the quality of the environment. This concept regards the premise that parasite specialists may prevail in more stable, whereas generalists prevail in more stressed environments (ZANDER & KESTING 1996). Therefore, the assumption is that specialized parasites can compete out generalists in waters of good quality, but are more affected by polluted waters (HOLMES & PRICE 1986). In polluted waters, sensitive hosts or larval stages of parasites may be absent, whereas generalists can better survive, because they are able to infect many hosts (ZANDER & KESTING 1996, ZANDER 2002). Therefore, a correlation of prevalence values of parasites by their appearance in one, two or more hosts (mono- vs. polytopic) was calculated (fig. 8). The points in the figure present all prevalence values of parasites assorted to the respective monotypic (one) or polytopic (two to four) hosts. The calculated regression line expresses the increasing importance of generalists by its steepness, and, therefore, the significance of eutrophication. In Blank Eck (see fig. 2) only a shallow slope was found, which indicates a moderate pollution, whereas in Dahmeshöved, Salzhaff and Flensburg fjord steeper lines indicate

**Tab. 3:** Prevalence of selected parasites in five gobies from Dahmeshöved (from ZANDER et al. 1994, ZANDER & KESTING 1996).
**Tab. 3:** Prävalenzen ausgewählter Parasiten in fünf Grundel-Arten von Dahmeshöved (aus ZANDER et al. 1994, ZANDER & KESTING 1996).

| **Parasites** **Hosts** | *Gobius niger* | *Gobiusculus flavescens* | *Pomatoschistus minutus* | *Pomatoschistus pictus* | *Pomatoschistus microps* |
|---|---|---|---|---|---|
| *Cryptocotyle concavum* | 8 | 36 | 11 | 54 | 90 |
| *Cryptocotyle lingua* | 36 | 1 | 6 | | |
| *Podocotyle atomon* | 5 | 35 | 29 | 28 | 1 |
| *Bothriocephalus scorpii* | 3 | 5 | 4 | | 4 |
| *Ligula pavlovskii* | 2 | 4 | 3 | | |
| *Echinorhynchus gadi* | 6 | | 3 | | 1 |
| *Pomphorhynchus laevis* | 7 | | 1 | | 3 |
| *Anissakis simplex* | 3 | 1 | 1 | | 2 |
| *Hysterothylacium aduncum* | 61 | 7 | 8 | 15 | 4 |
| *Contracaecum* sp. | 11 | | 2 | | |

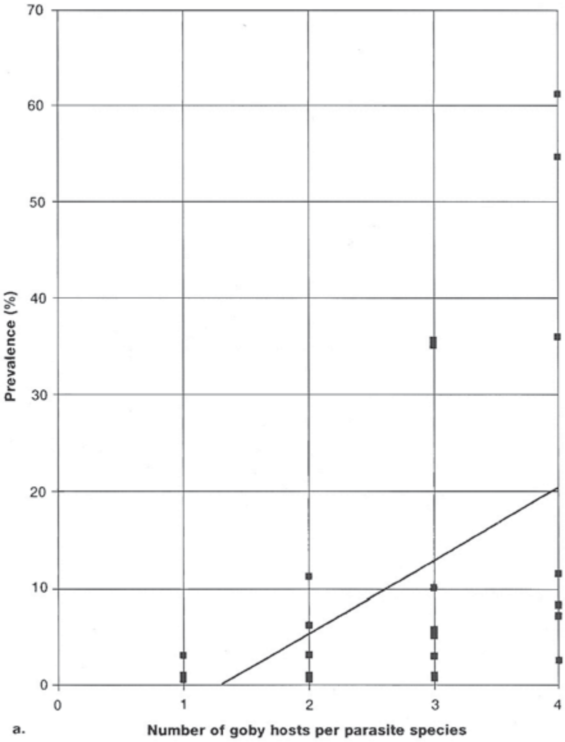
**Tab. 4:** Mean prevalence of parasites of four goby hosts from Dahmeshöved (D) and Blank Eck (B) (from ZANDER & KESTING 1996).
**Tab. 4:** Mittlere Prävalenzen der Parasiten bei vier Grundelarten von Dahmeshöved (D) und Blank Eck (B) (aus ZANDER & KESTING 1996).

| | *Gobiusculus flavescens* | | *Pomatoschistus minutus* | | *Pomatoschistus pictus* | | *Gobius niger* | |
|---|---|---|---|---|---|---|---|---|
| | D | B | D | B | D | B | D | B |
| **Digenea** | | | | | | | | |
| *Cryptocotyle concavum* | 36 | 15 | 11 | 1 | 55 | 10 | 36 | 21 |
| *Cryptocotyle lingua* | 1 | 1 | 6 | 3 | | | | |
| *Podocotyle atomon* | 35 | 5 | 5 | <1 | 10 | <1 | | |
| *Brachyphallus crenatus* | | 1 | | 1 | | | | |
| *Lecithaster confusus* | | 1 | | | | | | |
| *Asymphylodora demeli* | 1 | 1 | | | | | | |
| **Cestoda** | | | | | | | | |
| *Ligula pavlovskii* | | 4 | 3 | 3 | | | | |
| **Nematoda** | | | | | | | | |
| *Anisakis simplex* | 1 | | 1 | | | | 3 | |
| *Hysterothylacium aduncum* | 7 | 1 | 8 | 1 | | 2 | 61 | 7 |
| *Contracaecum* sp. | | | 2 | | | | 11 | 1 |
| **Acanthocephala** | | | | | | | | |
| *Corynosoma* sp. | | | 3 | 3 | | 3 | | 12 |
| *Pomphorhynchus laevis* | | | 1 | 1 | | | | |
| *Polymorphusminutus* | 1 | | 1 | | | | | |
| *Echinorhynchus gadi* | | | | | | | | |
| **Bivalvia** | | | | | | | | |
| Glochidia larvae | 1 | | | | | | | |

heavier pollution. Also the situation of the zero point of the line on the x-axis shows a trend for a shift to low values at lower stress. Most of the correlations were significant (ZANDER 2002). In the SW Baltic only positive correlations were found, in oligotrophic waters such as in some lakes even a negative correlation is to expect but was not investigated until now.

## 5. Component population and community

The basic parameter for component populations and communities is the prevalence. It is a preliminary to acknowledge the sensibility of a host to parasites in comparison to other species. Thus, among the gobies from Dahmeshöved differences become obvious by the prevalence



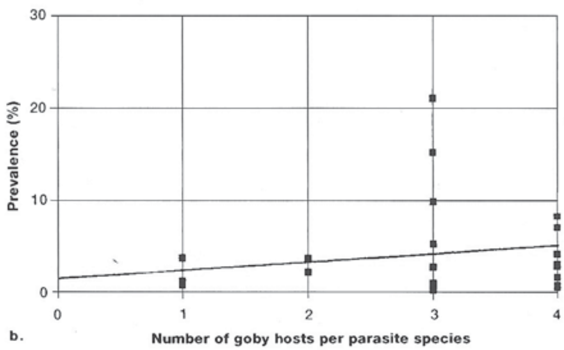




**Fig. 8:** The number of goby hosts (x-axis) infected by a parasite species arranged against their respective prevalences (y-axis). **a** Dahmeshöved ($p < 0.01$), **b** Blank Eck ($p > 0.1$) (from Zander & Kesting 1996).
**Abb. 8:** Anzahl der Grundelwirte, die von einer bestimmten Parasitenart befallen sind (X-Achse), geordnet nach deren jeweiligen Prävalenzen (Y-Achse). **a** Dahmeshöved ($p < 0.01$), **b** Blank Eck ($p > 0.1$) (aus Zander & Kesting 1996).

values of various parasites (tab. 5). Among five goby-species *Pomatoschistus minutus* presented relatively low prevalence values, whereas *Gobius niger* presented high infection by nematodes and low infection by digeneans, which were more frequently present in three other gobies (Zander et al. 1993, Zander & Kesting 1996). Among the investigated gobies *G. niger* is the only longer living species that may accumulate the nematode *Hysterothylacium aduncum*. The same species was also found in *Zoarces viviparus* (Zander 1991); on the other hand, metacercariae of *Podocotyle atomon* were observed to pass the intestinal tract of *G. niger* without the cyst was solved. A conspicuously high prevalence of *Cryptocotyle concavum* in *Pomatoschistus microps* (tab. 4) is caused by colonization of a new microhabitat in the host (see below).

Rohde (1982) distinguished the microhabitat as the place, where a parasite is regularly

**Tab. 5:** Infracommunity index (range 0-1). Bold: Important parasite-host combinations (from ZANDER 2004).
**Tab. 5:** Infra-Gemeinschaftsindex (Skala 0-1). Fett: Wichtige Parasit-Wirt-Kombinationen (aus ZANDER 2004).

| | *Gobius niger* | *Gobiusculus flavescens* | *Pomatoschistus minutus* | *Pomatoschistus pictus* | *Pomatoschistus microps* |
|---|---|---|---|---|---|
| **Ciliata** | | | | | |
| *Trichodina* ssp | | 0.09 | | 0.02 | |
| **Monogenea** | | | | | |
| *Gyrodactylus ssp.* | 0.01 | 0.27 | 0.09 | 0.08 | 0.13 |
| **Digenea** | | | | | |
| *Cryptocotyle concavum* | 0.21 | **0.33** | 0.26 | **0.45** | **0.69** |
| *Cryptocotyle lingua* | 0.23 | 0.05 | 0.07 | 0.16 | 0.04 |
| *Apatamon gracilis* | | 0.03 | | 0.01 | **0.37** |
| *Podocotyle atomon* | | **0.51** | **0.45** | **0.39** | **0.32** |
| *Aphalloides timmi* | | | < 0.01 | 0.01 | **0.59** |
| *Acanthostomum balthicum* | | < 0.01 | | | 0.13 |
| *Asymphylodora demeli* | 0.10 | 0.04 | 0.14 | 0.10 | 0.16 |
| **Cestoda** | | | | | |
| *Ligula pavlovskii* | | 0.04 | 0.07 | 0.01 | |
| **Nematoda** | | | | | |
| *Hysterothylacium aduncum* | 0.20 | | 0.12 | 0.06 | 0.02 |
| *Contracaecum* sp. | 0.08 | | | 0.05 | < 0.01 |
| *Anisakis simplex* | | | | 0.01 | <0.01 |
| *Rhaphidascaris scus* | 0.18 | 0.02 | 0.07 | 0.01 | 0.24 |
| *Ascarophis arctica* | 0.04 | | < 0.01 | 0.04 | 0.04 |
| **Acanthocephala** | | | | | |
| *Echinorhynchus gadi* | 0.20 | 0.20 | 0.16 | 0.12 | |
| *Acanthocephalus anguillae* | 0.02 | | < 0.16 | 0.01 | |

found from the macrohabitat as the habitat of its host. An analysis of three goby parasites revealed the possibility to change their special microhabitat (ZANDER et al. 1993). The nematode *H. aduncum* was mostly found in the genuine intestine but also in the stomach and rectum of host individuals, in *G. niger* also in the body cavity. *P. atomon* was generally living in the intestines but in *P. minutus* and *Gobiusculus flavescens* also in the stomachs in low prevalence. The digenean *C. concavum* was found mostly on the skin and pectoral fins, but in all *P. microps* and few *Pomatoschistus pictus* in the kidneys. Thus, also the ecological niche, which is a dynamic system between organism and environment, is in parasites accomplished by micro- and macrohabitat (ZANDER 1998a). Therefore, the analysis resulted in a wide niche of *C. concavum*, in a variable one of *H. aduncum* and in a narrow one of *P. atomon*.

Regarding species diversity (Shannon-Wiener-Index), prevalence values reveal differences in distinct host populations (ZANDER & KESTING 1996). Evenness was in three goby species in Blank Eck higher than in Dahmeshöved, only in *G. niger* the values were equal in both localities. Prevalence can also indicate changes during years and seasons. In Dahmeshöved evenness was lowest in spring and increased in summer until autumn (ZANDER & KESTING 1996). Only two values in autumn surpass the threshold of 0.6 which mean a relatively homogeneous diversity (fig. 9). This trend was also observed, if all five goby species were combined. In spring, when few parasites of the former year were still present, the evenness value was meanly 0.36 ± 0.12, in sum-

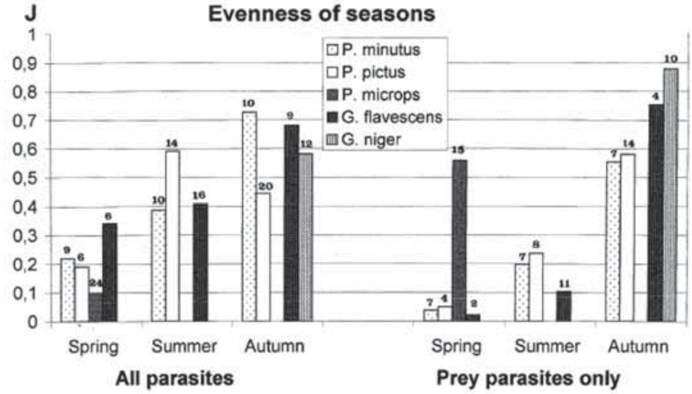



**Fig. 9:** Diversity of the parasite communities of five goby hosts from the SW Baltic at different seasons during the years 1997-2000, expressed as evenness. The numbers mark the respective parasite species numbers. Left: under regard of all parasites; right: only parasites transferred by prey organisms (from ZANDER 2005a).
**Abb. 9:** Diversität (ausgedrückt durch die Evenness) der Parasitengemeinschaften bei fünf Grundelwirten aus der SW-Ostsee von 1997-2000. Die Zahlen bedeuten die Anzahl der Parasitenarten. Links: unter Berücksichtigung aller Parasiten; rechts: nur über die Nahrung übertragene Parasiten (aus ZANDER 2005a).

mer, when rapid infection with generalists like *P. atomon* or *C. concavum* occur, it attained only 0.18 ± 0.06, and in autumn, when also the specialists have settled, it attained 0.69 ± 0.13.

## 6. Infrapopulation and community

The intensity is the basis for the investigation of a parasite population and community of a single host. The colonization of the kidney of the goby P*omatoschistus microps* by the digenean *Cryptocotyle concavum* from Fehmarn was very heavy with mean values of 300 and maximal values of nearly 3000 per single hosts (ZANDER 1998b). By comparing three localities, the host group with 64-127 metacercariae was the largest (30 %) in Fehmarn and Salzhaff by a mean intensity of ca. 100 metacercariae, whereas in Dahmeshöved the group of 32-63 larvae attained a mean intensity of ca. 50 metacercariae (fig. 10). The special situation of this host-parasite relationship will be described below.

The infection of single specimen of five goby hosts from Dahmeshöved revealed if compared differences in the ratio of parasite species numbers. These range from zero to eight parasite species, but only in *P. microps* were all and in *Pomatoschistus pictus* almost all. Most gobies fell in the group infected by one or two parasite species, only in *P. microps* groups with two and three parasite species dominated (ZANDER 2004). Individuals of this species hosted maximally eight parasite species, whereas the other four gobies presented maximally five per host individual. The reason for the special patterns of *P. microps* was the almost 100 % infection with *C. concavum* and some specialists, which were absent in other goby species. Regarding marine environments, HOLMES (1990) found also maximally eight parasite species in a surf perch individual. In freshwater single eels were at most infected by three parasite species though these hosts were of far greater size than gobies (KENNEDY 1990).

The structure of goby infra community can be measured by an infra community index (ICI = Mij/(Nj x Ij) ), which judges about the tendency of parasites to join the community (ZANDER 2004): Ij describes the mean of parasite species in the host j, Mij the ratio (numbers of multiple infected hosts j with parasite i and other parasites, Nj the ratio (numbers) of infected hosts j. As result, the greatest number of important parasites, which shared infra communities was found in

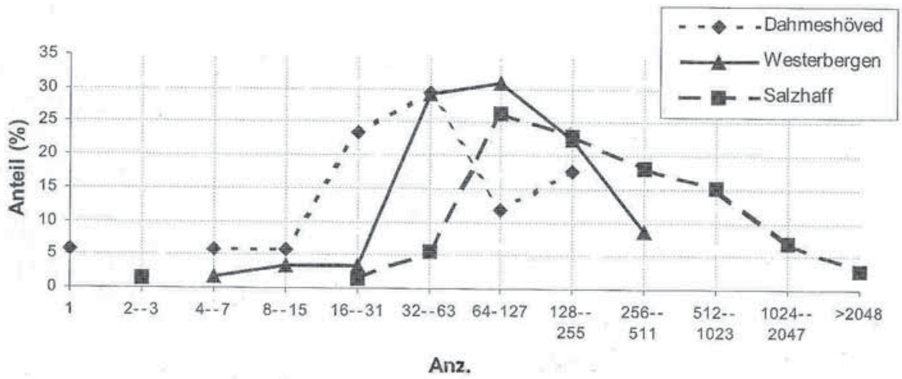



**Fig. 10:** Infection of kidneys of *Pomatoschistus microps* from three localities of the SW Baltic by metacercariae of the digenean *Cryptocotyle concavum* (from ZANDER 1998b).
**Abb. 10:** Befall der Nieren von *Pomatoschistus microps* aus drei Untersuchungsstellen der SW-Ostsee mit Metazerkarien des Digenen *Cryptocotyle concavum* (aus ZANDER 1998b).

*P. microps*: two digenean specialists (*Apatemon gracilis, Aphalloides timmi*) and two generalists (*Podocotyle atomon, C. concavum*) (tab. 5). *P. pictus* and *Gobiusculus flavescens* hosted the above mentioned generalists, whereas *Pomatoschistus minutus* hosted only the digenean *P. atomon* as a parasite which joined easily to the parasite community. *Gobius niger* was found to have no prominent parasite species; the highest index of this host was found in the nematode *Hysterothylacium aduncum*. The moderate or low indices of nematodes in all hosts were very conspicuous.

Regarding manifold infections three main microhabitats were analyzed in gobies (ZANDER 2004). Infections of skin and fins revealed prevalences of 0.6-14 % by two, and 0.3-4 % by three parasites in a single host. The body cavity was colonized by two parasites in two goby hosts at a lower level (0.4-4%) but by 62 % in *P. microps*, 12 % of the latter host harbored also three parasites. The intestinal tracts hosted contemporary two parasites by 8-20 % prevalence, three by 2-6 %, four in *P. minutus* by 0.7 % and *G. niger* by 1 %. *P. microps* is especially attractive for the specialist *A. timmi* and the generalist *C. concavum*, which is adapted to the kidney. These parasite species may be completed by the nematode generalists *H. aduncum*, *Contracaecum* sp. or *Anisakis simplex*.

## 7. Screens and filters of host infection by parasites

The way of colonization by parasites can be considered differently in the component, guild and supra community (BUSH et al. 1997). According to HOLMES (1990) the colonization depends on screen and filter mechanisms which excludes several parasites and influence, therefore, the final composition of the parasite community. If it is correlated to the model of distances as is used in the island theory (MACARTHUR & WILSON 1967) it can explain that the colonization of parasites is the more difficult the smaller the host (island) is and the greater its immune defense (distance from the source of immigration) is. Three categories can here be distinguished (ZANDER 2005a): 1. genetic distance, whereby the parasite population is influenced by the respective defense mechanisms of a single host specimen; 2. phylogenetic distance, whereby the varying defense systems of host populations are influenced; and 3. ecological (ontogenetic) distance, whereby the respective ways of life including cycles of parasites in several host guilds are influenced (fig. 11). The phylogenetic distance is not only responsible for the colonization of parasites but also for their maturation. If in the future the distances may become measurable,

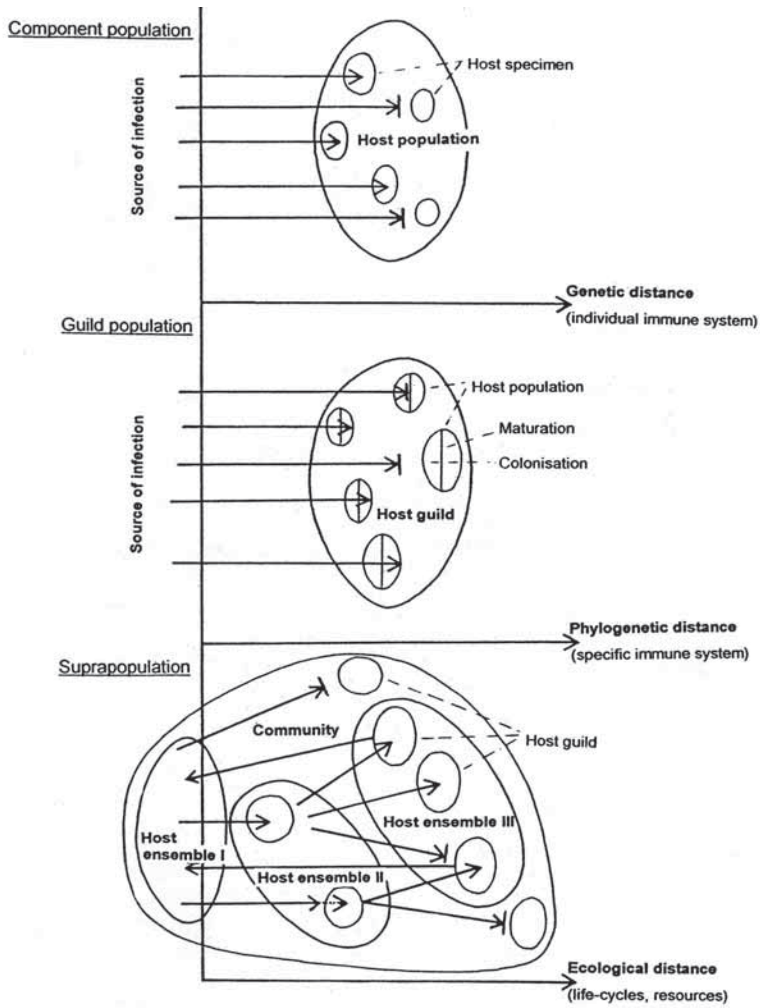



**Fig. 11:** A model of parasite infection under the influence of three handicaps. Above: The genetic distance is effective at the level of the component populations via the individual immune systems. Middle: The phylogenetic distance is effective at the level of the guild population via the respective specific immune system; this handicap consists of two patterns, the successful colonization by and maturation of the parasite. Below: Ecological distance is effective at the level of the supra population within a community via host characteristics such as life cycles and resource use; the ensembles represent the respective host phase of a parasite life cycle; different intermediate host guilds guarantee a high infection possibility of final host guilds. The arrows mark the distances which may be attained by distinct parasites (from ZANDER 2005a).

**Abb. 11:** Ein Modell des Parasitenbefalls unter dem Einfluss von drei Hindernissen. Oben: Die genetische Distanz ist auf der Stufe der Komponentenpopulationen auf Grund des individuellen Immunsystems der Wirte wirksam. Mitte: Die phylogenetische Distanz ist auf der Stufe der Gildenpopulationen aufgrund des artspezifischen Immunsystems wirksam; dieses Hindernis besteht aus zwei Merkmalen, der erfolgreichen Kolonisation und Reifung des Parasiten. Unten: Die ökologische Distanz ist auf der Stufe der Suprapopulation aufgrund der Merkmale der Wirte wie Lebensweise und Resourcennutzung wirksam; die Arten ähnlicher Lebensweise („essemblages") kennzeichnen ein bestimmtes Wirtsstadium im Lebenszyklus eines Parasiten; unterschiedliche Gilden von Zwischenwirten garantieren einen hohen Befall der Endwirtsgilden. Die Pfeile kennzeichnen die von bestimmten Parasiten eventuell erreichten Distanzen auf der Skala (aus ZANDER 2005a).

these values in combination with ecosystem parameters will characterize the ecological niche of a single parasite species.

## 8. Influence of brackish water on parasite host relationships

The parasites found in the Baltic Sea show special patterns caused by the physiological stress of brackish waters, which demands more energy under increasing osmoregulation for marine and limnetic organisms. Therefore, REMANE (1958) distinguished generally marine, limnetic, genuine brackish and migrating species. With exception of migrating species this classification is also valid for parasites. The peculiarities of parasites living in brackish waters like the Baltic Sea are compiled under four topics (ZANDER 1998a).

1. The suspension of specifity. The copepod parasite *Thersitina gasterostei* is distributed in high prevalence on the gills of its special host, *Gasterosteus aculeatus*, but by lower values also on other stickleback species and on non-related pipefish. The digenean *Bunocotyle cingulatus*, specific for the stickleback *Pungitius pungitius*, lives in the intestinal tract of this host, but was found in low prevalence in the non-related goby *Pomatoschistus minutus*. The specific parasites of *Pomatoschistus microps*, the digeneans *Aphalloides timmi* and *Apatemon gracilis*, were rarely found in other goby species (tab. 2) (ZANDER 2001). The crustacean *Crangon crangon* is a host, which is not infected by metazoan parasites in marine environments, but hosts the digeneans *Podocotyle atomon* and *Maritrema subdolum* in the Baltic (GOLLASCH et al. 1996). It is assumed that the stress of brackish water reduces the defense mechanisms of related hosts. This characteristic of decreased parasite specifity may correspond to the extension of habitats presented by freely living organisms in brackish waters (REMANE 1958). Similar results were also gained from snails, e.g. the periwinkle *Littorina saxatilis*, a specific first intermediate host of *Podocotyle atomon*, which is in the Baltic also infected by *Cryptocotyle concavum* and *Levinsiniella* sp. which live generally in *Hydrobia* snails (ZANDER et al. 2000).

2. New hosts. The digenean *Maritrema subdolum* can enlarge its life cycle, because gobiid fish may be used as third intermediate hosts in the Baltic (REIMER 1993, KESTING et al. 1996). This is a strategy, which facilitates the infection of its final hosts (birds), because the fish are larger than the small benthic crustaceans used as second intermediate hosts and, therefore, can be colonized by a larger numbers of parasites. This strategy may be advantageous in brackish waters, where suited hosts may be rare.

3. Reduction of life cycles. This is the opposite strategy to the former. Here the cercariae of the digenean *Microphallus clavifomis* and *Maritrema subdolum* remain in snails, the first intermediate hosts, and do not need to reach the second intermediate hosts, i.e. benthic crustaceans (KESTING et al. 1996, REIMER 1993). Consequently, these parasites can additionally attain to snail eating birds. *M. subdolum* is, therefore, able to change its normal three-host cycle into either a two- or a four-host cycle.

4. Coevolution of parasite and host in brackish waters. The genuine brackish water goby, *P. microps*, is infected by the digenean *C. concavum* that encysts in the kidney, where it accumulates several hundred or even thousand metacercariae (ZANDER 1998b). Thus, it has chance to harbor more parasites than on skin and fins as found in other fish species, and ensures infection possibilities of fish preying birds. The goby is not harmed by the parasite, differently to heavy inconvenience after infection of the fins of fish. Also the adult digenean *Aphalloides timmi*, which is found in *P. microps*, seems to be an exception choosing the body cavity as microhabitat.

In brackish waters there is a range between 5-8 ‰ salinity, where many fresh water and marine organisms cease to exist (species minimum, REMANE 1958). In contrast, genuine brackish water hosts were found to harbor at the species minimum the most parasites in the Schlei (KESTING et al. 1996, ZANDER & WESTPHAL 1998). In this locality, genuine brackish water hosts were the goby *P. microps*, the benthic peracarid crusta-

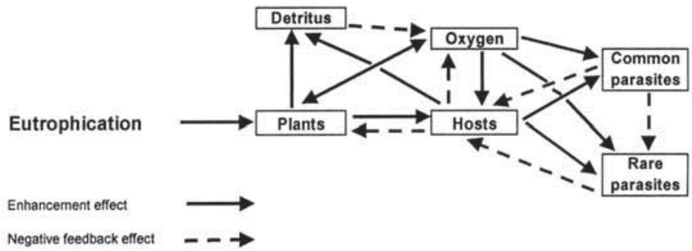



**Fig. 12:** Model of eutrophication effects on host and parasite populations in brackish waters comprising also positive and negative feedback reactions. The first consequence of eutrophication is increasing plant (algal) density (from ZANDER 2011).
**Abb.12:** Modell der Wirkung von Eutrophierung auf Wirt- und Parasitenpopulationen im Brackwasser mit ihren positiven und negativen Rückkopplungen. Die erste Folge der Eutrophierung ist eine gesteigerte Pflanzendichte, besonders von Algen (aus ZANDER 2011).

ceans *Idothea chelipes*, *Sphaeroma hookeri*, *Sphaeroma rugicauda*, *Gammarus duebeni*, *Gammarus zaddachi*, the planktonic copepod *Eurytemora hirundo*, and the snail *Hydrobia stagnalis*. Together with the reduced specifity of many parasites, there exists, therefore, an increased opportunity to harbor a parasite richness greater than the existing host richness.

## 9. Influence of eutrophication on parasite host relationships

In contrast to reduced salinity of brackish waters like the Baltic Sea, to which the organisms had the chance to adapt since 7000 years (KÖSTER 1995), eutrophication as stressor is a modern problem caused by human (GERLACH 1995). The input of phosphates and nitrates causes a yearly plant bloom. An initial effect of eutrophication lies in promoting the existence of herbi- and detritovores which are preferred intermediate hosts (KESTING & ZANDER 2000). An excessive growth of algae in spring leads to large oxygen deficiencies after their death (fig. 12) (ZANDER 2011). This situation influences the existence of other organisms, including parasites and is often combined with toxic substances which cause negative effects. These stressors affect not only hosts, but also free stages of parasites, miracidiae and cercariae of digeneans, coracoids of tape worms, larvae of nematodes and acanthellae of acanthocephalans. Additionally, the effect of stressors on host and parasite may differ, with the consequence that a harmed host can be better infested by parasites because of its reduced immune defense. This creates a network of interactions, including several feedback effects (fig. 12).

The investigated localities of Dahmeshöved and Blank Eck clearly differed in their oxygen balance and fewer periods of oxygen deficiency are found in Blank Eck than in Dahmeshöved (ZANDER & KESTING 1996). As mentioned above, in Blank Eck a higher diversity of the parasite community occurred than in Dahmeshöved, where some parasite species became dominant. The parasites of the free water are in a better situation under the extreme effect of pollution, because the pelagial provide often better conditions than the bottom. This was found in the inner Schlei fjord, where toxic mud reduces the numbers of benthic organisms (KESTING & ZANDER 2000). Therefore, parasites of the pelagial can survive longer than those of the bottom. But the ultimate result of increasing eutrophication can be the vanishing of all hosts and combined with these of all parasites.

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