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## Parasites of Baltic gobies – an example of evident annidation

### *Parasiten bei Grundeln der Ostsee – ein Fallbeispiel für offensichtliche Einnischung*

**summary** In the focus of this article are five fish species of the goby guild (Gobiidae) from the North and Baltic Sea. The influence of the abiotic factor salinity reveals differences in goby parasite communities between the marine North Sea and the brackish Baltic Sea. The regional parasite fauna of the SW Baltic Sea is repeated only partly in each locality which, therefore, is assumed to differ by several ecological conditions, e.g. eutrophication. The parasitological analysis of the single goby species (component community) mostly reveal congruent parasite communities but also some differences. Two such cases may evidence the evolutionary process of annidation. The digenan *Podocotyle atomon* is very abundant in four goby species but absent in *Gobius niger* because the metacercarian cysts of this parasite pass the intestine of the black goby without being digested. Metacercariae of the digenean *Cryptocotyle concavum* settle in the kidney of *Pomatoschistus microps* as a new microhabitat instead of the skin as in the other gobies. These results indicate a special coevolution and annidation which might be explained by an extreme population growth of parasites on or in the hosts. This situation forces to develop either special defense mechanisms as in *Gobius niger*, or to conquer new microhabitats as in *P. microps*. Therefore, extreme population growth leads to the process of annidation between host and parasites in order to avoid competition with other parasite species of high population density.

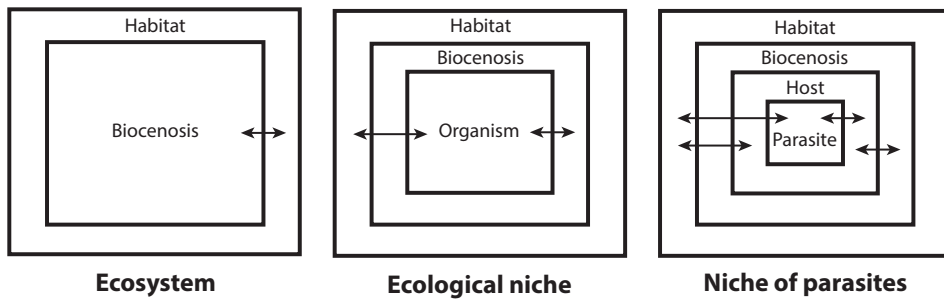
Zusammenfassung

Im Fokus dieser Abhandlung stehen als Wirte eine Gilde von fünf Arten der Fischfamilie Gobiidae aus Nord- und Ostsee. Der Salzgehalt als ein entscheidender abiotischer Faktor hat Unterschiede zwischen den Parasitengemeinschaften der marinen Nordsee und brackigen Ostsee zur Folge. Die regionale Parasitenfauna der SW Ostsee wiederholt sich nur teilweise in den einzelnen Lokalitäten dieser Region, wahrscheinlich auf Grund von jeweils unterschiedlichen ökologischen Faktoren, z. B. dem Grad der Eutrophierung. Die parasitologische Analyse der Standorte ergab einige Gemeinsamkeiten, aber im Fall der Digenen *Podocotyle atomon* und *Cryptocotyle concavum* auch Besonderheiten, die auf eine spezielle Koevolution und Einnischung mit ihren Wirten *Gobius niger* bzw. *Pomatoschistus microps* hinweisen. Bei *Gobius niger* werden spezielle Abwehrmechanismen gegen *Podocotyle atomon* entwickelt, bei *Pomatoschistus microps* erobert *Cryptocotyle concavum* ein neues Mikrohabitat. Der Auslöser ist die Konkurrenz bei Parasiten mit jeweils extremem Populationswachstum, die zu neuen Anpassungen und darauf folgender Einnischung führt.

## Introduction

Evolution is a phenomenon which occurs by several steps: mutation of genes, their recombination, adaptation of the genome to the respective organism and adaptation of the specimen to the population of a species. Annidation is according to Ludwig (1950) a factor of evolution which joins and can lead to speciation. It means the adaptation of an organism to a community in which it formerly was absent. The driving force is competition for resources which in some cases leads to extinction of one of the competitors but in other cases to a restriction of the respective resources. After successful annidation the organism creates its specific ecological niche by reciprocal interaction with biotic and abiotic factors. The term niche was introduced by Grinnell (1917) as the location where an organism is generally found (habitat niche). Elton (1927) regarded the functional aspect of an organism and included the prey of organisms into the niche-concept. Günther (1950) created the terms “autozoische Komponente” (attributes of the organism) and “ökische Komponente” (influence of environmental factors with which the organisms interact). Hutchinson (1957) acknowledged that the ecological niche is a multidimensional system, a hypervolume, which main dimensions are habitat, prey and time. Their use was advantageous in making an analysis easier. Pianka (1975, 1994) created the most modern definition by his short description of the niche as the optimal exploitation of the nature by an organism. This sentence includes all relationships between organism, habitat and biocenosis (Fig. 1b). The ecological niche is, therefore, congruent to the ecosystem, but on the autecological level where the organism is in the focus instead of the ecosystem which is the main case in the synecological level (Fig. 1a).

Nevertheless, until today the term ecological niche is discussed controversially. Whereas some authors follow the definition of Pianka (1975, 1994) as e.g. Sauer (1986) or, regarding fish, Zander (1997, 2006, 2009) other authors still persist on the understand-



**Fig. 1** Model of ecological systems. **a.** Ecosystem means the dynamical mutual relationship between biocenosis and habitat (synecological level). **b.** Ecological niche means the dynamical mutual relationship between organism and its environment – habitat and biocenosis (autecological level). **c.** Ecological niche of a parasite. A further compartment, the host, is enclosed in the dynamics of the system. According to Zander (1997).

**Abb. 1** Modell ökologischer Systeme. **a.** Ökosystem bedeutet die dynamischen Wechselbeziehungen zwischen Biozönose und Biotop (synökologische Stufe). **b.** Ökologische Nische bedeutet die dynamische Wechselbeziehung zwischen Organismus und seiner belebten und unbelebten Umwelt (autökologische Stufe). **c.** Die ökologische Nische eines Parasiten umfasst mit dem Wirt eine weitere Komponente, der die Dynamik des Systems komplexer macht. Nach Zander (1997).

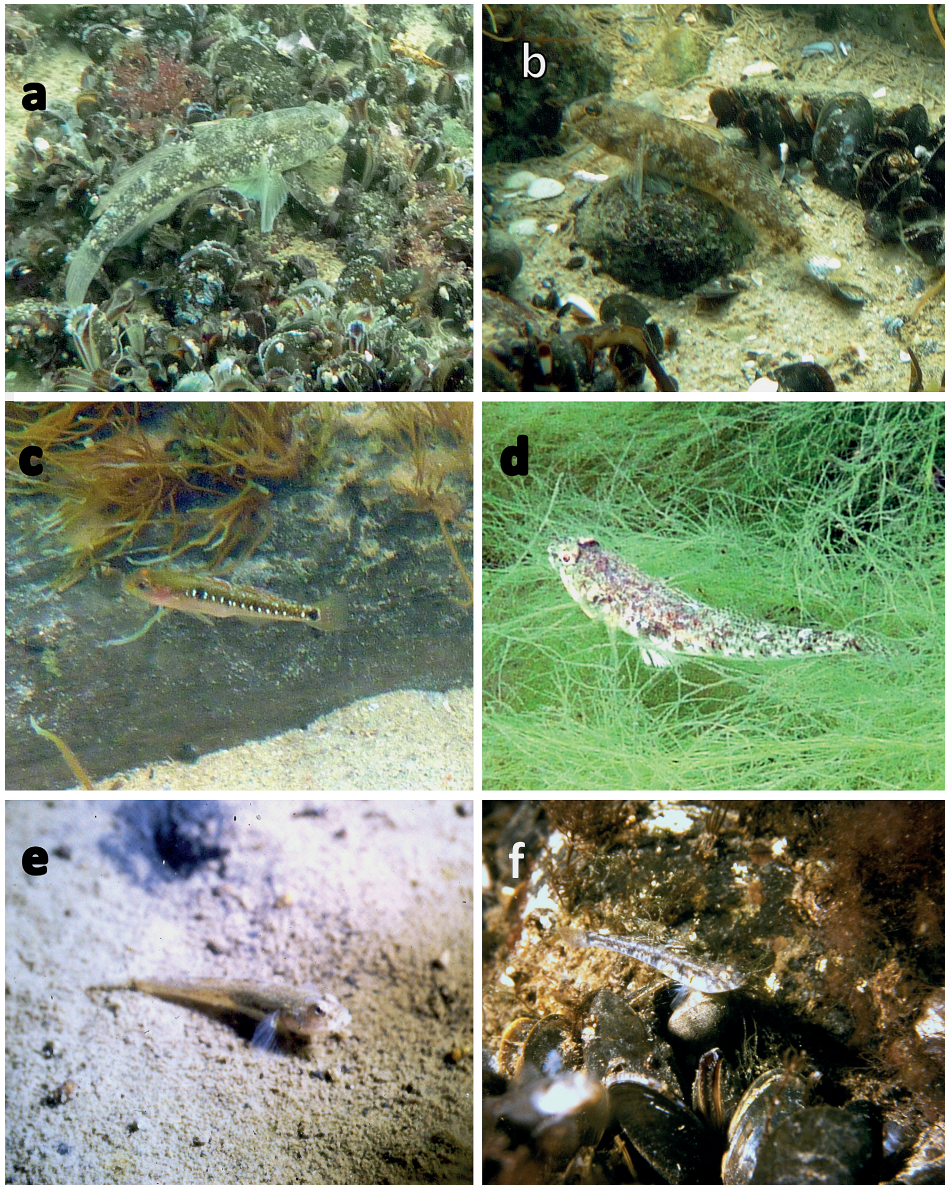
ing of this term as habitat which is influenced by a hypervolume of different factors. This view means a static system without the possibility for evolutionary processes and, therefore, also for annidation. Several authors even claim the existence of empty niches because species composition differs in separate but similar ecosystems (Levontin 1978, Walker and Valentine 1984). Regarding marine fish parasites, Kennedy et al. (1986) and Rohde (1994) proposed the existence of empty niches which could theoretically be occupied by suitable parasite species but are currently missing in the parasitocenosis. This theory of a statically organized niche has to be discussed below.

The ecological niche of parasites presents some peculiarities in contrast to the general niche (Fig. 1c). Parasites need two kinds of habitats: the microhabitat which describes the locality on or in the host, and the macrohabitat which is the niche of the host. Thus, the macrohabitat is relevant for the hosts, for ectoparasites and for free living stages of parasites. Furthermore, colonization and annidation are complicated in those parasites which change their hosts during the life cycles.

The aim of this study is, therefore, to reevaluate cases of annidation processes from own investigations on marine parasites which may support the niche definition of Pianka (1975). Also the application of parasite communities to the Island Theory of MacArthur and Wilson (1963) which was originally created for free living organisms is proven.

## Material

The results of former investigations on fish parasites from North and Baltic Sea are utilized for this reevaluation (Kesting et al. 1996, Zander 1999, 2003, 2004, 2005, 2009, Zander et al. 1984). The host objects are fish species of the family Gobiidae (Fig. 2). The discussion will also comprise the terms annidation, empty niches and Island-theory.



**Fig. 2** Photos of five species of Gobiidae from North Sea and Baltic Sea to which this review is referred. The slight differences of gobies in their habitat choice may be the reason for varying parasitocenoses, respectively. **a** and **b**: *Gobius niger* in two color variants. It inhabits pebble rich bottoms. It is the only species of this guild which live longer than one reproduction period. **c**: *Gobiussculus flavescens* present a suprabenthic way of life, but spawn on the substrate. **d**: *Pomatoschistus minutus* live on sand bottoms but the young for a long time in the suprabenthos. **e**: *Pomatoschistus microps* live in shallow water at the beach on sand-pebble bottoms. **f**: *Pomatoschistus pictus* prefer pebble-sand bottoms near the beach.

**Abb. 2** Fotos von fünf Gobiidae-Arten aus Nord- und Ostsee, auf die sich diese Rückschau bezieht. Die leichten Unterschiede in der Habitatswahl können der Grund für Abweichungen ihrer jeweiligen Parasitenzönosen sein. **a** und **b**: *Gobius niger* in unterschiedlichen Färbungen. Diese Art bewohnt Geröll reiche Böden. Es ist hier die einzige Art, die länger als eine Fortpflanzungsperiode lebt. **c**: *Gobiussculus flavescens* lebt suprabenthisch, laicht aber am Substrat. **d**: *Pomatoschistus minutus* lebt auf Sandböden, Jungfische aber auch längere Zeit suprabenthisch. **e**: *Pomatoschistus microps* lebt ufernah auf Sand-Geröll-Böden. **f**: *Pomatoschistus pictus* bevorzugt uferferne sandige Geröll-Böden.

## Results and Discussion

The prior event of annidation is a successful colonization. The first prerequisite is the presence of suited macro- and microhabitats. Tab. 1 presents the regional parasite fauna of ten hosts from the SW Baltic Sea and its appearance in 6 localities of this region (Zander 2003). Even though these localities show brackish conditions (salinities 11–18 ‰), it is possible that they differ in other factors. Thus the locality Blanck Eck presents the lowest number of species but also lowest level of eutrophication (Zander 2002). At the other end of the eutrophication scale are the localities Dahmeshöved and Salzhaff which attained the highest species richness but not the values of the regional parasite fauna.

Salinity is an abiotic factor which influences the parasite fauna of the goby hosts in great extent (Zander 2005). Tab. 2 presents the existence of several parasites from the North (marine salinity) or Baltic Sea (brackish salinity). Qualitative differences influence the digenean bird parasite, *Cryptocotyle concavum*, which was not found in the marine milieu because it is a genuine brackish organism, whereas the related *C. lingua* was also found in both milieus. *Ligula pavslovskii* (Cestoda) and *Brachyphallus crenatus* (Digenea) were also absent in the North Sea. Furthermore, quantitative differences exist in that the infection by several parasites is higher in the brackish Baltic Sea than in the North Sea. This is demonstrated by the abundance values of *Podocotyle atomon*, *Hysterothylacium* sp. and *Contracaecum* sp. and is compared in both regions (Tab. 2).

Another filter for a successful colonization is competition (Fig. 3). Competition occurs if two or more species use identical resources, especially, if these are short. After a parasite has successfully invaded a suitable microhabitat, competition with other parasites occurs and leads either to the extinction of one species or to the coexistence with the previous colonists. In the case that a microhabitat of the host is still not occupied the colonist can settle under distinct conditions and introduces a process of annidation. An evident example is the colonization of the kidney of the goby *Pomatoschistus microps* by cercariae of

Tab. 1 The percentage of parasite fauna from six localities related to the comprising regional fauna. Acc. Zander 2009

Tab. 1 Prozentsatz der Parasitenfauna von sechs Probestellen, bezogen auf die umfassende regionale Fauna

	Regional	Flensburg-Förde	Schlei	Blank Eck	W-Fehmarn	Dahmeshöved	Salzhaff
Digenea	48	31	18	9	21	28	36
Cestoda	12	6	5	1	2	7	7
Acanthocephala	10	2	5	3	0	8	3
Nematoda	18	12	3	5	11	8	0
Andere	12	8	6	2	1	6	6
<b>Sum %</b>	<b>100</b>	<b>59</b>	<b>37</b>	<b>20</b>	<b>35</b>	<b>57</b>	<b>52</b>

Tab. 2 Influence of the salinity on abundances of parasites in 3 goby species from North- (Helgoland) and SW-Baltic Sea (Dahmeshöved, Blank Eck) (acc. to Zander 2005). C=core species (abundance < 2), S=secondary species (abundance 0.2–2), R=rare species (abundance > 0,2) (acc. to Zander 2003).

Tab. 2 Einfluss des Salzgehalts auf die Abundanzen von Parasiten in 3 Grundelarten aus der Nordsee (Helgoland) und der SW Ostsee (Dahmeshöved, Blank Eck) (nach Zander 2005). C=Kernarten (Abundanz < 2), S=Sekundärarten (Abundanz 0.2–2), R=seltene Arten (Abundanz > 0,2) (nach Zander 2003).

	Helgoland			Dahmeshöved			Blank Eck	
	<i>P. microps</i>	<i>P. pictus</i>	<i>G. flavescens</i>	<i>P. microps</i>	<i>P. pictus</i>	<i>G. flavescens</i>	<i>P. pictus</i>	<i>G. flavescens</i>
<i>Cryptocotyle concavum</i>				C	C	S	R	S
<i>C. lingua</i>	R							
<i>Podocotyle atomon</i>	R			R		R		
<i>Brachyphallus crenatus</i>						R		R
<i>Lecithaster confusus</i>								R
<i>Asymphyiodora demeli</i>						R		
<i>Ligula pavlovskii</i>						R		R
<i>Proteocephalus</i> sp.			R					
<i>Bothriocephalus scorpii</i>						R		R
<i>Hysterothylacium</i> sp.	R	R		S	R	R	R	R
<i>Contracaecum</i> sp.	R	R	R	R			R	
<i>Echinorhynchus gadi</i>							R	R
<i>Caligus elongatus</i>			R					

the digenean *Cryptocotyle concavum* (Zander et al. 1984). *C. concavum* infects the skin of all other known hosts, also of related gobies but not the skin of *P. microps* (Tab. 3). This host harbors up to several thousand cysts in its kidney (Zander 1999, Zander et al. 1984). This situation gives space for another skin parasite, *Apatomon gracilis*, also a core species which, therefore, can settle in great numbers in the microhabitat skin.

An evolutionary process of adaptation was found also in the relationship of the digenean *Podocotyle atomon* and the goby *Gobius niger*. *G. niger* is the only species of the goby guild which lives longer than one reproduction period. The longer life span can lead to a heavy accumulation of parasites (Zander 2004). But even though the nematode *Hysterothylacium aduncum* and the digenean *Podocotyle atomon* were found in extreme high quantities in hosts of the Baltic Sea as was demonstrated in the eelpout, *Zoarces viviparus* (Zander 1991), they did not occur in *G. niger*. In contrast to all other species, the metacercariae of *P. atomon* are not digested in the gut of *G. niger*, and do not become infective. Therefore, the abundance value of this partnership is zero (Tab. 3) (Zander 2003). This phenomenon may be an adaptation by modifying the effect of ferments in the gut which solve metacercarian cysts. Thus, this small-sized host is saved against an excessive

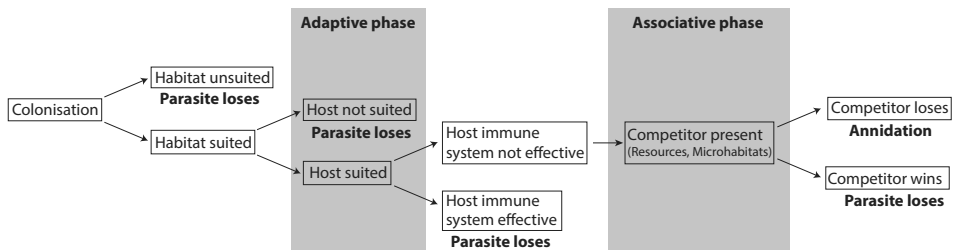


Fig. 3 Model of parasite annidation. The single steps are adaptations to habitat, host, host immune system and competition.

Abb. 3 Modell der Einnischung von Parasiten. Die einzelnen Stufen umfassen Habitat, Wirt, Immunsystem des Wirtes und Konkurrenz.

Tab. 3 Influence of host species of the goby guild on the intensity of infection by parasites. Core = core species (abundance < 2), S = secondary species (abundance 0.2–2), R = rare species (abundance < 0.2), O = special cases of no infection (acc. to Zander 2003).

Tab. 3 Einfluss der Wirtsart aus der Grundelgilde auf die Intensität der Infektion durch Parasiten. Core = Kernarten (abundance < 2), S = Sekundärarten (Abundanz 0.2–2), R = seltene Arten (Abundanz > 0.2), O = besondere Fälle von Nicht-Infektionen (nach Zander 2003).

	<i>Pomatoschistus</i>		<i>Pomatoschistus</i>	<i>Gobiusculus</i>	<i>Gobius</i>
	<i>microps</i>	<i>minutus</i>	<i>pictus</i>	<i>flavescens</i>	<i>niger</i>
<i>Cryptocotyle concavum</i> skin	O !	Core	Core	S	Core
<i>Cryptocotyle concavum</i> kidney	Core		R		
<i>C. lingua</i>	R	R	R	R	Core
<i>Podocotyle atomon</i>	S	Core	Core	Core	O !
<i>Apatemon gracilis</i>	Core		R	R	
<i>Aphalloides timmi</i>	Core		R		
<i>Acanthostomum balthicum</i>	R	R		R	
<i>Asymphylodora demeli</i>	R	R	R	R	R
<i>Ligula pavlovskii</i>	R		R	R	
<i>Bothriocephalus scorpii</i>			R		
<i>Hysterothylacium</i> sp.	R	R	R		S
<i>Anasakis simplex</i>		R	R		R
<i>Contracaecum</i> sp.	R		R		R
<i>Raphidascaris acus</i>	R	R	R	R	R
<i>Ascarophis arctica</i>		R	R		R
<i>Echinorhynchus gadi</i>		R	R	R	R

infection by several parasites in the microhabitat gut and, as consequence, against mortality. Such a process does not create a vacant niche but result in larger niche dimensions for competing gut parasites. Also in *Pomatoschistus microps* intestine parasites with high infection rates seem to compete because the digenean *Aphalloides timmi*, a specialist of

this host, is a core species and may restrict other parasites of this microhabitat, e.g. *Podocotyle atomon* that shows a lower abundance than in other hosts (Tab. 3). These examples may demonstrate several stages of the annidation process.

The host-parasite relationship is compared by several authors with the colonization of an island, where the hosts corresponds with an island and the parasite with a colonist. According to the Island Theory of MacArthur and Wilson (1963), its equilibrium of colonization is positively correlated to the size of islands and negatively to the distance to the mainland. Transferred to parasite-host-systems these components correspond to the size of host and its immune defense against parasites. Some authors enlarged the list of possible factors which influence colonization of parasites: the distribution range of parasites (Price 1980) and the phylogenetic time of appearance of their hosts (Gaugéan and Kennedy 1993) do not agree to the Island Theory. The results of the present contribution, the population density of parasites, can be added to the list of influencing factors; in the case of high values competition can lead either to the extinction of competing species or to a new niche. These examples of annidation may additionally stress the assumption that the niche is a dynamic system with relationships between both, organism and its environment.

The existence of empty niches is claimed by Rohde (1994) who presented following evidences: 1. in moderate climatic areas is the number of marine parasite species lower than in tropical areas, 2. hosts lose their parasites when they change into an extreme environment (fish which migrate from limnetic to marine waters or vice versa), 3. communities of insects on identical plant species vary in different geographical regions. Rohde, following the multidimensional niche of Hutchinson (1957), confuses obviously niche with habitat, he disregards that the niche is a system which dimension can in- or decrease. Its most important characteristic is the exploitation of resources (Pianka 1994). This leads within the biocenosis to a stable non-equilibrium (Reichholf 2008). The results of this reevaluation emphasize, therefore, the niche as a dynamic system which advances evolutionary processes like annidation. The assumption of vacant niches is, therefore, of no advantage because it presupposes a static system without the possibility for evolutionary progress.



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