Parasite interactions

Interactions in parasite communities

- Biotic factors
- Parasite interactions within the host
- Interspecific interactions
- Positive - disruption of host defence mechanisms by one parasite species can facilitate the use of different host species
- Negative - the presence of one species of parasite leads to reduction of population size, changes in distribution or limitation of reproduction of another species
- Intraspecific interactions

Ecological niche of parasites

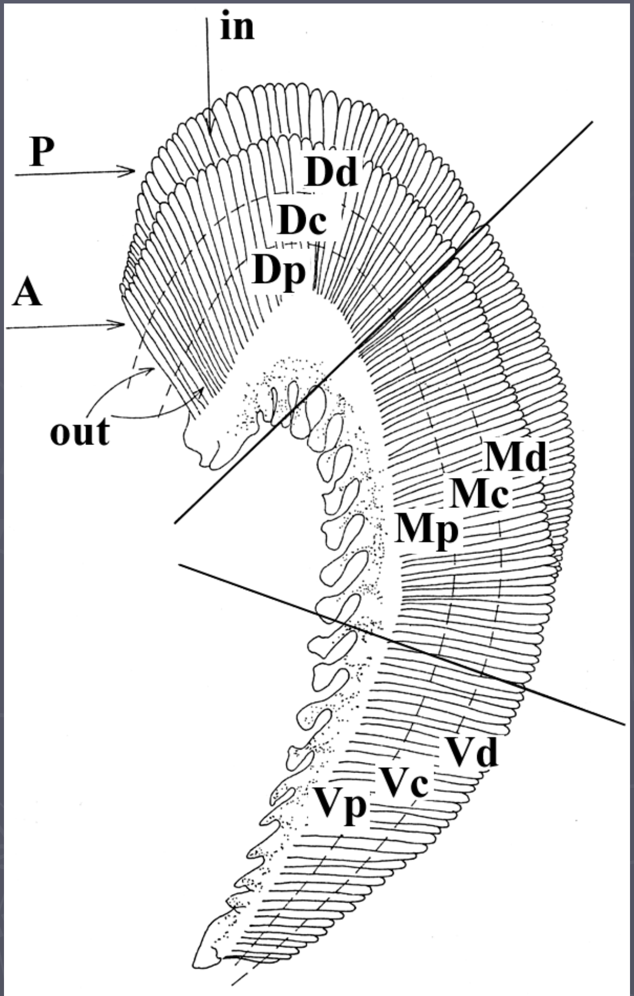
- Multidimensional space of parasite habitat defined by the biotic and abiotic variables
- Parasite occupies a specific position in host = habitat

  i.e. habitat of endoparasites – intestine
- Niche = determined by the range of all positions of all individuals of a given species

  Niche dimension = mean or median position

  (!!! in simple case a niche measured as unidimensional i.e. lentgh of intestine)

Ecological niche of parasites



Host habitat (gills) →
microhabitats

transversal
longitudinal
vertical
lateral
inner and outer surfaces

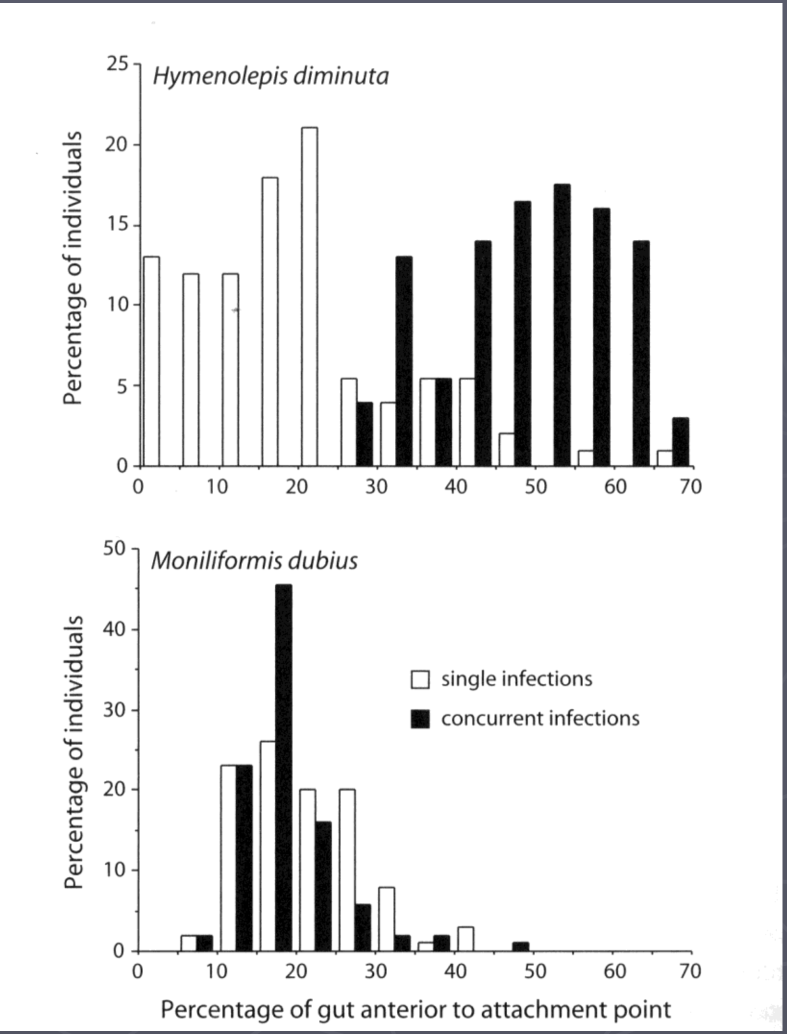
Basic versus realized ecological niche

- Hutchinson 1957
- Basic (preinteractive, precompetitive) - virtual range of positions where the parasite reproduces itself and survive in the absence of competitor
- Realized (postinteractive, postcompetitive)
  - subunit of basic niche reduced due to interspecific interactions

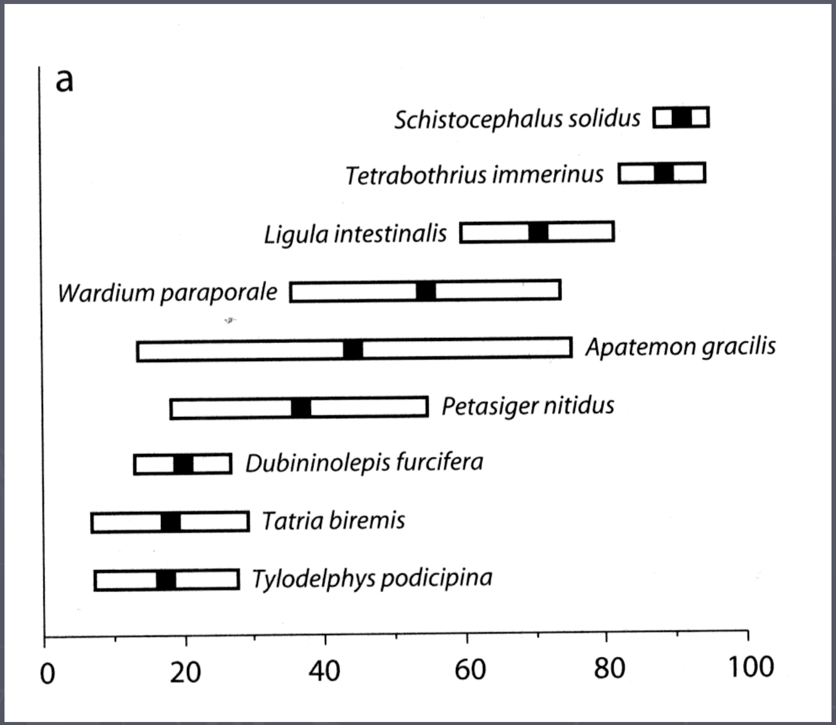
Fundamental and realized niches, niche overlap

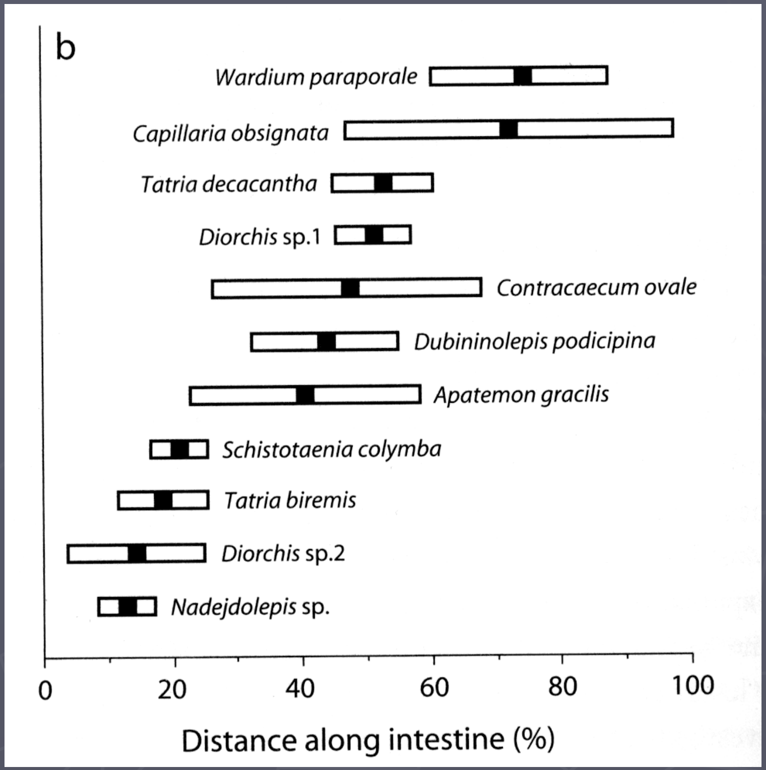
Ex. Distribution of *Hymenolepis diminuta* (Cestoda) and *Moniliformis dubius* (Acanthocephala) in the intestine of rats

Experimental infection
- single-species
- double-species



Fundamental niche of parasites





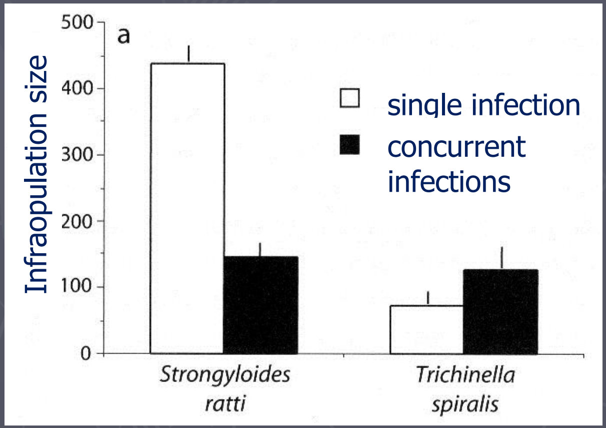
Ex. Basic niches of intestinal helminths (prevalence > 25%) in two species of grebes: (a) *Aechmophorus occidentalis*, (b) *Podiceps nigricollis*

Numerical responses to competition

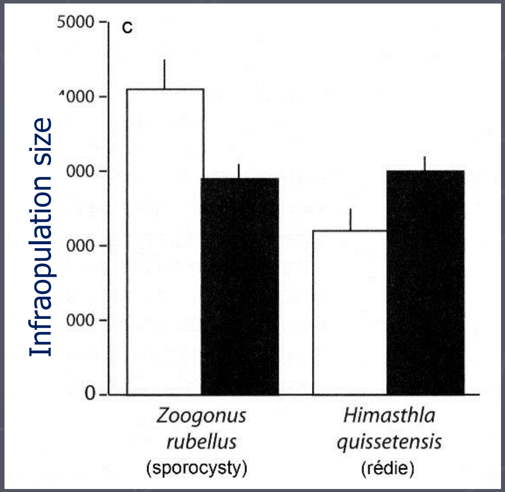
- reduction of parasite population size in the presence of other parasite species

  asymmetric output - affected only one species

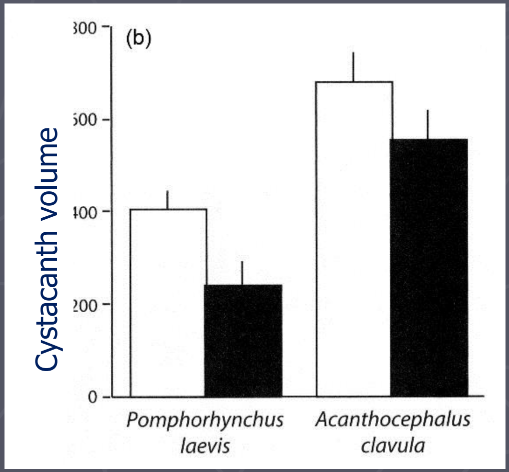
  symetric output – reduction of infrapopulation sizes in both species



2 nematode species in rats



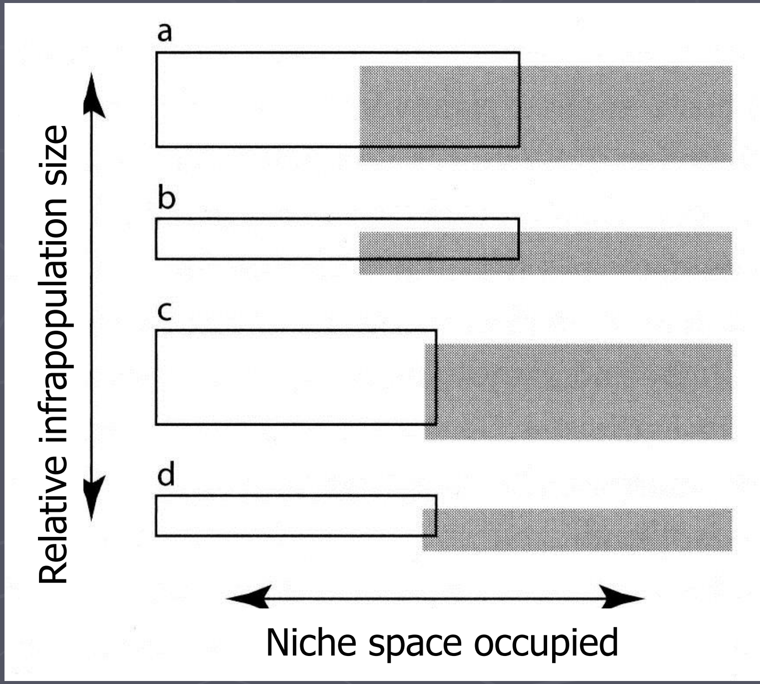
2 digenean species in IH (Mollusca)



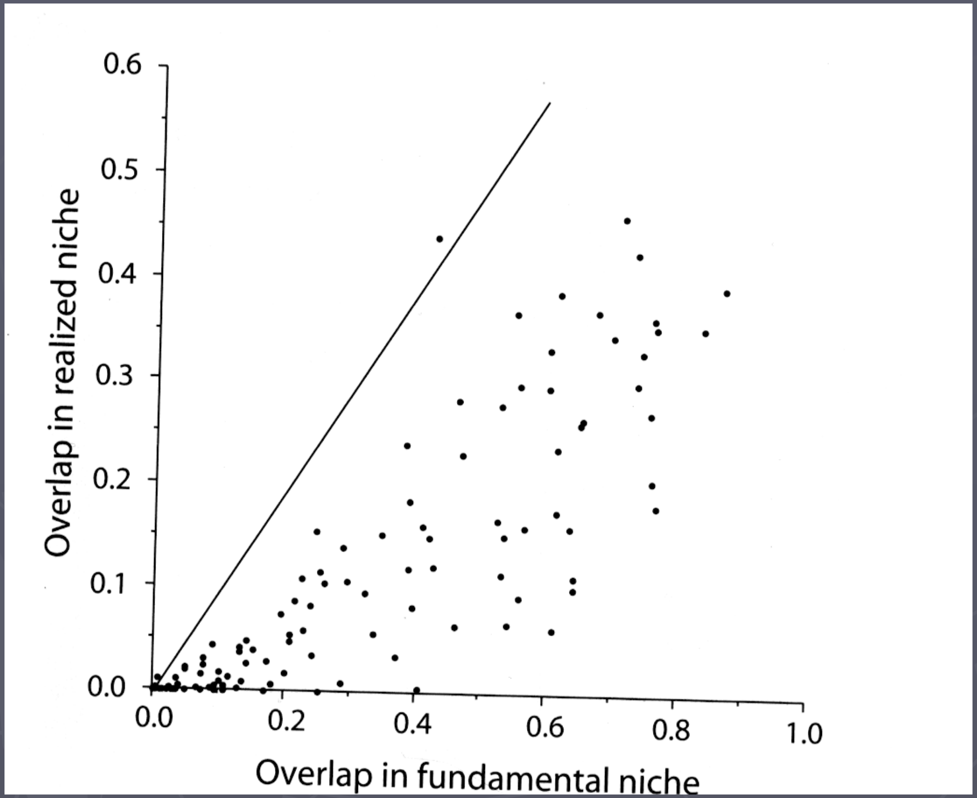
2 acanthocephalean species in IH (Amphipoda)

Functional response to competition

- Shift in realized niches in different species or reduction of niche overlap due to interactions
- Functional response occurs with or without numerical effects



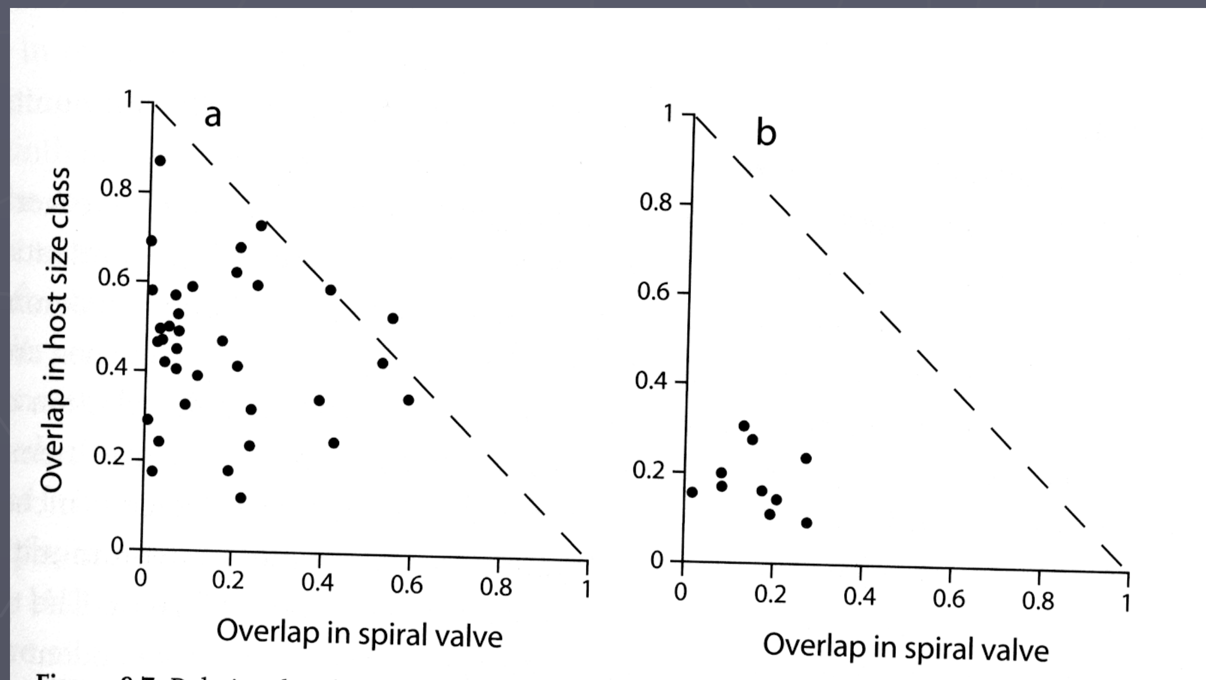
Relationship between the overlap in realized niche and the overlap in fundamental niche



Ex. 120 pairwise associations among 16 species of intestinal helminths in *Aythya affinis*

Overlap of multidimensional niche

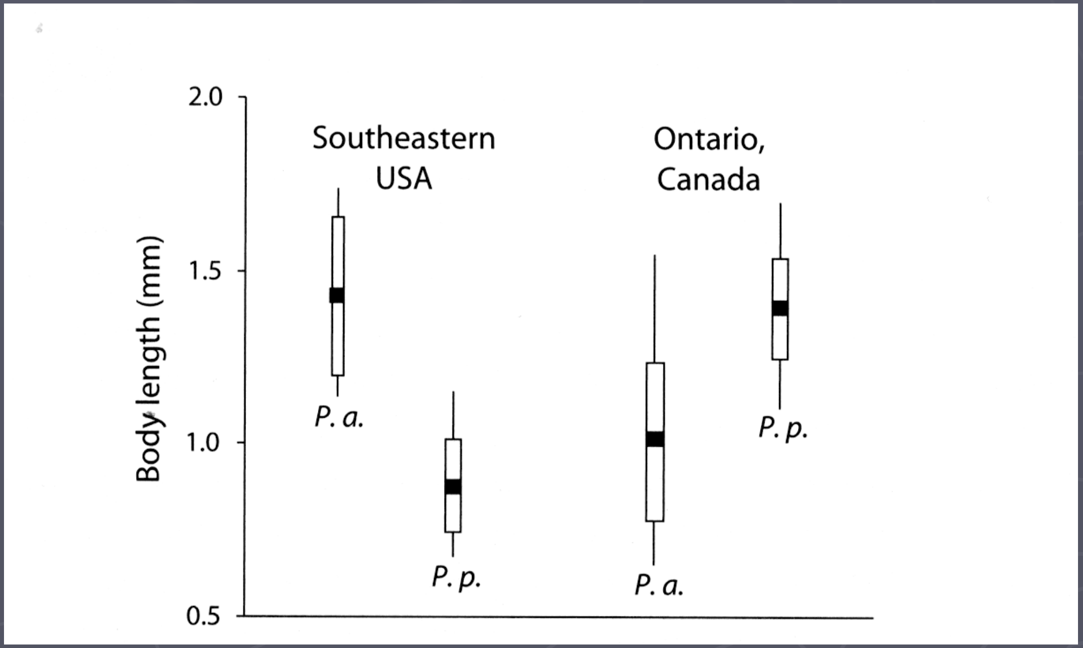
- Two-dimensional niche - high overlap only in one dimension



Ex. Overlap between pairs of cestodean species parasitizing in spiral valve of intestine in two species of elasmobranches (a) 9 species in *Urobatis halleri* (b) 5 species in *Leucoraja naevus*

Next type of functional response

- congeneric species with the same size (or morphology) in basic niches → divergence of size in overlapping niches – e.g. morphology of beaks of Galapagos finches



Ex. Body length in two co-occuring congeneric digenean species *Pharyngostomoides adenocephala* and *P. procyonis* parasitizing raccoons

Interactive versus non-interactive parasite communities

- Interactive community – competition
- Non-interactive community – species coexistence

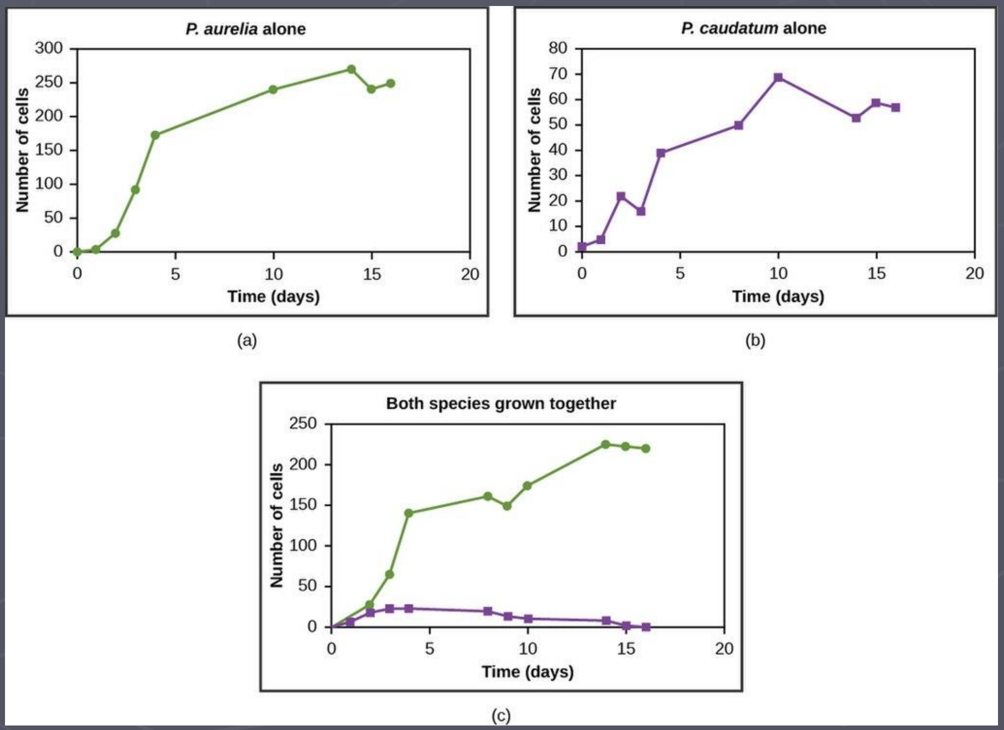
- Continuum between non-interactive and interactive community depending on niche space

- Saturated community – number of species cannot increase or number of species increases with decreasing niche size
- Non-saturated community – niche space free for parasite colonization, absence of competitors

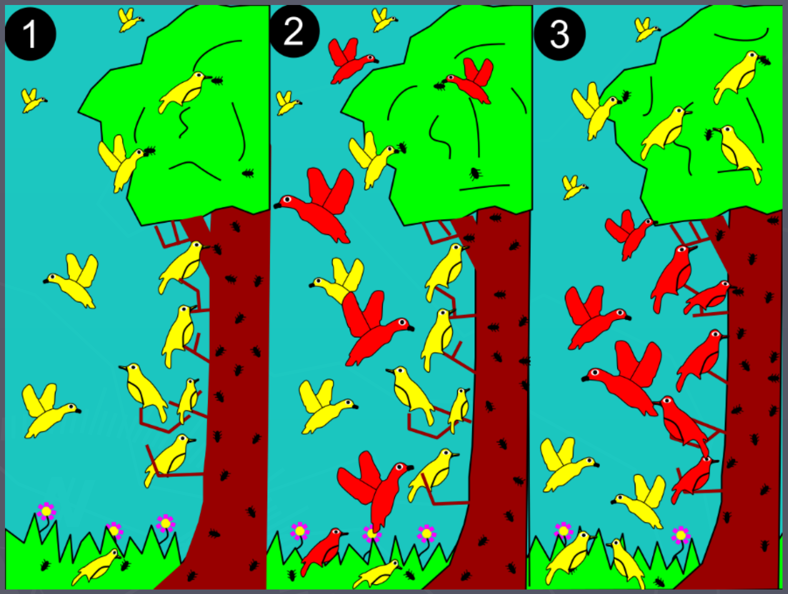
Competitive exclusion principle

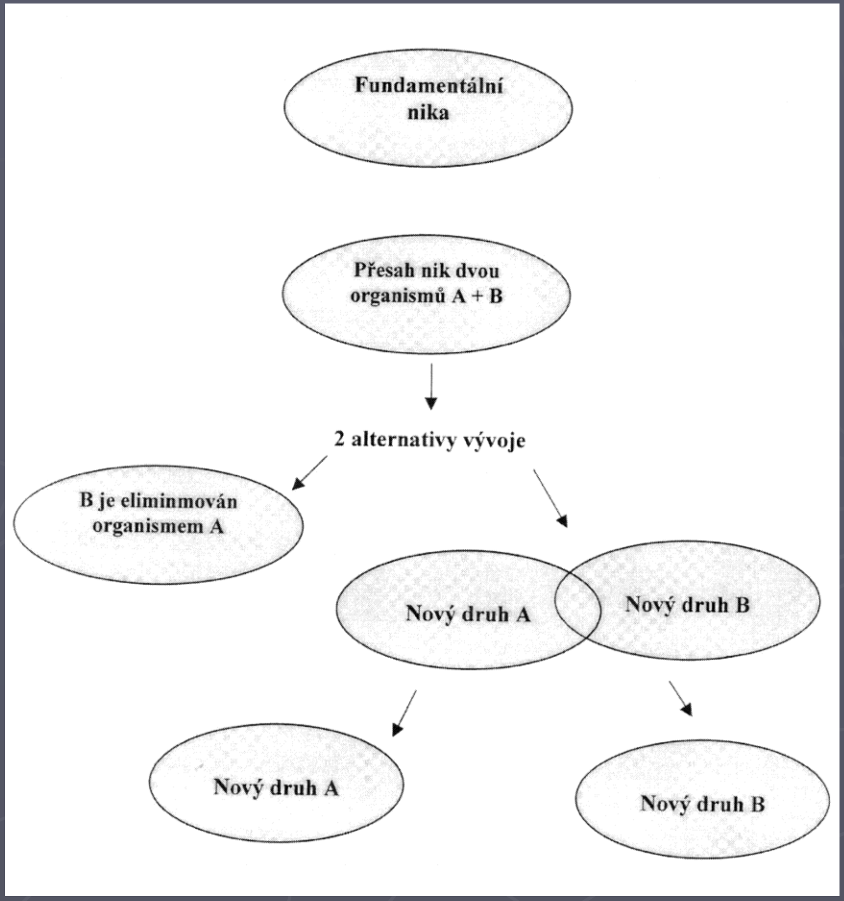
- Gause´s law, Gause (1934) – first experimental competiton
  - affecting species with similar ecological requirements →
  2 species with the same niche cannot coexist permanently
  2 species with the same ecology cannot coexist permanently

if 2 species coexist,
there was a differentiation
of realized niches



Competitive exclusion principle





the coexistence of competing species is allowed to differentiate niches, otherwise competitive exclusion

Ecological niche in parasites: dimensions

Rohde (1979)

- Host specificity
- Microhabitat
- Macrohabitat
- Geographical distribution
- Sex and age of hosts
- Season
- Food

Host specificity

- Restriction of a given parasite species to a given host species (or range of host species)
- Specialist vs. generalist

Table 8. Host specificity of parasites of fish in the Barents Sea. Host records from other seas are considered, records of accidental hosts in which parasites do not mature are not. Data from Polyanski (1966).

Parasitic group	Number of species	Percentage of species					
		In 1 host species	In > 1 species of 1 genus	In 1 family	Primarily in 1 family	In several families	Undetermined
Protozoa	25	21.7	4.3	17.4	21.7	8.7	26.2
Monogenea	21	52.4	9.5	33.3	4.8	0	0
Digenea	37	2.8	11.1	25.0	16.7	44.4	2.8
Cestoda	19	12.5	6.2	18.7	25.0	31.4	6.2
Nematoda	12	9.1	0	36.3	9.1	36.4	9.1
Acanthocephala	3	0	0	0	0	100.0	0
Hirudinea	3	33.3	33.3	33.3	0	0	0
Copepoda	15	6.7	20.0	27.0	33.2	6.7	6.7
Isopoda	1	0	0	0	100.0	0	0
Total	136	17.2	9.2	24.9	17.9	23.9	6.9

Microhabitats

- Preference of a parasite species for a specific microhabitat/-s (different morphology and physiology of microhabitats)

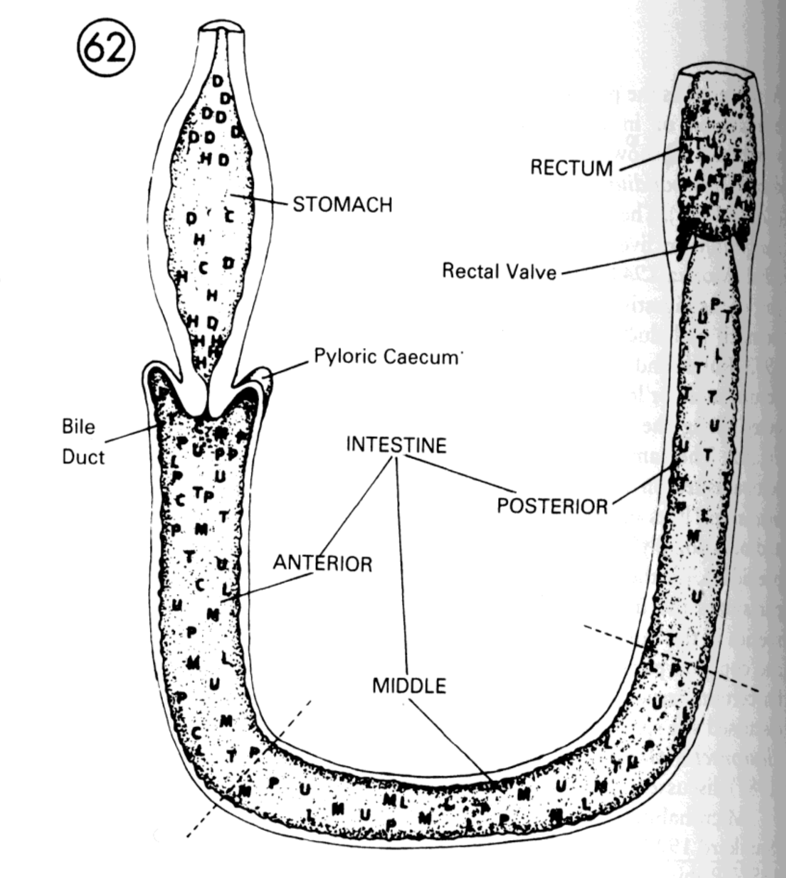


Fig. 62. The flounder gut opened to show the regional divisions and parasite distributions: A, *Pomphorhynchus* sp.; C, *Thynnascaris aduncum*; D, *Derogenes varicus*; H, *Hemiurus communis*; L, *Lecithaster gibbosus*; M, *Cucullanus minutus*; P, *Podocotyle* sp.; T, *Tetraphyllidean larvae*; U, *Cucullanus heterochrous*; Z, *Zoogonoides viviparus*. (After MacKenzie and Gibson 1970.)

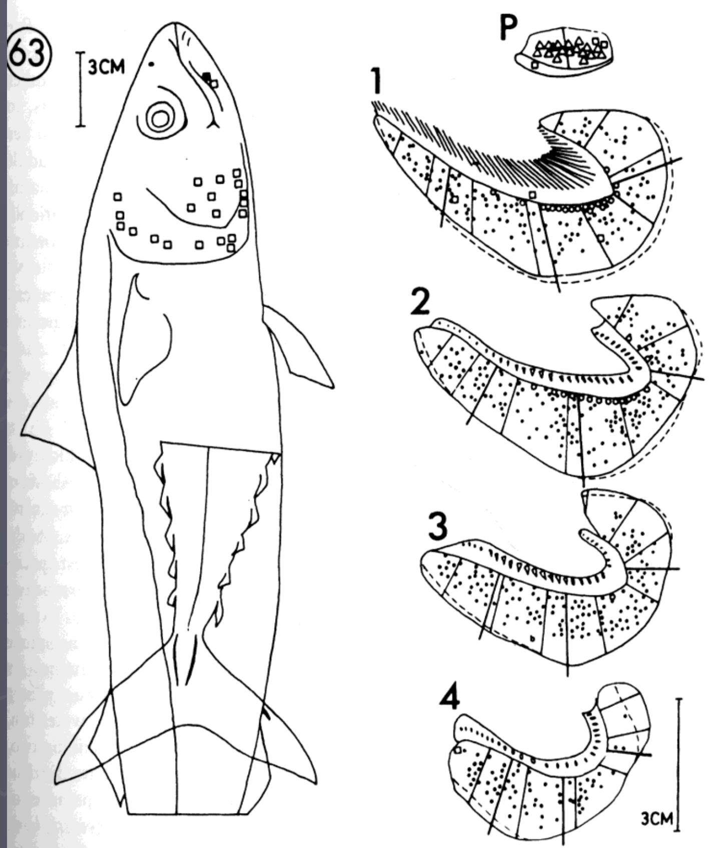


Fig. 63. Distribution of ectoparasites on the surface and in the mouth cavity of 122 *Scomber scombrus* at Helgoland, North Sea. (After Rohde 1980d.)
□ *Caligus pelamydis* in mouth cavity and on gills,
■ *C. pelamydis* in external fold of mouth;
● cysts;
○ *Kuhnia scombri* (1 circle = approx. 5 individuals);
Δ *Kuhnia* sp.
P = pseudobranch, 1–4 = gills nos 1–4.

Macrohabitats

- Habitat of hosts
- Sandy beach, rocky shore, estuary, deep sublittoral…
- Certain macrohabitats of a given host species, or several hosts from different macrohabitats
- Macrohabitat of parasites - narrower or wider than host habitat

- Ex. Larvae of nematodes parasitizing marine fish from Queensland

  - *Anisacis* – open water

  - *Contracaecum* – coastal shallow water

  - *Pseudoterranova*, *Thynnascaris* – intermediate distribution

Geographical distribution

- The spatial dimension of a niche, sometimes analogous to a macrohabitat
- Parasites - wider geographical range than host (more host species in different geographical areas)
  - narrow geographical range (one host species, infection only in part of area of host distribution)

Ex. *Diclidophora dinticulata* (Monogenea) – fish *Pollachius virensis* in the Barents Sea, *Merluccius merluccius* and *Gadus minutus* in the Atlantic

Ex. *Pseudothoracocotyla gigantica* (Monogenea) only Heron Island (Great Barrier Reef) on *Scomberomorus commerson* - commonly distributed in the Indian Ocean

Sex of host

- limited evidence
- Different food preferences, different composition of the epidermis of males and females
- Ex. *Discocotyle sagittata* (Monogenea) on *Salmo trutta* parasitizes 5-7 year old males more often than females
  Ex. *Calicotyle kroyeri* (Monogenea) is not present in gravid female stingrays *Raja radiata*

  Ex. males of snails *Hydrobia ulvae* in Britain are more parasitized by larval stages of digeneans than females of snails (16:1)

Age of host

- Preference for age category
- More common than gender preferences

- Ex. Bychowsky (1957) – many *Gyrodactylus* species – 100% mostly on young specimens of host

  Ex. *Diclybothrium armatum* (Monogenea) - absence on young sturgeons, 70-80% on adults

Food

Table 9. Food of some marine helminths. Modified from Rohde (1984a, sources therein).

Parasite	Food
Monogenea, Polyopisthocotylea	Blood, also low molecular organic compounds from water
Monogenea, Monopisthocotylea	Mucus, epithelial cells, sometimes blood
Didymozoida (Trematoda)	Blood and/or tissue fluid
Aporocotyle simplex (Trematoda)	Blood
Cestoda	Gut contents, tissue liquid
Nematoda	Gut contents, host tissue, or blood
Hysterothylacium bidentatum (Nematoda)	Fluid contents of stomach
Salvelinema walkeri (Nematoda)	Blood
Acanthocephala	Contents of intestine, tissue liquid
Hirudinea	Blood, some also prey
Larval Gnathiidae (Isopoda)	Blood
Copepoda	Blood, tissue, mucus

Niche heterogeneity in parasites

- Interactive niche heterogeneity – shift of niches in different species and reduction of niche overlap due to competition
- Spatial and temporal niche heterogeneity – i.e. seasonal occurrence of parasite species
- Niche heterogeneity facilitates parasite species coexistence in host
- If there is no niche heterogeneity → competitive exclusion of one species by the other one (e.g. larvae of digeneans in snails)

Ecological niche of parasite

- Predicted and limited localization on/in host - restricted (limited) niches
- Separation of niches between different species – niche segregation
- Limitations of the niche at the level of the microhabitats

Niche restriction in parasites

- Interactive segregation = functional response in the presence of competitor (i.e. intestinal parasites in *Podiceps*) - reduction of overlap in realized niches

- Selective niche segregation = strong competition over several generations - genetically fixed niche shift or reduction of overlap of fundamental and realized niches
  - evolutionary consequence of competition between sympatric species

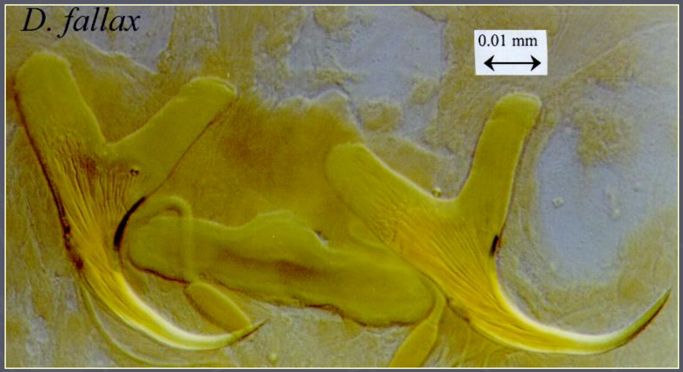
Evolutionary niche restriction in parasites

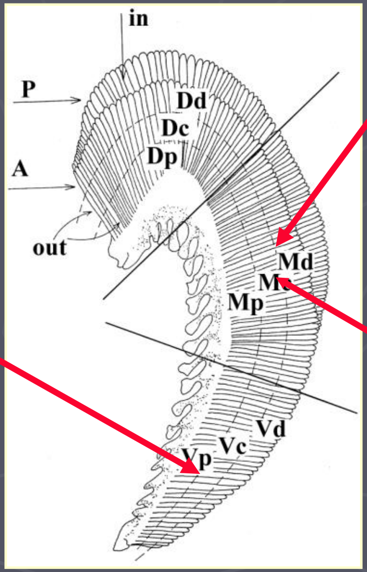
- Specific niches of parasites in the absence of current competiton
- product of past competition „ghost of competition from the past" – by the mechanisms of selective niche segragation
- independent on competition - many free niche space for parasite colonization and to facilitate intraspecific contacts and reproduction

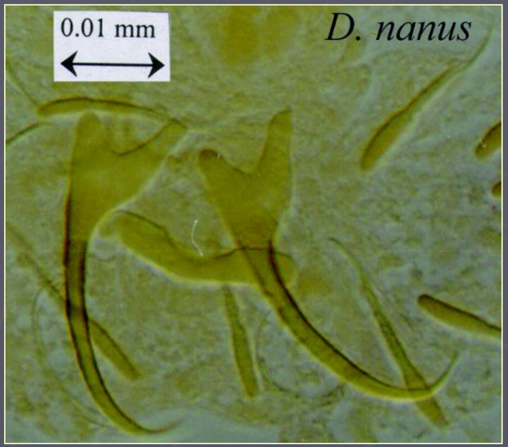
  e.g. Monogenea and Crustacea on fish gills – small infracommunities, many congeneric species on host

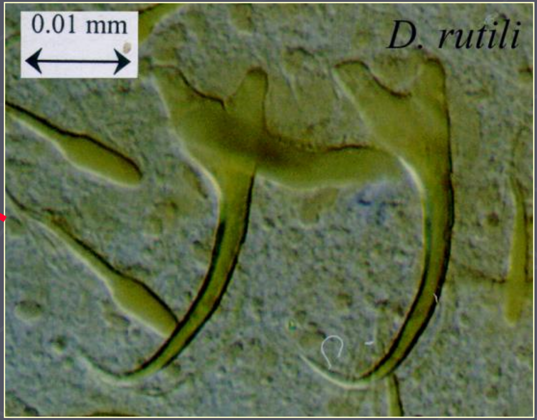
Specific niches of congeneric parasites

- Specialization and adaptation
- Morphology of attachment organ (haptor in monogeneans)









Dactylogyrus species in *Rutilus rutilus* (Cyprinidae)

Segregation of niches by specialization

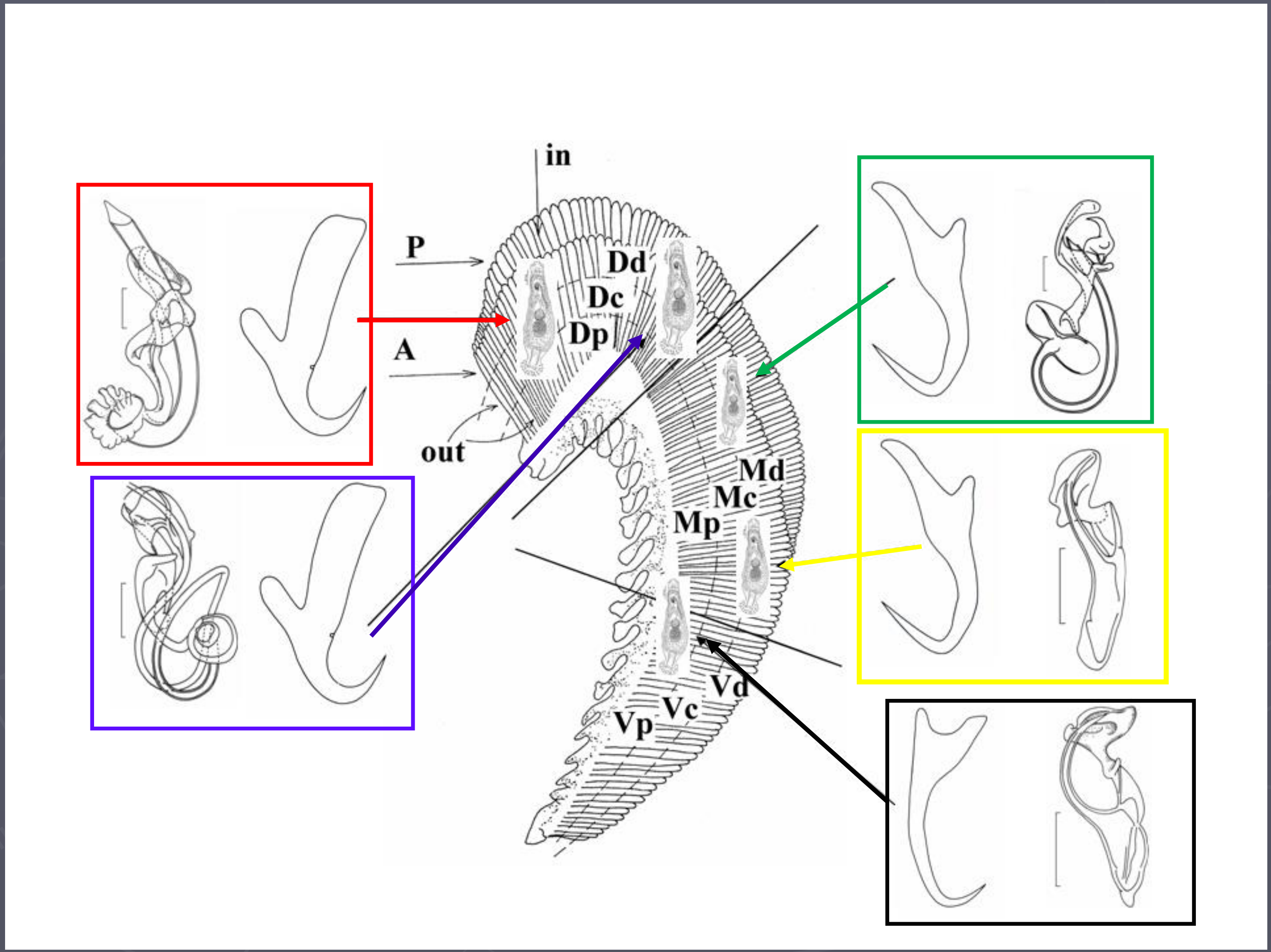
- Holmes (1990) - intestinal helminths

- Parasites select certain niches for localization, in the case of introduction to other niches, active movement to the preferred niche

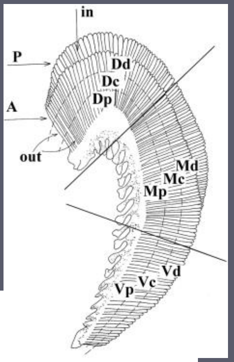
- The range of niches of adult parasites is smaller than in larvae - strict requirements for reproduction

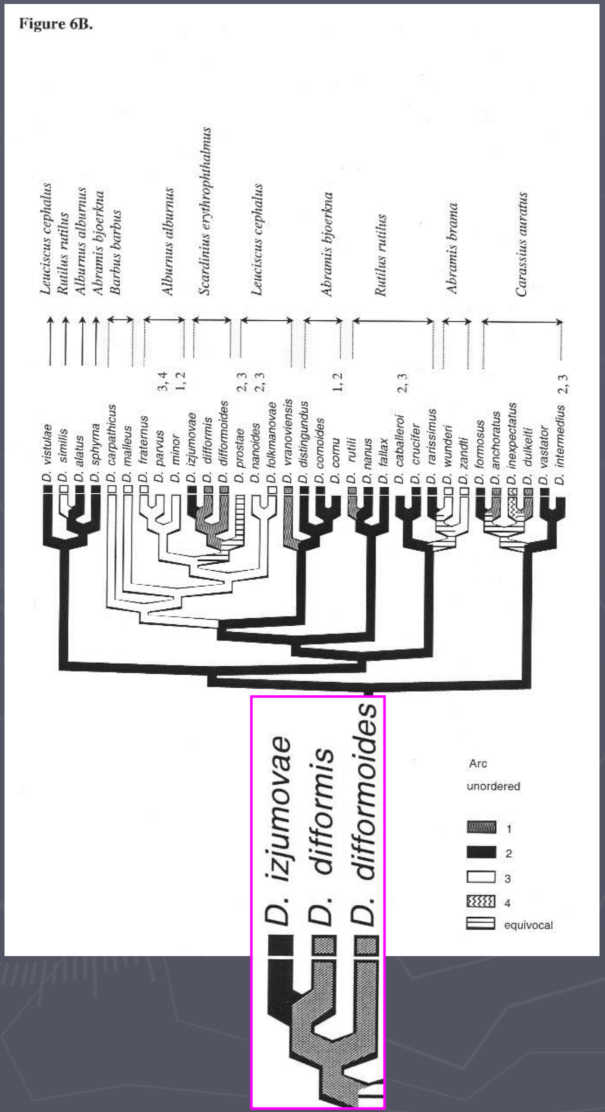
- The preferred location does not change in the case of increasing population density, and expanding the niche

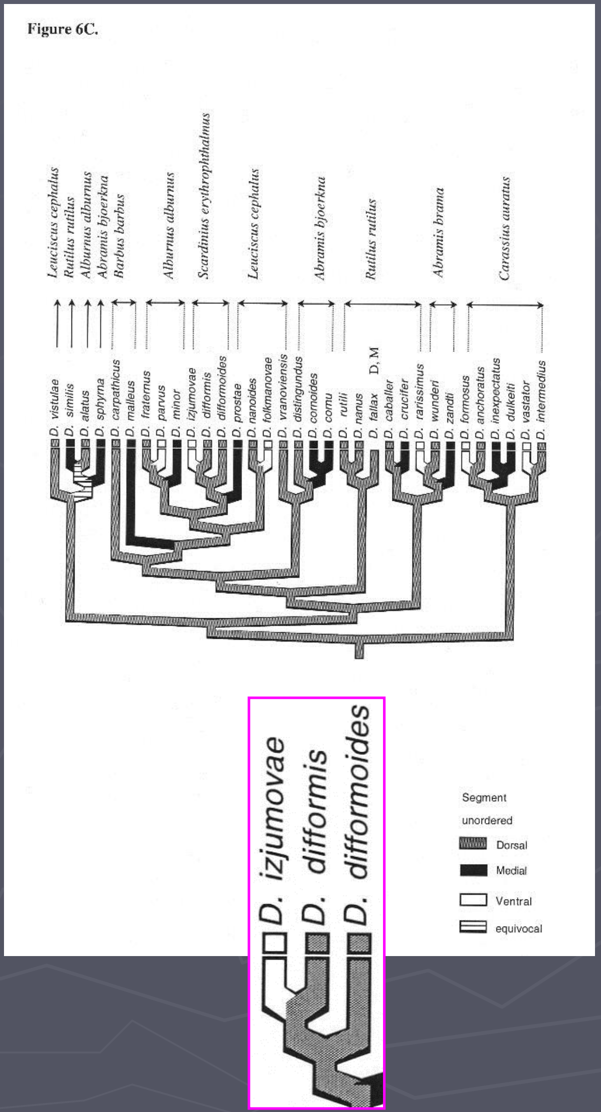
Reinforcement of reproductive barriers in congeneric parasites



Evolution of preferred niches in congeneric parasites







Quantification of ecological niche

- Niche width according to Levins (1968)

$$B = \frac{1}{\sum (p_j^2)}$$

where p_j is the proportion of individuals of a species found in sector j

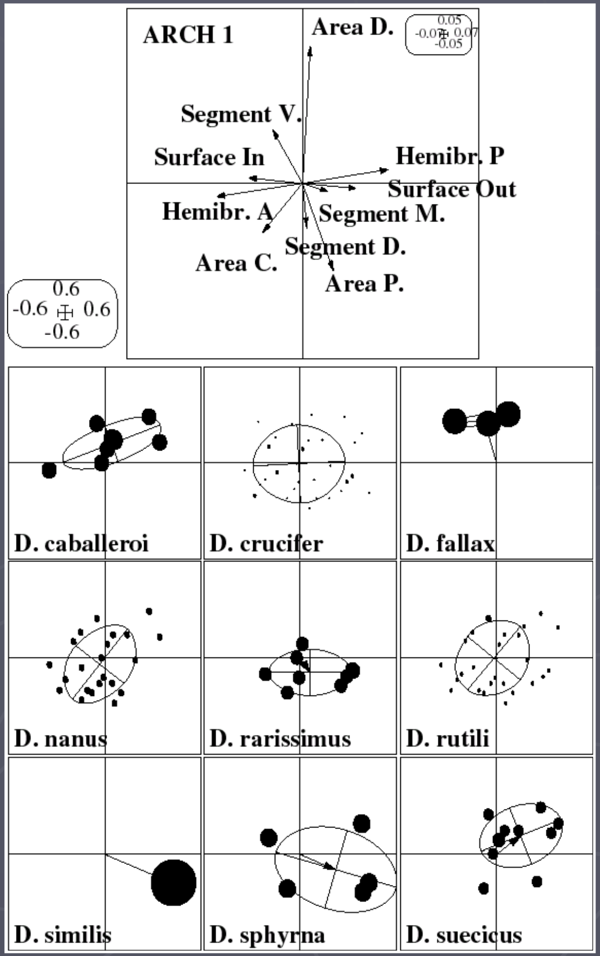
- Renkonen index of niche overlap (Renkonen, 1938)

$$R = 1 - \frac{\sum \left| p_{ia} - p_{ja} \right|}{2}$$

where p_{ia} is the proportion of individuals of species i in sector a, and p_{ja} is the proportion of individuals of species j in sector a

Quantification of ecological niche

- Outlying Mean Index (Dolédec *et al.*, 2000)
- Niche-oriented models (Tokeshi, 1990)



Coexistence of parasite species

- Niche preference
- Morphological adaptation
- Reproductive isolation
- Agregation - reduction of the overall intensity of competition through the aggregated use of fragmented resources (host)

Coexistence and aggregation of parasite species

- Aggregation model of species coexistence (Shorrocks, 1996)
- applied for parasites (Morand et al. 1999 - ectoparasites of marine fish)
- Interspecific aggregation is reduced in relation to intraspecific aggregation

Investigating the coexistence of congeneric parasites in fish

Agregation model of species coexistence (Shorrocks, 1996)

Intraspecific aggregation

$$J_1 = \frac{\sum_{i=1}^{p} \frac{n_{1i}(n_{1i}-1)}{m_1} - m_1}{m_1} = \frac{\frac{V_1}{m_1} - 1}{m_1}$$

n_{1i} is the number of species 1 in patch i
m_1 it the mean number of species 1 per patch
V_1 is the variance in number of species 1

Interspecific aggregation

$$C_{12} = \frac{\sum_{i=1}^{p} \frac{n_{1i} n_{2i}}{m_1 P} - m_2}{m_2} = \frac{Cov_{12}}{m_1 m_2}$$

n_{1i}, n_{2i}, m_{1i} m_{2i} are mean number and variance in number of species 1 and 2 per patch
P is the number of patch
Cov is covariance between a pair of species

Species coexistence

$$A_{12} = \frac{(J_1+1)(J_2+1)}{(C_{12}+1)^2}$$

Aggregation model applied for congeneric monogeneans

Intraspecific aggregation (J)

9 *Dactylogyrus* species

Interspecific aggregation (C)

24 pairs of *Dactylogyrus* positively aggregated

9 pairs of *Dactylogyrus* negatively aggregated

3 pairs of *Dactylogyrus* not evaluated

Species coexistence (A)

Reduction of interspecific aggregation in relation to intraspecific aggregation