SPECIFICITY AND HOST SUITABILITY OF *CUCULLANUS GENYPTERI* (NEMATODA : CUCULLANIDAE) IN THREE *GENYPTERUS* (OPHIDIIDAE) FISH HOST SPECIES FROM THE SOUTHEASTERN PACIFIC OCEAN

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Summary :

The host species constituted a relevant source of variation in morphometry, prevalence, abundance and reproduction of *Cucullanus genypteri* (Nematoda: Cucullanidae). The specimens were collected from three congeneric ling *Genypterus* (Ophidiiformes, Ophidiidae) fish host species. This study widens its geographic distribution from the southwestern Atlantic Ocean, Argentina, to the southeastern Pacific Ocean, Chile. Parasites were more specific to *Genypterus blacodes* because of the highest prevalence and abundance, which also were the most suitable hosts because of a higher fecundity. Phylogenetic hypotheses of the hosts based on other helminths of lings, as well as the ecological settings of this host-parasite system are discussed. Host suitability should be calculated by the relative net reproductive output of parasites inhabiting alternative and sympatric definitive hosts, rather than from prevalence and abundance data.

KEY WORDS : *Cucullanus genypteri*, *Genypterus* spp., fecundity, life-history, host phylogeny.

MOTS CLÉS : *Cucullanus genypteri*, *Genypterus* spp., fécondité, cycle évolutif, phylogénie de l'hôte.

Résumé : SPÉCIFICITÉ ET DEGRÉ D'ADÉQUATION À L'HÔTE DE *CUCULLANUS GENYPTERI* (NEMATODA : CUCULLANIDAE) DANS TROIS ESPÈCES DE POISSONS DU GENRE *GENYPTERUS* (OPHIDIIDAE) DE L'Océan PACIFIQUE

L'espèce-hôte constitue une importante cause de variation de la morphologie, de la prévalence, de l'abondance et de la reproduction pour des spécimens de *Cucullanus genypteri* parasitant trois espèces de Poissons du genre *Genypterus* (Ophidiiformes, Ophidiidae) dans le Pacifique sud-oriental, au large du Chili. Les parasites appartiennent à *Cucullanus genypteri*, une espèce récemment décrite dans l'Atlantique sud-occidentale. Ils sont plus spécifiquement inféodés à l'espèce *Genypterus blacodes* car c'est chez cette espèce qu'ils présentent la prévalence et l'abondance les plus élevées. L'espèce *Genypterus blacodes* est également l'hôte le plus adapté, car c'est chez elle que la fécondité du parasite est la plus élevée. Des hypothèses sur la phylogénie des hôtes, basées sur d'autres helminthes parasitant les espèces du genre *Genypterus* sont discutées, ainsi que les composantes écologiques de ce système hôte-parasite. Le degré d'adaptation devrait être évalué à partir du rendement reproductif net comparé des parasites chez différents hôtes définitifs sympatriques, plutôt qu'à partir des données d'abondance et de prévalence.

INTRODUCTION

It is well accepted that the mere list of alternative host species does not reveal which of them are better environments for parasite development. However, categorization of hosts as unsuitable, suitable and required has not been considered at the moment of quantifying host specificity (see Holmes, 1976, 1979; Rohde, 1980, 1994).

With the aim of assessing host specificity and host suitability, this research compares the morphology, morphometry, prevalence, abundance, sex ratio, proportion of mature females and fecundity of *Cucullanus genypteri* specimens that in the southeastern Pacific Ocean have been reported only in the three ling

Genypterus species inhabiting the area (Vergara & George-Nascimento, 1982; George-Nascimento & Huet, 1984; Rizzo, 1994): the golden ling *Genypterus blacodes* (Schneider, 1801), the red ling *G. chilensis* (Guichenot, 1848) and the black ling *G. maculatus* (Tschudi, 1846). *Cucullanus genypteri* was recently described by Sardella *et al.* (1997) in two ling *Genypterus* species from the southwest Atlantic Ocean. Host specificity is Rohde's index of relative abundance of a parasite in alternative hosts (Rohde, 1980, 1994). Host suitability is an index of the relative reproduction of a parasite among alternative host species. Our major goal was to assess if the three host species were habitats of different quality for the parasites, as seen from variations on parasite morphometry, and especially, on reproduction.

Genypterus (Ophidiiformes: Ophidiidae) species are distributed in the Southern Hemisphere only. *Genypterus blacodes* is the most widely distributed species and assumed to be the most primitive in the genus (Villalba & Fernández, 1986), although there are no specific phylogenetic hypotheses. The three host species

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in Chile have a different bathymetric distribution and occupy different habitats (Chong, 1984; Villalba & Fernández, 1986; Chong & Alveal, 1990). There is, however, some dietary overlap where most likely the prey responsible for the transmission of *Cucullanus genypteri* to their definitive hosts may be found (Henríquez & Bahamonde, 1964; Bahamonde & Zavala, 1981).

MATERIALS AND METHODS

In order to assess whether parasites belonged to one or more *Cucullanus* species, comparisons between specimens collected from the different hosts were made on their morphology and morphometry. Morphology of the mouth cavity, the head, the teeth, the spicules, and the number and distribution of caudal papillae were compared under SEM observations. Location of the excretory pore and deirids were qualitatively determined. Morphometry included the position of the vulva, oesophagus length, body length, body width, length of spicules and egg length and width, which were measured in mm or microns with a stereoscopic microscope furnished with a camera lucida. Body length, oesophagus length, position of the vulva, position of the cloaca and spicule length were also measured as a proportion of body length (%). The distance of the vulva is to the anterior end, and the distance of the cloaca to the posterior end. Maximum body length and body width of females were measured in more specimens because they were used for the estimation of parasite fecundity. Prevalence and abundance were based on the examinations of the viscerae of 28 golden lings, 36 red lings and 77 black lings, sampled offshore Talcahuano (36° 41'S, 73° 06'W), Chile, from November 1994 to June 1995, and on literature data from the same area (Vergara & George-Nascimento, 1982; George-Nascimento & Huet, 1984; Rizzo, 1994). Fishes were frozen to -20 °C until examination. Host specificity considered the index proposed by Rohde (1980) on abundance data. Host suitability is the mean number of eggs per female as a proportion of this variable summed across host species. The value of this index range between 0 and 1.

Comparisons on the reproductive aspects of parasites between hosts were on the sex ratio, the proportion of mature females, the fecundity and the relationship between fecundity and body volume. Females featuring eggs were considered to be mature. Statistical analyses on sex ratios and the proportion of mature females in the three host species were done through Chi-square tests on 3 × 2 contingency tables. Departure of the 1:1 sex ratio of parasites was done by a

goodness of fit Chi-square test for each host species. Fecundity, in number of eggs per mature female, was estimated as the proportion between the volume of the uteri and the volume of one egg. The volume of the uteri was assimilated to a cylinder and that of the egg to a sphere. The length and width of the body and the uteri were obtained out of drawings made through a camera lucida, and by using a curvimeter. Then, body volume was calculated, in mm³, by assimilating body shape to a cylinder. Egg diameter was the average of its maximum length and width. Mean egg volume was considered constant ($\bar{x} = 8.61 \times 10^{-5} \text{ mm}^3$, s.d. = $2.42 \times 10^{-7} \text{ mm}^3$) because there were no significant differences between host species (ANOVA, $F_{(2, 39)} = 1.34$; $P = 0.27$). A log-log linear regression of fecundity on body volume was carried out in 144 mature females. Statistical tests on the differences among host species in parasite morphometry and fecundity were One-way analysis of the variance of each variable. The variation of parasite fecundity with parasite body volume among host species was assessed with a covariance analysis on log transformed data (Sokal & Rohlf, 1981).

RESULTS

MORPHOMETRY OF *CUCULLANUS GENYPTERI* IN DIFFERENT HOSTS

Morphometry and morphology of specimens from lings of the Pacific Ocean revealed no remarkable differences with *Cucullanus genypteri* as described in lings *Genypterus blacodes* and *G. brasiliensis* from the southwest Atlantic Ocean by Sardella *et al.* (1997) (Table I).

Males showed no significant differences neither in body length ($F_{(2, 33)} = 0.21$; $P = 0.81$) nor in body width ($F_{(2, 29)} = 0.55$; $P = 0.58$). However, the length of the oesophagus ($F_{(2, 33)} = 5.22$; $P = 0.01$), and its proportional length ($F_{(2, 33)} = 10.91$; $P = 0.0002$), were larger in parasites from *G. blacodes* than in those from the two other host species. Although spicules were longer in specimens from *G. chilensis* ($F_{(2, 31)} = 3.57$; $P = 0.04$), the proportional length was similar ($F_{(2, 31)} = 2.64$; $P = 0.08$) (Table I).

Females had no significant differences in body length ($F_{(2, 170)} = 1.46$; $P = 0.23$), in the position of the vulva ($F_{(2, 26)} = 1.37$; $P = 0.27$), or in the position of the anus ($F_{(2, 26)} = 1.92$; $P = 0.17$). Nevertheless, they were wider in golden lings ($F_{(2, 141)} = 23.46$; $P < 0.0001$), and as a consequence of this, they also had a larger body volume ($F_{(2, 141)} = 10.58$; $P < 0.0001$) (Table IV). In addition, and similarly to males, the absolute length of the oesophagus ($F_{(2, 26)} = 36.07$; $P < 0.0001$) and the rela-

Geographical Origin	SW Atlantic								SE Pacific											
Host species	<i>Genypterus blacodes</i>								<i>Genypterus chilensis</i>								<i>Genypterus maculatus</i>			
Morphometric characters	<i>n</i>	<i>x</i>	Range		<i>n</i>	<i>x</i>	(s.d.)	Range	<i>n</i>	<i>x</i>	(s.d.)	Range	<i>n</i>	<i>x</i>	(s.d.)	Range				
Males																				
Total body length (mm)	10	19.6	18.6 - 23.0		14	20.4	(2.31)	15.5- 25.8	12	21.1	(1.41)	18.9-23.5	10	20.6	(3.60)	13.6-25.0				
Body width (μ)	10	350	260 - 460		12	337	(55)	250 - 450	10	345	(61)	250 - 425	10	360	(87)	200 - 450				
Oesophagus length (mm)	10	2.1	1.8 - 2.3		14	2.1	(0.40)	1.1 - 2.7	12	1.8	(0.29)	1.2 - 2.3	10	1.6	(0.45)	1.2 - 2.7				
Oesophagus length (%)	10	10.7	–	–	14	10.2	(1.15)	7.8 - 12.0	12	8.5	(1.38)	6.4 -10.7	10	7.7	(1.54)	5.4 -10.9				
Spicule length (mm)	10	1.1	1.04 - 1.2		13	1.1	(0.11)	0.9 - 1.3	12	1.3	(0.19)	1.0 - 1.7	9	1.1	(0.30)	0.6 - 1.5				
Spicule length (%)	10	5.7	–	–	13	5.3	(0.68)	3.8 - 6.2	12	6.0	(1.20)	4.9 - 8.6	9	5.1	(1.14)	3.3 - 7.1				
Females																				
Total body length (mm)	10	23.0	18.0 -28.7		85	24.5	(4.21)	14.0- 41.0	51	24.6	(5.21)	14.2-35.7	37	26.0	(5.27)	13.6-33.6				
Body width (μ)	10	360	320 - 530		75	720	(140)	400 -1,050	42	590	(104)	300 - 760	27	550	(120)	310 - 550				
Oesophagus length (mm)	10	2.5	1.8 - 2.6		10	2.6	(0.19)	1.3 - 2.7	9	1.9	(0.42)	1.5 - 2.7	10	1.6	(0.20)	1.2 - 1.8				
Oesophagus length (%)	10	10.8	–	–	10	9.8	(0.70)	8.3 - 10.6	9	7.2	(1.58)	4.5 - 9.5	10	7.1	(2.13)	3.6 -11.1				
Position of vulva (%)	10	65.5	–	–	10	61.6	(2.58)	57.1- 64.7	9	63.8	(4.32)	57.1-71.4	10	64.9	(6.00)	61.1-81.5				
Anus to tail (%)	10	1.9	–	–	10	1.9	(0.60)	1.1 - 2.9	9	1.5	(0.60)	1.1 - 2.9	10	1.4	(0.35)	0.9 - 2.4				
Egg size, large diameter (μ)	–	–	–	–	14	70	(8)	60 - 84	14	72	(9)	60 - 84	14	67	(14)	50 - 80				
Egg size, short diameter (μ)	–	–	–	–	14	40	(6)	36 - 48	14	40	(5)	36 - 48	14	36	(9)	24 - 48				

Table I. — Morphometric characters of *Cucullanus genypteri* in host species from the SW Atlantic (Sardella *et al.*, 1997) and the SE Pacific.

tive length of it ($F_{(2, 26)} = 9.28$; $P = 0.0009$) were greater in parasites collected from golden lings (Table I).

HOST SPECIFICITY AND HOST SUITABILITY

Cucullanus genypteri was more specific to golden lings because there they showed the highest prevalence and abundance (Table II). Rohde's specificity index based on abundance data ranged between 0.78 for these data and 0.93 for the published information (Table II).

Sex ratio of parasites in all three host species was not different ($\chi^2 = 2.93$; d.f. = 2; $0.10 < P < 0.25$), although females were in higher proportion than males in each host species (Table III).

The proportion of *C. genypteri* mature females was similar among host species (Table III). Females showed the greatest fecundity in *G. blacodes*, while *G. maculatus* and *G. chilensis* were not different among each other (Table IV). Fecundity increased with female body volume in all three host species (Simple regression analysis: $F_{(1, 142)} = 159.6$; $P < 0.0001$; $r^2 = 0.53$).

The covariance analysis showed no significant differences between host species in the slope of the regression of fecundity on body volume although there were significant differences in the elevations (Table V). Again, the regression in *G. blacodes* had the highest elevation, with no differences among the other two

Host species	<i>n</i>	P	A	Source
<i>Genypterus blacodes</i>	28	89.3	6.9	This study
	60	88.3	2.3	Riffo, 1994
<i>Genypterus chilensis</i>	36	74.9	3.2	This study
	80	72.5	3.6	Vergara & George-Nascimento, 1982
<i>Genypterus maculatus</i>	77	59.7	1.4	This study
	80	8.0	0.1	George-Nascimento & Huet, 1984

Table II. — Number of hosts examined (*n*), prevalence (P, %) and abundance (A) of *Cucullanus genypteri* in three *Genypterus* species from the southeastern Pacific Ocean.

Host species	<i>n</i>	<i>np</i>	<i>f</i>	χ^2	<i>mf</i>
<i>Genypterus blacodes</i>	17	170	112	16.52*	52
<i>Genypterus chilensis</i>	23	187	120	13.36*	50
<i>Genypterus maculatus</i>	28	75	56	17.28*	30

(Chi-square on proportion of mature females among host species = 0.86; d.f. = 2; $0.50 < P < 0.75$).

Table III. — Number of hosts parasitized (*n*), number of *Cucullanus genypteri* collected (*np*), number of females (*f*), Chi-square values on 1:1 sex ratio with 1 degree of freedom and number of mature females (*mf*) in three *Genypterus* host species. * = $P < 0.0001$.

host species (Fig. 1). Host suitability was 0.423 in golden lings, 0.243 in red lings, and 0.334 in black lings.

DISCUSSION

Cucullanus genypteri was described in the Southwestern Atlantic Ocean in *Genypterus blacodes* and *G. brasiliensis* (Sardella *et al.*, 1997). In the Pacific Ocean, the only phenotypic traits allowing to suspect the existence of more than one *Cucullanus* species are the longer oesophagus of parasites in golden lings, and the longer spicules of males collected from the red ling than in males collected from the two other hosts species (Table I). It would not be surprising, however, that electrophoretic analysis reveal that this is a species complex, as reported for several marine ascaroid nematodes and other helminth parasites (e.g., Bullini *et al.*, 1978; Nascetti *et al.*, 1986; Orecchia *et al.*, 1986; Paggi *et al.*, 1991; Nascetti *et al.*, 1993).

Source of variation	d.f.	SS	MS	F	P
Differences among separate slopes	2	0.0818	0.0409	1.10	0.336
Deviations in each group from its separate slope	138	5.1309	0.0372		
Deviations among intercepts	2	0.4788	0.2394	6.43	0.002
Error	140	5.2128	0.0372		
Total	143	12.5433			

* Common slope = 0.8337
Intercept for parasites in:
Genypterus blacodes = 3.532
Genypterus chilensis = 3.355
Genypterus maculatus = 3.322

Table V. — Summary of ANCOVA on fecundity of *Cucullanus genypteri* ($\log_{10}$, number of eggs per female) where the body volume ($\log_{10}$, mm³) is the covariable and the host species is the factor. d.f. = degrees of freedom, SS = sum squares, MS = mean squares, P = probability.

Host species	<i>n</i>	Volume	s.d.	Fecundity	s.d.
<i>Genypterus blacodes</i>	75	11.00	(6.75)	21,432	(10,676)
<i>Genypterus chilensis</i>	42	7.01	(3.29)	12,292	(8,199)
<i>Genypterus maculatus</i>	27	7.21	(4.03)	16,913	(10,358)

(Volume: $F_{(2, 141)} = 10.58$, $P < 0.0001$; Fecundity: $F_{(2, 141)} = 11.51$, $P < 0.0001$).

Table IV. — Body volume (mm³) and fecundity (number of eggs per female) in *Cucullanus genypteri* according to host species and summary of ANOVA. *n* = number of parasites examined.

The fact that *Cucullanus genypteri* is more prevalent and abundant in *G. blacodes*, as these and published data reveal (Table II, Vergara & George-Nascimento, 1982; George-Nascimento & Huet, 1984; Rizzo, 1994; Sardella *et al.*, 1997), indicates that it is more specific to it (Table II). Differences in prevalence and abundance among hosts species (Table II) can be explained by the differences in the habitats, bathymetric distribution and diet of the hosts. These facts suggest that the demographic exchangeability of this parasite among host species should be more associated to the distribution and vagility of the invertebrate intermediate hosts rather than to that of the definitive hosts (the stomatopod *Pterygosquilla armata* and the shrimp *Pleuroncodes monodon* are the main prey items shared by these three host species, Henríquez & Bahamonde, 1964; Bahamonde & Zavala, 1981), although different intermediate hosts may transmit the parasite to each ling species.

Parasite's fecundity, body size and morphology are more indicative of host suitability because most suitable hosts do not always have the highest prevalences and abundances (e.g.: Holmes, 1979; Ubeda *et al.*, 1994). According to recent analyses on the evolutionary correlates of life-history traits among parasitic nematodes of vertebrates, the mere fact that female parasites had a larger body volume in golden lings should have led to expect a higher reproductive output in this host (Morand, 1996). However, the fact that the elevations and not the slopes of the regressions between fecundity and body volume were higher in parasites from golden lings (Table V, Fig. 1) tells that the host's specific identity effect on fecundity is not the effect on the parasite's body volume only.

Results suggest that *G. blacodes* is the host that provides the best conditions for parasite development (Table IV, Fig. 1). Perhaps, *Cucullanus genypteri* has a longer time of association with *G. blacodes*. To our knowledge, the oioxenic blood fluke *Aporocotyle* species inhabiting the circulatory system of *Genypterus* species in Chile provide some support to these relationships between lings because *Aporocotyle ymakara*,

Fig. 1. — Log-log regressions between body volume (mm³) and fecundity (number of eggs) in *Cucullanus genypteri* females collected from a) *Genypterus blacodes*, b) *Genypterus chilensis*, and c) *Genypterus maculatus*.

which is found in *G. blacodes*, has been considered the most primitive blood fluke species in lings (see Villalba & Fernández, 1986).

We propose that host specificity and host suitability be separately assessed (see Downes, 1989 for a mixed use of the concepts). The former is a property of the parasite with obvious evolutionary connotations in host-parasite associations, although it has been formally defined in a way that has too many ecological sources of variation (Rohde, 1980, 1994). Host suitability, on the other hand, is a property of each of the host species where a parasite is found. We believe that the relative reproductive output of conspecific parasites in alternative hosts are a neat and simple way of quantifying the host suitability and its effects on parasite fitness.

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