

Ecological helminthology of wildlife animal hosts from South America: a literature review and a search for patterns in marine food webs

Helmintología ecológica en huéspedes animales silvestres de Sudamérica: revisión de la literatura y búsqueda de patrones en tramas tróficas marinas

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ABSTRACT

In this review I first summarize research on the helminth parasitism of wildlife animal hosts, done in South America during the last decade (1976-1985), with emphasis on ecological studies. I then describe and compare the taxonomic richness, host ranges and similarities for trophically-transmitted endohelminth assemblages reported in marine fishes from the northeast and southeast Pacific Ocean. I explore the relationship between taxonomic affinity, dietary overlap and similarity in helminth fauna among fish hosts, and also the relationship between parasite richness and host trophic level in pinniped-dominated sink food webs. Results show that research on the ecology of helminths in South America is just emerging, and that the existing host-parasite records for marine fish and pinnipeds conform to a general pattern of distribution of helminths in marine food webs.

Key words: Parasite richness, parasite similarity, marine fish, food webs.

RESUMEN

En esta revisión resumo los resultados de las investigaciones hechas en Sudamérica que, principalmente, tratan de aspectos ecológicos del parasitismo por helmintos en huéspedes silvestres, durante la última década (1976-1985). En seguida, describo y comparo la riqueza taxonómica, rangos de huéspedes y la similitud de las comunidades de helmintos transmitidos tróficamente, según han sido documentados para los peces marinos del océano Pacífico del nor y sudeste. Además, exploro la relación entre la afinidad taxonómica, la similitud dietaria y la similitud en helmintofauna entre los peces, y también la relación entre la riqueza parasitaria y el nivel trófico del huésped en ramas tróficas de "sumidero", dominadas por pinnípedos. Los resultados muestran que la investigación en la ecología de los helmintos está comenzando en Sudamérica, y que los registros huésped-parásito existentes para peces y pinnípedos parecen ajustarse a un patrón general de distribución de los helmintos en las tramas tróficas marinas.

Palabras claves: Riqueza parasitaria, similitud parasitaria, peces marinos, tramas tróficas.

INTRODUCTION

The most common approach to the study of the ecology of parasites in the context of interactions between trophic levels, the subject of this workshop, considers parasites as potential agents of host population regulation. I instead emphasize the importance of trophic interactions among hosts as the proximate mechanism by which some helminth parasites persist in any host community. The overall aims of this review are: First, to provide the background, and to comment on the gaps, trends, and areas on which further research

on ecological helminthology is expected in South America (S.A. hereafter). Second, to show that despite the scanty knowledge on the ecology of helminths in S.A., inference from the basic data on host-parasite records may provide a basis for testing the validity of some broad generalizations put forth in the eco-parasitological literature.

Despite the extent of current world communication in science, the lack of efficient transmission of information from and to the majority of S.A. research centers still persists. Several S.A. libraries, mainly in small cities, do not have an adequate

budget for supporting suscriptions to a reasonable variety of international journals. On the other hand, a large amount of S.A. research is published in journals of such a narrow circulation, that some of them remain unknown for years, even to the authorities specialized on the subject. This provides the justification for attempting a brief review that updates information to readers from and outside S.A. Consequently, in the first part I review the literature on host-helminth associations, in order to realize how much work has been done in S.A., directly or indirectly addressing ecological questions.

May's (1983, 1984) request for "more parasites in food web studies" inspired me to explore host community data in the second part of this review, where interactions between trophic levels constitute the mechanism by which helminths at larval stages accede to later ontogenetic stages. Thus, I emphasize studies in helminths transmitted through food to vertebrate predators, by consumption of either vertebrate or invertebrate prey that are the intermediate hosts of parasites (*sensu lato*, that is, including paratenic or transport hosts). I provide examples of how some assertions about the correlates of taxonomic richness, host ranges and similarity in helminth communities could be evaluated with data on host-parasite records for marine fishes and food webs from the Pacific coast of S.A. However, the data may be inappropriate for a critical evaluation of patterns when attempting to review the state of knowledge in a subject of recent development and in a geographic area dominated by developing countries. Therefore, I compare the information gathered in S.A. with that from a better surveyed area, the Pacific coast of North America (N.A. hereafter).

MATERIAL AND METHODS

First part

In order to describe the state of parasitological research in S.A., the number and subject of parasitological studies dealing with wildlife hosts was checked for every country (Guyana, French Guiana and Surinam arbitrarily excluded), by surveying the Helminthological Abstracts (Commonwealth Agricultural Bureaux) published

between 1976 and 1985. I tabulated by countries the number of papers dealing with the following five subjects: host and geographical records, descriptions of new species and life cycles, zoogeography and evolution of host-parasite associations, wildlife diseases, and reports on intensity or incidence of infections. I used a non exclusive categorization of papers, by subjects, in order to emphasize results of ecological interest. Studies of ecological interest were considered those on host-helminth zoogeography, evolution, effects of parasites upon hosts, and helminth populations and communities. Studies on life cycles, prevalence and intensity of infections by helminths were considered part of a descriptive stage in the development of parasitology, rather than of intrinsic ecological interest. However, description of helminth life cycles generally imply identification of biological associations involving more than two species. Among studies reporting quantitative estimates of parasitism, only those that included host (size, sex) or habitat variables as potential correlates of prevalence or intensity of infections, were considered of ecological interest.

Second part

I combined information from a variety of sources, in order to assess the existence of pattern in the numerical features (see Definition of terms, below) of the checklists analyzed.

Definition of terms

In every checklist, I recorded for each host genus the total number of cestode, nematode and acanthocephalan genera (hereafter labeled CNA), as well as their host status (intermediate or definitive host, according to whether the record was a larval or adult stage of the parasite, respectively). I considered the combined number of CNA because they have a common mode of transmission, that is, through food consumption. Parasite richness is the number of CNA genera reported for each host genus. Host range is the number of host genera from which a parasite genus has been reported, regardless of how heavily and frequently the various host genera are infected (Rhode 1984). The

number of cases of parasitism in each checklist is the sum of host ranges for each parasite genus or the sum of parasite richness for each host genus. I omitted digenetic trematodes because they are not strictly linked to trophic transmission and further, they have not been studied extensively in the Southeastern Pacific Ocean.

Data bases

Perú: Records of CNA helminths in marine fish were obtained from reports, communications to congresses and publications as summarized by Tantaleán *et al.* (1982), and from the papers of Durán & Oliva (1980), Escalante & Carvajal (1981, 1984), and Escalante (1984)¹. The host-parasite matrix has 32 fish genera and 37 CNA genera, and is shown in Appendix I. Data on the relative abundance of 17 demersal fish genera, as reported by Samamé *et al.* (1978), was used to assess its correlation with the CNA parasite richness reported for those fish.

Chile: Records of CNA helminths in marine fish came from the following publications: Fernández & Villalba (1985a) for nematode genera, and scattered published and kindly facilitated unpublished records and checklists on cestode and acanthocephalan genera (Van Cleave 1921, Yáñez 1950, Carvajal & Goldstein 1969, 1971, Carvajal 1971, 1974, 1977, Euzet & Carvajal 1973, Carvajal & Dailey 1975, Dailey & Carvajal 1976, Cattán 1977, Carvajal & Cattán 1978, Carvajal & Campbell 1979, Carvajal *et al.* 1979, Cattán *et al.* 1979, Soto & Carvajal 1979, Campbell & Carvajal 1980, Carvajal & Jeges 1980, Oliva 1982, Vergara & George-Nascimento 1982, George-Nascimento & Huet 1984, Fernández 1985, Villalba & Fernández 1985, J Carvajal, L Durán, R Mendoza, M Oliva and C Villalba, personal communications). The binary host-parasite matrix has 57 fish genera and 47 CNA helminth genera (Appendix II).

Maximum body size of 42 fish host genera (Mann 1954), and sample size of 28 host genera (the sum of the number of host

individuals examined, when reported by the authors consulted in this review), were explored in their correlation with CNA parasite richness. Host dietary composition, both qualitative and quantitative, was used to assess the relationship between the similarity in diet and in helminth fauna among fish hosts, with published and unpublished data for 14 fish species (Delfin 1903, Bahamonde 1950, 1953a, 1953b, Bahamonde & Cárcamo 1959, Henríquez & Bahamonde 1964, Rosario 1970, Etcheberry 1978², Konchina 1980, Molina *et al.* 1980, Moreno & Zamorano 1980, Bahamonde & Zavala 1981, Ojeda 1981³, R Mendoza, H Arancibia, personal communications). Taxonomic affinity among these 14 species was assessed by categorizing each host pairwise comparison in decreasing order of relatedness: fishes in the same genus, family, order, Class, or in different Class, according to Nelson (1976). These fish species are indicated in Fig. 3b with asterisks; CNA recorded in these fish are summarized in Appendix II, and prey items identified in those fish are listed in Appendix III. The sink food web where parasite richness by CNA genera was examined according to host trophic level was built by consulting the following sources: diet of the S.A. sea lion *Otaria flavescens* Shaw (George-Nascimento *et al.* 1985), indicated in parenthesis in Fig. 3b; helminth fauna of the S.A. sea lion (George-Nascimento & Carvajal 1981; and CNA helminth genera found in their fish prey (Appendix II).

Pacific coast of North America: Records on CNA helminths are from Love & Moser (1983). This checklist differs from those of S.A. in that it includes helminth records beyond the Eastern Pacific coast of N.A. Thus, parasite richness appears exaggerated in widely distributed fish. It is hoped that this effect be somewhat reduced by considering hosts and parasites at the genus level. Data on the maximum body size of

1) ESCALANTE H (1984) Cestodes parásitos de peces: Descripción de seis nuevas especies de tetrarínquidos y hallazgo de un nuevo huésped de *Diphyllbothrium pacificum*. Tesis Depto. de Microbiología y Parasitología, Universidad Nacional de Trujillo, Perú, 36 pp.

2) ETCHEBERRY C (1978) Algunos aspectos biológicos de tiburones, predominantes en las pesquerías de arrastre y espinel, capturados en la zona de Talcahuano. Informe Práctica Profesional, Departamento de Biología y Tecnología del Mar, Sede Talcahuano, Pontificia Universidad Católica de Chile, 127 pp.

3) OJEDA FP (1981) Estructura comunitaria de peces demersales en el extremo austral de Chile: explicación ecológica de patrones latitudinales, batimétricos y de simpatria. Tesis, Facultad de Ciencias, Universidad de Chile, 91 pp.

227 fish genera from Miller & Lea (1972), were used to explore the correlation with parasite richness. Data used when sink food webs were the units explored for addressing the existence of differences in parasite richness between hosts of different trophic level were: diet of pinnipeds living in the California current (Antonelis & Fiscus 1980; Table 2); CNA helminth genera of those pinnipeds (Dailey 1975: Tables 83 through 89, 92 and 93); and parasite richness by CNA helminth genera as reported in their fish prey (Love & Moser 1983).

Statistical methods and classification techniques

The existence of differences between checklists in the proportions of intermediate and definitive host genera, and of parasite genera at larval and adult stages, was tested by means of Chi-square tests. I tested the significance of differences in location and dispersion among frequency distributions of parasite richness, and of host ranges, by means of Smirnov tests. Correlation coefficients calculated between parasite richness and any other variable are Spearman's r_s (Conover 1980).

Similarity in parasite fauna among host genera was assessed by means of the number of shared helminth genera, and by the Jaccard's index for binary data (Legendre & Legendre 1983). Absolute numbers of parasite genera shared by hosts were considered more informative about the possible similarity in biology among hosts, than merely taking into account their similarity values. No attempt was made to extrapolate the results with binary data to a situation in which quantitative data on parasites were available. In addition to Jaccard's index, similarity in diet among hosts was assessed by means of Morisita's index (modified by Horn 1966, *vide* Hurlbert 1978), for data on numbers of prey individuals. In order to detect whether taxonomic affinity and similarity in diet (binary and quantitative) among hosts were relevant explanatory variables of the similarity in helminth fauna (measured by the absolute number of CNA genera shared or by Jaccard's index), I matched each pairwise comparison (in CNA, diet, or taxonomic affinity, $n = 91$), and tested the significance of the amount

of variance in CNA similarity explained by, first, taxonomic affinity, and then, by similarity in diet among 14 fish species from Chile, using an ANCOVA on the ranked variables (Conover & Iman 1982).

The clustering technique used was WPGMA (Sneath & Sokal 1973), because sampling over hosts and parasites has not been at random (Legendre & Legendre 1983), but biased toward fish frequently occurring in commercial catches, and toward those parasite taxa that happened to be of interest to taxonomists.

RESULTS AND DISCUSSION

Part one:

Literature review of helminthology in South America

Taxonomic and life cycle studies

Four hundred out of 476 (84%) helminthological studies done in wildlife animal hosts of South America during 1976-1985 and whose abstracts appeared in the Helminthological Abstracts, deal with host records, life cycles or taxonomic research on helminths. These topics are by far the major subject of research in the area (Table 1). From an historical perspective, helminth faunal studies and surveys, the basic step for broad analyses in host-helminth community structure, began in the XIX century, with foreign (mainly European) expeditions, and continue in this century with scattered studies. This is the current state of the art in South America.

Through time, reasonably broad faunal records have been gathered. For example, Cattán & George-Nascimento (1982) reviewed the helminthological reports of autochthonous and introduced Chilean terrestrial and marine mammalian species. Since then, three new reports on these hosts have been added (Carvajal *et al.* 1983, Fernández & Villalba 1985b, 1986). A similar review had been published in Argentina (Lombardero 1980). However, some parasitic and host groups in certain areas still remain poorly studied (*e.g.*, monogeneans and digenetic trematodes in marine fish from Chile, thus rendering premature Rhode's (1978, 1980) assertion of an impoverished trematode fauna in marine fish hosts of this area. See Oliva &

TABLE 1

Number of helminthological studies published during the last decade in South America (1976-1985), by subjects and countries, as cited in the Helminthological Abstracts.

Número de estudios helmintológicos publicados en la última década en Sudamérica (1976-1985), por tópicos y países, según citas de Helminthological Abstracts.

	Taxonomic Studies	Life Cycles	Evolution & Zoogeography	Wildlife Diseases	Prevalence & Intensity	Ecology	Total
Argentina	53	7	1	0	0	4	67
Bolivia	0	0	0	0	0	0	0
Brazil	145	6	2	3	21	7	195
Chile	43	2	1	3	26	5	77
Colombia	33	1	5	2	2	2	41
Ecuador	6	1	0	0	0	0	7
Paraguay	14	0	0	0	2	2	18
Peru	26	4	1	0	4	1	34
Uruguay	13	2	0	0	1	0	16
Venezuela	41	3	3	1	0	2	49
Total	374	26	13	9	56	23*	N/A

* Year and number of the abstract in the Helminthological Abstracts, by South American countries, for those 23 studies considered to be of interest in ecology of hosts or of helminth parasites: Argentina: (1977) = 5293, 5294; (1980) = 4949; (1983) = 3370. Brazil: (1977) = 4136; (1978) = 4383; (1979) = 173; (1981) = 3106; (1982) = 5465; (1984) = 1203; (1985) = 4711. Chile: (1977) = 461; (1979) = 5794; (1980) = 2032; (1983) = 2368, 4811. Colombia: (1979) = 5392, 5704. Paraguay: (1982) = 938; (1984) = 3429. Peru: (1985) = 2305. Venezuela: (1980) = 154; (1985) = 2803.

Muñoz (1985), Oliva (1984a, 1985, 1986), and Villalba (1985) for some recent contributions to the topic.

Zoogeographic and evolutionary studies

Studies dealing with zoogeography or evolutionary aspects of helminth parasitism are few in S.A., accounting for 2.7% of the total number of studies in the last decade (Table 1). The earlier contributions that dealt with S.A. parasitic fauna mainly noticed the zoogeographic affinities of parasites, or other symbionts, with that of their hosts. For example, Von Ihering (1891) found zoogeographical affinities between S.A. and New Zealand because of the vicariant distributions of crustaceans and temnocephalids. Manter (1967) found similar affinities between the trematode fauna of freshwater fish of S.A. and Africa, based on data from the extensive studies of Travassos (1934) and Szidat (1954). Recently, Brooks (1981) has applied quantitative phylogenetic methods to the helminths of freshwater stingrays from S.A.

Other recent S.A. work includes the study of the zoogeographical origin of hake (*Merluccius* spp.), based on a re-proposed

phylogeny of *Aporocotyle* spp. (Digenea) (Fernández & Durán 1985). Durette-Desset *et al.* (1976) described a new species of strongylid nematode in two species of sympatric and congeneric cricetid rodents (*Akodon olivaceus* and *A. sanborni*). Close relatives of the parasite had been previously found only in primitive Australian marsupials. They interpreted this finding as representing a case of host capture, and predicted that related species should occur in S.A. marsupials.

Evolutionary relationship of elasmobranchs and cestodes, in several cases closely linked, have been explored in *Rhinebohrrium* spp., reported to be host specific in *Psammobatis* spp. (Euzet & Carvajal 1973). A frequently overlooked aspect of these studies is the intermediate host which may also be coevolutionarily engaged in the life cycle. To my knowledge, evidence is lacking on the extent to which prey (intermediate hosts), are also closely linked in the evolution and speciation of parasites (Freeman 1973, Brooks *et al.* 1985). Such studies should shed light on the possibility of coevolved food sub-webs, traced by parasites, as indicators of evolved predator-prey relationships.

Effects of parasites on hosts

Effects of parasites on host fitness or welfare are found, out of ecological context, in human and veterinary medical studies where some detrimental effects on patients' health have been estimated. Reports from wildlife hosts have contributed 2% of the papers in parasitology during the last decade, and mainly consist in histopathological findings of parasitic diseases (Table 1). Probable effects of parasites upon the fitness of a wildlife host (e.g., parasitic castration), have been documented in S.A. in the association key hole limpet (*Fissurella* spp.)–digenetic trematode (*Proctoeces humboldti*). Intensities of infection vary according to geographical locality of sampling and apparent differential susceptibilities among limpet species (Bretos & Jirón 1980, Bretos *et al.* 1983, Osorio *et al.* 1986, M Bretos, C Moreno, M Oliva, personal communications).

Several Chilean naturalists are currently exploring the possibility of quantifying the impact of *Proctoeces* on the reproductive capacity of the host. This goal may prove elusive because the key hole limpet is a sequential, asynchronous brooder (Bretos *et al.* 1983; e.g., partial castration (Kabat 1986)). In any case, this seems to be an excellent opportunity to link the impact of parasitism to intertidal zone ecology, given that several key species such as pejesapo (*Scyases sanguineus*), key hole limpets and mytilids (Paine & Palmer 1978, Castilla & Durán 1985, Santelices *et al.* 1986), may be involved in the life cycle of the parasite (George-Nascimento & Quiroga 1983, Oliva 1984b, Osorio *et al.* 1986).

Quantitative and ecological studies on helminths

Helminth communities have been hierarchically classified (Holmes & Price 1986), mainly because helminth populations are classified this way. Infrapopulations and infracommunities are found in individual hosts. Suprapopulations, component communities and compound communities constitute higher levels of organization that involve populations and communities of parasites and hosts (see Margolis *et al.* 1982 and Holmes & Price 1986, for definition of terms). Usually, questions at

these community levels, despite their differences in perspective and subjects, use the same sampling units: individual hosts. Consequently, those differences consist mainly in the way data are handled and analyzed.

A major fraction of the parasitological literature in S.A. and elsewhere deals with medical problems of humans and the living resources they exploit. Although research on these diseases has received extensive funding because of its importance in human autecology, it has rarely been considered from an ecological perspective. Among the exceptions are the work of Bucher & Schofield (1981), an analysis of the landscape epidemiology of Chagas disease, and the work of Neghme & Silva (1971), on the environmental correlates (rainfall) of the prevalence of human trichuriasis and ascariasis in Chile. Studies exploring the existence of correlation between prevalence or intensity of infections with some other host or habitat variables are a minor fraction of those reporting quantitative estimates of parasitism in wildlife animals.

This latter type of studies represent 11.8% of the S.A. papers in helminthology during the last decade, and seem to be the natural next step in accumulating knowledge on the subject (Table 1). Although some of these papers are also of ecological interest (e.g., Cattán & Videla 1976, Cattán *et al.* 1976, Vergara & George-Nascimento 1982, Villalba 1982, George-Nascimento *et al.* 1983, George-Nascimento & Huet 1984, Mendoza 1984⁴, Fernández 1985)⁵ the bulk of them are point estimators of prevalence or intensities of infection that have not been analyzed according to any host or habitat variable. Among the exceptions is the report on the helminth assemblage inhabiting the digestive tract of *Octodon degus* (Rodentia), where there seem to be environmental (seasonal),

4) MENDOZA R (1984) Contribución al conocimiento del parasitismo en la corvina *Cilus gilberti* (Abbot 1899). Memoria de Título, Facultad de Ciencias Agropecuarias y Forestales, Departamento de Medicina Veterinaria, Universidad de Concepción, Chillán, Chile, 71 pp.

5) VILLALBA C (1982) Estudio preliminar de los parásitos de *Mugiloides chilensis* (Molina 1782) recolectados en caleta Cascabeles y en caleta Reque. Tesis, Facultad de Ciencias Biológicas y Recursos Naturales, Departamento de Zoología, Universidad de Concepción, Chile, 92 pp.

and host sex and age (body weight), correlates of prevalence and intensity of infection that deserve further exploration (Cattan *et al.* 1976, Cattan & George-Nascimento 1978).

Several other host-parasite associations are influenced by climatic or physiographic features. For instance, mussels (*Perna perna*) from areas exposed to strong wave action were not infected by the larval *Bucephalus* (Digenea) (Umiji *et al.* 1976) whereas hosts from more projected sites showed a prevalence of 15-20%. The only S.A. report on the infection dynamics of an helminth transmitted through food in a wildlife host is that of George-Nascimento & Vergara (1982). They showed that catsharks (*Schroederichthys chilensis*) began to be infected at a given size by a nematode (*Proleptus niedmanni*, see Fernández & Villalba 1985a), and suggested that crabs *Cancer plebejus* were the intermediate host because their presence as prey in catshark's stomach was correlated with the helminth's prevalence. Further research corroborated that the crab was the intermediate host of the parasite (Carmona 1984)⁶. This single study suggests that predation dynamics and parasite infrapopulation dynamics, when studied in combination, yield results that may bridge the gap between parasitologists and ecologists.

Ecological differences among sympatric taxonomically - related hosts have been suggested as the possible cause of differences in their parasite loads. Two species of Chilean cusk-eels (*Genypterus chilensis* and *G. maculatus*), differ in the prevalence and intensity of infections by two loosely specific parasites, *Anisakis* sp. and *Corynosoma* larvae, and a shared ectoparasitic copepod *Lepeophtheirus yañezi* (Vergara & George-Nascimento 1982, George-Nascimento & Huet 1984). These differences were interpreted as indicators of food and habitat partitioning among hosts. The same type of inferences have been advanced for helminths of sympatric species of leptodactylid frogs from Brazil (Fabio 1982). Microhabitat occupancy by conspecific or closely related parasites inhabiting the same

host individuals have been reported in monogeneans from the gills of South Atlantic fish (Suriano 1975), and in monogeneans parasitizing a fish ectoparasitic copepod (Villalba 1985). Another example reveals that *Echeneibothrium* spp. diverge in scolex morphology, in a way that matches the topography of villi in the spiral valve of their common host *Raja* sp. (Carvajal & Dailey 1975). These cases could fit the population - concentration hypothesis (Rhode 1979) or the microhabitat - specialization hypothesis (Price 1984), but conclusive evidence is lacking.

Parasite infracommunity ecology has not been focused in S.A. studies, mainly because the data on helminth assemblages from individual hosts are usually combined and analyzed separately for each parasite taxon across the whole host sample. Although infracommunity studies use the same sampling units as those for component communities (individual hosts), differential handling of data turn them in studies of infrapopulation or component communities, rather than of infracommunities (Holmes & Price 1986). Extant reports on helminth species or assemblages remark changes in composition, prevalence and intensities of infections with host size (or age) and inferred food niche shifts. Examples of this are reports in jack mackerels (*Trachurus murphyi*), red cusk-eels (*Genypterus chilensis*), black cusk-eels (*Genypterus maculatus*) and croakers (*Cilus gilberti*) (Vergara & George-Nascimento 1982, George-Nascimento *et al.* 1983, George-Nascimento & Huet 1984, Mendoza 1984 (see footnote 4)).

Part two:

Taxonomic richness and similarity in component helminth communities of marine vertebrate hosts

In this part I explore the usefulness of analyses of host-parasite records for revealing patterns in distribution and composition of parasitic assemblages in marine systems involving vertebrate hosts and trophically transmitted helminths. The approach employed here is at the component helminth community level because host taxa are the units on which patterns are searched for (Holmes & Price 1986).

The analyses attempt to detect patterns in three aspects. First, in the frequency

6) CARMONA R (1984) Nematodiasis en la jaiba *Cancer plebejus* Poeppig. Informe Práctica Profesional, Departamento de Biología y Tecnología del Mar, Pontificia Universidad Católica de Chile, Sede Talcahuano, 51 pp.

distributions of parasite richness by CNA helminths in marine fishes, as recorded from three areas in the Eastern Pacific Ocean, and according to the host status. In the same vein I explore the existence of correlations between parasite richness and sample size, host relative abundance, host maximum body size, host dietary breadth, and trophic level. Second, I search for patterns in the frequency distributions of host ranges of CNA helminths, according to developmental stage, in the same three geographical areas. Third, I look for patterns of similarity in CNA helminth fauna among hosts coming from selected food webs, specially emphasizing its relationship with dietary overlap and taxonomic affinity among hosts.

Distribution of parasite richness

Two main questions addressed here are: a) Are there significant differences between checklists in the parasite richness of the fish host genera?; b) Are some of the host variables considered here, relevant in explaining the variance in parasite richness?

Before comparisons are made, it must be recalled that the number of fish genera surveyed for CNA helminths increases from Perú to U.S.A. (Table 2), and that fish may be, apart from singly, simultaneously intermediate and definitive hosts of CNA genera. Thus, when comparing checklists in the relative proportions of fish as hosts of different status for the parasites, I assigned hosts according to their simultaneous or single condition, in mutually exclusive categories. In the two S.A. checklists there is a similar proportion of fish genera reported as intermediate hosts only (50-53%), definitive only (25-24%), or both kinds simultaneously (25-23%). This is in sharp contrast with the checklists of U.S.A., where 52% of the host genera are simultaneously intermediate and definitive hosts for CNA genera (Chi-square test, $X^2 = 21.9$, 4 d.f., $P < 0.001$, Table 2). This may be due to the more thorough studies carried out in N.A., and to the wider scope of the N.A. checklists. Unfortunately, the task of estimating the proportion of host genera infected with CNA in any community may not be accomplished with

TABLE 2

Parasite richness by CNA genera reported in marine fishes from the Peruvian, Chilean and U.S.A. coasts, according to the host status for their parasites (Interm. = intermediate, Defin. = definitive)

Riquezas parasitarias por géneros de CNA reportadas en peces marinos de las costas peruana, chilena y de E.E.U.U., según el status del huésped para sus parásitos (Interm. hosts = huéspedes intermediarios, Defin. hosts = huéspedes definitivos).

	PERU			CHILE			U.S.A.		
	Interm. hosts	Defin. hosts	Total	Interm. hosts	Defin. hosts	Total	Interm. hosts	Defin. hosts	Total
Number of host genera with a given parasite richness									
PARASITE RICHNESS									
Number of parasite genera/host genus									
1	14	11	17	21	14	27	49	51	39
2	4	3	6	11	6	10	28	17	30
3	1	0	1	5	2	8	14	13	25
4	0	0	1	1	2	1	11	8	17
5	2	1	1	1	2	4	7	6	3
6	2	0	1	0	1	1	7	3	4
7	0	0	3	2	0	2	5	7	6
8	0	0	0	1	0	2	3	4	7
9	1	1	1	1	0	1	3	2	7
10	0	0	1	0	0	0	1	0	4
>10	0	0	0	0	0	1	5	10	25
TOTAL	24	16	32	43	27	57	133	121	167

data of checklists because hosts have been generally surveyed for some of their parasites rather than for their whole parasite faunas.

Cumulative frequency distributions of parasite richness in marine fishes from Perú, Chile and the Pacific coast of U.S.A. reveal a common feature: the bulk of the hosts are parasite-poor (Table 2). I used the maximum parasite richness reported for a fish genus, expressed as a fraction of the total number of CNA genera in the checklist, in order to compare the relative parasite richness among the checklists. This index yielded similar values in Perú (0.27), Chile (0.23), and U.S.A. (0.27), suggesting that it does not vary widely with the size of the host-parasite checklist. However, there is a significantly lower relative abundance of host genera with two or less CNA genera in the U.S.A. checklist, than in either from the southern hemisphere (Smirnov test, $P < 0.01$, Table 2). This latter result is probably due to the smaller sample sizes and less complete faunal studies and surveys carried out in S.A. Perhaps, another demonstration of this is that the number of individuals sampled per fish genus in Chile is significantly correlated with the parasite richness reported for those fish ($r_s = 0.51$; $n = 28$ host genera; $P < 0.01$).

When examining the parasite richness of fish according to the host status for the parasites (intermediate or definitive hosts), the frequency distributions of parasite richness for definitive hosts were found not to be different from those for intermediate hosts in each checklist (Smirnov test; $P < 0.01$; Table 2). In addition, parasite richness for equivalent types of hosts were similar between checklists (Smirnov test; NS; Table 2), exception made of a marginally significant higher proportion of definitive hosts carrying two or less CNA genera in Perú than in U.S.A. (Smirnov test; $P < 0.1$; Table 2).

There are at least four other host variables that may help to explain the variance in parasite richness: body size, relative abundance, dietary breadth and trophic level (Polyansky & Bychowsky 1963, Price 1980, Leong & Holmes 1981, Price & Clancy 1983, Rhode 1984, Kennedy *et al.* 1986). Host maximum body size is a significant explanatory variable of the variance in CNA parasite richness in the U.S.A. checklist ($r_s = 0.32$; $n = 227$;

$P < 0.001$), but not in the Chilean checklist ($r_s = 0.10$; $n = 42$; $P > 0.50$). Although this lack of correlation in the Chilean checklist may be due to inadequate sampling, the correlation coefficient obtained in the U.S.A. checklist indicates that host body size does not explain a large fraction of the variance in CNA parasite richness in marine fishes, a result similar to that found in freshwater fishes (Price & Clancy 1983).

Parasite richness revealed to be significantly correlated with relative abundance of Peruvian demersal fish ($r_s = 0.66$; $n = 17$ host genera; $P < 0.01$), suggesting that the faunal exchange hypothesis (Neraasen & Holmes 1975, Leong & Holmes 1981) may hold here. Dietary breadth, considered either as the absolute number of prey taxa in the diet of each of the 14 fish genera from Chile, or as the diversity of prey taxa in the diets (measured by Shannon's index), revealed not to be significantly correlated with CNA parasite richness ($r_s = 0.18$ and $r_s = -0.28$, respectively; $n = 14$; NS). Although this result does not agree with the expectation of Kennedy *et al.* (1986), that dietary breadth could be a factor affecting parasite richness or diversity in helminth communities, more quantitative assessments are needed before generalizations are made.

The host trophic level hypothesis (Price & Clancy 1983), was tested by comparing the parasite richness of predators and prey in two sink food webs (*sensu* Cohen 1978): one where the top predator is the S.A. sea lion *Otaria flavescens*, and another where five pinniped species inhabiting the California Current constitute the "sink" of the food web. Sink food webs were considered the appropriate units for testing this hypothesis because, as opposed to community food webs, trophic levels are clearly differentiated as a consequence of being defined by the choice of predators, all their prey, plus the prey taken by the prey of those predators and so on (*sensu* Cohen 1978).

In the Chilean sink food web, seven fish taxa eaten by the S.A. sea lions are among the richest in CNA fauna when compared to the whole set of 57 fish genera surveyed in the area. This may be due to the more thorough parasitological studies made on these fish prey species (see prey indicated in parenthesis in Fig. 2b). However, the fact that parasite richness of S.A. sea lions (four CNA genera) is lower than several

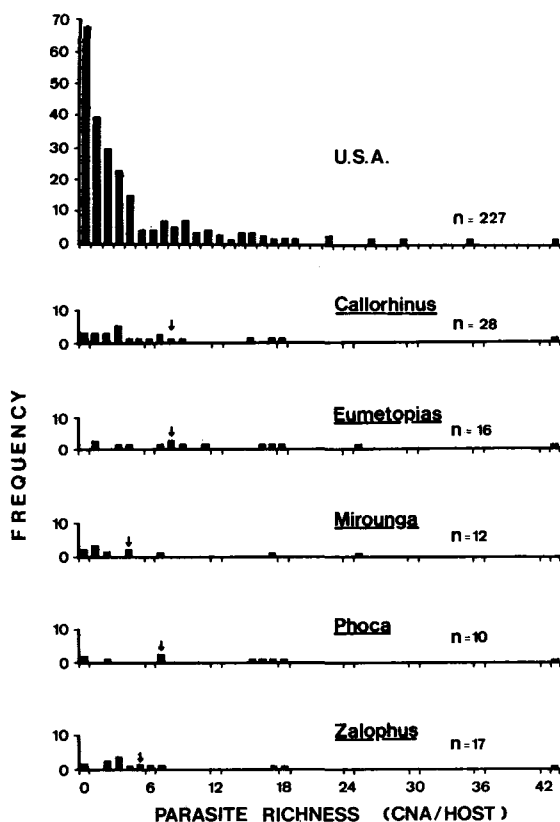


Fig. 1: Frequency distribution of CNA parasite richness (number of CNA genera per host genus), in marine fishes of the Pacific Coast of U.S.A. (top), and in the fish prey of five pinniped genera inhabiting the area. Numbers indicate total number of fish genera for each frequency distribution. Arrows indicate parasite richness of each pinniped genus.

Distribución de frecuencias de riquezas parasitarias por helmintos CNA (número de géneros de CNA por género de huésped), en peces marinos de la costa del Pacífico de E.E.U.U., y en los peces presa de cinco géneros de pinnípedos que habitan en esa área. Los números señalan el número total de géneros de peces para cada distribución de frecuencias. Las flechas señalan la riqueza parasitaria de cada género de pinnípedo.

of their prey is not a sampling artifact, given that the same is seen for each of the pinniped genera in the sink food web of N.A. (Fig. 1), for which an adequate knowledge of their helminth fauna may be assumed. It may be argued, however, that this case can be better explained by the fact that helminth communities of pinnipeds are probably impoverished when compared to those inhabiting in their terrestrial host ancestors (Anderson 1984). Although the assertion may be correct in this case (Delyamure 1955), more

evidence is needed on the significance of the differences in parasite richness between host trophic levels, and other host variables, in this and other ecosystems, and for a variety of host and parasite taxonomic or community assemblages. Meanwhile, a general overview of what is known on trophically transmitted helminths casts doubt on the validity of the trophic level hypothesis, because there is no clearcut difference in parasite richness at least between terrestrial mammals of low and high trophic levels.

Distribution of host range

I here address the following question: Are the frequency distributions of host ranges similar between checklists? Before attempting an answer it must be remarked that the number of CNA genera recorded per checklist increases from Perú to U.S.A. (Table 3), and that CNA helminths, as a consequence of the different status of hosts for parasites, may be found at larval or adult stage in marine fish. By means of a mutually exclusive categorization of CNA genera in each host-parasite matrix (according to whether they have been found at larval stage only, adult stage only, or both), I tested the significance of the differences between checklists, in the proportions of CNA genera found at different developmental stages. Results show significant differences, although in each checklist the bulk of CNA genera have been reported at adult stage only (between 57 and 80%), then at larval stage only (between 7 and 35%), and finally some at both larval and adult stage, but usually in different fish host taxa (between 8-13%, Chi-square test $X^2 = 31.0$; $P < 0.001$; Table 3).

In order to answer the question of differences in the host ranges of parasites between checklists, I compared the cumulative frequency distributions with and without making distinctions between developmental stages of the parasites. Results show that in each checklist, frequency distributions are dominated by helminths with narrow host ranges. The only significant difference between checklists in the total host range of parasites (regardless of the developmental stage), is between Perú and U.S.A.: the former has a higher proportion of CNA genera whose host range is one, than the latter (Smirnov

TABLE 3

Host ranges and number of cases of parasitism reported for Helminth genera (CNA) parasitizing marine fish genera from the Peruvian, Chilean and U.S.A. coasts, according to the developmental stage of the parasites.

Rangos de huéspedes y número de casos de parasitismo registrados para géneros de Helmintos (CNA) en géneros de peces marinos de las costas peruana, chilena y de E.E.U.U., según el estado de desarrollo de los parásitos.

	PERU			CHILE			U.S.A.		
	Larval stages	Adult stages	Total	Larval stages	Adult stages	Total	Larval stages	Adult stages	Total
Number of parasite genera with a given host range									
HOST RANGE									
Number of host genera/parasite genus									
1	5	20	22	3	26	25	6	60	58
2	3	2	5	1	8	7	5	28	27
3	1	1	1	3	2	3	4	19	19
4	2	1	4	1	2	2	2	8	11
5	1	0	1	3	0	3	2	7	11
6	1	0	0	0	0	3	2	1	2
7	1	0	2	0	0	0	0	0	2
8	1	0	1	0	0	0	0	1	0
9	1	0	1	0	0	0	1	1	3
10	0	0	0	2	0	2	1	1	1
>10	0	0	0	2	0	2	6	11	22
TOTAL	16	24	37	15	38	47	32	145	157
Number of cases of parasitism									
	56	31	87	98	56	154	447	448	885

test; $P < 0.05$). I used the maximum host range of a given CNA genus, expressed as a fraction of the total number of host genera in each matrix, in order to compare the relative host range between the checklists. These are 0.28 in Perú, 0.49 in Chile and 0.52 in U.S.A., suggesting a trend of the relative host range to increase with size of the checklists.

When comparing host ranges by developmental stage of the parasites (larval and adult stages) in each checklist it was found that parasites at larval stage have wider host ranges than at adult stage, and thus, although CNA genera at larval stage are fewer in each checklist than those at adult stage, they account for half or more of the cases of parasitism reported (Smirnov test; $P < 0.05$; Table 3). In addition, frequency distributions of host ranges for parasites at larval stage are similar between checklists, but those for adult parasites of fishes from Perú and Chile show a higher proportion of adult CNA with host ranges

of 2 or less, than the U.S.A. checklist (Smirnov test; $P < 0.01$). These results probably reflect a gradient of historical research on the topic, suggesting that through time reports on the more conspicuous parasitism by larval stages (large parasites, widely distributed, cumulative infections), are followed by records of the CNA adults in fish. CNA adults are found or reported later probably because they usually require a higher effort to achieve taxonomic identification than larval stages, and also because they are found in a narrower range of hosts than larval stages. However, this result may also be due to the U.S.A. list being an "optimized" checklist that maximizes host-parasite records.

Helminth sharing among hosts

The main question in this section is: Is there any obvious relationship between the similarity in host ecology, or in taxonomic affinity among hosts, with their similarity

in CNA helminth fauna? This potential similarity in helminth fauna among hosts has been described to be determined by host phylogeny, host morphology and host food (Holmes & Price 1980, Freeland 1983, Holmes 1986). In the S.A. and N.A. checklists the high right-skewness of both the frequency distributions of CNA richness and of host ranges, leads one to expect by chance alone a low mean number of helminth genera shared among hosts.

An initial qualitative inspection of the dendrograms reveals that in the Peruvian checklist the highest numbers of CNA genera shared occur among fish genera from different families and orders (e.g., *Trachurus-Scomber* and *Sciaena-Merluccius*, Fig. 2a). The former fish pair shares five CNA genera and both species are pelagic: a suggestive habitat commonality; but the second host pair, also sharing five CNA genera, does not share a common habitat. A similar contrasting figure is seen in the Chilean checklist (Fig. 2b). Although one of the fish pairs that share six CNA genera (*Macruronus-Merluccius*) has species belonging in the same family (*Merlucciidae*), and inhabiting the demersal community (Ojeda 1983), another pair, *Genypterus-Cilus*, also sharing six helminth genera, has species that belong in different orders, and live in different habitats (Mann 1954). The fact that the highest numbers of shared helminth genera are found not necessarily among closely related fish is because the bulk of this similarity among hosts depends on sharing parasites at larval stage (compare Fig. 3a and 3b). This is so because parasites at larval stage in marine fish have wider host ranges than parasites that use them as definitive hosts.

The quantitative assessment of the relative importance of the similarity in diet and the taxonomic affinity among hosts on the similarity in their trophically transmitted helminth fauna is a task unfinished in ecological helminthology. I explored this topic from two perspectives and in two types of data sets. First, I tested the significance of the amount of variance in the number of CNA genera shared by 14 fish species from Chilean waters (12 of these are from the demersal community, and two others are the coastal fish species *Mugiloides chilensis* and *Cilus gilberti*), that is explained by their taxonomic affinity and dietary overlap. This data set constitutes a community food web (*sensu* Cohen 1978) that

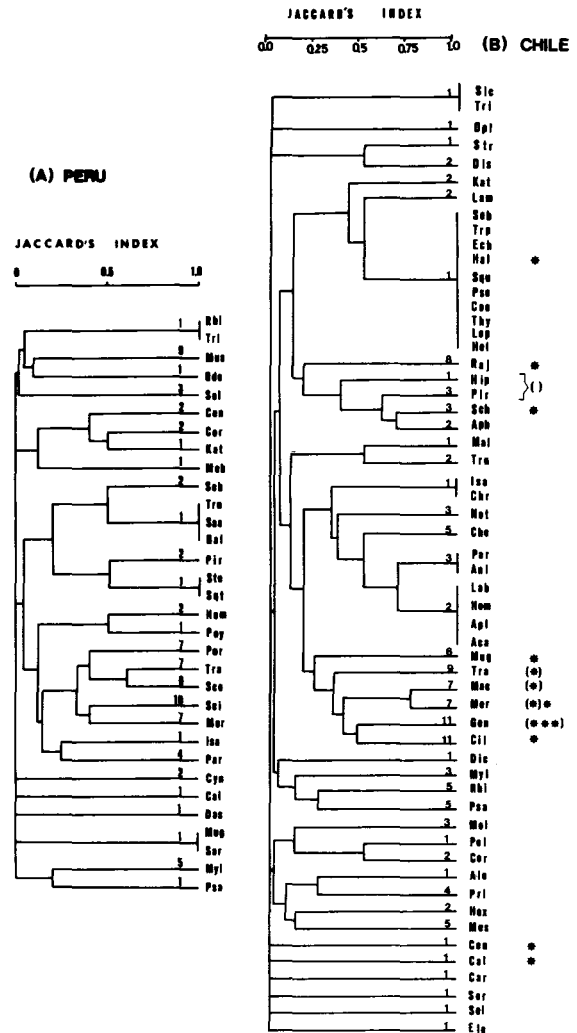


Fig. 2: Similarity in trophically transmitted helminth fauna (CNA genera, measured by Jaccard's index), among marine fish genera from Peru and Chile. Numbers on each branch are parasite richness of hosts. Asterisks in the right margin of the Chilean dendrogram indicate the 14 fish species whose dietary information was available for analysis of the relationship between taxonomic affinity, dietary parameters and parasite similarity. Parenthesis indicate fish taxa consumed by S.A. sea lions, whose parasite richness was used for testing the trophic level hypothesis (see text).

Similitud en helmintofauna transmitida tróficamente (géneros de CNA, medida por el índice de Jaccard), entre géneros de peces marinos de Perú y Chile. Los números en cada rama del dendrograma señalan la riqueza parasitaria de los huéspedes. Los asteriscos en el margen derecho del dendrograma de Chile indican las 14 especies de peces cuya información dietaria estaba disponible para el análisis de la relación entre los parámetros dietarios y la similitud en helmintofauna. Los paréntesis indican los taxa de peces consumidos por el lobo marino común, que fueron usados para someter a prueba la hipótesis del nivel trófico (ver texto).

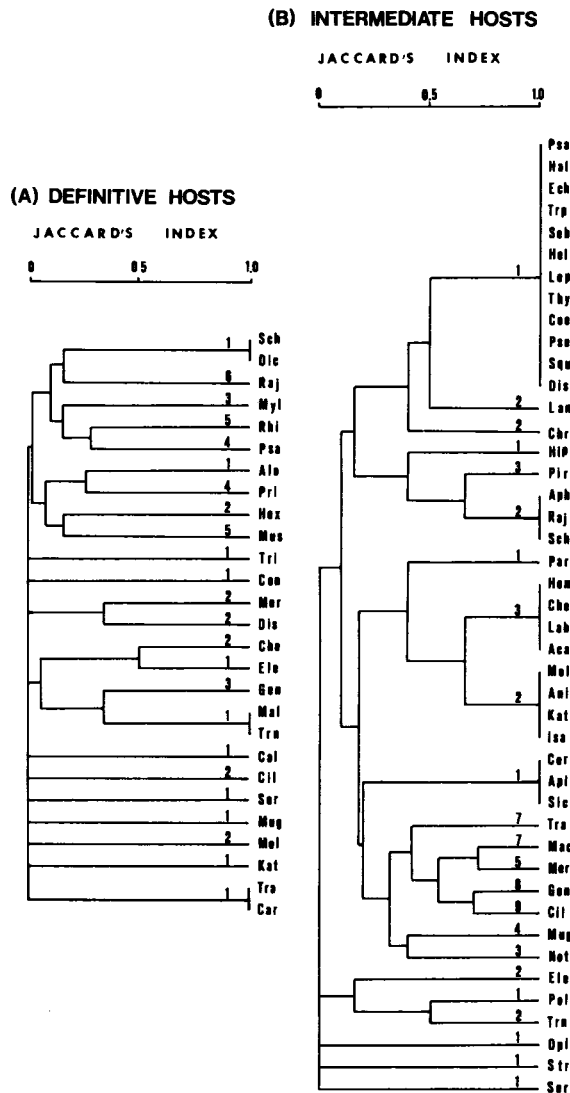


Fig. 3: Similarity in trophically transmitted helminth fauna (CNA genera, measured by Jaccard's index), among marine fish genera of Chile, according to the developmental stage of parasites: definitive or intermediate hosts.

Similitud en helmintofauna transmitida tróficamente (géneros de CNA, medida por el índice de Jaccard), en géneros de peces marinos de Chile, según el estado de desarrollo de los parásitos: Huéspedes definitivos e intermedarios.

involves hosts from a variety of taxonomic categories. Second, I tested the significance of the correlation between the similarity in CNA fauna and in diet among five related host taxa from a given geographic area. These are the same five pinniped genera inhabiting the California Current considered in the test of the trophic level hypothesis (Fig. 1).

In the Chilean community food web, the taxonomic affinity among hosts accounts for 42.5% of the variance in the ranked numbers of CNA genera shared by fish ($F [4, 85] = 16.2$; $P < 0.001$; Figure 4a). A marginally significant additional amount of the variance is explained by the hosts' ranked similarity in diet, as measured by the Morisita's index ($F [1, 85] = 2.73$; $P = 0.1$). The same analyses on the ranked similarities in CNA fauna and in diet among hosts, when both are measured by the Jaccard's index, yielded slight lower coefficients of determination (r -square). The simple correlation analysis that yielded the highest value was that between the quantitative dietary overlap measured by the Morisita's index and the similarity in CNA fauna measured by the Jaccard's index ($r_s = 0.20$; $n = 91$; $P = 0.05$). In Fig. 4b it can be seen that low dietary overlaps may be associated with both low and high values of Jaccard's similarity in CNA fauna. The lower amount of variance in the ranked numbers of CNA genera shared by fish, as explained by their dietary overlap when the taxonomic affinity had been first considered in the ANCOVA, may be interpreted as similarity in diet and taxonomic affinity being not independent variables ($F [4, 85] = 3.88$; $P < 0.01$). As far as the bulk of the shared helminth fauna among fish are larval helminths (see Fig. 3a and 3b), this low correlation suggests use of invertebrates as first intermediate hosts for parasites (Hurst 1984). The amount of variance in helminth sharing explained by the taxonomic affinity is considered in this case an artifact due to use of presence-absence data. This assertion is justified by the differential rates of infection known to occur among some of these generalist parasites in several of the fish species studied (e.g., Cattán & Videla 1976, Carvajal *et al.* 1979, Vergara & George-Nascimento 1982; George-Nascimento *et al.* 1983, George-Nascimento & Huet 1984, Mendoza 1984 (see footnote 4); Fernández 1985).

In the N.A. sink food web, results revealed a lack of significant correlation between the similarity in diet among pinnipeds (38 fish genera consumed by five pinniped genera) and in their helminth fauna (11 CNA genera; $r_s = 0.01$; $n = 10$; NS). In this case, although the mean similarity in CNA fauna is high among hosts (mean Jaccard's similarity = 61.0;

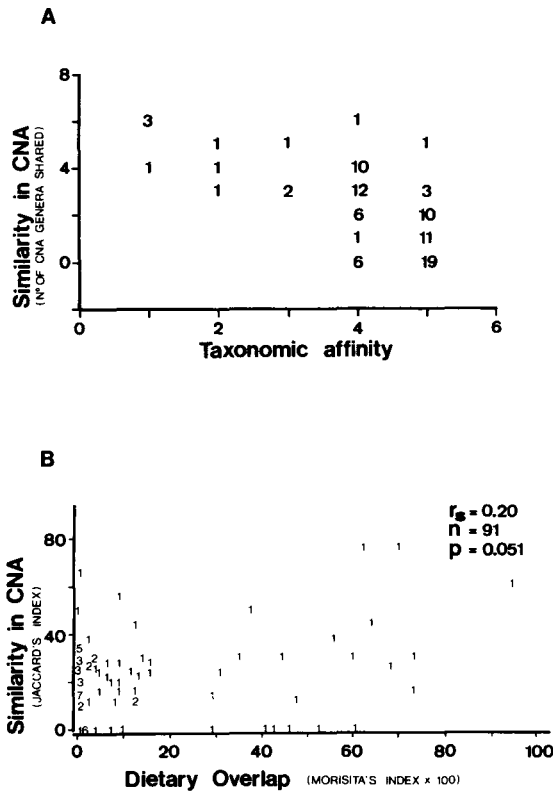


Fig. 4: Relationship between (a) the number of CNA genera shared and the taxonomic affinity among hosts, and (b) the similarity in CNA fauna (Jaccard's index), and dietary overlap (Morisita's index) among 14 fish species from Chilean waters signalled with asterisks in Fig. 2b. Categories of taxonomic affinity are 1 = Congeneric species; 2 = Confamilial species; 3 = Conordinal species; 4 = Species of the same Class, 5 = Species of different Classes. Numbers in the graph space indicate observations per point.

Relación entre (a) el número de géneros de CNA compartidos y la afinidad taxonómica entre los huéspedes, y (b) la similitud en CNA fauna (índice de Jaccard) y la superposición dietaria (índice de Morisita), en 14 especies de peces de aguas Chilenas, señaladas con asteriscos en la Fig. 2b. Las categorías de afinidad taxonómica son 1 = Especies congénicas; 2 = Especies de la misma familia; 3 = Especies del mismo orden; 4 = Especies de la misma Clase; 5 = Especies de distinta Clase. Los números en el espacio del gráfico indican observaciones por punto.

s.d. = 15.5; $n = 10$), their similarity in diet is not (mean Jaccard's similarity = 17.7; s.d. = 7.7). Hence, the only plausible explanation is that as far as pinnipeds have similar parasite taxa due to their relatedness, their parasites at larval stage are widely distributed among prey taxa, and hence no reason exists for expecting a tight relation-

ship between both variables. This result is in agreement with Mauchline & Gordon's (1984) expectation on the lack of a strong correlation between the similarity in diet and in helminth fauna, in demersal fishes.

CONCLUDING REMARKS

In order to understand S.A. parasitological studies, it must be recalled that "some intrinsically ecological subjects, such as parasitology,... have only recently... seen themselves as allied with ecology" (McIntosh 1980: 9). However, nowadays Dobson & Hudson (1986) consider that the role of parasites as a relevant potential factor in structuring host communities "seems to be fully accepted" because of their inclusion in the community ecology textbooks recently published.

Because of the recent development of theoretical expectations around ecological parasitology, S.A. work addressing the ecology of helminths or their ecological implications in host populations and communities is very scarce. The available information from S.A. reveals that more field and experimental studies on ecological parasitology need to be done at all hierarchical levels of parasite populations and communities. Ecological parasitology is just emerging as a field of study in S.A.: there are several unexplored host-parasite systems that offer excellent opportunities to test predictions arising from theoretical work. But first, parasitology must enter into the minds of ecologists and into the ecology programs not simply as an interaction analogous to predator-prey relationships. Implications of parasitism for host ecology, in evolutionary as well as in ecological time, are not only those of detrimental effects of parasites on hosts (e.g., Anderson & May 1978). In fact, the parasites dealt with in this review (macro-parasites), belong to the group with lowest abilities to regulate host populations (Toft 1986). But at the same time they are fully linked to food webs, that is to host communities, and in this manner they may shed light on community evolutionary ecology (e.g., Noble 1960, Campbell *et al.* 1980).

The evidence here gathered does not allow clear conclusions about how inadequately has the parasite richness of Peruvian and Chilean fish been studied. The positive

correlation of parasite richness with sample size in the Chilean checklist, the higher relative abundance of host genera with one or two parasite genera in the Chilean and Peruvian checklists, the higher proportion of fish with adult and larval stages of CNA in the U.S.A. checklist, the increasing value of the maximum relative host range with size of the checklist, and the lack of a significant correlation with host body size in the Chilean checklist, all suggest inadequate sampling.

However, the lower proportion of parasite-poor fish and the higher proportion of adult CNA genera in U.S.A. may merely reflect that this checklist includes parasite records beyond the North American coast (Love & Moser 1983). The similar maximum relative parasite richness (as a fraction of the total number of genera in the matrix), the shape of the frequency distributions of parasite richness and host ranges, the correlation of richness with relative abundance (Peruvian checklist), the pattern of differences in host ranges between adult and larval stages in each checklist, and the consistent differences in parasite richness between pinnipeds and their fish prey, all suggest that CNA parasites, even at the primary level that they have been studied in S.A., conform to a general pattern of distribution in marine food webs. These results suggest that studies of this nature could provide the initial steps in the attempt of describing and analyzing patterns in component helminth communities. More thorough attempts should consider, for example, quantitative information on parasitological parameters.

A final comment on the trophic level hypothesis follows: Although the bulk of CNA genera reported in marine fishes are found at adult stage (mainly elasmobranch cestodes), they have narrower host ranges than the few CNA genera living as larvae in fish (mainly teleosts). These latter instead mature in fish vertebrate predators (teleosts, elasmobranchs, birds, and mammals), and use many trophic links and intermediate host taxa for transmission to host in top trophic levels. The evidence reveals that, although pinnipeds eat prey of intermediate to high trophic level, they are not the richest in CNA parasite fauna in any of the sink food webs where they are the top predators (see Fig. 1). This evidence does not support the proposition

of Price & Clancy (1983) and other authors stating that parasite richness increases monotonically with host trophic level. I here propose that the highest parasite richnesses should be found at intermediate trophic levels simply because hosts at those levels harbor both larval and adult stages of the parasites in the community. What probably increases with host trophic level is the proportion of parasite taxa per host taxon that reach their sexual maturity in that host.

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Appendix I
Apéndice I

Appendix I: Host-parasite matrix of 37 CNA genera reported in 32 marine fish genera of Peru. Coded names of host and parasite genera at the matrix margins are fully written at the bottom. A number (1) indicates the report of an adult stage of a parasite, and (2) of a larval stage.

Matriz huésped-parásito para 37 géneros de CNA registrados en 32 géneros de peces marinos de Perú. Los nombres codificados de los géneros de parásitos y huéspedes en los márgenes, están escritos en forma completa al pie de la matriz. Un número (1) indica el registro de un estado adulto del parásito, y (2) de un estado larval.

	G	N	D	C	C	L	P	T	N	G	O	P	O	R	A	R	C	A	A	P	C	A	P	E	P	C	C	T	R	P	D	P	F	P	P	T	
	Y	E	L	I	L	A	A	T	E	Y	R	T	H	R	H	N	H	I	C	N	H	O	C	H	C	R	U	O	E	H	S	A	O	L	R	A	E
	R	O	O	P	E	L	C	E	N	B	I	O	Y	O	T	I	L	A	I	O	N	H	I	C	L	L	R	G	A	G	S	E	O	O	R	T	
MYL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
PSA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RHI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
TRI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MUS	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1
CAL	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
TRN	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
TRA	0	0	0	0	0	2	0	0	2	2	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	
SAA	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
SCO	0	0	0	2	0	2	0	0	2	2	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
SCB	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0		
CYN	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0		
SCI	0	0	0	2	0	2	2	0	2	2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	1	0	0	2	2	0	0	0	0		
POR	0	0	0	2	0	2	0	2	0	2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0		
MUG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
ISA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0		
SEL	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0		
PAR	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0		
HEM	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
MER	0	0	0	2	1	2	2	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0		
GAL	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
ODO	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
SAR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
COR	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
KAT	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
CEN	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0		
POY	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
PIR	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
STE	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
MOB	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
SQT	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DAS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	

HOSTS: MYL = *Myliobatis*, PSA = *Psammobatis*, RHI = *Rhinobatos*, TRI = *Triakis*, MUS = *Mustelus*, CAL = *Callorhynchus*, TRN = *Trachinotus*, TRA = *Trachurus*, SAA = *Sarda*, SCO = *Scomber*, SCB = *Scomberomorus*, CYN = *Cynoscion*, SCI = *Sciaena*, POR = *Paralanchurus*, MUG = *Mugil*, ISA = *Isacia*, SEL = *Seriotelella*, PAR = *Paralabrax*, HEM = *Hemilutjanus*, MER = *Merluccius*, GAL = *Galeichtys*, ODO = *Odontesthes*, SAR = *Sardinops*, COR = *Coryphaena*, KAT = *Katsuwonus*, CEN = *Centropomus*, POY = *Polyclems*, PIR = *Paralichthys*, STE = *Stellifer*, MOB = *Mobula*, SQT = *Squatina*, DAS = *Dasyatis*. PARASITES: GYR = *Gyrocotyle*, NEO = *Neobothriocephalus*, GLO = *Glossobothrium*, DIP = *Diphyllobothrium*, CLE = *Clestobothrium*, CAL = *Callitetrarhynchus*, LAC = *Lacistorhynchus*, PTE = *Pterobothrium*, TEN = *Tentacularia*, NYB = *Nybelinia*, GRI = *Grillotia*, OTO = *Otobothrium*, PHY = *Phyllobothrium*, ORY = *Orygmatobothrium*, RHO = *Rhodobothrium*, ANT = *Anthobothrium*, RHI = *Rhinebothrium*, CIL = *Callobothrium*, ACA = *Acanthobothrium*, ANI = *Anisakis*, PHO = *Phocanema*, CON = *Contraeacum*, ACH = *Acanthocheilus*, PHI = *Philometra*, ECC = *Echinocephalus*, PRL = *Proleptus*, CUL = *Cucullanelus*, COR = *Corynosoma*, TEG = *Tegorhynchus*, RHA = *Rhadinorhynchus*, PSG = *Pseudogrilltia*, DAS = *Dasyrhynchus*, POE = *Poecilancistrum*, FLO = *Floriceps*, PRO = *Prochristianella*, PAR = *Parachristianella*, TET = *Tetrarhynchobothrium*.

