Richness and similarity of helminth communities in the tropical cichlid fish *Cichlasoma urophthalmus* from the Yucatan Peninsula, Mexico

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SUMMARY

The composition, richness and similarity of helminth communities in a tropical freshwater fish were determined in samples of *Cichlasoma urophthalmus* collected from 7 localities of broadly similar age and character situated along the northern coast of the Yucatan peninsula, Mexico. The component communities exhibited a unique combination of characteristics for a freshwater fish. They were dominated by digeneans, with all other helminth groups being numerically inferior. A common suite of species could be recognized, but many of its members were generalists and not cichlid specialists. Species richness and number of individuals per host were high, but diversity was low, reflecting high dominance by one species. Intra- and inter-locality similarity levels were low, and local variation high. In respect of species richness and digenean dominance, the communities resembled those in Australian tropical anguillids, but in respect of low diversity, similarity and high dominance they are more similar to helminth communities of northern temperate fish.

Key words: helminth community, tropics, *Cichlasoma urophthalmus*, community diversity, Mexican parasites.

INTRODUCTION

It has been suggested that helminth communities of freshwater fish are stochastic assemblages and isolationist in character (Kennedy, 1990). Kennedy also considered that the regular co-occurrence at substantial population densities of more than one helminth species would seldom occur in freshwater habitats, and therefore inter-specific competition was unlikely to be a major determinant of community composition.

However, most data on helminth communities of freshwater fish have been obtained from north temperate latitudes, and few studies apart from that of Kennedy (1995) have examined composition and diversity of parasite communities in tropical fish. Helminthological investigations of tropical freshwater Mexican cichlid fish (Salgado-Maldonado, 1993; Pineda-Lopez, 1994) have indicated that they contain rich assemblages of helminth parasites, composed mainly of metacercarial and adult trematodes, and that a group of cichlid specialist species appears to be widely distributed among Central American cichlids. *Cichlasoma urophthalmus* is, for several reasons, a good model to study helminth communities of tropical freshwater fish. It occurs throughout the Usumacinta ichthyological province of Central America (see Miller, 1966), ranging from southern Mexico (the limit of its range) to Guatemala and Honduras, and can be found in many types of freshwater habitats as well as in coastal lagoons of raised salinity. It is often locally abundant, to the extent of dominating the fish fauna in bodies of water it inhabits, and this ensures the availability of hosts for examination. Moreover, *C. urophthalmus* supports important local fisheries. Finally, some background data on the helminth parasites themselves have been obtained by Salgado-Maldonado (1993) and Pineda-López (1994).

There are therefore 2 principal aims of the present study: (1) to describe for the first time the richness and diversity of helminth communities in *C. urophthalmus* and to examine the similarity of communities within and between 7 localities in the Yucatan Peninsula, Mexico and (2) to compare these communities with those described from freshwater fish of north temperate latitudes and of tropical latitudes.

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MATERIALS AND METHODS

Localities and sampling

The Yucatan peninsula in southeastern Mexico (Fig. 1) is almost flat. Surface run off is minimal. The whole drainage of the peninsula is sub-surficial and

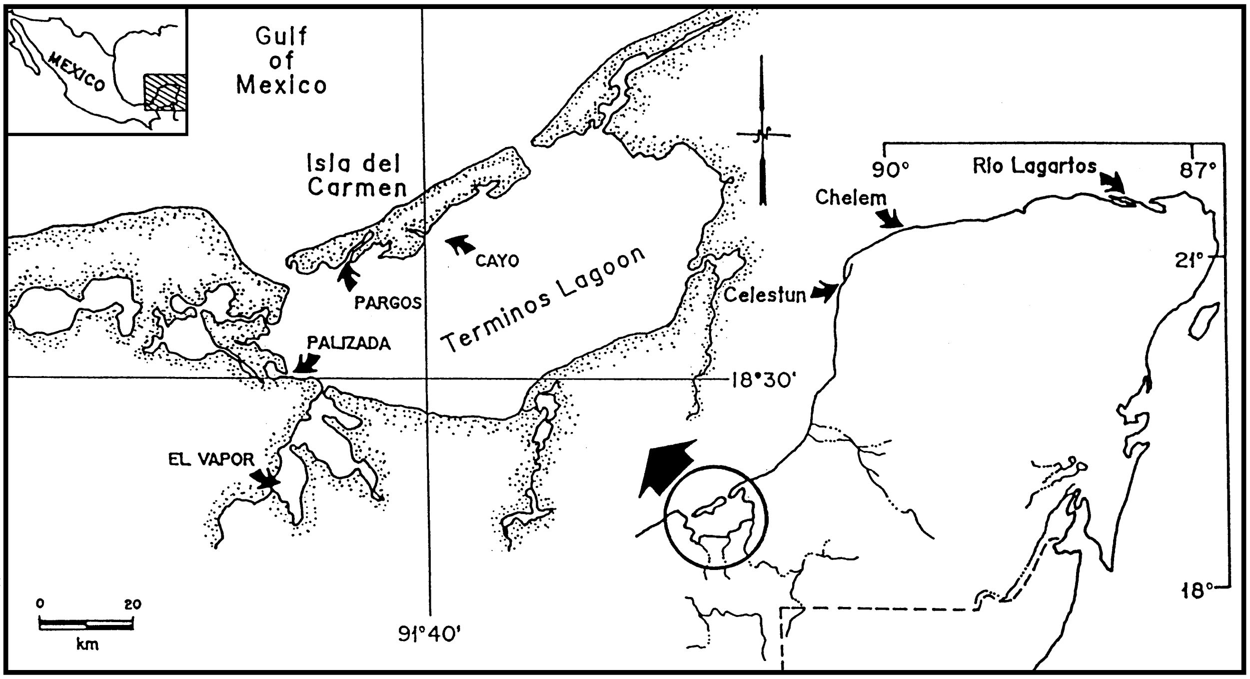

Fig. 1. The Yucatan peninsula, Mexico. Collection sites are shown.

includes an extensive net of subterranean channels and caverns through which the water flows slowly to the north estuarine borders. All open caverns, holes and other topographical formations that connect the inner subterranean waters to the surface land are known locally as 'cenotes'.

Seven localities were selected for sampling (Fig. 1). El Vapor lagoon, Palizada, Pargos and Cayo are sites situated inside Terminos Lagoon (Fig. 1), the largest coastal lagoon in Mexico (area 2500 km^2, average depth 3·5 m). The other localities (Fig. 1), a cenote near Rio Lagartos Lagoon and the coastal lagoons of Celestun and Chelem, fed by freshwater springs and rain water, are widely separated. Pargos and Cayo (Fig. 1), are both essentially marine, salinity being 22–35 % throughout the year (Kemp *et al.* 1988); no other cichlid species inhabits these localities and all fish are marine or estuarine species (Yañez-Arancibia *et al.* 1980; Vargas Maldonado *et al.* 1981). Cayo is situated on Isla del Carmen, which separates the main body of Terminos Lagoon from the Gulf of Mexico waters (Fig. 1), and Pargos is a narrow channel almost bisecting the Isla del Carmen. There is no physical barrier precluding the movement of fish from one side of Terminos Lagoon to the other. However, *C. urophthalmus* populations in Cayo and Pargos are believed to remain discrete, localized and isolated from populations in other parts of Terminos and migrations into or out of them rarely, if ever, occur (Yanez-Arancibia *et al.* (1980) and contemporary, unpublished fishery investigations). As many as 10 species of cichlids have been reported from El Vapor and other freshwater sites including Palizada in Terminos Lagoon (Toral & Reséndez-Medina, 1973). The cenote at Rio Lagartos contains only freshwater fish species; at least one other cichlid species was seen whilst sampling. Additional cichlid species inhabit Chelem (Zizumbo-Villareal, 1989) but *C. urophthalmus* is the only species of cichlid in Celestun. Both of these lagoons contain marine and estuarine components in their fish communities. In all sample sites, *C. urophthalmus* was abundant and often the dominant species. Detailed descriptions of collection sites are given by Salgado-Maldonado (1993).

Throughout the study period, some localities were sampled monthly but others less frequently. In order to minimize seasonal influences in this study, samples taken in the dry season only (November–May) are considered. To minimize influences due to age of host, analyses are restricted to adult fish (they cannot be aged more precisely). The total number of fish examined from each locality varied (Table 1), but sample sizes were considered adequate since cumulative species richness curves indicated that > 90 % of the helminth species found from each locality were recovered from just 12–15 fish.

Fish were captured using nets or by angling, transported alive to the laboratory and examined for helminths over the following 48 h. All organs and tissues, except blood and bones, were examined under a dissecting microscope by routine procedures described by Salgado-Maldonado (1993). All individuals of each helminth species were counted and recorded separately for each fish. Large numbers of metacercariae were found encysted in the intestinal walls: to count these, the whole section of the intestine containing the cysts was pepsin-digested, for 5–8 h, after which free cysts were counted in a 1 ml sample and then scaled up for the known

Table 1. The relative abundance of each helminth species as a proportion (p_i) of the total number of all helminths of all species found in *Cichlasoma urophthalmus* in 7 localities of the Yucatan Peninsula

(/c = component species in the locality.)

	Localities						
Helminth species	El Vapor	Palizada	Pargos	Cayo	Celestun	Chelem	Lagartos
Phyllodistomum lacustris†	0·00001						
Diphtherostomum brusinae†				0·02			
Stephanostomum sp.†				0·14/c			
Homalometron pallidum†	0·00008						
Crassicutis cichlasomae†	0·004/c	0·015			0·0006/c	0·009/c	0·008/c
Helicometrina nimia†				0·09/c			
Oligogonotylus manteri†	0·0002/c	0·57/c	0·34/c		0·003/c	0.23/c	0·001/c
Genarchella isabellae†	0·0008/c	0·0026					0·0008/c
Lecithochirium floridense†			0·1	0·01	0·0000006		
**Perezitrema bychowskyi*	0·003/c						
**Oligogonotylus manteri*†	0·98/c	0·02/c			0·99/c	0·52/c	0·89/c
**Drepanocephalus spathans*	0·0003				0·0002/c		
**Echinochasmus zubedakhaname*					0·002/c		
**Ribeiroia ondatrae*	0·001/c						
**Phagicola angrense*†	0·001/c	0·10/c	0·07	0·04	0·00008/c	0·004	0·09/c
**Ascocotyle leighi*	0·00005	0·03					0·00006/c
**Clinostomum complanatum*	0·001/c	0·06/c	0·07		0·0000006	0·12/c	0·001/c
**Diplostomum compactum*	0·000024					0·003	
**Posthodiplosthomum* sp.	0·00006						
*‘*Neascus*’	0·0009/c	0·005/c					0·001/c
*Trypanorhyncha gen. sp.†					0·00000019		
*Proteocephalidae gen. sp.†	0·00002				0·000002	0·002	
*Tetraphyllidea gen. sp.†		0·008/c	0·05	0·54/c	0·000009	0·001	
Neoechinorhychus golvani†	0·000014	0·06/c		0·008	0·000002		
**Hexaglandula mutabilis*		0·01/c		0·008	0·000004	0·003	0·000005
Spirocamallanus sp.†	0·000014						
Mexiconema cichlasomae	0·0002/c	0·03/c	0·13	0·11/c	0·0005/c	0·003	0·00002/c
**Camallanus* sp.†	0·000005						
**Procamallanus* sp.†	0·000009						
**Goezia* sp.	0·00002						
**Contracaecum* sp.	0·001/c	0·06/c	0·21/c		0·0001/c	0·11/c	0·0006/c
Total no. of parasites	203354	381	38	114	1579782	548	202158
No. of fish examined	85	19	28	42	120	30	26
No. of fish infected (%)	100	100	39·2	66·6	100	100	100

* Larvae/immature.
† Intestinal species.

volume of digested tissue. Terminology of parasite infections follows definitions given by Margolis *et al.* (1982).

Community structure

Analyses were carried out at the component community level (Holmes & Price, 1986) i.e. all of the helminths in all of the individuals of *C. urophthalmus* in each of the specific collection sites. The measures of component community structure adopted were: the total number of helminth species per locality and mean number of helminth species per fish, the number of component species (as defined by Bush, Aho & Kennedy, 1990), dominance, and mean Simpson's and Brillouin indices per fish. All indices are defined and calculated as in Magurran (1988) using natural ($\log_2$) logarithms in appropriate cases. To examine the local and regional distribution of species, the procedures of Bush & Holmes (1986) were applied in order to identify core and satellite species, i.e. testing for a significant correlation between prevalence and mean intensity of helminth species and plotting the frequency distribution of prevalence of each species by locality.

Communities within individual fish were compared within and between localities using the Jaccard similarity index, as calculated in Magurran (1988). As reported by Esch *et al.* (1988), the similarity between each pair of fish in a given locality was determined separately, and the mean of all possible pair combinations was obtained. This procedure was carried out for autogenic and allogenic species separately to stress the importance of colonization ability. Autogenic and allogenic species were defined as in Esch *et al.* (1988). Comparison of community

Table 2. The relative abundance of each intestinal helminth species as a proportion (p_i) of the total number of all intestinal helminths of all species found in *Cichlasoma urophthalmus* in 7 localities of the Yucatan Peninsula

(/c = component species in the locality.)

	Localities						
Parasite species	El Vapor	Palizada	Pargos	Cayo	Celestun	Chelem	Lagartos
Phyllodistomum lacustris	0·004						
Diphtherostomum brusinae				0·03			
Stephanostomum sp.				0·16/c			
Homalometron pallidum	0·017						
Crassicutis cichlasomae	0·75/c	0·02			0·17/c	0·04/c	0·79/c
Helicometrina nimia				0·11/c			
Oligogonotylus manteri	0·036/c	0·86/c	0·68/c		0·82/c	0·94/c	0·1/c
Genarchella isabellae	0·17/c	0·004					0·08/c
Lecithochirium floridense			0·21	0·02	0·0002		
*Trypanorhyncha gen. sp.					0·0005		
*Proteocephalidae gen. sp.	0·004				0·0005	0·007	
*Tetraphyllidea gen. sp.		0·01/c	0·1	0·65/c	0·003	0·007	
Neoechinorhnchus golvani	0·002	0·09/c		0·01	0·0005		
Spirocamallanus sp.	0·003						
**Camallanus* sp.	0·001						
**Procamallanus* sp.	0·002						
Total no. of parasites	1027	252	19	95	5611	134	1998
No. of fish infected (%)	87·0	94·7	17·0	52·3	90·0	89·6	100

* Immature.

similarity between localities was carried out in a similar manner, resulting in a mean value for each pair of localities. All correlations were carried out using Spearman's Rank tests.

Analyses were first carried out on all helminths, i.e. helminths of all species recovered from all habitats examined. Helminths inhabiting the gastrointestinal tract (intestinal helminths) were then analysed separately in order to compare the intestinal component communities with previously published data.

RESULTS

General characteristics

Altogether, 31 taxa of helminths (larvae and adult *Oligogonotylus manteri* are here considered as separate taxa), of which 20 were digeneans, were found in the 350 fish from the 7 localities (Table 1). In all but 2 localities, Pargos and Cayo, all fish were infected with 1 or more species. The number of species varied between localities, from a maximum of 22 in El Vapor to a minimum of 7 in Pargos. The number of individuals was also very variable between localities, with a minimum of 38 in Pargos but exceeding 200 000 in El Vapor and Lagartos and a million in Celestun. Neither the total number of individuals nor species was significantly correlated with the number of fish examined. The major contributors to these very high densities were always metacercariae of *O. manteri*. These metacercariae were encysted in the intestinal wall, in contrast to the adults which were found in the lumen. Other species of metacercariae were also abundant in some localities, such that with the exception of 2 localities, Palizada and Cayo, digenean metacercariae comprised the greater proportion of the total helminth component communities.

An identical pattern is evident when only intestinal component communities are considered (Table 2). Prevalence levels were lowest in Pargos and Cayo, and the numbers of individuals were also highest in El Vapor, Lagartos and Celestun. Adult trematodes, *O. manteri* in 4 of 7 localities and *C. cichlasomae* from 2 localities, were the major contributors to observed worm densities.

Common and rare species

Only 2 species, *P. angrense* and *M. cichlasomae*, were found in all 7 localities, and only 2, *C. complanatum* and *Contracaecum* sp., in 6 localities (Table 1). Several other species were widely distributed and occurred in 5 localities, but there were also several species with restricted distributions, being found in only 1 or 2 localities. The widespread species were generally, but not always, component species (Table 3). The maximum number of component species in a locality was 11 and the minimum 5 in the group of the 5 richest localities: in Pargos and Cayo the number of component species fell to 2 and 4 respectively. Component species could be autogenic

Table 3. Prevalence of selected component species of helminths of *Cichlasoma urophthalmus* in 7 localities of Yucatan peninsula, Mexico

	Localities						
	El Vapor	Palizada	Celestun	Chelem	Lagartos	Pargos	Cayo
*O. manteri**	21·1	47·4	80·8	44·8	69·2		
O. manteri	10·6	89·5	88·3	82·7	88·5	10·7	
C. cichlasomae	80·0		25·8	13·8	100		
M. cichlasomae	17·6	21·0	63·3		11·5	10·7	21·4
*Ph. angrense**	30·6	31·6	25·0		92·3		
*C. complanatum**	30·6	36·8		24·1	65·4		
Contracaecum sp.*	25·9	26·3	42·5	55·1	57·6	14·2	

* Larvae.

Table 4. Diversity characteristics of the component communities of helminths of *Cichlasoma urophthalmus* in the Yucatan Peninsula

(Metacercariae and adults of *Oligogonotylus manteri* were counted as separate taxa (see text). Om, *O. manteri*; Cra, *C. cichlasomae*; Tetr., Tetraphyllidea gen. sp.)

	Localities						
Characteristics	ElVapor	Palizada	Pargos	Cayo	Celestun	Chelem	Lagartos
All species							
Total no. of species	23	13	7	9	15	11	11
Mean no. of species	3·6	3·4	0·6	0·95	4·2	2·5	6·07
±S.D.	±1·8	±1·0	±0·9	±0·9	±1·7	+1·0	±1·2
No. of component species	11	10	2	4	8	5	10
No. of Autogenic species	14	7	4	7	9	6	5
No. of Allogenic species	9	6	3	2	6	5	6
Mean no. of individuals	2392·4	20·0	1·4	2·71	13164·8	18·9	7775
±S.D.	±9692	±12·3	±2·6	±4·4	±17997	±50·6	±9854
Proportion of individuals							
autogenic	0·99	0·71	0·63	0·94	0·99	0·77	0·90
allogenic	0·006	0·28	0·36	0·05	0·003	0·22	0·09
Simpson's Index	0·63	0·53	0·9	0·49	0·84	0·62	0·71
±S.D.	±0·26	±0·2	±0·18	±0·2	±0·23	±0·24	±0·25
Brillouin Index	0·54	0·63	0·07	0·09	0·31	0·44	0·56
±S.D.	±0·41	±0·3	±0·2	±0·2	±0·42	±0·29	±0·44
Dominant species	Om*	Om	Om	Tetr*	Om*	Om*	Om*
Intestinal species only							
No. of species	10	5	3	6	7	4	3
Mean no. of species	1·3	1·4	0·25	0·61	1·2	1·03	2·2
±S.D.	±0·76	±0·7	±0·57	±0·68	±0·7	±0·5	±0·65
No. of component species	3	3	1	3	2	2	3
No. of autogenic species	10	5	3	6	7	4	3
Mean no. of individuals	12·0	13·2	0·67	2·26	46·7	4·6	76·8
±S.D.	±12·7	±10·6	±2·28	±4·41	±74·5	±4·6	±66·0
Simpson's Index	0·86	0·85	0·97	0·96	0·91	0·93	0·69
±S.D.	±0·19	±0·22	±0·09	±0·13	±0·2	±0·1	±0·1
Brillouin Index	0·15	0·16	0·02	0·03	0·12	0·05	0·45
±S.D.	±0·21	±0·26	±0·1	±0·12	±0·22	±0·12	±0·28
Dominant species	Cra	Om	Om	Tetr*	Om	Om	Cra

* Larvae.

or allogenic. The species contributing most to helminth abundance were also almost always component species, although the converse was not always the case, e.g. *Stephanostomum* sp. was a component species in Cayo but was not the most abundant species. A similar situation pertains in respect of component species in intestinal communities only. It is clear that in both total and intestinal communities, there is a group of recurring common and widespread species.

There was a significant positive correlation between the mean intensity and prevalence of each

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Table 5. Mean (±S.D.) similarity, Jaccard Index, of helminth communities between individual fish in each sample

(Each value represents the mean of all possible pair combinations of fish within a sample.)

Locality	No. of hosts analysed	Total species similarity	Total similarity: Due to autogenic species	Total similarity: Due to allogenic species	Similarity due to intestinal species only	No. of comparisons
El Vapor	85	0·22 ± 0·17	0·27 ± 0·26	0·13 ± 0·23	0·40 ± 0·37	3570
Palizada	19	0·28 ± 0·16	0·41 ± 0·25	0·15 ± 0·28	0·55 ± 0·36	171
Pargos	28	0·01 ± 0·09	0·01 ± 0·08	0·01 ± 0·13	0·01 ± 0·06	378
Cayo	42	0·07 ± 0·21	0·07 ± 0·21	0·005 ± 0·07	0·05 ± 0·21	861
Celestun	87	0·45 ± 0·20	0·58 ± 0·29	0·26 ± 0·4	0·57 ± 0·38	3741
Chelem	30	0·37 ± 0·25	0·43 ± 0·35	0·26 ± 0·39	0·58 ± 0·43	435
Lagartos	26	0·56 ± 0·16	0·65 ± 0·20	0·50 ± 0·24	0·74 ± 0·22	325

Table 6. Mean (±S.D.) Jaccard similarity of total helminth communities between pairs of localities for the 7 locations

(Each value represents the mean of all possible combinations of each pair of fish between the 2 localities; from El Vapor and Celestun, 45 hosts were randomly selected for this analysis. Numbers of paired comparisons, which will vary with each combination of localities, are not included.)

	Palizada	Pargos	Cayo	Celestun	Chelem	Lagartos
El Vapor	0·09 ± 0·11	0·02 ± 0·08	0·012 ± 0·061	0·13 ± 0·15	0·10 ± 0·14	0·25 ± 0·15
Palizada		0·05 ± 0·12	0·028 ± 0·084	0·30 ± 0·19	0·29 ± 0·20	0·27 ± 0·13
Pargos			0·02 ± 0·11	0·06 ± 0·14	0·07 ± 0·17	0·04 ± 0·07
Cayo				0·03 ± 0·09	0·01 ± 0·04	0·02 ± 0·05
Celestun					0·34 ± 0·22	0·30 ± 0·15
Chelem						0·25 ± 0·13

species when data are pooled across all localities (total species: $r_s = 0{\cdot}83$, $P < 0{\cdot}001$; intestinal species only: $r_s = 0{\cdot}9$ $P < 0{\cdot}001$). This suggests that the most prevalent, and hence widely distributed, species in the pooled data, were also the most abundant. When localities were considered separately, mean intensity and prevalence were significantly positively correlated in El Vapor ($r_s = 0{\cdot}75$ $P < 0{\cdot}001$), Celestun ($r_s = 0{\cdot}94$ $P < 0{\cdot}001$), Chelem ($r_s = 0{\cdot}72$ $P < 0{\cdot}01$) and Lagartos ($r_s = 0{\cdot}81$ $P < 0{\cdot}005$). Correlations were positive for Palizada ($r_s = 0{\cdot}27$ $P = 0{\cdot}36$) and Cayo ($r_s = 0{\cdot}44$ $P = 0{\cdot}23$), but not significant. The correlation for Pargos ($r_s -0{\cdot}94$ $P = 0{\cdot}057$) was negative and significant but is not considered to be of biological relevance as it almost certainly reflects the low number of species (4) at this locality.

Frequency distributions of prevalence of the parasite species were examined in respect of total species and intestinal species only for each of 6 localities (Pargos being excluded because of the small number of species). The frequency distributions showed no common, consistent pattern and in the majority of cases were unimodal. There was no evidence of bimodality and thus of the existence of core and satellite species *sensu* Hanski (1982), but only of a suite of common species.

Richness and dominance

Even though species richness (number of species) equalled or exceeded 9 in 6 of 7 localities (Table 4), total component communities in the same localities exhibited high levels of dominance (p_i *max* $> 0{\cdot}5$) (dominance being defined as the proportion of the total sample that is due to the most abundant species: Table 1) and 6 of the localities were dominated by the same species, *O. manteri*. When intestinal species only are considered, all localities again exhibited high levels of dominance (p_i *max* $> 0{\cdot}6$) (Table 2) and 4 were dominated by *O. manteri*.

Similarity

The similarities within these helminth communities (Table 5) were highly variable. Mean similarities between pairs of hosts from the same population ranged from 0·01 (Pargos) to 0·56 (Lagartos). However, despite this variation, it is apparent that similarity values were lowest in Pargos and Cayo and highest within Celestun and Lagartos. Similarity values in respect of autogenic species were consistently higher than those of allogenic species in all samples except that from Pargos.

The similarity index in comparisons between localities was variable (Table 6). It ranged from 0·01 to 0·34 and for most pairs of localities (12/21) similarity was lower than 0·1. Pargos and Cayo consistently showed the lowest levels of similarity with any of the other localities, whereas the comparisons of Lagartos with El Vapor, Palizada, Celestun and Chelem, and Palizada with Celestun and Chelem, and Celestun with Chelem showed the highest values of similarity. Similar patterns were evident when intestinal communities only were considered. Similarity between localities was generally lower than that observed within localities.

DISCUSSION

The component helminth communities of *C. urophthalmus* in Yucatan are, in general, species rich. Overall, 31 taxa were recorded from this study, with a maximum of 23 from El Vapor. This makes this not only the richest single locality but also the richest helminth component community yet known from any species of freshwater fish studied to date (Kennedy, 1995). What could not have been expected was the overwhelming richness of digenean species or of larval stages: of the 31 taxa, 20 were digeneans and 19 were larval stages. Such a species composition is, to date, unique for helminth communities of freshwater fish. In temperate latitudes, helminth communities of freshwater fish appear more varied in composition and species of acanthocephalans are often more strongly represented (Leong & Holmes, 1981; Valtonen & Crompton, 1990; Kennedy, 1990, 1993), whereas in tropical anguillids acanthocephalans are poorly represented and digeneans and nematodes contribute most to species richness (Kennedy, 1995). We suggest, albeit tentatively, that richness of digenean species may be a characteristic of helminth communities in tropical freshwater fish.

Although there was variation in helminth community composition and richness, localities could be separated into 2 quite distinct groups. Five of the localities were truly freshwater; in these, all fish were infected, community composition closely corresponded to the above description, and the dominant species was *O. manteri*. The second group comprised only Pargos and Cayo. Both these localities were essentially marine, helminth richness was lower, a smaller proportion of fish was infected, especially with freshwater species, and the helminth community in Cayo was dominated by marine Tetraphyllidea. Each community is distinctive, and despite the fact that both localities are situated in Terminos Lagoon and close to each other, similarity between them was very low ($0{\cdot}018 \pm 0{\cdot}1$). Even intra-locality similarity was unusually low, especially in Pargos. Their peculiar compositions undoubtedly reflect the marine conditions and the impact these have on the parasite fauna of what is regarded as a fundamentally freshwater fish species. Pargos and Cayo will thus not be considered further. The remainder of this discussion will focus on the other group of 5 freshwater localities.

Not only did the communities in these 5 localities exhibit high helminth species richness, but they were also characterized by high helminth intensities. This was especially true of El Vapor, Celestun and Lagartos. The vast numbers of individuals were due entirely to metacercariae of *O. manteri*, and this species dominated all the freshwater helminth communities. The life-cycle of *O. manteri* is particularly well suited to these conditions: cichlids can be infected by consuming infected snails or by active cercarial penetration, following which they encyst as metacercariae and accumulate over time, and even post-cyclical transmission is believed to occur by larger cichlids feeding on smaller individuals (for details of this complex life-cycle see Scholtz *et al.* (1994)). It is thus not surprising that this adaptable cichlid specialist should be able to reach such exceptional densities and dominate so many widespread localities.

Clearly, conditions in the lagoons favour digeneans in general. The high concentration of calcium carbonate in the water, warm temperatures and high productivity favour development of dense mollusc populations (Scholtz *et al.* 1994). The shallowness of the lagoons and the benthic, territorial behaviour of *C. urophthalmus* and its preference for mangroves and submerged vegetation will bring it into proximity to snails, whilst the size and abundance of this cichlid makes it a common prey item in the diet of fish-eating birds. These features, and continual feeding and activity throughout the year, will facilitate transmission of all digeneans and the opportunistic nature of the host diet and variety of prey that it consumes will favour the development of a rich and diverse digenean community (Kennedy, Bush & Aho, 1986).

Despite the variation in helminth species richness between localities, it was possible to identify a suite of common species that influenced the richness of the component communities and contributed to the similarity of communities between localities. The species comprising this suite were not core species *sensu* Hanski, (1982) such as were identified in helminth communities of ducks (Bush & Holmes, 1986). They were simply a group of commonly co-occurring species such as were identified in the helminth communities of *Salmo trutta* by Hartvigsen & Halvorsen (1993) and *Anguilla reinhardtii* by Kennedy (1995). The majority of species in the common suite were digeneans, but also included 2 species of nematodes. The suite included specialist – generalist and autogenic – allogenic species in equal proportions; however, the predominant species was again the cichlid specialist (Scholz *et al.*

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1994) digenean *O. manteri*. Not all specialists found in the course of the study were part of this suite of common species. *Neoechinorhynchus golvani* is a cichlid specialist (Pineda-Lopez, 1994), but occurred at low densities in only 3 of the 5 localities and was a component species in only 1 of them. The composition of the common suite can be considered to reflect those of the component communities in general, in that the specialists can be considered to form the phylogenetic component of the communities and the generalists the ecological component (Kennedy & Bush, 1994). However, because of the dominance of *O. manteri* in all the communities, it can be concluded that the phylogenetic element played the major part in characterizing the communities and was responsible for most of the similarity between them. The ecological component contributed more to locality differences in species richness, as the prevalence and abundance of the generalist species reflected local conditions, the presence of other fish species in a locality and chance colonizations. It is not surprising that the ecological component should contribute so much to the species richness of helminth communities in a host at the limits of its range and so far from its S. American heartland (Kennedy & Bush, 1994). It is, perhaps, slightly surprising that the phylogenetic component should still play such a major role as a determinant of community composition, but this can be interpreted in terms of the particularly favourable conditions for digeneans in the lagoons.

Other aspects of the helminth communities in *C. urophthalmus* were also unexpected. Although, given their tropical location, the species richness of the communities was to be expected, the low diversity of both total and intestinal communities was not. In previous studies, species richness and diversity have, not surprisingly, been found to be positively correlated (Kennedy *et al*. 1986; Kennedy, 1995). The explanation for the low diversity in this study is to be found in the high levels of dominance by *O. manteri*. Levels of similarity between communities from different localities are also lower than might have been expected, given the existence of a common suite and the dominance of one species. Even neighbouring localities such as Palizada and El Vapor, both in Terminos Lagoon, showed a low level of similarity ($0{\cdot}09 \pm 0{\cdot}11$). Much of the similarity was due to autogenic species, in contrast to the situation in Britain, where allogenic species generally contribute more to similarity (Esch *et al*. 1988), but similar to the situation in Australian eels (Kennedy, 1995). The low similarity levels suggest that the factors promoting differences between parasite communities in lakes have a greater influence than those promoting similarity, a conclusion also reached in respect of helminth communities in fish of British reservoirs (Hartvigsen & Kennedy, 1994).

Overall, the helminth communities of *C. urophthalmus* in Yucatan exhibited an unusual combination of characteristics. Some of these are individually evident in helminth communities of freshwater fish from other parts of the world, but the combination here appears to be unique. The species richness of helminth communities in *C. urophthalmus* (range 11–23 total, 5–12 intestinal) is generally higher than observed in the tropical *A. reinhardtii* (the only tropical species with which a detailed and valid comparison can be made) in Australia (range 7–15 total, 3–9 intestinal) (Kennedy, 1995). The 2 hosts are also similar in that all individuals examined were infected. However, the communities differ with respect to dominance and diversity. In only 1 Australian community did total component community dominance exceed 0·5 and in only 4 intestinal component communities did it exceed the same value, whereas in none of the 5 freshwater Mexican localities did either total or intestinal component community dominance fall below 0·5. Diversity was also much higher in the Australian eels: communities in Australian eels showed high richness and diversity, those in Mexican cichlids exhibited high richness but low diversity. A comparison between the helminth communities of *C. urophthalmus* and that of *Amia calva* confirms the unusual nature of the former since helminth communities of *A. calva* are both rich and diverse (Aho, Bush & Wolfe, 1991).

Comparisons with helminth communities of temperate freshwater fish indicate that those of the cichlid are much richer. Leong & Holmes (1981) reported 16 helminth species from 1 species of fish in Cold Lake, Alberta, Canada, and Esch *et al*. (1988) a maximum of 9 species from 1 fish population in Britain, but the mean number of intestinal species per component community in northern temperate freshwater fish is only 2·9 (Bush *et al*. 1990). Helminth densities are also much higher in Yucatan. On the other hand, the community diversity of helminths in *C. urophthalmus* is far more similar to that found in helminth communities of temperate fish than in tropical eels. Helminth communities in freshwater fish in Britain are also characterized by high dominance indices and low diversity indices (Esch *et al*. 1988; Kennedy, 1990, 1993), and similarity levels both within and between localities are low (Esch *et al*. 1988). Indeed, the values of diversity and dominance recorded from the helminth communities in the 5 freshwater localities in Yucatan are strikingly similar to those recorded from helminth communities of *Anguilla anguilla* in a small stream in Britain (Kennedy, 1993).

The helminth communities of *C. urophthalmus* thus show some features in common with communities from other tropical fish (mainly those of community composition and species richness) and others in common with communities from temperate fish (mainly those of community dominance and diversity). Suites of common species have been recognized in both tropical (Kennedy, 1995) and temperate (Hartvigsen & Halvorsen, 1993) fish, but unlike those in cichlids these are composed almost entirely of specialists. Why these helminth communities from Yucatan should be so distinctive is not known: it may reflect the particular conditions there, or the nature and history of the cichlids there. What this study has indicated is the need for more investigations into parasite communities of tropical fish. Until the results from these are known, it will be impossible to determine whether generalizations on helminth communities from fish and birds and on isolationist versus interactive communities (Kennedy *et al*. 1986) are of global value or apply only to the temperate regions in which they were first made.

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