TEMPORAL VARIATION IN THE HELMINTH PARASITE COMMUNITIES OF THE PACIFIC FAT SLEEPER, *DORMITATOR LATIFRONS,* FROM TRES PALOS LAGOON, GUERRERO, MEXICO

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ABSTRACT: Temporal variation in the helminth parasite communities of the Pacific fat sleeper, *Dormitator latifrons*, from Tres Palos Lagoon, Guerrero, Mexico, was studied at the component community and infracommunity levels. In total, 185 host specimens were collected between April 2000 and March 2001. Eight parasite species were identified: *Clinostomum complanatum, Echinochasmus leopoldinae, Ascocotyle (Phagicola) longa, Pseudoacanthostomum panamense, Saccocoelioides* sp., *Parvitaenia cochlearii, Neoechinorhynchus golvani,* and *Contracaecum* sp. The communities had low numbers of parasite species and diversity, and contained only generalist parasites. Nested (nonrandom) species composition was observed in the infracommunities during all climatic seasons. The variation in nestedness intensity was attributed to a process of sequential colonization by the most common parasite species, because some were more abundant in the dry season, and others were more abundant in the rainy season.

Parasite communities experience temporal structural changes related to seasonal variations in biotic and abiotic environmental factors; these variations can be reflected in species composition and density over time (Zander and Kesting, 1998; Fiorillo and Font, 1999; Zander et al., 1999, 2002; Zander, 2003, 2004, 2005). Most studies designed to examine the seasonal variation in parasite community composition have been carried out in fishes from temperate regions (Mhaisen et al., 1988; Zander and Kesting, 1998; Zander et al., 1999; Klimpel et al., 2003; Zander, 2003; Fellis and Esch, 2004; Zander, 2004; Simková, 2005; Zander, 2005). Many processes have been suggested to influence the seasonal variation in parasite communities in these regions, for example, temperature and other abiotic factors (Eure, 1976; Chubb, 1979; Granath and Esch, 1983); intermediate host abundance (Esch and Fernandez, 1993; Zander and Kesting, 1998; Zander et al., 1999; Fellis and Esch, 2004; Zander, 2004); and changes in host abundance, reproductive and feeding behavior (Mhaisen et al., 1988; Klimpel et al., 2003; Fellis and Esch, 2004; Simková, 2005), and immunity (Kennedy and Hine, 1969; Zander and Kesting, 1998).

There is currently very little research on temporal variation in the parasite communities of tropical or subtropical areas, where temperature changes are not as extreme (Leong, 1986; Fiorillo and Font, 1999; Steinauer and Font, 2003; Vincent and Font, 2003). In these areas, recruitment of helminths might correlate with other factors such as wet–dry seasons, or year-round recruitment (Fiorillo and Font, 1999; Steinauer and Font, 2003).

Research on temporal variation in the parasite communities in Mexico has been done on freshwater cichlids (Salgado-Maldonado, 1993; Pineda-Lopez, 1994; Jiménez, 2003; Vidal-Martinez and Poulin, 2003). These studies have shown high variation in parasite abundance over time in response to alterations generated by the seasonal dry/rain cycle, which affects the parasite species recruitment process (Salgado-Maldonado, 1993), or in response to seasonal increases in host feeding and reproductive activity influenced by seasonal water temperature fluctuations (Jiménez, 2003; Jiménez-García and Vidal-Martínez, 2005). Pineda-Lopez (1994), however, suggested that helminth communities in tropical climates exhibit a stable structure over time.

No studies have been done to date on helminth parasite species composition over time in a tropical brackish-water fish in Mexico. *Dormitator latifrons* is widely distributed and highly abundant in almost all the Pacific coastal lagoons of Mexico, and is 1 of the most characteristic fish species of the lagoon systems in the state of Guerrero (Yañez-Arancibia and Díaz-González, 1977). The region's pronounced dry and rainy seasons notably affect Tres Palos Lagoon, leading to questions about whether or not this seasonal variation affects the parasite community of *D. latifrons* in this tropical, brackish environment. The present study objective was to describe temporal composition and variation in the helminth parasite community of *D. latifrons*, and to identify possible biotic and abiotic factors responsible for temporal variation.

MATERIALS AND METHODS

Tres Palos Lagoon (16°47′N, 99°39′W) is on the Pacific coast of Mexico, 25 km east of Acapulco (Violante-González, 2006) (Fig. 1). It has a surface area of 55 km² (5,500 ha) and ranges in depth from 0.5 to 8 m. Constant urban waste discharge into the lagoon by means of the Sabana River causes it be eutrophic (Violante-González, 2006). As a result, primary productivity is very high (80–106 µg/L⁻¹ chlorophyll-*a* concentration), particularly during the rainy season (Banderas and González, 2000). The region experiences 2 distinct climatic seasons, a rainy period from June to November (precipitation ≈ 430 mm), and a dry time from December to May (precipitation ≈ 100 mm) (Violante-González, 2006). In the present study, the surface water temperature (measured at 0.5-m depth) and salinity were measured monthly with a YSI model 33, at San Pedro las Playas, where *D. latifrons* specimens were collected.

In total, 185 adult *D. latifrons* specimens were collected with the use of gill nets between April 2000 and March 2001. The 1-yr sampling period was divided into 4 3-mo periods: April–June, July–September, October–December, and January–March. The number of specimens examined per sampling period ranged from 46 to 47 fish (Table I). Fish sex and total length were recorded. A complete necropsy was done on all hosts, including all organs. Internal and external metazoan parasites collected from the hosts were processed according to Lamothe-Argumedo (1997). Voucher specimens of all taxa were deposited in the National Helminth Collection, Institute of Biology, National Autonomous University of Mexico, Mexico City (CNHE: 4901, 4903, 4904, 4906, 4911, 4912, 4917, 4920). A species-richness sampling effort curve was applied to determine if sample size was sufficient to recover the highest possible proportion of parasite species, and thus to characterize ade-

State of Guerrero, Mexico
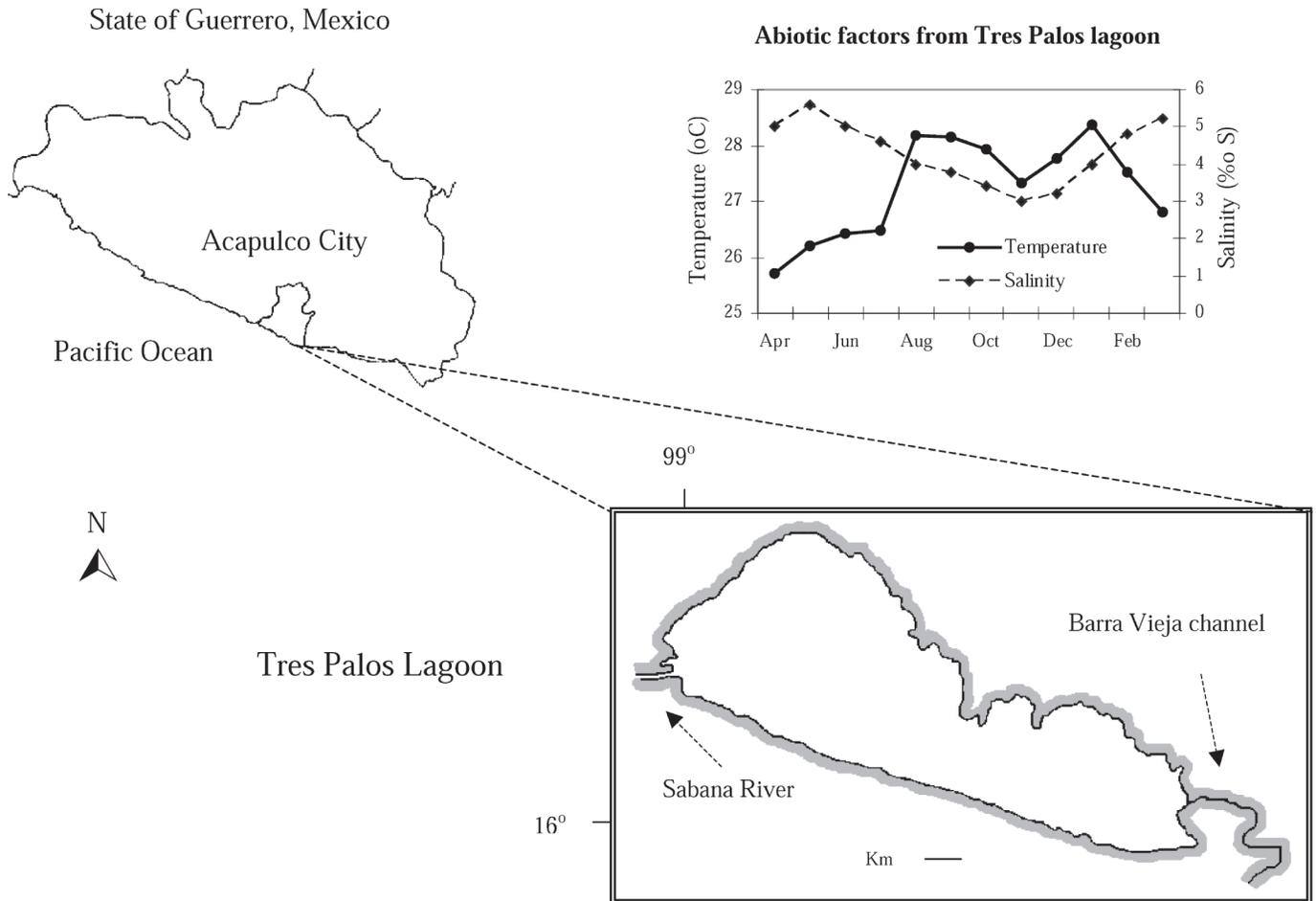
Abiotic factors from Tres Palos lagoon

FIGURE 1.   Location of Tres Palos Lagoon in the state of Guerrero, Mexico. (Insets: temperatures and salinity recorded during a 1-yr sampling period.)

quately the component communities (Aho et al., 1991). Cumulative species curves were plotted per sampling period, and the observed values fitted to the Clench model to assess any asymptotic trend (Clench, 1979).

Autogenic parasite species were defined as those that reach maturity in aquatic hosts and thus have a limited ability to colonize new locations. Allogenic species were those with birds or mammals as definitive hosts and whose natural migrations favor dispersion, giving them a wide geographic distribution (Esch et al., 1988). Active transmission was defined as movement of a parasite to a host by its own means, whereas passive transmission was defined as movement of a parasite from 1 host to another without energy expenditure by the parasite (Bush et al., 2003). The host-range concept (Rohde, 2005) was used to classify the parasite species as specialists or generalists. According to this concept, a specialist parasite species is one that has a marked affinity for a specific host family, genus, or species, whereas a generalist is one that parasitizes a number of families. An Olmstead–Tukey association test (Sokal and Rohlf, 1998) was applied to classify the parasite species based on infection parameters of prevalence and abundance: dominant (abundant and frequent), common (low abundance but frequent), rare (low abundance and low frequency), and indicators (abundant but low frequency). Numerically dominant species were those with more than 40% prevalence and a mean abundance of 10 or more parasites per fish, common species were those with less than 40% prevalence and mean abundance of less than 10 parasites per fish, rare species were those with prevalence below 5% and mean abundance below 5 parasites per fish, and indicator species were those with mean abundance >10 parasites and prevalence <5%.

Variation in species composition over time was described with the

use of prevalence (percent infected host) and mean abundance (mean number of parasites per examined fish), calculated and applied according to Bush et al. (1997) for each helminth species per sampling period. To determine possible differences in infection parameters between sampling periods, G-tests were used for prevalence and a 1-way ANCOVA for abundance, with total length as a covariate to control the influence of host size. Normality was determined with the Kolmogorov–Smirnov test with the use of Lilliefors' approach (Sokal and Rohlf, 1998). When important deviations from normality were found, the data were transformed to Naperian logarithms ($\ln[X + 1]$). The significance of all statistical analyses was established at $P = 0.05$, unless stated otherwise.

Analyses were made at the component community and infracommunity levels (Holmes and Price, 1986); that is, we considered all the helminth parasites in all the hosts collected per sampling period and all the helminth parasites in an individual fish. The component community parameters included total number of parasite species, total number of individual parasites, the Shannon–Wiener index (H) as a measure of diversity, species evenness (equitability) (Krebs, 1999), and the Berger–Parker index (BPI) as a measure of numerical dominance (Magurran, 1991). Component community predictability was determined by measuring quantitative and qualitative similarities between sampling periods. The Jaccard index was used for qualitative analysis and the percentage of similarity (PS) index for quantitative analysis (Krebs, 1999). Kruskal–Wallis tests were used to determine significant differences in the component community parameters between sampling periods at this level. Correlations were made with the use of the Spearman range coefficient (r_s) (Krebs, 1999). The infracommunities were described by the mean number of helminth parasite species per fish, mean number of parasite individuals per fish, and the mean value of the Brillouin

TABLE I. Prevalence (upper value) and mean abundance (lower value) ± standard deviation of helminth parasites of the fat sleeper, *Dormitator latifrons*, from Tres Palos Lagoon, Guerrero, Mexico. Colonization strategy: Au = autogenic species, Al = allogenic species. Distribution: Fw = freshwater; Mw = marine water; Bw = brackish water.

Sampling periods	Dry season April–June 2000	Rainy season July–September	Rainy season October–December	Dry season January–March 01	Au/Al	Microhabitat	Transmission form
Number of hosts	46	47	46	46			
Mean total length (cm)	21.46 ± 1.97	22.96 ± 1.73	20.79 ± 1.80	21.90 ± 1.64			
Digenea (adult)							
Saccocoelioides sp.[Fw]	11.1 0.2 ± 0.8	32.4 1.3 ± 5.2	50.0* 9.9 ± 22.1*	58.3* 4.6 ± 8.1	Au	Intestine	Passive
Digenea (larvae)							
Ascocotyle (Phagicola) longa[Fw]	8.3 0.2 ± 1.5				Al	Heart	Active
Clinostomum complanatum[Fw]	22.2 0.8 ± 2.9	21.6 5.3 ± 54.9	8.3 0.1 ± 0.6	16.7 2.1 ± 18.7	Al	Liver, mesentery	Active
Echinochasmus leopoldinae[Fw]	75.0* 315.1 ± 371.4*	27.0 2.5 ± 6.0	25.0 2.1 ± 6.7	54.4* 172.2 ± 408.9*	Al	Gills	Active
Pseudoacanthostomum panamense[Mw,Bw]	47.2* 3.2 ± 6.3	16.2 1.2 ± 4.3		22.2 1.1 ± 5.0	Au	Gills, muscle	Active
Cestoda (larvae)							
Parvitaenia cochlearii[Fw]	13.9 3.3 ± 38.7	8.1 0.4 ± 0.6	55.6* 17.3 ± 54.8*	30.6 3.6 ± 23.2	Al	Liver	Passive
Acanthocephala (adult)							
Neoechinorhynchus golvani[Fw]	100 52.0 ± 54.4*	94.6 21.4 ± 40.4	83.3 19.1 ± 20.0	97.2 39.6 ± 41.5*	Au	Intestine	Passive
Nematoda (larvae)							
Contracaecum sp.[Fw]	5.6 0.5 ± 10.6	10.8 0.2 ± 0.8	11.1 0.3 ± 1.4	5.6 0.1	Al	Liver, mesentery	Passive

* $P < 0.05$.

diversity index (H′) per fish. The host specimens were pooled into 3 size classes based on total length, i.e., ≤19 cm, ≥20 and ≤22 cm, and ≥23 cm. A 1-way ANCOVA was used to determine significant differences in infracommunity parameters between sampling periods.

Nestedness of parasite infracommunities between sample periods was tested with the use of the ''nestedness temperature calculator'' (Atmar and Patterson, 1995). This calculator considers a random matrix in terms of disorder, or entropy. The relationship between entropy and heat is used to quantify a randomness matrix in terms of temperature, with 0° representing minimum entropy (perfect nestedness) and 100° representing maximum entropy (randomness). This is done by building a presence–absence matrix of parasite species in each infracommunity for each sample. The nestedness temperature calculator packs the observed data into the matrix to concentrate presences in the upper left-hand corner as much as possible, while preserving the primary information (species-per-site data) within the matrix. The packed matrix is then compared with a maximally nested equivalent to identify unexpected presences and absences. For each observed matrix a $T°$ value is calculated where 0° represents a perfectly nested matrix and 100° a completely random matrix. The significance of a derived $T°$ was estimated with a t-test, with the use of a normal distribution of 500 Monte Carlo simulated $T°$ values. As a complement to this analysis, the infracommunity index (ICI) (Zander, 2004), which describes the frequency of double and multiple infections by a single parasite species in a distinct host, was calculated as follows: $ICI = (M_{ij}/N_j) \times I_j$, where I_j = mean of parasite species in host (j = mean infracommunity); M_{ij} = the ratio (numbers) of multiple infected host j with parasite i and other parasites; N_j = the ratio (numbers) of infected host j.

RESULTS

Abiotic factors

Water temperature (measured at 0.5-m depth) varied only slightly between sampling periods, ranging from 25.9 C (April 2000) to 28.4 (January 2001) (Fig. 1). Salinity also varied minimally, ranging from 3.0 (November 2000) to 5.8 ppm (May 2000), indicating an oligohaline environment (Fig. 1).

Species composition

Eight helminth parasite species were identified in the 185 *D. latifrons* specimens collected during the 1-yr study period (April 2000 to March 2001), including 5 digeneans, 1 cestode, 1 acanthocephalan, and 1 nematode (Table I). Six parasite species were found as larvae in different organs, such as the heart, liver, mesentery, muscles, and gills (see Table I). In contrast, only 1 adult digenean (*Saccocoelioides* sp.) and an adult acanthocephalan (*N. golvani*), both intestinal parasites, were recovered. Five of the species found in the larval stage were classified as allogenic, because they mature in ichthyophagous aquatic birds living in the lagoon. Autogenic species included the 2 species collected as adults, as well as the metacercariae *P. panamense* (Table I). All the helminth parasites were classified as generalists because they have been recorded in other hosts from different families living in the same lagoon (data not shown; see Violante-González, 2006).

Seasonal variation in parasite species

No significant difference was observed between parasite species prevalence and mean abundance parameters for male and female hosts ($P > 0.05$); therefore, both sexes were pooled for subsequent statistical analyses. The prevalence of at least 3 parasite species differed significantly between sampling periods (Table I). Higher infection percentages were observed for *E. leopoldinae* in the 2 dry seasons (April–June, 75%; January–

March, 54%) ($G = 37.48$, $P < 0.05$), for *P. cochlearii* in October–December (55%) ($G = 50.27$, $P < 0.05$), and for *Saccocoelioides* sp. in 2 contiguous periods (October–December 2000 and January–March 2001) ($G = 34.55$, $P < 0.05$). Five of the parasite species had variable mean abundance over time (Table I): *E. leopoldinae* and *N. golvani* had the highest mean abundance in April–June and January–March (1-way ANCOVA $F = 35.63$; $F = 9.41$, $P < 0.05$) (both dry seasons); only *P. panamense* was more abundant in April–June (1-way ANCOVA $F = 7.81$, $P < 0.05$); and *Saccocoelioides* sp. and *P. cochlearii* had higher mean abundance values in October–December (rainy season) (1-way ANCOVA $F = 4.78$; $F = 8.53$, $P < 0.05$, respectively).

Component community

Table II shows the descriptors of the helminth component communities of *D. latifrons* through the sampling periods. All examined *D. latifrons* specimens were infected, with 9.7% parasitized by only 1 species, and 90.3% having mixed infections. Of the total number of host specimens, 33.8% were infected with 3 parasite species, and 14.5% had up to 4 parasite species. Based on cumulative species curves, the sample sizes used were sufficient to recover all dominant parasite species, and the number of missing rare species in some sampling periods was minimal (1–2 species) (data not shown).

Between 6 and 8 parasite species were collected in each sampling, though the number did not vary significantly between periods (Kruskal–Wallis H = 4.91, $P > 0.05$). Total number of individual parasites ranged from 1,342 (July–September) to 13,493 (April–June), and varied significantly between periods (Kruskal–Wallis H = 9.03, $P < 0.05$), with the highest total number of individuals collected during April–June (dry season) (Table II). The digenean *E. leopoldinae* numerically dominated during the 2 dry season periods, whereas the acanthocephalan *N. golvani* dominated in the 2 rainy periods (Table II). The Shannon–Wiener diversity index values ranged from 0.77 to 1.77 (Table II). Qualitative similarity within each sampling period ranged from 0.72 in July–September to 0.96 in April–June, and quantitative similarity ranged from 33.31 (October–December) to 61.39% (January–March). The only significant difference in community similarity was observed between periods at the quantitative level (Kruskal–Wallis H = 9.12, $P < 0.05$), and was higher in the 2 dry season sampling periods (Table II).

Infracommunities

The mean number of parasite species ranged from 2.1 ± 1.0 (July–September) to 2.8 ± 1.1 (April–June period) and the mean number of parasite individuals ranged from 36.5 ± 48.9 (July–September) to 375.3 ± 360.3 (April–June period) (Table II). Brillouin diversity index values varied from 0.53 ± 0.39 (April–June) to 0.69 ± 0.40 (October–December).

All hosts were adults, though body size differed significantly between sampling periods (1-way ANOVA $F = 7.97$, $P < 0.05$). The largest hosts were collected in July–September (22.96 ± 1.73), and the smallest in January–March (21.46 ± 1.97). Overall, host length was positively correlated with mean number of individual parasites ($r_s = 0.368$, $P < 0.05$, n = 185). Size class analysis indicated that the lowest values for mean number of parasite species and individual parasites were ob-

TABLE II. Characteristics of the helminth parasite component communities and infracommunities of *Dormitator latifrons* from Tres Palos Lagoon, Guerrero, Mexico, during a 1-yr period. Climatic season: dry season (D), rainy season (R). BPI = Berger-Parker index; H = Shannon-Wiener diversity index; J = Jaccard index; PS = percentage of similarity; Echi = *Echinochasmus leopoldinae*, Neo = *Neoechinorhynchus golvani*. Au = autogenic species; Al = allogenic species.

| | Component communities | | | | | | | | | Infracommunities | | |
Sampling period	No. of hosts	No. of species	No. of parasites	BPI	Dominant species	H	Evenness	J	PS	Mean number of species	Mean number of individuals	Mean value of Brillouin index
April–June 2000[D]	46	8	13,493	0.84	Echi[Al]	0.77	0.26	0.96	58.96	2.8 ± 1.1	375.3 ± 360.6	0.53 ± 0.39
July–September[R]	47	7	1,342	0.70	Neo[Au]	1.47	0.52	0.72	39.47	2.11 ± 1.0	36.5 ± 48.9	0.53 ± 0.47
October–December[R]	46	6	1,827	0.42	Neo[Au]	1.77	0.68	0.68	33.31	2.33 ± 0.8	51.1 ± 71.5	0.69 ± 0.41
January–March 2001[D]	46	7	7,294	0.84	Echi[Al]	0.86	0.31	0.82	61.39	2.75 ± 1.0	202.7 ± 331.2	0.63 ± 0.38

served in the smallest host-size class in all sampling periods (Fig. 2).

Mean number of parasite species was generally higher in the April–June (dry) and January–March (dry) periods (1-way AN-COVA $F = 4.37$, $P < 0.01$), and mean number of individuals was also significantly higher during these periods (ANCOVA $F = 22.84$, $P < 0.0001$). No significant differences were observed in the mean Brillouin diversity index values between sampling periods (1-way ANCOVA $F = 1.29$, $P > 0.05$).

Testing for nestedness

Table III shows the values of nestedness for each sampling period in Tres Palos Lagoon. Nestedness occurred during all 4 periods, but only its intensity (lowest value $T°$) was highest in July–September (rainy season) ($T° = 15.82°$). Species composition remained almost unchanged in all 4 periods, although the rank assigned to each species inside the packed component community matrix did vary between periods. Only the acanthocephalan *N. golvani* was top ranked in all 4 periods, and this was also the only parasite species considered dominant in all 4 sampling periods (Table III).

The infracommunity index values (ICI) indicated that 4 parasite species had a higher number of double or multiple co-occurrences with other parasite species (ICI > 0.20) in all 4 periods, although this only occurred consistently with *N. golvani*. This parasite species exhibited the highest number of co-occurrences in July–September (ICI = 0.448), when the maximum nestedness value was observed (Table III).

DISCUSSION

The results indicate that even though species composition, richness, and diversity of the parasite communities were rather similar throughout the study period, some parasite species presented temporal changes in their infection levels. Two biotic factors were considered as possible causes of the temporal variations observed, i.e., alterations in the recruitment processes of some allogenic parasite species as result of environmental changes originated by the dry and rainy seasons that influence the availability of intermediary hosts, and changes in the feeding and reproductive behavior of *D. latifrons* that influence the recruitment of intestinal autogenic species. The temporal variation pattern observed depends, therefore, on how the parasite invades the host (Chubb, 1979), i.e., its form of transmission.

Three of the 8 metazoan parasite species identified in *D. latifrons* are new geographical records for Tres Palos Lagoon, Guerrero, Mexico, i.e., *E. leopoldinae*, *A.* (*P.*) *longa*, and *P. cochlearii*. The remaining 5 have been reported previously from this location (Garrido-Olvera et al., 2004). Of the identified species, only 3 were autogenic (mature in aquatic hosts); i.e., *Saccocoelioides* sp. and *N. golvani* mature in *D. latifrons*, and *P. panamense* matures in *Hexanematichthys guatemalensis*. The other 5 species all mature in the aquatic birds, *Casmerodius albus egretta* (great egret) and *Phalacrocorax olivaceus* (Neotropic cormorant), that inhabit Tres Palos Lagoon (Violante-González, 2006) and were thus classified as allogenic, i.e., *C. complanatum*, *E. leopoldinae*, *A.* (*P.*) *longa*, *P. cochlearii*, and *Contracaecum* sp.

Five of the parasite species were identified exclusively as larval stages, indicating that *D. latifrons* mainly acts as an in-
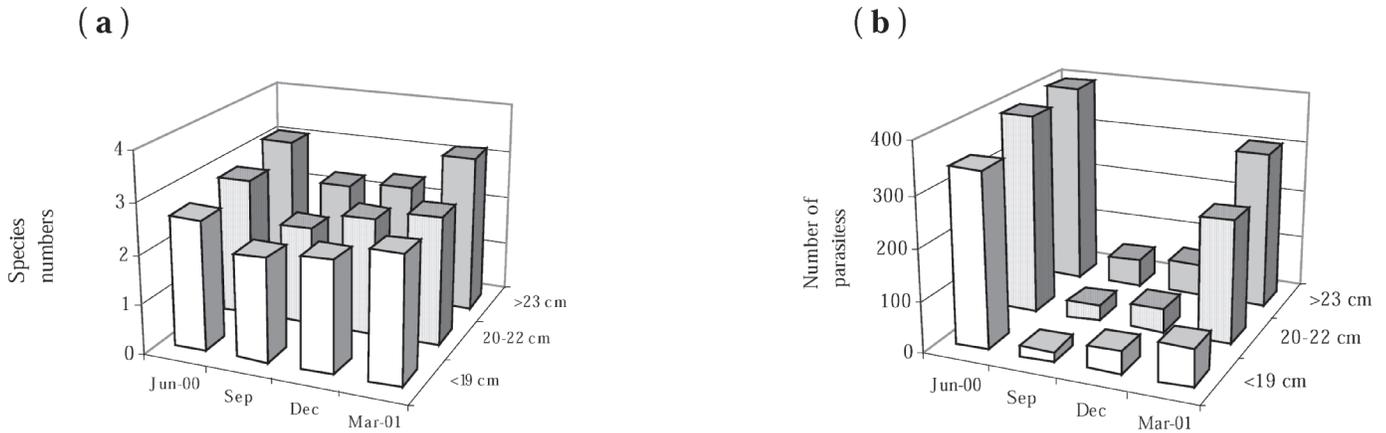
(a)

(b)

FIGURE 2.   Infracommunities. Mean number of helminth parasite species (**a**), and mean number of parasite individuals (**b**) for 3 size classes of *Dormitator latifrons* host.

termediate host to helminth parasite species in Tres Palos Lagoon (Zander et al., 1999). All 8 identified parasite species were generalists. The digeneans were clearly the numerically dominant group, representing 62.5% of all helminth species in the *D. latifrons* component community. High digenean abundance in coastal lagoons may be linked to the high temperatures and high productivity of eutrophic systems. These factors favor development of large herbivorous snails and crustacean populations, which act as intermediate hosts for parasites such as digeneans and acanthocephalans (Valtonen et al., 1997; Zander et al., 1999). Moreover, the shallow depth of coastal lagoons and the detritophagous habits of *D. latifrons* (Yañez-Arancibia and Díaz-González, 1977) place it in vicinity of the snails that act as primary intermediate hosts for digenean species.

These results coincide with others reported for eutrophic estuarine systems in other latitudes, in which generalist parasites (mainly digeneans) dominate and specialists are a minor element of the parasite communities (Zander, 1998; Zander and Reimer, 2002).

Species composition of the *D. latifrons* component community exhibited a clear freshwater influence as 6 of the 8 identified species are of freshwater origin. This may be linked to the lagoon's oligohaline condition (4.30 ± 0.85%), the result of its greater freshwater contribution from rainfall and its temporally limited connection with the sea during the rainy season (Violante-González, 2006). A similar situation has been reported for low-salinity (0.5–3.5%), temperate brackish environments in which marine parasite species represented only 12.69% of total recovered species from 31 host fish species, and freshwater parasite species dominated community composition (Valtonen et al., 2001).

At least 2 of the most abundant species (*E. leopoldinae* and *N. golvani*) exhibited clear temporal variation in mean abundance between climatic seasons, with both species reaching their highest mean abundance during the dry season. Currently, data for Tres Palos Lagoon are insufficient to make a definitive explanation of this variation. In the case of *E. leopoldinae*, however, its higher mean abundance may be due to greater recruitment of infective stages (cercariae) during this period (Moravec et al., 2002). Tres Palos Lagoon experiences relative environmental stability during the dry season (December–May) (Violante-González, 2006). This can favor the transmission of par-

asites such as *E. leopoldinae*, through higher availability of intermediary hosts (snails), as well as of other actively transmitted digeneans such as *C. complanatum* and *P. panamense*, which both had high mean abundance during at least 1 dry season (Table I).

In contrast, during the rainy season (July to November) environmental conditions in the lagoon become unstable in response to the addition of high volumes of organic matter transported by the contiguous Sabana River and other tributaries. This causes a high mortality of benthonic invertebrates, such as snails, which are buried by silt (Violante-González, 2006). However, the addition of organic matter to the lagoon also enhances productivity during the rainy season (Banderas and González, 2000), favoring the transmission process of other helminths that use crustaceans as primary hosts, such as the allogenic cestode *P. cochlearii*, which was most abundant during the most intense rainy period (October–December, Table I).

A similar dynamic was reported by Salgado-Maldonado (1993) in a study of the parasite communities of the cichlid *Cichlasoma urophthalmus* in Celestun Lagoon in southeast Mexico. Although the transmission process was continuous year-round, it registered a drastic fall in the early rainy season. This dynamic may explain, therefore, the temporal variation among allogenic parasite species, but is not applicable to intestinal autogenic species.

In this sense, the higher abundance of the acanthocephalan *N. golvani* in the dry season may be linked to higher levels of feeding activity by *D. latifrons* during this period. During its July–October (rainy season) reproductive period (data not shown), *D. latifrons* exhibits reduced feeding activity, which may explain the lower *N. golvani* mean abundance recorded during this season (Table I). In particular, the ostracods, crustaceans considered to be the first intermediate host of the acanthocephalan *N. golvani* (Salgado-Maldonado, 1993), were scarce in the stomachs of *D. latifrons* during the rainy season.

Temporal variation in infection levels of the acanthocephalan *Neoechinorhynchus agilis* was also related to reproductive aspects of its host *Liza abu* (Mhaisen et al., 1988). Indeed, many studies have shown that seasonal variation in the diet and amount of food ingested by hosts is clearly linked to parasite population dynamics and structure of parasite communities (Esch et al., 1988; Zander and Kesting, 1998; Fiorillo and Font,

TABLE III. Composition of helminth parasite species according to the sampling periods, and their position (rank) within packed component community matrices. Higher values of infracommunity index (ICI > 0.20) and significant values of nestedness temperature index $T°$ are in bold. Classification of parasite species: dominant (D), common (C), rare (R), and indicators (I).

Helminth	April–June 2000			July–September			October–December			January–March 2001		
	Rank	Status	ICI	Rank	Status	ICI	Rank	Status	ICI	Rank	Status	ICI
Neoechinorhynchus golvani	1	D	**0.353**	1	D	**0.448**	1	D	**0.358**	1	D	**0.354**
Echinochasmus leopoldinae	2	D	**0.265**	3	I	0.128	4	R	0.107	3	D	0.162
Pseudoacanthostomum panamense	3	D	0.167	5	R	0.077				5	R	0.081
Clinostomum complanatum	4	R	0.079	4	I	0.102	6	R	0.036	6	R	0.061
Parvitaenia cochlearii	5	I	0.049	7	R	0.038	2	D	**0.238**	4	I	0.111
Saccocoelioides sp.	6	R	0.039	2	C	0.154	3	D	**0.215**	2	D	**0.212**
Ascocotyle (Phagicola) longa	7	R	0.029									
Contracaecum sp.	8	R	0.020	6	R	0.051	5	R	0.048	7	R	0.020
Number of hosts	46			47			46			46		
Number of species	8			7			6					
$T°$	**18.19°**			**15.82°**			**22.36°**			**22.65°**		
P	0.00002			0.00005			0.0004			0.0007		

1999; Zander et al., 2002; Klimpel et al., 2003; Zander, 2003; Fellis and Esch, 2004; Zander, 2004, 2005).

Abiotic factors, such as temperature and salinity, were not highly variable during the study period, and were therefore not considered important in determining helminth parasite community structure. This also coincides with Zander and Kesting (1998), who reported that salinity was not an important abiotic factor for the presence of fish parasite species in the brackish Baltic Sea, whereas the degree of eutrophication appeared to have more influence.

The parasite communities in this lagoon had low numbers of species and diversity at both studied levels (component and infracommunity, Table II), a scenario that is also typical in many parasite communities of gobies (Gobiidae: Teleostei) in eutrophic brackish water in temperate latitudes (Zander et al., 1999).

A possible explanation for the low richness of parasite species in this host may be related to the low-complexity food-web structure in this lagoon; food-web structure is known to affect parasite species richness and diversity in many freshwater systems (Carney and Dick, 2000; Marcogliese, 2001). Zooplankton are not very diverse, and the macrobenthos, including molluscs, are scarce, being represented by just 6 species (Stuardo and Villarroel, 1976). The impoverished biodiversity in this system clearly restricts intermediate host availability in the food web, reducing the opportunity for transmission of higher numbers of parasite species (Carney and Dick, 2000; Marcogliese, 2001).

At the component community level, both community composition and number of parasite species were similar throughout the study period. Total number of parasite individuals, however, exhibited clear seasonal variation, being significantly higher in both dry seasons (Table II). This was attributed to the higher abundance of *E. leopoldinae* and *N. golvani* during these periods. The high qualitative similarity between sampling periods at this level (0.72–0.96), suggests that the community has high predictability year-round. The higher qualitative similarity resulted from the constant presence of a group of 4 abundant and frequent species, i.e., *E. leopoldinae*, *Saccocoelioides* sp., *P. cochlearii*, and *N. golvani*.

The positive significant correlation of mean number of parasite individuals with total host length, and the analysis considering the 3 size classes, indicate that larger hosts harbored more parasite individuals and more parasite species than smaller ones (Fig. 2). This is attributed to the facts that larger, i.e., older, fish (1) offer larger target areas for parasites transmitted by cercariae, (2) ingest larger quantities of food, and (3) have had more time to accumulate parasites than smaller, i.e., younger, fish (Zander and Kesting, 1998; Fiorillo and Font, 1999; Poulin, 2000; Bush et al., 2003; Fellis and Esch, 2004; Zander, 2004).

Although host size may have a significant effect on infracommunity structuring, it did not affect the present results. For example, the largest hosts were collected in July–September (rainy season), but the mean number of parasite species and individuals was lower during this period than in the dry season (Table II). When the influence of host size was removed statistically from the analyses on temporal variation between climatic seasons, the nature of the observed temporal patterns in the parasite infections dynamics infers a biological effect, and is

not a result of changes in host demographics (Fiorillo and Font, 1999).

The presence of nestedness in all the sampling periods suggests that a certain degree of structure was apparent in infracommunity species composition over time; i.e., a certain order existed in the species composition. This means that the parasite species with high prevalence were present in all infracommunities class (rich or poor), whereas the rare ones were mainly in infracommunities rich in species (Poulin and Valtonen, 2001).

Several processes have been suggested as generators of nestedness within infracommunities, including passive sampling and sequential colonization of parasite species (Carney and Dick, 2000). The passive sampling hypothesis, based on probability, predicts that common species will occur in many hosts and rare species in fewer hosts, producing a nested pattern. The nestedness observed here may have been caused by the high stability in species composition, which is reflected in the high qualitative similarity values (0.72–0.96, Table II). However, because some of the dominant parasite species occurred in a higher number of double or multiple co-occurrences with other parasite species (ICI > 0.20, Table III) and were more abundant in different seasons, a sequential colonization process may explain the variation in nestedness intensity observed during the study period.

Nestedness can, therefore, be considered a common feature for the parasite infracommunity composition of *D. latifrons* in Tres Palos Lagoon, which coincides with reports for other fish species from other locations (Carney and Dick, 2000; Poulin and Valtonen, 2001; Valtonen et al., 2001; Vidal-Martinez and Poulin, 2003; Norton et al., 2004). Thus, temporal variation in the recruitment process of some of the main parasite species can be considered as an important influence on nestedness intensity.

Clearly, more research is needed on temporal variation in the parasite communities of this and other hosts over longer periods (Zander, 2005) to understand better the mechanisms that influence variation in eutrophic tropical brackish water parasite communities.

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