RICHNESS AND STRUCTURE OF AN ODONATA LARVAL ASSEMBLAGE FROM RÍO PINOLAPA, TEPALCATEPEC, MICHOACÁN, MEXICO IN RELATION TO THEIR HABITAT CHARACTERISTICS

J.A. GÓMEZ-ANAYA and R. NOVELO-GUTIÉRREZ

Instituto de Ecología, A.C. Red de Sistemática. Carretera Antigua a Coatepec 351, El Haya, 91070, Xalapa, Veracruz, Mexico

antonio.gomez@inecol.edu.mx; − rodolfo.novelo@inecol.edu.mx

The odon. larval assemblage from Río Pinolapa (RP) in the municipality of Tepalcatepec, Michoacán, is described. Sampling was conducted twice in each season (8 trips in total), and additionally some physicochemical variables of the river channel were recorded. Strata (shores, riffles and eddies) and seasonal variation of assemblages are described and compared using classical diversity measures such as Shannon's diversity index, Simpson's diversity index as a dominance measure, Margalef's richness index and Pielou's evenness index. For comparing strata and seasonal diversity the Renyi's diversity profiles were used. A Cluster Analysis was performed on a Bray-Curtis similarity matrix to explore the faunal relationships among year seasons and strata. CCA was also performed to investigate the relationships between the physicochemical and species abundance matrixes. As results, 28 spp. (12 Zygoptera and 16 Anisoptera) were recorded as larvae. Most abundant species were *Erpetogomphus elaps*, *Brechmorhoga praecox* and *Phyllogomphoides luisi*. The highest number of spp. was registered in winter and the lowest in summer. Among strata the highest abundance was recorded in riffles, although the shoreline had the largest number of spp. The most similar assemblages were those of autumn and winter. Shore habitats were more heterogeneous than eddies and riffles and this could explain the larger number of species. The Clench's model explains better the data. Additionally, we used the slope of cumulative number of spp. curve for assessing completeness of the RP list. CCA was significant, with pH, autumn, shoreline and riffles the most important variables. This means that species variation is related to physicochemical, temporal and strata conditions in RP.

INTRODUCTION

The estimation of biodiversity has become one of the major goals for ecologists up to now (MAGURRAN, 2004). Conservation of biodiversity requires the knowledge of its patterns and magnitude (BASELGA & NOVOA, 2008), where the process of making an inventory of unknown assemblages, as well as describing new species, represents the first step in understanding that biodiversity, and also the foundation for any later research related to biodiversity. Unfortunately, this kind of work has received relatively little attention by many journals, propitiating a great abandonment by researchers (WHEELER, 2004; WHEELER et al., 2004; DE CARVALHO et al., 2005).

Different methods for biodiversity assessment have been developed as an indicator of ecosystem conditions, conservation goals, management and environmental monitoring (SPELLERBERG, 1991). Usually, the number of species is the more used measure of diversity (MAYR, 1992; MORENO, 2000). However, diversity depends not only on the number of species but also on the relative abundance of them. Generally, species are distributed according to hierarchical abundance classes, from some very abundant to some very rare. As some species become more abundant and others become rarer, the lower the biodiversity of the community will be. Then, the conservation of biodiversity is mainly a problem concerning to the ecological behavior of the rare species.

In this manner, measuring the relative abundance of species will allow us to identify those species that, due to their rareness in the community, are more sensitive to environmental changes (MORENO, 2001) and, consequently, more exposed to extirpation.

On the other hand, Odonata have become among the most used aquatic insect groups in ecological quality assessment today, because they are relatively large, abundant, widely distributed, easy to collect, the larvae are rather sedentary and easy to rear in laboratory, and there is limited genetic variation (HELLAWELL, 1986). Also, they are relatively easy to identify in comparison with other groups (STORK, 1994), and are generally well represented in aquatic samples (HAMMOND, 1994). Moreover, they respond quickly to environmental stress (NOSS, 1990). Fortunately, the identification of immature stages has been developed in the last two decades in Mexico. However, an important gap still remains on the knowledge of the structure and function of Mexican Odonata assemblages, with relatively few studies dealing with this subject (NOVELO-GUTIÉRREZ & GONZÁLEZ-SORIANO, 1991; GÓMEZ-ANAYA et al., 2000; NOVELO-GUTIÉRREZ et al., 2002; ALONSO-EGUÍALIS, 2004). The exploration of patterns in time and space of Odonata larval assemblages can supply basic data for future research.

The goal of this work was to describe the structure and seasonal variation of the Odonata larval assemblage from the Río Pinolapa and relate it to environmental factors.

STUDY AREA

The Río Pinolapa (RP) is located at (19°00.524N; 103°01.456W), municipality of Tepalcatepec, in Michoacán State, Mexico (Fig. 1). The sampling site is at 616 m asl. Average gradient was 0.02 (1°08'44.75", n = 7), minimum = 0.006 (0°20'37.57"), maximum = 0.042 (2°24'18.03"). Average depth = 0.11 m (IC = 0.05 - 0.19 m, n = 8); average width = 2.18 m (IC = 0.65 - 3.71 m, n = 8); current velocity = 37.58 m/s (IC= 28.57 - 46.58 m/s, n = 8); discharge = 9.16 m³/s (IC = 3.32 - 21.65 m³/s). Averages of physicochemical variables were: temperature = 28.03°C (IC = 27.02- 29.04°C, n = 30), pH = 8.47 (IC = 8.33-8.61, n = 30), conductivity = 666.83 μS/cm (IC = 640.70 - 692.96 μS/cm, n = 30) and oxygen = 7.78 ppm (IC = 7.05 - 8.51 ppm, n = 30).
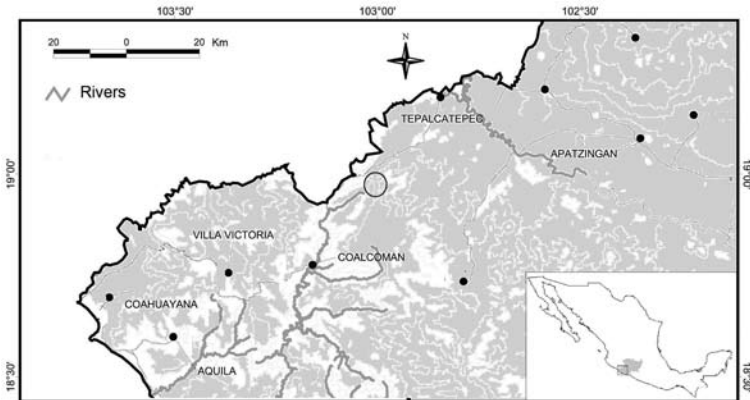

Fig. 1. Sampling site (empty circle) in municipality of Tepalcatepec, Michoacán, México.

MATERIAL AND METHODS

COLLECTING. − Larvae were collected twice in each season (8 trips in total) at shores, and in riffles (at mid-channel) and eddies. Usually, sampling was done at the end of the first third and at the beginning of the last third of each season. We used an aquatic D-frame net, and samples were preserved in 96% alcohol with one replacement before 24 h. A stereomicroscope was used to separate and quantify all larvae to the species level. In addition to the larval sampling, physicochemical variables such as pH, dissolved oxygen, temperature and conductivity were recorded for each sample. Depth, width, and current velocity were measured and discharge was then calculated. The gradient (slope) was measured at seven points of the 500 m long sampling transect according to RESH et al. (1996).

DIVERSITY MEASURES AND DATA ANALYSIS. − Richness and composition, as well as classical diversity measures such as the Shannon's diversity index (H'), the Simpson's index (D), the Margalef's richness index (M_g), and the Pielou's evenness index (J) were used in order to describe the Odonata assemblages by season, strata and as a whole (MORENO, 2001). Also, the Renyi's diversity profiles (TÓTHMÉRÉSZ, 1995, 1998; JAKAB, 2002) were used for comparing diversity, as proposed by SOUTHWOOD & HENDERSON (2000). In this method when the value of the scale used as a parameter is low, the method is extremely sensitive to the presence of rare species. As the value of the scale increases, diversity is less sensitive to rare species. At a high value, the method is sensitive only to common species. The result of this scale-dependent characterization of diversity can be used in a graphical form to visualize the diversity relations of assemblages. This curve is usually

called 'the diversity profile of the assemblage'. It is important to stress that curves of two diversity profiles may intersect. For two communities, the intersection of the diversity profiles means that one of the communities is more diverse for rare species, while the other one is more diverse for common species. The Species Diversity & Richness package v. 3.0 was employed to generate the Renyi's values, exporting them to an Excel spreadsheet to show them graphically.

THEORETICAL RICHNESS. – An estimate of the theoretical richness using non parametric estimators Chao2, Bootstrap, and upper limit of Mao Tau was carried out, using Estimates 8.0 (COLWELL, 2006). Additionally, parametric methods as richness estimators by extrapolation were also used, which apply the observed curve of species accumulation for modeling the addition of new species in relation to the sampling effort (PALMER, 1990; SOBERÓN & LLORENTE, 1993). The Clench's (CLENCH, 1979) and Linear dependence models were applied, as exemplified by JIMÉN-EZ-VALVERDE & HORTAL (2000). Likewise, the slope on the cumulative species curve was used to assess the completeness of assemblages (HORTAL & LOBO, 2005). The slopes were obtained by means of the first derivative of the Clench's and Linear dependence functions (NOVELO-GUTIÉR-REZ & GÓMEZ-ANAYA, 2009).

CLUSTER ANALYSIS. – Beta diversity was assessed by methods of classification. A Cluster Analysis (CA) on a Bray-Curtis (BC) similarity matrix [(1-W) where W = BC dissimilarity)] and the Unweighted Pair Group Method with Arithmetic mean (UPGMA) were used to explore the faunal relationships among seasons and strata. This analysis was performed using PC-ORD ver 4.5 (Mc-CUNE & GRACE, 2002).

CANONICAL CORRESPONDENCE ANALYSIS. – The Canonical Correspondence Analysis (CCA), a direct ordination method, was used to relate species abundance with environmental variables (TER BRAAK & SMILAUER, 1998). The number of environmental variables was then reduced using the automatic forward selection option in the CANOCO 4.5 program. The statistical significance of the relationship between the species and the set of environmental variables was tested by a Monte Carlo permutation test, using an F-ratio of the sum of all eigenvalues as the statistical test (TER BRAAK and PRENTICE, 1988).

RESULTS

SEASONAL PHYSICOCHEMICAL VARIATION

Temperature, pH and conductivity had higher averages in summer, while oxygen was highest in spring. In fact, oxygen decreases gradually from spring to winter (Tab. I). All pH values were slightly alkaline. Oxygen levels were very low in winter when both abundance and species richness were highest.

LARVAL RICHNESS AND COMPOSITION

A total of 3,278 Odonata larvae belonging to 28 species (12 Zygoptera and 16 Anisoptera), 16 genera and six families were collected (Tab. II). *Erpetogomphus elaps* (50.21%) was the dominant species; other numerically important species were *Brechmorhoga praecox* (14.16%) and *Phyllogomphoides luisi* (6.72%) (Fig. 2). A further 61.54% of all species occurred in low abundance (<1%) and were considered rare.

Table I
Averages and 95% confidence intervals for the physicochemical variables of Río Pinolapa

	Temperature	-95%	95%	pH	-95%	95%	Conductivity	-95%	95%	Oxygen	-95%	95%
Spring	31.90	31.29	32.51	8.68	8.56	8.81	706.33	647.6	765.1	10.5	9.55	11.45
Summer	34.95	34.34	35.56	8.95	8.83	9.08	752.00	693.3	810.7	7.28	6.33	8.23
Autumn	26.18	25.75	26.61	8.11	8.02	8.19	567.83	526.3	609.4	8.68	8.01	9.36
Winter	20.93	20.32	21.54	8.50	8.37	8.63	740.17	681.4	798.9	3.74	2.78	4.69

SEASONAL NUMERICAL DOMINANCE

During spring *Erpetogomphus elaps* (38.73%), *Argia oenea* (17.40%), and *Progomphus marcelae* (14.95%) dominated numerically. Only seven species were detected in summer (four of which were gomphids), with very low total and relative abundances. No coenagrionid was recorded in this season. *E. elaps* (44.15%) and *B. praecox* (28.39%) dominated in autumn. Finally, during winter *E. elaps* (60.10%) dominated the assemblage. *Argia tezpi* (8.74%) and *Phyllogomphoides. luisi* (6.52%) were present as codominant species together with *E. elaps*. It is interesting to note that while *E. elaps* clearly dominated throughout the year in the larval stage, the imagoes were not very commonly encountered.

SEASONAL ASSEMBLAGES

Table III and Figure 3 show the seasonal ecological parameters. The smallest number of species was recorded in summer, spring and autumn were intermediate, and the highest number of species was found in winter. The abundance pattern seems to follow the richness one, being higher in winter and lower in summer. Shannon's diversity index (*H'*) seems to vary little throughout the four seasons, although it was a little higher in spring. Dominance (*D*) was higher in winter, mainly due to the great abundance of *E. elaps*. Renyi´s diversity profiles are shown in Figure 4. The summer pattern was a straight line. It showed the minimum number of species for $\alpha = 0$ (the basic structure of assemblages), but for values up to 2 (Simpson index) the pattern showed that summer diversity was the highest.

SIMILARITY

The Odonata larval assemblages from autumn and winter were the most similar, mainly due to their high and similar abundance (Fig. 5), nevertheless, they were quite different in richness sharing a high number of species (13). Some species like *Argia oculata*, *Erpetogomphus cophias* and *Paltothemis lineatipes* were exclusively

Table II

Richness and composition of seasonal Odonata larval assemblages from Río Pinolapa

| Taxa	Key	Spring	%	Summer	%	Autumn	%	Winter	%	Total	%
Number of individuals		410	12.45	20	0.61	1452	44.32	1396	42.61	3278	
Number of species		15	55.56	7	25.93	16	59.26	22	81.48		100
ZYGOPTERA											
Calopterygidae											
Hetaerina											
americana	*Heam*	-	-	4	20.0	22	1.52	7	0.50	33	1.01
Platystictidae											
Palaemnema											
domina	*Pado*	23	5.64	-	-	16	1.10	54	3.87	93	2.84
Coenagrionidae											
Argia funcki	*Arfu*	7	1.72	-	-	-	-	-	-	7	0.21
A. oculata	*Aroc*	-	-	-	-	3	0.21	-	-	3	0.09
A. oenea	*Aroe*	71	17.40	-	-	14	0.96	53	3.80	138	4.21
A. pallens	*Arpa*	1	0.25	-	-	-	-	8	0.57	9	0.27
A. pulla	*Arpu*	-	-	-	-	-	-	6	0.43	6	0.18
A. tezpi	*Arte*	1	0.25	-	-	20	1.38	122	8.74	143	4.37
Enallagma											
novaehispaniae	*Enno*	5	1.23	-	-	-	-	2	0.14	7	0.21
E. semicirculare	*Ense*	-	-	-	-	-	-	3	0.21	3	0.09
Telebasis salva	*Tesa*	2	0.49	-	-	-	-	-	-	2	0.06
Protoneuridae											
Protoneura cara	*Prca*	-	-	-	-	-	-	1	0.07	1	0.03
ANISOPTERA											
Gomphidae											
Erpetogomphus											
bothrops	*Erbo*	-	-	-	-	-	-	1	0.07	1	0.03
E. cophias	*Erco*	-	-	-	-	1	0.07	-	-	1	0.03
E. elaps	*Erel*	158	38.73	7	35.0	641	44.15	839	60.10	1645	50.21
Progomphus											
clendoni	*Prcl*	13	3.19	2	10.0	9	0.62	8	0.57	32	0.98
P. lambertoi	*Prla*	1	0.25	-	-	91	6.27	1	0.07	93	2.84
P. marcelae	*Prma*	61	14.95	-	-	8	0.55	65	4.66	134	4.09
Phyllogomphoides											
luisi	*Phlu*	21	5.15	2	10.0	106	7.30	91	6.52	220	6.72
P. pacificus	*Phpa*	-	-	2	10.0	9	0.62	8	0.57	19	0.58
Libellulidae											
Dythemis											
nigrescens	*Dyni*	-	-	-	-	-	-	7	0.50	7	0.21
Brechmorhoga											
praecox	*Brpr*	5	1.23	2	10.0	412	28.37	45	3.22	464	14.16
Erythrodiplax sp.	*Ersp*	-	0.00	-	-	-	-	7	0.50	7	0.21
Macrothemis											
inacuta	*Main*	7	1.72	-	-	-	-	-	-	7	0.21
M. pseudimitans	*Maps*	28	6.86	1	5.0	83	5.72	60	4.30	172	5.25
Paltothemis											
lineatipes	*Pali*	-	-	-	-	3	0.21	-	-	3	0.09
Perithemis											
domitia	*Pedm*	-	-	-	-	-	-	2	0.14	2	0.06
Pseudoleon											
superbus	*Pssu*	6	1.47	-	-	14	0.96	6	0.43	26	0.79
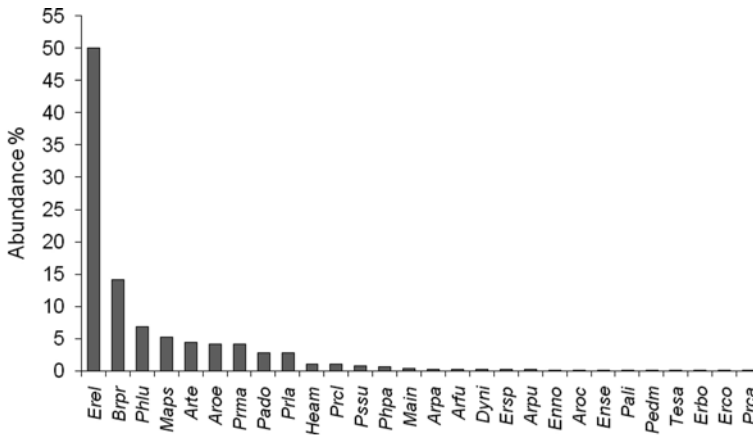
Fig. 2. Relative abundance of Odonata species from Río Pinolapa. Key to species in Table II.

recorded in autumn, while others as *Argia pulla*, *Enallagma semicirculare*, *Protoneura cara*, *Dythemis nigrescens* and *Erythrodiplax* sp., were only found in winter. Summer contains an assemblage of very few species.

DIVERSITY AND ABUNDANCE BY STRATA

Table IV shows the ecological parameters of the Odonata larval assemblages by strata of RP. Number of species in the shores was almost twice as much of that of the riffles (middle-channel), and more than twice as much of that of eddies. However, the abundance was higher in the middle-channel of the water body. The diversity H' was higher in the shores while the dominance did in eddies. The major amount of larvae in all strata was *Erpetogomphus elaps*, however, in the riffles we found a higher proportion of *Brechmorhoga praecox* (24.42%). When diversity is compared and ordered using the Renyi's profiles (Fig. 6), it fol-

Table III

Seasonality of the ecological parameters of Odonata larval assemblages at Río Pinolapa

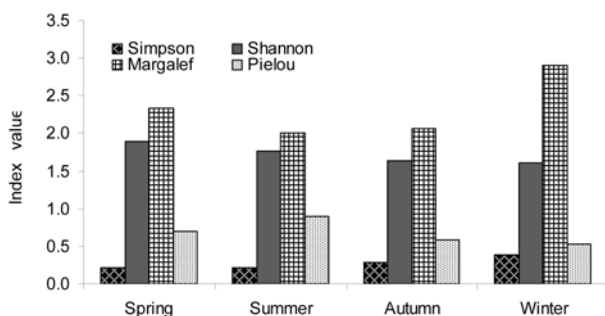|	Spring	Summer	Autumn	Winter	Total
Number of species	15	7	16	22	28
Number of specimens	401	20	1452	1396	3269
Simpson (*D*)	0.22	0.21	0.29	0.38	0.29
Shannon-Weaver (*H'*)	1.89	1.76	1.63	1.61	1.85
Margalef richness (*R*)	2.34	2.00	2.06	2.90	3.09
Pielou evenness (*J*)	0.70	0.90	0.59	0.52	0.57

Fig. 3. Ecological parameters per season of the Odonata larval assemblage at Río Pinolapa. Collections were made between March 2005 and January 2006.

lows the gradient shores>riffles>eddies. This fact confirms that shores contain the highest diversity of Odonata larvae in RP.

THEORETICAL RICHNESS ESTIMATION

NON-PARAMETRIC MODELS. – The cumulative species curves generated by non parametric estimators Chao2, and Bootstrap are shown in Figure 7. The estimated number of species was 41.4, and 32.4 species, respectively, which gave a sampling efficiency of 67.6%, and 86.3, respectively. These richness estimators indicate a lack of register from 4 to 13 species. The estimated number of species using the Mao Tau upper limit of class interval was 34.7, which means that still should be added to the list 6-7 species, being the efficiency of the total sampling effort of 80%. The number of species with a single individual (singletons) was 3, with two individuals (doubletons) was 2, the number of unique species was 11, and for duplicated ones was 3.

PARAMETRIC MODELS. – Figure 8 shows cumulative species curves generated by the Clench's and Linear dependence functions. The first function predicted 30.67 species and explained 98% of data variation, while the second one predicted 25.74 species and explained 95% of data variation. The Clench's model indicates that there are 3 species to be registered yet, and the linear dependence in-

Table IV
Ecological parameters of the Odonata larval assemblages by stratum at Río Pinolapa

Index/stratum	Shores	Riffles	Eddies
Number of species	25	14	10
Number of specimens*	1062	1713	323
Simpson (D)	0.27	0.32	0.47
Shannon-Weaver (H')	1.93	1.54	1.18
Margalef's richness (R)	3.44	1.61	1.56
Pielou's (J) eveness	0.60	0.60	0.51

* Some samples were excluded because of a lack of enough data field.
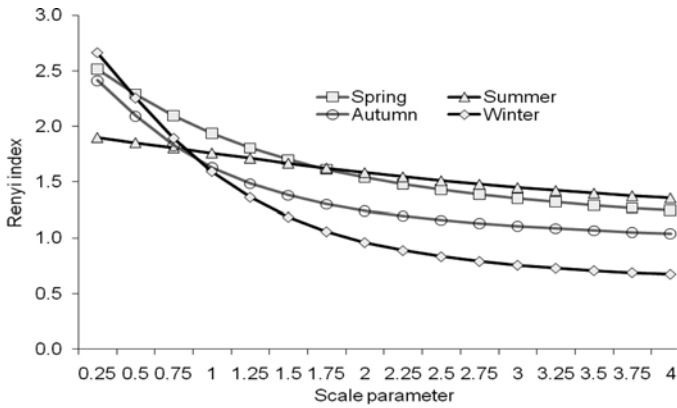
Fig. 4. Renyi's diversity profiles for the four seasonal Odonata larval assemblages from Río Pinolapa.

dicates the list has been completed. Based on the explained variance (R^2, determination coefficient), the Clench's estimation explained better the data variation; its prediction is considered further. Finally, slopes for both curves were 0.10 for Clench's function and 0.04 for Linear dependence.

THE SPECIES-ENVIRONMENT RELATIONSHIPS

The results of the CCA were globally significant (trace = 0.937, F = 1.59, p <0.05, Tab. V). The first three axes offered a good solution to the ordination of the physicochemical variables and abundance of species, since from the total variability in the data (inertia = 3.701), it was possible to explain 87.9% by means of these group of axes. The significance test of the first canonical axis showed it was significant (eigenvalue = 0.292, F = 2.822, p <0.05).
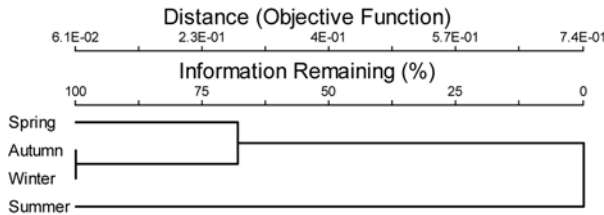

Fig. 5. Dendrogram showing the faunal relationships among the year seasons assemblages of Odonate larvae. Based on a Bray-Curtis similarity matrix and the unweighted pair-group arithmetic averaging (UPGMA).

Table V
Results of the canonical correspondence analysis (CCA) of log-transformed odonata larvae
abundance as a function of their environmental variables

Axes	1	2	3	4	Total inertia
Eigenvalues	0.29	0.25	0.18	0.09	3.705
Species-environment correlations	0.82	0.85	0.76	0.66	
Cumulative percentage variance					
of species data	7.9	14.7	19.5	22	
of species-environment relation	31.2	58	76.9	86.8	
Sum of all eigenvalues					3.705
Sum of all canonical eigenvalues					0.937

The first axis was the most important, explaining 31.2% of variance, and it was also the most strongly correlated with pH, riffles and autumn. The second axis explained 26.8% of variance, and it correlated strongly with conductivity. The third and fourth axes explained only 16.7% and 12.1% of variance, respectively, and were not considered further.

When the distribution of the species in the eight collections and three strata is analyzed together with the CCA of the Figure 9, it is possible to make the following precisions: *Paltothemis lineatipes, Erpetogomphus cophias, Progomphus*
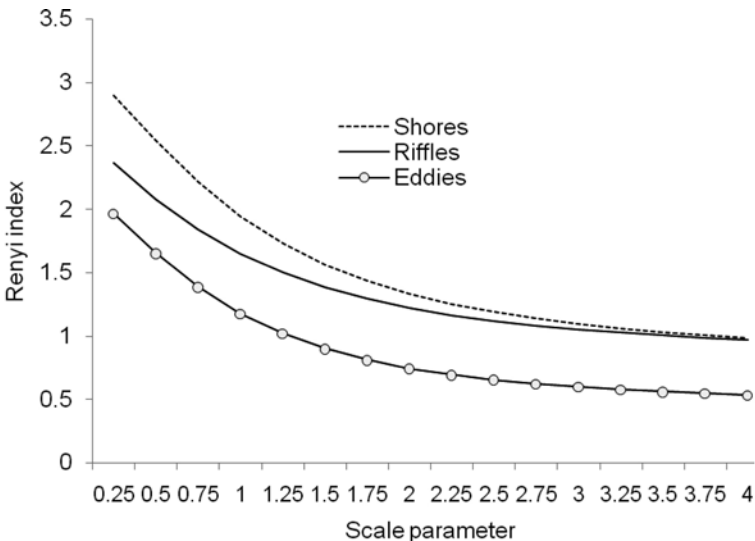

Fig. 6. Renyi's diversity profiles for three strata assemblages of Odonata larvae from Río Pinolapa. Profiles differ mainly at their basic level of structure, the number of species. Profiles never cross in α range from 1 to 4. Values of Renyi when α = 4 were: shores profile = 0.982, riffles profile = 0.969 and eddies profile = 0.535.

lambertoi, and *Hetaerina* a*mericana* do associate well with the autumn. Particularly, *P. lambertoi* was registered almost in 100% (91 out of 92 specimens) from the shores at the beginning of the autumn. *Argia oenea* and *Palaemnema domina* were almost invariably registered from the riffles and at late winter. Only seven larvae of *Macrothemis inequiunguis* were registered from late spring on shores.

DISCUSSION

GENERAL ASPECTS

A total of 28 Odonata species (12 Zygoptera and 16 Anisoptera) were found and 3,276 larvae were identified in this work. The size of the Odonata larval assemblage from RP is similar to other Mexican water bodies reported (ALONSO-EGUÍALIS, 2004; GÓMEZ-ANAYA et al., 2000; NOVELO-GUTIÉRREZ & GONZÁLEZ-SORIANO, 1991; NOVELO-GUTIÉRREZ et al., 2002; BOND et al., 2006). Usually, the most speciose families are Libellulidae and Coenagrionidae. In this case Coenagrionidae, Gomphidae and Libellulidae were best represented. The single genus *Argia* contributed 50% of Coenagrionidae; in Gomphidae three genera contributed more or less equally, and in Libellulidae seven genera contributed to the diversity.

DIVERSITY AND ABUNDANCE

The highest and lowest species richness was found in winter and summer, respectively. The greatest abundance of individuals was recorded in autumn and
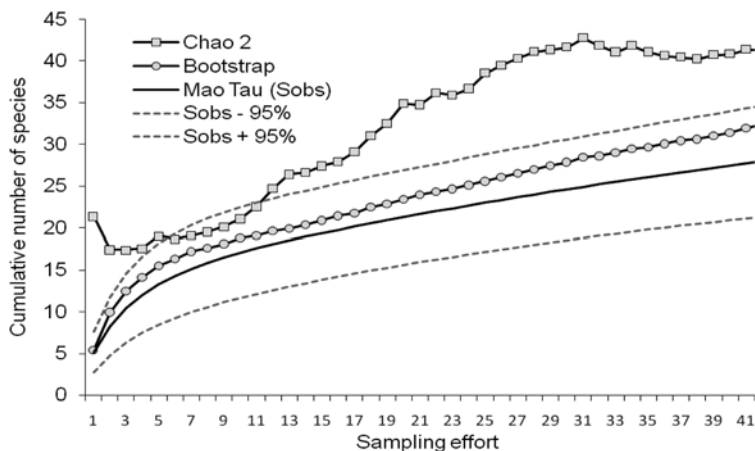

Fig. 7. Cumulative species curves generated by non-parametric estimators Mao Tau (S_{obs}), Chao2, and Bootstrap for the Odonata larval assemblage from Río Pinolapa.
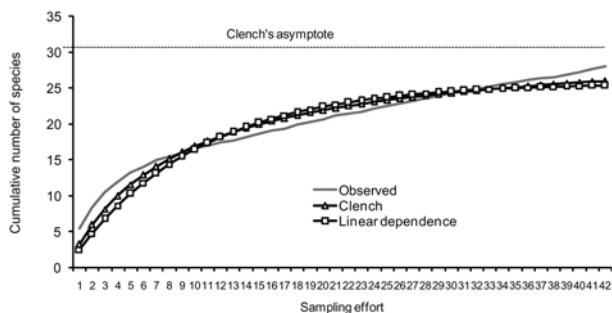
Fig. 8. Cumulative species curves generated by the Clench's function (a = 3.68, b = 0.12, asymptote = 30.67, R = 0.98), and linear dependence function (a = 2.63, b = 0.102, asymptote = 25.74, R = 0.95), for the Odonata larval assemblage from Río Pinolapa. The slope was estimated by the first derivative of Clench's function [$a/(1+b*n)^2$] and the first derivative of Linear dependence function [$a*exp(-b*n)$].

winter. This could be due to the emergence pattern of the seasonal species. Most of them emerge during the dry season (at the end of the winter and through the spring). Thus, when the rains come in the summer, very few species are present as larvae. Summer is the season with a great reproductive activity, so that when autumn comes, there are large populations of larvae of the majority of odonate species. Later, as time goes on, abundance decreases through mortality until the lower abundances in spring and then, with emergence of the adults, even lower in summer. Among strata, the highest species richness was found at shoreline and the lowest in eddies; while the highest abundance occurred in riffles and the lowest in eddies. Eddies were the most simplified stratum, usually with a muddy bottom and some decaying leaves, and lacking any kind of aquatic plant; this could result in the lowest richness and abundance. Richness distribution pattern was different to that of abundance in RP. Thus, 55.39% of all abundance was recorded in riffles, 34.20% in shorelines and 10.40% in eddies. The most abundant species in all three strata was *Erpetogomphus elaps*, with 53.79%, 32.44%, and 13.77%, respectively. This species is, apparently, the best adapted to different conditions in time and space in RP, despite having a restricted period as adults (late summer to early autumn).

RENYI'S DIVERSITY PROFILES

Diversity ordering can be performed by using a diversity index family (TÓTH-MÉRÉSZ, 1995), as proposed by SOUTHWOOD & HENDERSON (2000). The Renyi's diversity profiles method has been poorly used in comparing and ordering diversity of aquatic macroinvertebrate assemblages (SIPKAY *et al.* 2007) and even less used with Odonata assemblages (JAKAB et al., 2002). In this method a scale parameter (alpha) is related to the abundance-dominance structure of the community. At different values of the scale the function is sensitive to rare, common, and intermediate-abundance species. When comparing two Renyi diversity profiles, if they do not cross each other, it means that the upper profile represents

a more diverse assemblage under any common measure of diversity; but if these profiles do cross each other once, it means that one assemblage is more diverse when rare species are weighted more heavily (low alpha), and the other assemblage is more diverse when common species are weighted more heavily (high alpha). When the diversity profiles cross each other, the communities cannot be ordered according to their diversity, because one of them is more diverse for rare species, the other for common ones. Renyi's diversity is sensitive to rare species for small values of the scale, whereas it is sensitive to abundant species for larger values of the scale. Seasonal diversity profiles crossed once, mainly for $\alpha<1$ values (Figure 4). It means that these assemblages are mainly different in rare species. Strata profiles do not cross; however, shore and riffles profiles were similar in abundant and frequent species ($\alpha>2$), and, definitively, eddies profile was the least diverse.

Species distribution must meet the ecological requirements of all stages in the life cycle (CORBET, 1999). Although the imagoes have more mobility than immature, adequate substrates must be present for the larval emergence (rocks, vegetation, twigs, etc.). In consequence, the disturbance of the original conditions (e.g. riparian vegetation) will affect richness (SMITH et al., 2007). In RP the major diversity in shores can be explained because of major microhabitat heterogeneity. In shores we observed different size of rocks, sand, algae, plants, roots, mud, leaf packs, detritus, and different combinations of these substrates. Number of substrates in riffles and eddies or combinations of them were limited. In shores we found 10 Zygoptera species (1 calopterygid, 1 platystictid, 1 protoneurid, 7 coenagrionids), and 15 Anisoptera (7 gomphids and 8 libellulids). All Zygoptera species are endophitic in oviposition and they can find the needed substrates in shores. Gomphids and libellulids females lack ovipositor and they release their eggs on the water surface near the shores.

Most of the riffle samples of RP come from shallow and smooth flowing water places. In riffles we found 14 species (5 Zygoptera and 9 Anisoptera). *Brechmorhoga praecox* was the most abundant species in this stratum, as have been reported to different species of this genus (CORBET, 1999), and particularly for this species (BOND et al., 2006). Most of *B. praecox* larvae were caught, mainly, at the end of autumn. They exhibit different disruptive color patterns, being cryptic at sand and fine gravel bottom. Must of Coenagrionidae species were recorded from shores, except *Argia oenea* and *A. tezpi* which were more abundant in riffles.

CUMULATIVE CURVES OF SPECIES

The non-parametric estimation achieved by Bootstrap agrees well with the parametric estimation made by Clench function, which predicted 31 species (3 species more to be added). For parametric estimations, we chose initially the model

that better fitted data using the coefficient of determination (R^2). This model was the Clench's function. Then, we used the slope of the curve evaluated at the maximum sampling effort by the first derived of both functions, as an approach of completeness of the list, according to JIMÉNEZ-VALVERDE & HORTAL (2003), and HORTAL & LOBO (2005). Although the slope was smaller with the Linear dependence (0.04), we believe this function underestimates the number of species (since it predicted fewer species than the recorded ones). We think few species could exist yet to be added to the list for the studied section of the river. The slope of the first derived of Clench (0.10) is relatively small, supporting the idea that the list is practically complete.

CCA

Several authors have explored the relationship between some environmental factors and odonate faunas using multivariate techniques (SAMWAYS, 2003; SCHINDLER et al., 2003; HOFFMANN & MASON, 2005; OPPEL, 2005; CARCHINI, 2007; FLENNER & SAHLÉN, 2008; SATO & RIDDIFORD, 2008; HAMASAKI et al., 2009). In this work the CCA showed significant correlation between both environmental and species matrices. Additionally, the CCA biplot allowed visualization of some particular facts and the establishment of some hypotheses on species-species and environment-species relationships. For example, *Palaemnema domina* and *Argia oenea* are well associated with riffles stratum, indicating similar ecological requirements. *P. domina* is usually
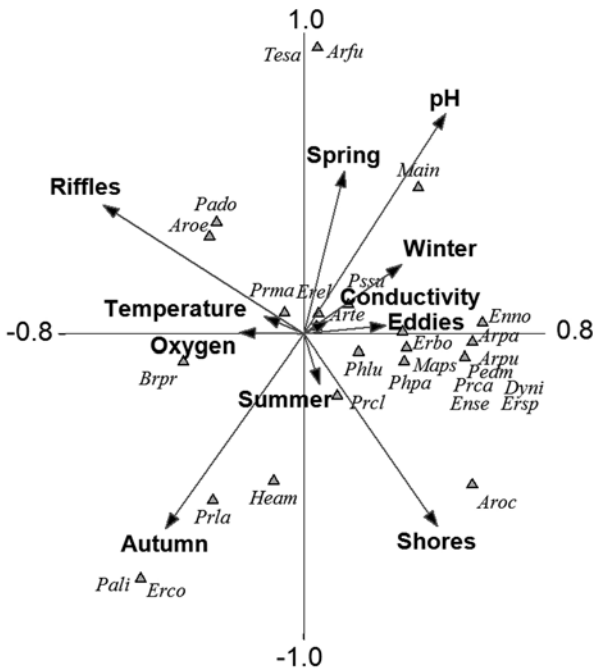

Fig. 9. Biplot of CCA ordination showing environmental variables (arrows) most strongly correlated with axes CC1 and CC2 and species in triangles. Seasons and strata were included in CCA as dummy variables. In terms of predicting larval assemblage composition, important environmental variables have longer arrows than less important ones.

found under mid-sized rocks (8-10 cm diam.) in riffles, as is *A. oenea*, although this last species is found also commonly among rough gravel. *Erpetogomphus elaps* is close to the origin on Figure 9, meaning it is the most ubiquitous species in RP. Apparently, the larvae are well adapted to both erosional and depositional environments. Moreover, it was found in every collection and through all seasons.

FINAL CONSIDERATIONS

Contrary to species lists from lentic water bodies (lakes, lagoons, ponds) which can be considered complete lists because one can sample the whole water body, the 28 recorded species in the RP survey represent just a part of a bigger assemblage. This bigger assemblage extends up and down stream changing in richness, composition, and abundance with changes in river conditions. From this point of view, the assemblage here described represents a relatively local measure of this group of insects, and also a measure of the conservation status of the river. It is possible that for many species with low abundance and distribution in space (strata) and time (seasons), the best conditions for their reproduction could be up or down stream. In this bigger assemblage the floristic, climatic, altitudinal and microhabitat changes should be considered, because the more the changes in the river conditions, the larger the species list should be.

REFERENCES

ALONSO-EGUÍALIS, P.E., 2004. *Ecología de las asociaciones de Odonata en la zona de influencia de las microcuencas afectadas por la presa Zimapán, Querétaro e Hidalgo*. PhD Thesis, Univ. Autón. Querétaro.

BASELGA, A. & F. NOVOA, 2008. Coleoptera in a relict forest of Spain: implications of hyperdiverse taxa for conservation strategies. *Ann. ent. Soc. Am*. 101(2): 402-410.

BOND, J.G., R. NOVELO-GUTIÉRREZ, A. ULLOA, J.C. ROJAS, H. QUIROZ-MARTÍNEZ AND T. WILLIAMS, 2006. Diversity, abundance, and disturbance response of Odonata associated with breeding sites of Anopheles pseudopunctipennis (Diptera: Culicidae) in Southern Mexico. *Environ. Ent*. 35(6): 1561-1568.

CARCHINI, G., V. DELLA BELLA, A.G. SOLIMINI & M. BAZZANTI, 2007. Relationships between the presence of odonate species and environmental characteristics in lowland ponds of central Italy. *Ann. Limnol*. 43(2): 81-87.

DE CARVALHO, M.R., F.A. BOCKMANN, D.S. AMORIM, M. DE VIVO, M. DE TOLEDO-PIZA, N.A. MENEZES, J.L. DE FIGUEIREDO, R.M.C. CASTRO, A.C. GILL, J.D. McEACHRAN, 2005. Revisiting the taxonomic impediment. *Science* 307: 353.

FLENNER, I. & G. SAHLÉN, 2008. Dragonfly community re-organisation in boreal forest lakes: rapid species turnover driven by climate change? *Insect Conserv. Divers*. 1: 69-179.

GÓMEZ-ANAYA, J.A., R. NOVELO-GUTIÉRREZ & R. ARCE-PÉREZ, 2000. Odonata de la zona de influencia de la Central Hidroeléctrica "Ing. Fernando Hiriart Balderrama" (PH Zimapán), Hidalgo, México. *Folia ent. mex.* 108: 1-34.

HAMASAKI, K., T. YAMANAKA, K. TANAKA, Y. NAKATANI, N. IWASAKI & D.S. SPRAGUE, 2009. Relative importance of within-habitat environment, land use and spatial autocorrelations for determining odonate assemblages in rural reservoir ponds in Japan. *Ecol. Res.* 24: 597-605.

HAMMOND, P.M., 1994. Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Phil. Trans. R. Soc. Lond.* (B) 345: 119-136.

HELLAWELL, J.M., 1986. *Biological indicators of freshwater pollution and environmental management.* Elsevier, London.

HOFFMANN, T.A. & C.F. MASON, 2005. Habitat characteristics and the distribution of Odonata in a lowland river catchment in eastern England. *Hydrobiologia* 539: 137-147.

HORTAL, J. & J. LOBO, 2005. An ED-based protocol for optimal sampling of biodiversity. *Biodivers. Conserv.* 14: 2913-2947.

JAKAB, T., Z. MÜLLER, G. DÉVAI & B. TÓTHMÉRÉSZ, 2002. Dragonfly assemblages of a shallow lake type reservoir (Tisza-Tó, Hungary) and its surroundings. *Acta zool. Acad. Sci. hung.* 48(3): 161-171.

JIMÉNEZ-VALVERDE, A. & J. HORTAL, 2003. Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Rev. Ibérica Aracnol.* 8: 151-161.

MAGURRAN, A.E., 2004. *Measuring biological diversity*. Blackwell, Oxford.

MAYR, E., 1992. A local flora and the biological species concept. *Am. J. Bot.* 79: 222-238.

McCUNE, B. & J.B. GRACE, 2002. Distance Measures. *In*: B. McCune, J.B. Grace & D.L. Urban, [Eds], *Analysis of ecological communities,* pp. 45-57. MJM Software Design, Gleneden Beach.

MORENO, C.E., 2001. *Métodos para medir la biodiversidad*. M&T-Manuales & Tesis SEA, Vol. 1. Zaragoza.

MORENO, C.E. & G. HALFFTER, 2000. Assessing the completeness of bat biodiversity inventories using species accumulation curves. *J. appl. Ecol.* 37: 149-158.

NOSS, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conserv. Biol.* 4: 355-364.

NOVELO-GUTIÉRREZ, R. & E. GONZÁLEZ-SORIANO, 1991. Odonata de la Reserva de la Biosfera "La Michilía", Durango, México, 2: larvas. *Folia ent. mex*. 81: 107-164.

NOVELO-GUTIÉRREZ, R., J.A. GÓMEZ-ANAYA AND R. ARCE-PÉREZ, 2002. Community structure of Odonata larvae in two streams in Zimapán, Hidalgo, Mexico. *Odonatologica* 31(3): 273-286.

OPPEL, S., 2005. Habitat associations of an odonate community in a lower montane rainforest in Papua New Guinea. *Int. J. Odonatol.* 2: 243-257.

RESH, V.H., M.J. MYERS & M.J. HANNAFORD, 1996. Macroinvertebrates as biotic indicators of environmental quality. *In*: F.R. Hauer & G.A. Lamberti, [Eds], *Methods in stream ecology,* pp. 647-667, Acad. Press, San Diego.

SAMWAYS, M.J., 2003. Threats to the tropical island dragonfly fauna (Odonata) of Mayotte, Comoro archipielago. *Biodivers. Conserv.* 12: 1785-1792.

SATO, M. & N. RIDDIFORD, 2008. A preliminary study of the Odonata of S'Albufera Natural Park, Mallorca: status, conservation priorities and bio-indicator potential. *J. Insect Conserv.* 12: 539-548.

SCHINDLER, M., C. FESL & A. CHOVANEC, 2003. Dragonfly associations (Insecta, Odonata) in relation to habitat variables, a multivariate approach. *Hydrobiologia* 497: 169-180.

SIPKAY, C.S., L. HUFNAGEL, A. RÉVÉSZ & G. PETRÁNYI, 2007. Seasonal dynamics of an aquatic macroinvertebrate assembly (Hydrobiological case study of Lake Balaton, No. 2).

Appl. Ecol. environ. Res. 5(2): 63-78.

SMITH, J., M.J. SAMWAYS & S. TAYLOR, 2007. Assessing riparian quality using two complementary sets of bioindicators. *Biodivers. Conserv*. 16: 2695-2713.

SOUTHWOOD, T.R.E. & P.A. HENDERSEN, 2000. *Ecological methods.* [3rd edn] Blackwell, Oxford.

SPELLERBERG, I.F., 1991. *Monitoring ecological change*. Cambridge Univ. Press, Cambridge/U.K.

STORK, N.E., 1994. Inventories of biodiversity: more than a question of numbers. *In*: P.L. Forey, C.J. Humphries & R.I. Vane-Wright, [Eds], *Systematics and conservation evaluation,* pp. 81-100. Clarendon Press, Oxford.

TER BRAAK, C.J.F., 1988. Partial canonical correspondence analysis. *In*: H.H. Bock, [Ed.], *Classification and related methods of data analysis,* pp. 551-558, North-Holland, Amsterdam.

TER BRAAK, C.J.F. & P. SMILAUER, 1998. CANOCO reference manual and user´s guide to Canoco for Windows: software for canonical community ordination, version 4. Ithaca, NY.

TÓTHMÉRÉSZ, B., 1995 Comparison of different methods for diversity ordering. *J. Veget. Sci.* 6: 283-290.

TÓTHMÉRÉSZ, B., 1998. On the characterization of scale-dependent diversity. *Abstr. Bot.* 22: 149-156.

WHEELER, Q.D., 2004. Taxonomic triage and the poverty of phylogeny. *Philos. Trans. R. Soc. Lond.* (B) 359: 571-583.

WHEELER, Q.D., P.H. RAVEN & E.O. WILSON, 2004. Taxonomy: impediment or expedient? *Science* 303: 285.