

Diversity, Abundance, and Disturbance Response of Odonata Associated with Breeding Sites of *Anopheles pseudopunctipennis* (Diptera: Culicidae) in Southern Mexico

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Environ. Entomol. 35(6): 1561–1568 (2006)

ABSTRACT Odonate nymphs are important predators of the immature aquatic stages of mosquitoes. Populations of the malaria vector *Anopheles pseudopunctipennis* Theobald (Diptera: Culicidae) can be efficiently reduced by extraction of filamentous algae from river pools in southern Mexico. Here, we examined the influence of this intervention on the diversity of odonates associated with mosquito breeding pools after annual extractions of algae from river pools in a 3-km section of the Coatán River, over a period of 2 yr. Odonate sampling was performed at monthly intervals in control and treated sections of the river for 4–5 mo after extraction in both years and before extraction in 1 yr. In total, 16 species, 10 genera, and 6 families of odonates were collected. Shannon diversity index values declined significantly during a period of 1 mo in 2001 and >5 mo in 2002. However, the abundance of odonates captured was not affected by algal extraction. In contrast, year-to-year variation in the diversity and abundance of the odonate community was strongly influenced by precipitation and river volume. Despite the importance of algae in river ecology, we conclude that the mosquito control intervention resulted in minimal impact on the odonate community in southern Mexico.

KEY WORDS diversity, disturbance, extraction of filamentous algae, Odonata, community recovery

Immature Odonata occupy a great diversity of aquatic habitats but are generally most abundant in lowland streams and ponds. The predatory nymphs are an important part of aquatic food webs and the aquatic stages of mosquitoes comprise a significant part of the diet of many immature odonates (Ward 1992, Westfall and Tennesen 1996). Indeed, odonates were one of the first arthropods to be examined as biological control agents against mosquitoes, but difficulties with colonization, production, and handling impeded their deployment (Legner 1995).

The use of the odonates as environmental quality indicators had been the subject of debate. It may be argued that, because of the complex requirements of habitat of each species, the presence of a vigorous and diverse fauna of these insects will always be a reliable indicator of stability, health, and integrity of an aquatic ecosystem (Chovanec 1994, 1998, Foote and Rice Hornung 2005). Others believe that the odonates are of minor or irregular value as bioindicators, except in

specialized habitats (Carchini and Rota 1985). Nevertheless, odonate communities have become an increasingly important tool in studies on the ecological evaluation of aquatic systems (Schmidt 1985, Osborn 2005).

Recently, extraction of filamentous algae from riverside pools was shown to be a highly effective intervention resulting in control of the malaria vector, *Anopheles pseudopunctipennis*, during the peak period of vector activity by this species in southern Mexico (Bond et al. 2004). Filamentous algae of the genera *Spirogyra* and *Cladophora* represent food sources and predator refuges for mosquito larvae and are also highly attractive to ovipositing females (Bond et al. 2005). Habitat manipulation procedures of this kind represent temporally discrete pulse perturbations of aquatic systems, resulting in an instantaneous change in the availability of resources: algae in the case of the phytophagous community and prey items in the case of the predator community (Pickett and White 1989).

Relatively few studies have addressed the influence of discrete perturbations on the diversity and abundance of aquatic invertebrate communities (Resh et al. 1996, Billheimer et al. 1997, Wildhaber and Schmitt 1998, Poulton et al. 2003, Harrison et al. 2004). Because of their trophic position and sensitivity to environmental degradation, dragonflies and damselflies are useful subjects for research on the effects of anthro-

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pogenic perturbation and are highly sensitive to changes in habitat quality (Wilson 1997).

The extraction of filamentous algae from river pools in southern Mexico presented the opportunity to evaluate of consequences of this practice on the Odonata community associated with *An. pseudopunctipennis* breeding sites. Specifically, we examined changes in odonate diversity and the process of community recovery after annual perturbations performed over 2 yr.

Materials and Methods

Study Area. The study was performed during two dry seasons, February to June 2001 and January to May 2002, in a 6-km section of the River Coatán, 25 km northeast of the town of Tapachula, Chiapas, Mexico, between the villages of Unión Roja and La Boquilla at an altitude between 297 and 675 m above sea level. River discharge is reduced during the dry season, resulting in the appearance of interconnected pools in which filamentous algae proliferate. These pools are favored by ovipositing mosquitoes for the development of their offspring. The pools are joined by stretches of riffles and smooth flowing water. The climate in this region is tropical subhumid with a wet season from May to October and dry season from November through April. The annual average rainfall is 4,200 mm, average annual temperature is 25°C, and relative humidity is 60–90% most of the year.

Experimental Design. The intervention aimed at reducing the *An. pseudopunctipennis* population by extraction of filamentous algae has been described previously (Bond et al. 2004). Briefly, the 6-km section of river was divided into two zones, each of 3 km. In 2001, the upstream zone was selected for extraction of filamentous algae (treated zone) from all the river pools of water. Because of the large scale of the experiment, it was not possible to perform strict controls, for example, sites in a number of nearby rivers that were not subjected to the intervention. Therefore, we used a comparative approach involving the downstream 3-km zone that was left undisturbed as an untreated contrast zone. In 2002, the treated and untreated contrast zones were switched, and the experiment was repeated. Manual extraction of filamentous algae from the entire area of each pool in the treated zone was performed over a 7-d period with the use of garden rakes covered with mosquito netting. The bottom of the pools was not disturbed during this procedure. The start of the study on the impacts to odonates was taken to be the first day after extraction of algae from all pools in the treated zone had been completed.

Odonata Sampling and Identification. Monthly samples of aquatic odonates were taken in each zone during 5 mo/yr. In 2001, a sample was taken immediately before extraction of algae, whereas in 2002, all samples were taken after extraction. Each month, five subsamples per zone were taken from each of five pools located at intervals of \approx 500 m apart. Aquatic stages were collected using an aquatic entomological net of 24 by 46 cm and mesh size of 0.9 mm situated

to catch drifting insects at the outflow of the sampling area. All the samples were taken in pools connected to riffles with substrates of rubble, gravel, and sand. Odonates were disturbed and encouraged to drift by agitating the substrate using the traveling kick method (Pollard 1981) for a 5-min period over a 5-m² area of the pool. Samples sites were never resampled. Samples from each pool were placed in 95% ethanol. In the laboratory, odonates were identified to genus and species level using dichotomous keys (Westfall and May 1996, Novelo-Gutiérrez 1997a, b, Needham et al. 2000). The specimens identified from each set of five pools were combined for diversity index estimates.

Odonate Community Diversity. The diversity of odonates was estimated by means of the Shannon index (Magurran 2004). The accuracy of index values was estimated by jackknifing, which permitted a reduction in the bias in our estimate of the population value and provided an SE. Confidence intervals for the statistic were calculated by bootstrap with replacement. Index values for the disturbed versus untreated zone were compared by *t*-test with degrees of freedom calculated by harmonic interpolation (Southwood and Henderson 2000). Probability values derived from *t*-tests were corrected for multiple comparisons by the Benjamini and Hochberg (1995) false discovery rate adjustment, which is less conservative than the Bonferroni method and ensures fewer type II errors. The Shannon index assumes that all taxa are represented in the overall sample. To validate this, the cumulative number of species observed during the sampling procedure each year was plotted against sampling effort (the number of samples taken per zone during each 5-mo sampling period). Cumulative curves were analyzed by regression to identify statistical relationships between zones and species accumulation rates.

Physico-Chemical Measurements. The following physical-chemical parameters were measured in situ: dissolved oxygen (mg/liter), pH, and conductivity (μ S/cm), using appropriate portable meters (Hanna Instruments, Leighton Buzzard, UK), temperature (°C), current velocity (m/s), and river discharge (m³/s), calculated from current velocity, width, depth and riverbed substrate characteristics (Needham and Needham 1962). Differences between the mean physico-chemical parameters in each contrast zone in both years were determined by multivariate analysis of variance (ANOVA) multiple comparisons with Tukey's honestly significant difference (HSD) test. Meteorological data were obtained from a weather station located next to the village of El Retiro, \approx 1 km from the central dividing point between treated and untreated sections of the river.

Results

Odonate Community Diversity. In total, 965 individuals comprising 6 families, 10 genera, and 16 species of odonates were registered during sampling from both zones over the 2-yr study. The total number of individuals captured in each zone was approximately three times greater in 2002 compared with 2001

Table 1. Abundance of Odonata species associated with breeding sites of *An. pseudopunctipennis* identified during 2 yr of sampling in the River Coatán, Chiapas, Mexico

| Species | Family | 2001 | | 2002 | |
|---|-------------------|-----------|------------|-----------|------------|
| | | Untreated | Extraction | Untreated | Extraction |
| <i>Argia oenea</i> Hagen | Coenagrionidae | 20 | 25 | 79 | 88 |
| <i>Argia</i> sp. | Coenagrionidae | 0 | 0 | 0 | 1 |
| <i>Brechmorhoga praecox</i> (Hagen) | Libellulidae | 50 | 67 | 124 | 233 |
| <i>Brechmorhoga vivax</i> Calvert | Libellulidae | 6 | 0 | 3 | 0 |
| <i>Erpetogomphus elaps</i> Selys | Gomphidae | 16 | 8 | 16 | 5 |
| <i>Erpetogomphus eutainia</i> Calvert | Gomphidae | 0 | 0 | 9 | 0 |
| <i>Erpetogomphus</i> sp. | Gomphidae | 13 | 4 | 49 | 7 |
| <i>Erythemis plebeja</i> (Burmeister) | Libellulidae | 0 | 0 | 8 | 3 |
| <i>Hetaerina cruentata</i> (Rambur) | Calopterygidae | 0 | 0 | 8 | 0 |
| <i>Heteragrion tricellulare</i> Calvert | Megapodagrionidae | 0 | 1 | 0 | 1 |
| <i>Macrothemis pseudimitans</i> Calvert | Libellulidae | 2 | 2 | 1 | 2 |
| <i>Palaemnema</i> sp. | Patystictidae | 17 | 13 | 30 | 39 |
| <i>Phyllogomphoides</i> sp. | Gomphidae | 1 | 1 | 3 | 0 |
| <i>Phyllogomphoides suasus</i> (Selys) | Gomphidae | 0 | 2 | 4 | 2 |
| <i>Progomphus clendonii</i> Calvert | Gomphidae | 0 | 0 | 0 | 1 |
| <i>Progomphus</i> sp. | Gomphidae | 0 | 0 | 1 | 0 |
| Total | | 125 | 123 | 335 | 382 |

(Table 1). The most abundant species were *Brechmorhoga praecox* (Hagen), *Argia oenea* Hagen, and *Palaemnema* sp., which comprised 49.1, 22.0, and 10.3% of the total capture, respectively. Plots of cumulative species curves all showed a tendency to reach a plateau, indicating that the great majority of species of odonates present in the river were likely represented in the sampling program (Fig. 1A and B). Regression of Ln (cumulative number of species sampled) against sampling effort revealed that the rate of accumulation of species (as indicated by the slope of the regression) was statistically similar in both zones during 2001 ($F_{1,48} = 2.89$; $P = 0.096$), but differed significantly from one another in 2002 ($F_{1,48} = 5.60$; $P = 0.022$).

Sampling before algal extraction in 2001 confirmed no difference in odonate diversity in treated versus untreated contrast sites (Fig. 2A; Table 2). Extraction of filamentous algae resulted in a significant reduction in diversity in the sample taken 1 mo after the intervention, whereas the diversity of samples taken at 2–4 mo after extraction were similar to those from untreated pools.

Pretreatment sampling was not performed in 2002 (Fig. 2B; Table 2). The diversity index value was similar to that of the untreated zone at 1 mo after extraction of algae, but subsequent diversity values in treated pools remained below those of untreated pools for the following 4 mo until the experiment ended when the river volume increased and eliminated river pools at the onset of seasonal rains. Diversity values in both zones also fluctuated more widely in 2002 than 2001. However, the effect of algal extraction on odonate diversity was greater in 2002 and persisted for the 5-mo duration of the study (Fig. 2B; Table 2).

Jackknifing indicated that diversity index values were slightly underestimated in all cases (Table 3). The magnitude of the error was small: 4.7 and 7.9% for the untreated and treated zones, respectively, in 2001, compared with 6.0 and 1.4% for the same zones, respectively, in 2002.

In 2001, maximum diversity values (H_{max}) were the same in both zones in the pretreatment and were in

the range 1.10–1.79 in the untreated zone compared with 1.39–1.61 in the extraction zone at post-treatment times (Table 2). In 2002, the ranges of H_{max} values were 1.39–2.20 in the untreated zone and 1.39–1.79 in the extraction zone. Evenness values (defined as $J' = H'/H_{max}$) in the abundance of odonate species, for which absolute evenness has a value of 1.0, were consistently greater in the untreated zone with range of

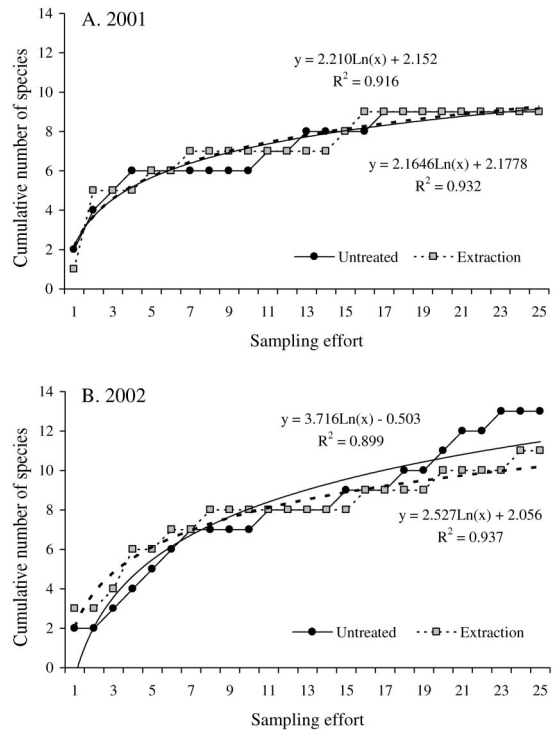


Fig. 1. Regression of Ln (cumulative number of odonate species sampled) against sampling effort (number of samples taken) in (A) 2001 and (B) 2002. Dashed and solid lines indicate regressions for treated and untreated zones, respectively.

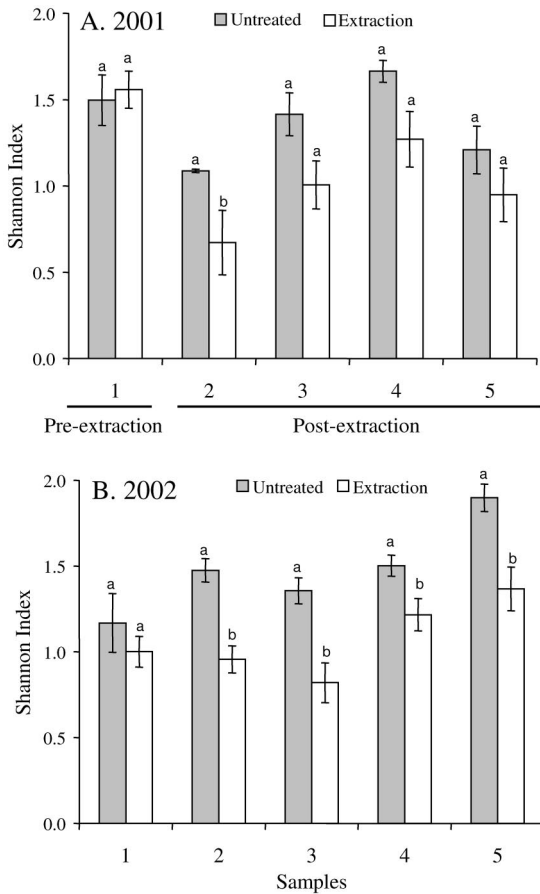


Fig. 2. Shannon index values for odonates calculated after extraction of filamentous algae from pools in the River Coatán, Mexico, in (A) 2001 and (B) 2002. Sampling was performed at monthly intervals. A pre-extraction sample was performed in 2001. Vertical bars indicate SEM. Columns headed by identical letters are not significantly different for within sample comparisons between contrast sites (details given in Table 2).

0.75–0.99 compared with the extraction zone with a range of 0.48–0.75 in 2001, except for the pretreatment sample (Table 2). This pattern was repeated in 2002 with a range of 0.70–0.93, which was higher in the untreated zone compared with 0.53–0.76 in the extraction zone.

Physico-Chemical Measurements. Water temperatures during the experimental period in 2002 were ≈ 1.5 – 2°C higher in untreated and extraction zones than during 2001 (Table 4). Dissolved oxygen levels did not differ significantly between untreated and extraction pools in 2001 but were elevated in untreated pools in 2002. The pH values in the untreated zone were significantly higher in 2001, but not in 2002. Conductivity was significantly reduced in extraction zones in both years compared with the untreated zone. Current velocity did not differ according to zone or year, but river depth, width, and discharge were all significantly greater in 2001 compared with 2002. This

was clearly related to differences in rainfall between years: mean monthly precipitation during the experimental period was 288 mm in 2001 compared with 184 mm in 2002.

Discussion

Habitat manipulation involving the extraction of filamentous algae can successfully control the malaria vector, *An. pseudopunctipennis* for periods of up to 8 wk (Bond et al. 2004). Despite the importance of algae in river ecology (Stevenson et al. 1996), this intervention resulted in minor but detectable changes in the taxa richness of the Odonata community associated with river pools. However, the abundance of odonates captured from pools in untreated and treated sections of the river was similar in both years. Shannon index values were significantly depressed after algal extraction for a period of 1 mo before returning to values similar to those of the untreated zone in 2001 and for a period exceeding 5 mo in 2002. However, differences between years (annual variation) tended to be similar in magnitude to the differences observed between zones within a particular year.

Use of the Shannon index as a diversity metric has been criticized as being oversensitive to sample size (Southwood and Henderson 2000, Magurran 2004), resulting in biased estimates (Lande 1996), yet Shannon measures are far less sensitive to sample size than species richness measures (Kempton 1979). Indeed, Shannon values are the only measures of diversity that weigh all species in proportion to their frequencies in each sample rather than favoring common or rare species as Simpson or species richness metrics do, making them the best general purpose measures of diversity (Jost 2006). The Shannon index is also the most widely applied diversity index in aquatic systems (Washington 1984).

The abundance and species richness of odonates diminishes with increasing latitude and altitude (Corbet 1999). To date, a total of 330 described species, 82 genera, and 15 families has been recorded in Mexico (González and Novelo 1996). With a total of 16 species, 10 genera, and 6 families registered over 10 mo of sampling during 2 yr, the River Coatán seems to harbor an elevated diversity of Odonata. A comparable study performed in the North of Mexico reported five genera from four families associated with *An. pseudopunctipennis* breeding sites (Delgado-Gallardo et al. 1994). This is likely because of a combination of cup-dipping sampling, which was unlikely to provide a representative sample of benthic invertebrates, and the subtropical location of the U.S. border region with correspondingly reduced diversity compared with the tropical south of Mexico where the current study was performed. Other studies performed in California and Chile have reported very few species of odonates (Rogers 1998, Figueroa et al. 2003). In contrast, Eliécer (2001), reported 15 genera and 7 families of odonates present in a 6-mo study in Panama.

Table 2. Shannon index values calculated to determine the effect of extraction of filamentous algae from breeding sites of *An. pseudopunctipennis* on the community of aquatic Odonata during 2001 and 2002

| Sample | Contrast | N | S | H' | H _{max} | J' | VarH | t _c | df | P _{adj} |
|--------|----------|-----|---|---------|------------------|---------|---------|----------------|---------|------------------|
| 2001 | | | | | | | | | | |
| 1 | U | 21 | 6 | 1.49670 | 1.79176 | 0.83532 | 0.02137 | | | |
| 1 | E | 27 | 6 | 1.55508 | 1.79176 | 0.86958 | 0.01146 | 0.339 | 40.503 | NS |
| 2 | U | 25 | 3 | 1.08757 | 1.09861 | 0.98994 | 0.00009 | | | |
| 2 | E | 26 | 4 | 0.67230 | 1.38629 | 0.48496 | 0.03502 | 2.216 | 26.134 | 0.048 |
| 3 | U | 15 | 5 | 1.41537 | 1.60944 | 0.87942 | 0.01537 | | | |
| 3 | E | 21 | 4 | 1.00639 | 1.38629 | 0.72596 | 0.01924 | 2.198 | 35.889 | NS |
| 4 | U | 32 | 6 | 1.66530 | 1.79176 | 0.92942 | 0.00401 | | | |
| 4 | E | 22 | 5 | 1.27076 | 1.60944 | 0.78957 | 0.02577 | 2.286 | 28.898 | NS |
| 5 | U | 32 | 5 | 1.20915 | 1.60944 | 0.75129 | 0.01914 | | | |
| 5 | E | 27 | 4 | 0.94881 | 1.38629 | 0.68442 | 0.02396 | 1.254 | 56.789 | NS |
| 2002 | | | | | | | | | | |
| 1 | U | 10 | 4 | 1.16828 | 1.38629 | 0.84274 | 0.02956 | | | |
| 1 | E | 101 | 6 | 1.00113 | 1.79176 | 0.55874 | 0.00802 | 1.139 | 16.045 | NS |
| 2 | U | 95 | 6 | 1.47480 | 1.79176 | 0.82310 | 0.00457 | | | |
| 2 | E | 126 | 6 | 0.95675 | 1.79176 | 0.53397 | 0.00615 | 5.004 | 220.989 | <0.001 |
| 3 | U | 113 | 7 | 1.35596 | 1.94591 | 0.69683 | 0.00576 | | | |
| 3 | E | 56 | 4 | 0.82001 | 1.38629 | 0.59151 | 0.01350 | 3.862 | 104.549 | 0.001 |
| 4 | U | 48 | 5 | 1.50188 | 1.60944 | 0.93317 | 0.00380 | | | |
| 4 | E | 53 | 5 | 1.21587 | 1.60944 | 0.75546 | 0.00877 | 2.551 | 90.184 | 0.031 |
| 5 | U | 69 | 9 | 1.89826 | 2.19722 | 0.86394 | 0.00635 | | | |
| 5 | E | 46 | 6 | 1.36710 | 1.79176 | 0.76299 | 0.01602 | 3.551 | 81.190 | 0.002 |

U, untreated zone; E, extraction zone; N, total no. of odonates in sample; S, number of species identified in sample; H', Shannon index; H_{max}, maximum diversity; J', evenness (H'/H_{max}); VarH', variance in H'; t_c, t value calculated as described in Magurran (2004); P_{adj}, probability after false discovery rate adjustment for multiple comparisons (Benjamini and Hochberg 1995); NS, not significant (α = 0.05).

In general, a greater abundance and a greater number of species of Odonata were observed in both contrast zones in 2002 compared with those sampled in the previous year. This was associated with reduced precipitation and lower river volume (width, depth, and discharge) in 2002 compared with 2001. The dry

season also ended several weeks earlier in 2001, with mean precipitation of 135 mm in March 2001 compared with 21 mm in March 2002. Elevated river discharge is likely to have been responsible for reducing odonate populations directly, by physical removal and increased drift, or indirectly, by removal of potential

Table 3. Values of total diversity of aquatic Odonata obtained by Jackknifing for untreated and algal extraction zones performed in the River Coatán, Chiapas, Mexico

| Contrasts | Number of analyzed samples | Values for H' | Pseudovalues φ | Jackknifed φ (±SE) | Confidence limits Range of 95%*1 | Error (%) | Discussion |
|------------|----------------------------|---------------|----------------|--------------------|----------------------------------|-----------|---|
| 2001 | | | | | | | |
| Untreated | All the samples | 1.68130 | | | | | |
| Untreated | (1,2,3,4) | 1.76459 | 1.34814 | | | | |
| Untreated | (1,2,3,5) | 1.59760 | 2.01610 | | | | |
| Untreated | (1,2,4,5) | 1.63369 | 1.87174 | 1.75962 ± 0.12598 | 1.40990-2.10934 | 4.65830 | Population parameter was lightly underestimated |
| Untreated | (1,3,4,5) | 1.70274 | 1.59554 | | | | |
| Untreated | (2,3,4,5) | 1.60998 | 1.96658 | | | | |
| Extraction | All the Samples | 1.39362 | | | | | |
| Extraction | (1,2,3,4) | 1.44101 | 1.20406 | | | | |
| Extraction | (1,2,3,5) | 1.38347 | 1.43422 | | | | |
| Extraction | (1,2,4,5) | 1.38871 | 1.41326 | 1.50308 ± 0.25815 | 0.78659-2.21970 | 7.85408 | Population parameter was lightly underestimated |
| Extraction | (1,3,4,5) | 1.49662 | 0.98162 | | | | |
| Extraction | (2,3,4,5) | 1.12147 | 2.48222 | | | | |
| 2002 | | | | | | | |
| Untreated | All the samples | 1.79867 | | | | | |
| Untreated | (1,2,3,4) | 1.53465 | 2.85475 | | | | |
| Untreated | (1,2,3,5) | 1.81668 | 1.72663 | | | | |
| Untreated | (1,2,4,5) | 1.85641 | 1.56771 | 1.90736 ± 0.24127 | 1.23759-2.57712 | 6.04269 | Population parameter was lightly underestimated |
| Untreated | (1,3,4,5) | 1.85420 | 1.57655 | | | | |
| Untreated | (2,3,4,5) | 1.79555 | 1.81115 | | | | |
| Extraction | All the samples | 1.14251 | | | | | |
| Extraction | (1,2,3,4) | 1.05668 | 1.48583 | | | | |
| Extraction | (1,2,3,5) | 1.08243 | 1.38283 | | | | |
| Extraction | (1,2,4,5) | 1.18211 | 0.98411 | 1.15809 ± 0.12035 | 0.82310-1.49218 | 1.36401 | Population parameter was lightly underestimated |
| Extraction | (1,3,4,5) | 1.21647 | 0.84667 | | | | |
| Extraction | (2,3,4,5) | 1.15538 | 1.09103 | | | | |

*: t_{0.05(n-1)} SEφ = (2.776) (SE); ¹confidence intervals were calculated by Bootstrap.

Table 4. Mean \pm SD physico-chemical parameter values recorded in untreated and extraction zones of River Coatán, Chiapas, Mexico, during 2001 and 2002

| Contrast zones | Temperature (°C) | Dissolved O ₂ (mg/liter) | pH | Conductivity (μ S/cm) | Current velocity (m/s) | Depth (m) | Width (m) | Discharge (m ³ /s) |
|----------------|------------------|-------------------------------------|------------------|----------------------------|------------------------|------------------|------------------|-------------------------------|
| 2001 | | | | | | | | |
| Untreated | 25.2 \pm 1.4a | 6.97 \pm 1.01a | 8.96 \pm 1.48a | 65.5 \pm 12.1a | 0.19 \pm 0.02a | 0.26 \pm 0.06a | 5.96 \pm 1.33a | 0.28 \pm 0.12a |
| Extraction | 25.2 \pm 1.3a | 6.13 \pm 0.75a | 7.57 \pm 1.39b | 50.1 \pm 14.0b | 0.20 \pm 0.02a | 0.26 \pm 0.06a | 6.24 \pm 1.51a | 0.31 \pm 0.15a |
| 2002 | | | | | | | | |
| Untreated | 27.3 \pm 1.7b | 8.25 \pm 1.99b | 7.51 \pm 0.94b | 60.4 \pm 10.0a | 0.19 \pm 0.03a | 0.21 \pm 0.04b | 4.67 \pm 0.73b | 0.16 \pm 0.05b |
| Extraction | 26.8 \pm 1.4b | 5.86 \pm 2.33a | 6.74 \pm 1.24b | 49.5 \pm 11.1b | 0.20 \pm 0.04a | 0.20 \pm 0.03b | 4.27 \pm 0.76b | 0.15 \pm 0.04b |

All means based on five observations at each of four sample dates in 2001 (pretreatment measurements excluded) and five sample dates in 2002. Values followed by the same letters are not significantly different for comparisons within columns (Tukey HSD, $P > 0.05$). Table from Bond (2005).

prey items (Brittain and Eikeland 1988). Current velocity or river discharge exercise a major influence on benthic invertebrates and can be the principal factor determining population densities and community diversity (Resh et al. 1998, Thompson et al. 2002, Bond and Downes 2003). Both flow variation and the removal of algae may have resulted in additional indirect effects on odonates and their predators, including birds and fish. Such effects include the removal of physical refuges or changes in odonate oviposition responses to treated river pools. Alternatively, increased drift in response to flow rate can mask the effects of predation by redistributing predators and prey (Thompson et al. 2002).

The importance of filamentous algae resides in their ability to act as refuges against predators (Sih 1986, Orr and Resh 1989), reduce current velocity (Hall 1972), provide direct and indirect food sources by harboring an important epiphytic microbial community (Wetzel and Søndergaard 1998, Stanley et al. 2003), and increase the physical heterogeneity of the habitat (Cardinale et al. 2002). Filamentous algae may also provide chemical and visual cues to ovipositing mosquitoes (Orr and Resh 1992, Rejmankova et al. 1996), and their physical characteristics can positively influence macroinvertebrate community diversity, particularly for the Chironomidae, and species of Trichoptera and Plecoptera (Downes et al. 2000).

Plots of cumulative number of species against sampling effort indicated that sampling provided a representative sample of odonates in the River Coatán. Interestingly, the curves could be closely fitted to regression models with statistically similar slopes, indicating that the rate of detection of previously unsampled species was the same in both zones, but differed significantly between years.

Jackknife estimates indicated that Shannon index values were very slightly underestimated (1.3–7.85%). All mean index values fell well inside the corresponding 95% confidence intervals determined by bootstrap. These estimates represent a substantial improvement in accuracy compared with the previous study on the diversity of *An. pseudopunctipennis* breeding sites, based on the Simpson diversity index, in which jackknife procedures indicated a 31% error in the calculated values (Delgado-Gallardo et al. 1994). Estimates of evenness in genera abundance were

greater in the untreated zone compared with the extraction zone in both years of the study, indicating that the estimated diversity in that zone was closer to the expected maximum diversity values of the community. We assume this to be a direct consequence of the intervention; removal of algae resulted in diminished species richness in the treated pools.

We conclude that extraction of filamentous algae from *An. pseudopunctipennis* breeding pools results in a measurable reduction in the diversity of the odonates community in river pools. Recovery was achieved over a period of \sim 2 mo in 2001 and $>$ 5 mo in 2002. However, fluctuations in diversity arising from year-to-year variation in river volume were equal or greater than those arising from habitat manipulation for mosquito control.

Acknowledgments

We thank J. S. Aguilar, J. Covarrubias, J. L. Espinosa, and E. Pérez for assistance with field studies and J. Valle for statistical support. The study was supported by SIBEJ 20000502025. Voucher specimens have been deposited in the entomological collection of ECOSUR, Tapachula, Mexico.

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Received for publication 21 May 2006; accepted 9 September 2006.
