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Large branchiopod assemblages common to Mexico and the United States

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Abstract

We present observations on the frequency of large branchiopod associations found in north-central Mexico, and in Arizona, USA. Of a total of 25 species involved in these assemblages, 12 were common in both areas. Fifty-eight (43.3%) of the ponds in Mexico, and seventy-eight (47%) of those in Arizona had two or more species present. The combinations of species which occurred with highest frequency were *Streptocephalus mackini* with *Thamnocephalus platyurus* for Arizona, and *T. platyurus, Triops* sp., and *Leptestheria compleximanus* for Mexico. In Mexico, and Arizona, as in many parts of the world, multispecies assemblages of large branchiopods are a common phenomenon. Therefore, the 'common rule' of 'one-phyllopod-per-habitat' advanced by Weise (1964) is inconsistent with field observations. Furthermore, since cases of co-occurrence of two or more congeneric species of Anostraca and Notostraca are not uncommon, generalizations about congeners not coexisting remain applicable only for the Spinicaudata and Laevicaudata. On the basis of the literature, and of observations in the field and in the laboratory, we list potential factors contributing to the co-occurrence of several species within a pond.

Introduction

Most large branchiopod species live in ephemeral ponds. During the wet phase of a pond, only a single species of large branchiopod may be present, different species may occur in neighbouring ponds, or individuals of several species may co-occur in the same pond. When multiple species co-occur in the same pool they may or may not co-exist temporally.

Packard (1877) reported some time ago that *Streptocephalus texanus* Packard, *Thamnocephalus platyurus* Packard, *Triops* sp., *Leptestheria compleximanus* (Packard), *Cyzicus mexicanus* (Claus), and *Lynceus brevifrons* (Packard) were collected from the same ponds. This assemblage of six species includes representatives of all four large branchiopod orders (Fryer, 1987), i.e. two Anostraca, one Notostraca, two Spinicaudata, and one Laevicaudata. Pennak (1953, 1978, 1989), in his influential book *Freshwater Invertebrates of the United States* wrote concerning the large banchiopods: 'With few exceptions, a pond never contains more than one species of a particular genus at a time'. However, several authors seem to have misinterpreted Pennak, and missed some of the relevant literature. Thus, Weise (1964) notes that the co-occurrence of two or more species had reported, but suggested these are only exceptions to what he called the common rule of 'one-phyllopod-per-habitat'. Weise (1964) claimed that no record of more than three species was known, and maintained that his report of four species from a road-side pond in Kansas was the first, when in fact, the species he reported (two anostracans, one notostracan and one conchostracan) were four of the six already recorded together by Packard (1877). Like Weise, Huggins (1976) mistakenly wrote: 'although the sympatric occurrence of some species of Anostraca has been noted by other authors, no references could be located noting the sympatric occurrence of species of Anostraca and Notostraca'. However, the three species (two anostracans, and one notostracan) he reported from Kansas also included species from the assemblage recorded by Packard (1877). More recently, Debrey et al. (1991) reported the sympatric occurrence of one anostracan, one notostracan and one conchostracan in a pond from Wyoming. They also claimed that their's was the first record of sympatry of these three orders. They also erroneously stated that their's were the first records of *Leptestheria compleximanus* and *Streptocephalus dorothae* Mackin from the state. As pointed out by Graham (1995) in a discussion of the many errors in their paper, Horne (1967) reported the former and Belk (1983) the latter.

An old explanation for what was thought to be the infrequent co-occurrence of several large branchiopod species in a pond was given by Gissler (1883) who advanced the hypothesis, 'It is very likely that the secretion of the antennal gland is antagonistic to other species'. Moore (1963) called Gissler's idea the 'species-incompatibility theory'. However, after experimentation, Moore (1963) rejected this theory as an explanation of why *Eubranchipus moorei* Brtek (misindentified by him as *Eubranchipus holmanii* (Ryder)) were not active at the same time as *Streptocephalus sealii* Ryder in pools know to support both species, but in different seasons.

Since Packard (1877), many reports of species co-occurrence from most continents have been published. Several studies have even reported recurrent groupings of large branchiopod species, either in space (i.e. the same assemblage in two or more ponds in a certain area) or through time during separate wet phases in a specific pond. Spatial recurrences of the same assemblages have been reported by Gauthier (1933) (Algeria), Prophet (1963b) (Oklahoma and Kansas, USA), Sublette & Sublette (1967) (New Mexico), Dimentman (1981) (Israel), Geddes (1983) (Australia), Alonso (1985) (Spain), Hammer & Appleton (1991a) (Natal, South Africa), Thiéry (1991) (western Morocco), Lepiney (1961) (North Africa), King et al. (1996) (California USA) and Petrov and Cetkovic (this volume) (Yugoslavia), Vekhoff (this volume) (Russia). Temporal recurrence of specific assemblages were reported by Nourisson & Aguesse (1961) (France), Daborn (1977) (Alberta, Canada), Donald (1983) (Alberta, Canada), and MacKay et al. (1990) (New Mexico, USA).

In this work, we report observations on the frequency of large branchiopod associations found in two areas of North America, the northern central part of Mexico, and the state of Arizona, USA (Figure 1). Also, on the basis of literature, and observations in the field and the laboratory, we list a series of general factors which may contribute to the co-occurrence of large branchiopod species.

Material and methods

Material from Mexico was collected (from 1981 to 1989), identified by A.M. Maeda-Martínez, and deposited at the Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León (UANL), and at the Escuela Superior de Biología, Universidad Juárez del Estado de Durango (Maeda-Martínez, 1987, 1991). Additional species records were obtained from Belk (1973), Moore (1958, 1966), Moore & Young (1964) and Strenth & Littleton (1990), and from the crustacean collection of the Facultad de Ciencias Biológicas, UANL, and Denton Belk's private collection. Material from Arizona was collected (from 1963 to 1974) and identified by D. Belk (Belk, 1974, 1977, 1992), and deposited in his collection. Additional species records came from collections at the University of Arizona. Figure 1 shows the main collection areas in Mexico and Arizona.

Data were treated according to the following conditions: (1) Some localities consisted of a group of ponds, but every pond was considered separately from the others; and (2) some collections were taken from the same pond but at different dates, only the collection with the highest number of species was included in the analysis.

A total of 134 ponds in Mexico, and 166 ponds in Arizona were sampled. The list of species, and the list of abbreviations of species names used throughout the text are shown in Table 1. *Branchinecta* sp. A (Otero fairy shrimp) and *Branchinecta* sp. B (Kaibab fairy shrimp) are undescribed species. In the case of *Triops* populations, we use *Triops* sp. because there is a taxonomic problem with the determination of the North American species (Sassaman, 1991; Sassaman et al., 1997).

For each taxon the total number of occurrances and the number of co-occurrances was determined (Table 1). Details of large branchiopods assemblages, locations, and dates from Mexico, and Arizona are presented in Appendices 1 and 2. A matrix of co-occurrences for each area was made, and Fager's index of affinity (Southwood, 1966) was calculated (Tables 2 and 3). This index is defined by:

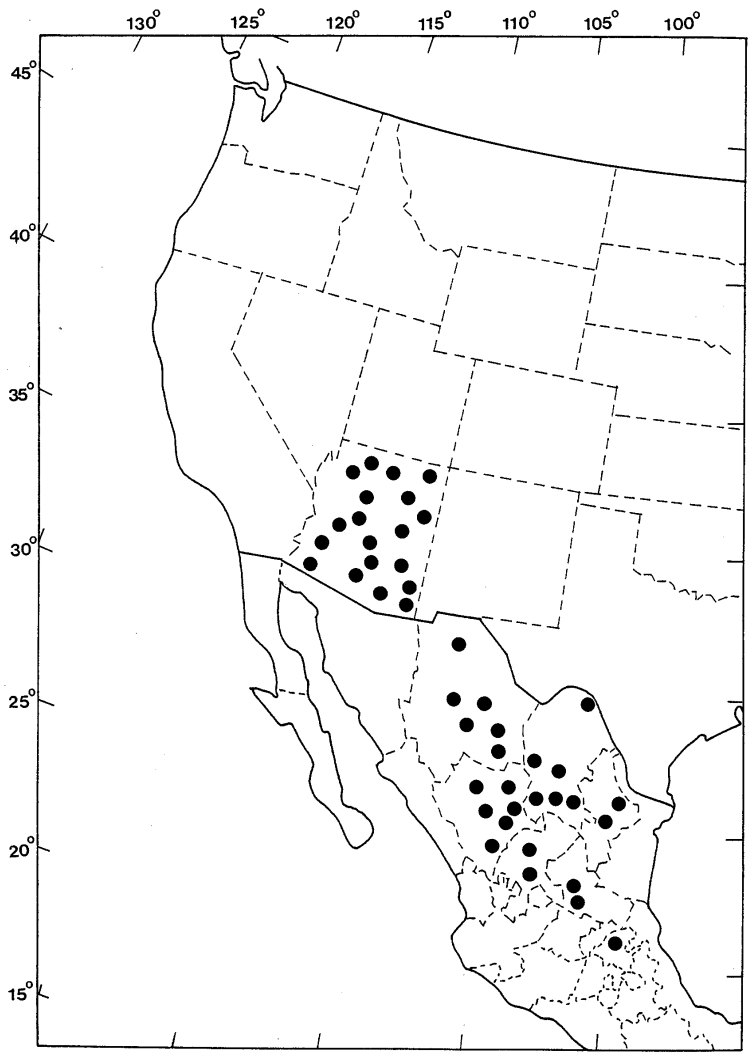

Figure 1. Main collection areas in Mexico and Arizona, USA.

$$I_{AB} = \frac{2J}{n_A + n_B}$$

where J = number of joint occurrences, n_A = total number of occurrences of species A, and n_B = total number of occurrences of species B. This index provides a measure of the frequency with which species occur together (Southwood, 1966). The most frequent large branchiopod combinations, along with additional records obtained from assemblages reported from California, Colorado, Kansas, New Mexico, Oklahoma, Texas, Utah, and Woming are listed in Table 4. The ordinal composition of the assemblages (Appendices 1 and 2) was used to determine the 'ordinal structure' of the assemblages (Table 5).

Results

Of a total of 25 large branchiopod species involved, 19 occurred in Mexico, 18 in Arizona, and 12 were common to both areas (Table 1). From 134 ponds in Mexico, 76 (56.7%) were scored with one species, and 58 (43.3%) with two or more species (Appendix 1), including 26 (19.4%) with two, 10 (7.4%) with three, five (3.6%) with four, nine (6.7%) with five, five (3.6%) with six, two (1.4%) with seven, and one (0.7%) with eight species. From 166 ponds in Arizona, 88 (53.0%) were recorded with one species, and 78 (47%) with two or more species (Appendix 2), including 49 (29.5%)

with two, 18 (10.8%) with three, eight (4.8%) with four, one (0.6%) with five, and two (1.2%) with six.

Eubranchipus bundyi Forbes, *Branchinecta lindahli* Packard, *B.* sp. B, *Streptocephalus sealii*, and *S. similis* Baird only sporadically co-occurred with other species (co-occurrence $< 30\%$). *Branchinecta belki* Maeda-Martínez, Obregón-Barboza and Dumont, *B.* sp. A, *Streptocephalus linderi* Moore, and *Lynceus brachyurus* Müller often co-occurred with other species (co-occurrence 30–60%). *Branchinecta packardi* Pearse, *Streptocephalus dorothae, S. mackini* Moore, *S. texanus, Caenestheriella setosa* (Pearse), *Eocyzicus digueti* (Richard), *Eulimnadia cylindrova* Belk, and *E. texana* (Packard) very often co-occurred with other large branchiopod species (co-occurrence 60–90%). The large branchiopods which normally co-occurred with other large branchiopods (co-occurrence $> 90\%$) are the widely distributed *Thamnocephalus mexicanus* Linder, *T. platyurus*, *Triops* sp., *Leptestheria compleximanus*, *Lynceus brevifrons*, and the Mexican endemics *Streptocephalus moorei* Belk, *S. guzmani* Maeda-Martínez, Belk, Obregón-Barboza and Dumont, and *Paralimnetis mapimi* Maeda-Martínez (Table 1).

The pairs of species which showed the highest affinity index (0.40 or more) were: *Branchinecta belki-B.* sp. A, *Streptocephalus mackini-Thamnocephalus platyurus*, *T. platyurus-Triops* sp., *T. platyurus-Leptestheria compleximanus*, *Triops* sp.-*L. compleximanus*, and *L. compleximanus-Lynceus brevifrons* (Tables 2 and 3). Looking at those species which occur in the study area and including literature records from other states in USA, the most frequent large branchiopod combinations are *S. mackini–T. platyurus*, *T. platyurus–Triops* sp., *S. mackini-Triops* sp., *Triops* sp.-*L. compleximanus*, and *S. texanus-Triops* sp., with 52, 43, 38, 29, and 24 records, respectively (Table 4). The most frequent three species-combinations are *S. mackini-T. platyurus-Triops* sp., and *T. platyurus-Triops* sp.-*L. compleximanus*, with 19, and 18 records, respectively (Table 4).

As to the structure of the assemblages, anostracans were the dominant taxon. In 90% of the two-species assemblages, one was an anostracan, and in the cases of assemblages of three or more species, anostracans were always present (Table 5).

We found the co-occurrence of the following congeneric species: (1) two *Branchinecta* species in three ponds in México, (2) two *Streptocephalus* species in five ponds in México, and in three ponds in Arizona, (3) three *Streptocephalus* species in one pond in Coahuila, and (4) *Thamnocephalus mexicanus* and *T. platyurus* co-occurred in five ponds in México, and in two ponds in Arizona (Appendices 1 and 2).

Discussion

In Mexico and Arizona, as in many parts of the world, multispecies assemblages of large branchiopods are a frequent phenomenon. Therefore, the eronerous idea of 'one-phyllopod-per-habitat' (Weise, 1964) must be abandoned. Furthermore, the old 'species-incompatibility theory' of Gissler (sensu Moore, 1963), appears inconsistent with field observations and should also be abandoned.

We found eight large branchiopods species which normally co-occurred with other large branchiopods species (co-occurrence $> 90\%$). The fairy shrimp *Thamnocephalus platyurus* was always found co-occurring with other large branchiopod species in the 70 ponds from which it was collected. Similarly, Prophet (1963b) observed that all pools inhabitated by *T. platyurus* also contained *S. texanus*, but that the reverse was not the case.

Recurrent assemblages can be found across very large areas. For example, the grouping of *Thamnocephalus platyurus-Triops* sp.-*Leptestheria compleximanus* occurs over a distance of about 3,000 km from Wyoming, USA to San Luis Potosí, Mexico (Figure 2). The most frequent large branchiopod combinations found in this study, included species assemblages of the genera *Streptocephalus*, *Triops*, and *Leptestheria*. In Africa, Gauthier (1933), Hamer & Appleton (1991a), and Thiéry (1991) also found assemblages including the same genera.

Many cases of co-occurrence of two or more congeneric species of Anostraca are known. These records include species of *Branchinella* (Geddes, 1983), *Branchinecta* (Broch, 1988; Cohen, 1981, 1983; Daborn, 1975a,b, 1977; Donald, 1983; Fugate, 1993; Lynch, 1958, 1960, 1964; Maynard & Romney, 1975; Simovich & Fugate, 1992), *Chirocephalus* (Brtek, 1976; Hartland-Rowe, 1967; Mura, 1985; Petrov & Cetkovic, 1997), *Eubranchipus* (Dexter, 1953, 1956; Donald, 1983), *Streptocephalus* (Belk, 1973, 1977; Dexter, 1953, Hamer & Appleton, 1991a; Mackin, 1942; Mertens & Dumont, 1989; Moore, 1958, 1966; Sublette & Sublette, 1967), *Tanymastigites* (Thiéry, 1991), and *Thamnocephalus* (Moore, 1966, Moore & Young, 1964). In our study, we found the co-occurrence of congeneric species of *Branchinecta*,

Table 1. Large branchiopods involved in assemblages found in Mexico and Arizona, USA, with the abbreviations used. N = total number of ponds in which the species occurred; n = number of ponds in which the species co-occurred with another species

Taxa	Abbreviation	Mexico			Arizona		
		Total	Co-occur		Total	Co-occur	
		N	n	%	N	n	%
ANOSTRACA							
Eubranchipus							
bundyi	Eb	–	–	–	18	3	16
Branchinecta							
belki	Bb	4	2	50	–	–	
lindahli	Bl	–	–	–	31	9	29
packardi	Bp	12	9	75	4	4	100
sp. A	Bsa	5	3	60	–	–	–
sp. B	Bsb	–	–	–	7	1	14
Streptocephalus							
dorothae	Sd	–	–	–	31	22	70
guzmani	Sg	4	4	100	–	–	–
linderi	Sl	5	3	60	–	–	–
mackini	Sm	92	40	43	56	40	71
moorei	Smo	1	1	100	–	–	–
sealii	Sse	–	–	–	7	2	28
similis	Ssi	10	3	30	–	–	–
texanus	St	18	18	100	4	1	25
Thamnocephalus							
mexicanus	Tm	8	6	75	4	4	100
platyurus	Tp	26	26	100	44	44	100
NOTOSTRACA							
Triops							
sp.	Ts	34	30	88	40	38	95
SPINICAUDATA							
Caenestheriella							
setosa	Cs	11	11	100	4	3	75
Eocyzicus							
digueti	Ed	5	5	100	4	3	75
Leptestheria							
compleximanus	Lc	17	17	100	15	14	93
Eulimnadia							
cylindrova	Ec	4	2	50	1	1	100
texana	Et	13	9	69	12	8	66
LAEVICAUDATA							
Lynceus							
brachyurus	Lba	–	–	–	6	3	50
brevifrons	Lbe	8	7	87	1	1	100
Paralimnetis							
mapimi	Pm	2	2	100	–	–	–

Streptocephalus, and *Thamnocephalus*. Furthermore, Thiéry (1991) reports *Triops cancriformis mauritanicus* Ghigi and *T. granarius* (Lucas) as co-occurring in four localities in Morocco, and Sassaman et al. (1997) report the co-occurrence of two species of *Triops* in Arizona and in Kansas USA.

Table 2. Matrix of co-occurrences from 134 ponds in Mexico. For abbreviations of species names, see Table 1. Lower part shows the number of records in which the species co-occurred. Upper part shows the Fager's affinity index ($\times 100$)

	Bb	Bp	Bsa	Sg	Sl	Sm	Smo	Ssi	St	Tm	Tp	Ts	Cs	Ed	Lc	Ec	Et	Lbe	Pm
Bb		–	40	–	–	2	–	–	20	–	–	6	–	–	11	–	–	–	–
Bp	0		27	13	–	12	–	–	27	–	17	26	17	–	–	13	–	–	–
Bsa	1	2		29	–	4	–	–	10	–	15	11	–	–	–	29	–	–	–
Sg	0	1	1		–	8	–	–	9	17	29	16	–	22	19	25	–	–	–
Sl	0	0	0	0		–	–	13	–	15	14	–	13	–	–	–	–	–	–
Sm	1	6	2	4	0		2	–	16	2	34	37	17	8	26	4	13	12	2
Smo	0	0	0	0	0	1		–	–	–	8	6	–	33	11	–	–	–	–
Ssi	0	0	0	0	1	0	0		14	11	12	–	–	–	–	–	–	–	–
St	2	4	1	1	0	9	0	2		15	29	35	21	17	29	–	13	–	20
Tm	0	0	0	1	1	1	0	1	2		31	10	–	31	8	–	19	–	20
Tp	0	3	2	4	2	20	1	2	6	5		55	17	34	54	14	22	19	15
Ts	1	6	2	3	0	23	1	0	9	2	16		27	15	51	5	30	19	11
Cs	0	2	0	0	1	9	0	0	3	0	3	6		13	29	–	17	32	–
Ed	0	0	0	1	0	4	1	0	2	2	5	3	1		36	22	11	–	29
Lc	1	0	0	2	0	14	1	0	5	1	11	13	4	4		10	13	40	21
Ec	0	1	1	1	0	2	0	0	0	0	2	1	0	1	1		–	–	–
Et	0	0	0	0	0	7	0	0	2	2	4	7	2	1	2	0		–	27
Lbe	0	0	0	0	0	6	0	0	0	0	3	4	3	0	5	0	0		–
Pm	0	0	0	0	0	1	0	0	2	1	2	2	0	1	2	0	2	0	

Table 3. Matrix of co-occurrences from 166 ponds in Arizona, USA. For abbreviations of species names, see Table 1. Lower part shows the number of records in which the species co-occurred. Upper part shows the Fager's affinity index ($\times 100$)

	Eb	Bsb	B1	Bp	Sd	Sm	Sse	St	Tm	Tp	Ts	Cs	Ed	Lc	Ec	Et	Lba	Lbe
Eb		–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	25	–
Bsb	0		–	–	–	–	14	–	–	–	–	–	–	–	–	–	–	–
Bl	0	0		–	–	9	–	–	–	8	17	–	–	13	–	9	–	–
Bp	0	0	0		6	–	–	25	–	4	18	–	25	32	–	–	–	–
Sd	0	0	0	1		9	–	–	6	32	37	17	11	9	6	–	–	–
Sm	0	0	4	0	4		–	–	10	64	29	–	–	23	–	15	–	–
Sse	1	1	0	0	0	0		–	–	–	–	–	–	–	–	–	15	–
St	0	0	0	1	0	0	0		–	–	9	–	–	11	–	–	–	–
Tm	0	0	0	0	1	3	0	0		4	–	–	–	11	–	13	–	–
Tp	0	0	3	1	12	32	0	0	1		40	–	4	24	–	21	–	–
Ts	0	0	6	4	13	14	0	1	0	17		9	9	25	5	12	–	5
Cs	0	0	0	0	3	0	0	0	0	0	2		–	–	–	–	–	–
Ed	0	0	0	1	2	0	0	0	0	1	2	0		11	–	–	–	–
Lc	0	0	3	3	2	8	0	1	1	7	7	0	1		–	22	–	–
Ec	0	0	0	0	1	0	0	0	0	0	1	0	0	0		–	–	–
Et	0	0	2	0	0	5	0	0	1	6	3	0	0	3	0		–	–
Lba	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0		–
Lbe	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	

Thus, Pennak's (1953, 1978, 1989) statement that ponds rarely contain congeners appears to be applicable for now only to the Spinicaudata and Laevicaudata.

Our results are based on the simultaneous occurrence of several large branchiopod species at one time. Thus, the frequency of associations reported here are likely underestimated in terms of pool basins contain-

Table 4. Records of the most frequent large branchiopod combinations from assemblages found in Mexico and Arizona, with additional literature records from California (CA) (Eng et al., 1990; Simovich & Fugate, 1992), Colorado (CO) (Pearse, 1912), Kansas (KS) (Creaser, 1930; Huggins, 1976; Packard, 1877), New Mexico (NM) (Dexter, 1953; Sublette & Sublette, 1967), Oklahoma (OK) (Creaser, 1930; Moore, 1965), Texas (TX) (Horne, 1971; Moore, 1965; MacKay et al., 1990), Utah (UT) (Creaser, 1930), and Wyoming (WY) (Horne, 1967; Lynch, 1964). For abbreviations of species names see Table 1

Species combination	Mexico	Arizona	Literature records	Total
Sd–Tp	–	12	NM (2)	14
Sd–Ts	–	13	NM (2)	15
Sm–St	9	–	TX (1)	10
Sm–Tp	20	32	–	52
Sm–Ts	23	15	–	38
Sm–Cs	9	–	–	9
Sm–Lc	14	7	–	21
Sm–Et	9	5	–	14
St–Tp	6	–	CA (2), CO (1), KS (4), NM (3), OK (1), TX (2), WY (2)	21
St–Ts	9	1	KS (3), NM (2), TX (6), UT (1), WY (2)	24
St–Lc	5	1	KS (4), NM (2), TX (2), UT (1), WY (1)	16
Tp–Ts	16	17	CA (1), KS (3), NM (2), TX (2), WY (2)	43
Tp–Ed	5	1	–	6
Tp–Lc	11	7	KS (1), NM (2), WY (2)	23
Ts–Cs	6	2	NM (2), TX (5), WY (1)	16
Ts–Lc	13	7	KS (2), NM (2), OK (1), TX (2), WY (2)	29
Ts–Et	7	3	OK (1), TX (1)	12
Lc–Lbe	5	–	NM (2), TX (2)	9
Sd–Tp–Ts	–	6	NM (2)	8
Sm–St–Tp	5	–	–	5
Sm–St–Ts	5	–	–	5
Sm–Tp–Ts	8	11	–	19
Sm–Tp–Lc	8	5	–	13
Sm–Tp–Et	1	3	–	4
St–Tp–Ts	4	–	KS (3), NM (2), TX (2), WY (2)	13
Tp–Ts–Ed	3	1	–	4
Tp–Ts–Lc	10	3	KS (1), NM (2), WY (2)	18
Tp–Ts–Et	3	2	–	5
Tc–Cs–Lc	4	–	NM (1), TX (2), WY (1)	8
Bl–Sm–Tp–Ts	–	2	–	2
Sd–Sm–Tp–Ts	–	2	–	2
Sm–St–Tp–Ts	4	–	–	4
Sm–St–Tp–Lc	2	–	–	2
Sm–Tp–Ts–Lc	8	2	–	10
Sm–Tp–Ts–Lbe	3	–	–	3
Sm–Ts–Cs–Et	2	–	–	2
St–Tp–Ts–Lc	2	–	KS (1), NM (2), WY (2)	7

Table 4. (continued)

Species combination	Mexico	Arizona	Literature records	Total
Tp–Ts–Ed–Lc	2	1	–	3
Tp–Ts–Cs–Lc	3	–	NM (2), WY (1)	6
Tp–Ts–Lc–Et	1	1	–	2
Tp–Ts–Lc–Lb	3	–	KS (1), NM (2)	6
Sm–St–Tp–Ts–Lc	2	–	–	2
Sm–Tp–Ts–Cs–Lc	2	–	–	2
Sm–Tp–Ts–Cs–Lbe	2	–	–	2
Sm–Tp–Ts–Lc–Lbe	3	–	–	3
Tp–Ts–Cs–Lc–Lbe	2	–	–	2
Sm–Tp–Ts–Cs–Lc–Lb	2	–	–	2

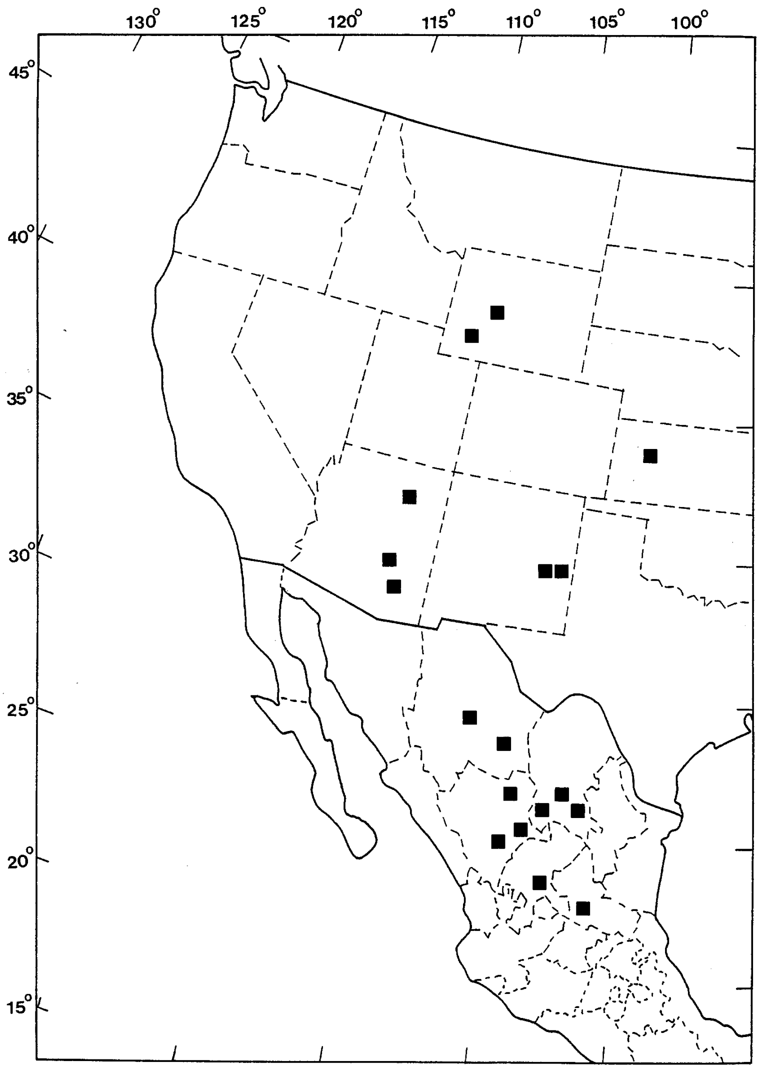

Figure 2. Approximate location of large branchiopod assemblage records for the three-species combination *Thamnocephalus platyurus-Triops* sp.-*Leptestheria compleximanus*.

Table 5. 'Taxonomic Structure' of the assemblages and their percentages recorded from 58 ponds in México and 78 ponds in Arizona. A = anostracans, N = notostacans, C = conchostracans, and n = number of records of assemblages with the indicated structure

Species number	Structure			Mexico		Arizona	
	A	N	C	n	%	n	%
2	2	–	–	8	30.7	24	48.9
	1	1	–	8	30.7	12	24.4
	1	–	1	9	34.6	8	16.3
	–	1	1	–	–	5	10.2
	–	–	2	1	3.8	–	–
				26	100	49	100
3	3	–	–	6	60	1	5.5
	2	1	–	1	10	8	44.4
	2	–	1	1	10	5	27.7
	1	1	1	2	20	4	22.2
				10	100	18	100
4	3	1	–	1	20	3	37.5
	3	–	1	–	–	1	12.5
	2	1	1	4	80	3	37.5
	2	–	2	–	–	1	12.5
				5	100	8	100
5	4	1	–	2	22.2	–	–
	4	–	1	1	11.1	–	–
	3	1	1	2	22.2	–	–
	3	–	2	–	–	1	100
	2	1	2	2	22.2	–	–
	2	–	3	1	11.1	–	–
	1	1	3	1	11.1	–	–
				9	100	1	100
6	4	1	1	1	20	–	–
	3	1	2	2	40	2	100
	2	1	3	2	40	–	–
				5	100	2	100
7	5	1	1	1	50	–	–
	3	1	3	1	50	–	–
				2	100	–	–
8	3	1	4	1	100	–	–

ing multiple species since several species do not always co-exist temporally. For example, Sublette & Sublette (1967) demonstrated large branchiopod species succession in the weekly phenology of fauna from playas in New Mexico and Texas, USA, and Hathaway and Simovich (1996) implicated differential developmental rate in the offset appearance of co-occurring anostracans in California, USA.

It has also been demonstrated that zooplankton species may show a non-random pattern of association (Dodson, 1979, 1987; King et al., 1996). Dodson (1987) found a significant positive association among *Triops*, conchostracans, and anostracans. The association of *Branchinecta mackini* Dexter and its predator *Branchinecta gigas* Lynch is well known (Daborn, 1975b, 1977). However, Dodson (1979) maintains that 'Distinct associations are the result of a constellation of the proper chemical, physical, and biological factors and, for that reason, distinct associations are expected to be uncommon'. Dodson (1979) also concluded that in any geographic area, the zooplankton distribution pattern is likely to be, to some degree, also a reflection of the distribution pattern of chemical and physical factors. Jefries (1988) suggested that even when important correlations between biotic and abiotic factors have been defined (e.g. Friday, 1987; Fryer, 1985; Jefries, 1988), species composition may vary widely and often unpredictably between ponds of the same area, probably due to Talling's 'element of chance' which states that not every species will necessarily have colonized all available habitats.

Friday (1987) grouped the possible factors which influence the diversity and composition of pond communities into: (1) biogeographical: (a) pond age, (b) isolation, and (c) pond area; and (2) habitat characteristics: (a) habitat diversity, (b) competition and predation, and (c) water chemistry. Ebert & Balko (1987) indicated that species richness of different groups of taxa responded differently to the characteristics of pool area, and the frequence of drying in temporary pools in California. Crustacean and rotifer species richness were more highly correlated with the number of times a pool dried than with pool area (Ebert & Balko, 1987). King et al. (1996) reported that differences in crustacean assemblages among pools in northern California corresponded with physical and chemical factors of the habitat such as depth, solute concentrations, elevation and biogeographic region, and with existing geologic/floristic-based habitat descriptions. They also pointed out that other factors such as historical factors (past colonization, vicariance, or other chance events), and ecological interactions (competition, predation) may be influential in determining species assemblages.

A wide range of explanatory factors of the distribution and co-occurrence of large branchiopods have been given, including climate (Gauthier, 1933; Rzóska, 1961), hatching temperature (Moore, 1963; Belk,

Table 6. Factors potentially contributing to the co-occurrence of several species of anostracans, notostracans, or conchostracans in a single temporary pond

Habitat factors	
1.	Pond refills during different seasons.
2.	Chemical characteristics of water, e.g., salinity, pH, oxygen concentration, alkalinity, etc.
3.	Physical characteristics of the water body.
	3.1 Temperature.
	3.2 Pond size. Physical structures and length of wet phase.
	3.3 Inert suspended particles, e.g. clay.
4.	Pond richness in food resources.
5.	Interspecies interactions, e.g., competition, predation, dispersal agents, etc.
6.	Pond in favorable location for receiving cysts (= resting eggs) from diverse or distant areas.
7.	Pond in an ecotone joining regions containing different allopatric species.
Species factors	
1.	Differences in feeding strategies.
2.	Differences in growth rates, maturation size, and reproductive strategies.
3.	Differences or affinities in hatching responses.
4.	Differences or affinities in preferences or tolerances (ecological amplitude) to the physical and chemical environmental conditions, in both wet and dry phases.
5.	Differences in behavior.
Historic factors	
1.	Presence of relict species.
2.	Merger of the ranges of once allopatric species resulting from geologic and climatic processes.
3.	Merger of the ranges of once allopatric species resulting from dispersal agents.
4.	Merger of the ranges of once allopatric species resulting from anthropogenic environmental modification.

1977; Hathaway & Simovich, 1996), hatching pattern (Simovich & Hathaway, 1997), physical and chemical water conditions (temperature, dissolved oxygen, salinity, ion concentrations) (Prophet, 1963a, 1963b; Horne, 1967; Anderson, 1971; Simovich & Fugate, 1992; King et al., 1996, Simovich, in press), physical forces and subsequent biotic responses (MacKay et al., 1990), food availability (Daborn, 1978), different ionoregulatory capabilities and osmoregulation (Broch, 1969; Gonzalez et al., 1996), growth and maturation rate (Belk, 1991; Hathaway & Simovich, 1996), thermal tolerance (Belk, 1992) passive dispersal (Anderson, 1971), habitat morphometry (Anderson, 1971), predators (Anderson, 1971; Hamer and Appleton, 1991a), historical factors (Alonso, 1985), ephemerality-interruption of competition (King et al., 1996) and cyst bank influences (Simovich, in press).

Donald (1983) proposed that the discontinuous presence and yearly changes of species were potentially the result of (1) colonization and extinction, (2) long-term viability of anostracan eggs, and (3) species-specific differences in requirements for embryonic development and egg hatching. Alonso (1985) proposed that the assemblages are usually made up of species with similar environmental requirements that exhibit some type of segregation in feeding or behavior. Hamer & Appleton (1991a, 1991b) found that the species number appeared to be related to (1) pond area and habitat duration, and (2) the presence of vegetation which controls the amount of detritus available. Thiéry (1991) pointed to four factors as contributing to species assemblages: (1) climatic and water characteristics favouring the co-occurrence of naturally allopatric species, (2) in turbid environments a diversity of food types, created by organic matter attached to clay, may allow resource partitioning, (3) size differences, and (4) horizontal or vertical segregation of species.

On the basis of literature and our observations in the field, we conclude that the probable factors contributing to the co-occurrence of several large branchiopod species can be divided into three categories. These are: (1) habitat factors, (2) species factors, and (3) historic factors (Table 6).

Finally, it is important to point out that for a better understanding of the factors determining different large branchiopod assemblages, more detailed limnological surveys of their habitats, including studies on organic matter, detritus, nanoplankton, and phytoplankton, supplemented by studies on competition and predation, and their natural food and feeding habits, are clearly needed.

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Appendix 1. Large branchiopod assemblages recorded from seven states of México. For abbreviations of species names see Table 1. N = total number of species in the assemblage, code = state locality: DG = Durango, CH = Chihuahua, CO = Coahuila, HG = Hidalgo, NL = Nuevo León, SL = San Luis Potosí, and ZA = Zacatecas, and date = month and year of field collection.

species																					
Bb	Bp	Bsa	Sg	Sl	Sm	Smo	Ssi	St	Tm	Tp	Ts	Cs	Ed	Lc	Ec	Et	Lbe	Pm	N	code	date
								×	×	×	×		×	×		×		×	8	DG01	09.81
	×	×	×		×					×	×				×				7	CO10	10.85
					×			×		×	×	×	×	×					7	CO13	09.81
					×			×		×	×					×		×	6	CH21	07.83
					×	×				×	×		×	×					6	CH24	08.71
			×		×			×		×	×			×					6	CO09	05.81
					×					×	×	×		×			×		6	DG12	07.85
					×					×	×	×		×			×		6	SL01	07.70
					×					×	×			×			×		5	CH02	09.85
					×					×			×	×	×				5	CH22	08.71
	×	×			×					×	×								5	CO10	02.84
			×		×					×	×			×					5	CO10	10.85
			×		×				×	×			×						5	CO10	07.82
	×				×			×		×	×								5	CO11	10.85
×					×			×			×			×					5	CO13	10.85
					×					×	×			×		×			5	DG06	07.82
					×						×	×		×			×		5	DG14	07.85
					×					×	×					×			4	CH20	09.85
	×				×			×				×							4	CO05	12.82
					×						×	×				×			4	CO08	07.82
									×	×	×					×			4	NL03	09.78
					×					×	×			×					4	ZA04	07.68
								×			×			×					3	CO03	10.81
×		×						×											3	CO13	12.89
					×						×					×			3	CO14	09.85
				×					×	×									3	CO17	04.63
	×				×			×											3	CO24	05.85
					×					×	×								3	DG08	09.83
					×			×		×									3	DG20	08.71
							×	×	×										3	NL06	09.85
				×			×			×									3	NL07	07.54
	×				×							×							3	ZA03	05.87
					×									×					2	CH04	09.85
					×												×		2	CH07	09.85
					×					×									2	CH14	09.85
					×											×			2	CH18	09.85
					×											×			2	CH19	09.85
				×								×							2	CO01	03.83
					×					×									2	CO04	10.81
					×					×									2	CO05	07.86
					×						×								2	CO06	06.86
	×										×								2	CO09	02.81
					×			×											2	CO12	10.81
					×						×								2	CO16	06.84
									×	×									2	CO23	07.69
														×			×		2	DG02	09.85
	×									×									2	DG07	05.82

Appendix 1. (continued)

species																					
Bb	Bp	Bsa	Sg	Sl	Sm	Smo	Ssi	St	Tm	Tp	Ts	Cs	Ed	Lc	Ec	Et	Lbe	Pm	*N*	code	date
					×						×								2	DG13	07.85
					×												×		2	DG19	08.39
								×			×								2	DG21	10.87
								×				×							2	DG22	08.88
					×							×							2	DG27	08.88
					×						×								2	HG01	07.85
								×			×								2	NL05	02.84
							×			×									2	NL13	06.56
							×	×											2	SL05	07.54
	×							×											2	SL07	06.87
					×									×					2	ZA02	07.85

Appendix 2. Large branchiopod assemblages recorded from Arizona, USA. For abbreviations of species names see Table 1. N = total number of species in the assemblage, code = catalog number in the collections of D. Belk (DB) and University of Arizona (UA). Date = month and year of field collection.

species																				
Eb	Bl	Bp	Bsb	Sd	Sm	Sse	St	Tm	Tp	Ts	Cs	Ed	Lc	Ec	Et	Lba	Lbe	N	code	date
		×		×					×	×		×	×					6	DB001	08.71
	×				×				×	×			×		×			6	DB135	10.72
					×			×	×				×		×			5	DB237	07.74
		×					×			×			×					4	DB005	09.71
	×				×				×	×								4	DB129	10.72
					×				×	×			×					4	DB016	10.71
				×	×				×				×					4	DB039	10.71
					×				×	×					×			4	DB078	06.72
				×	×				×	×								4	DB090	06.72
				×	×				×	×								4	DB092	06.72
	×				×								×		×			4	DB132	10.72
				×						×				×				3	DB033	09.71
					×				×	×								3	DB097	08.72
					×				×	×								3	DB100	08.72
					×				×				×					3	DB103	08.72
				×					×	×								3	DB106	08.72
				×						×	×							3	DB111	08.72
				×						×	×							3	DB112	08.72
				×					×	×								3	DB113	08.72
×						×										×		3	DB172	06.73
					×				×	×								3	DB017	10.71
					×				×	×								3	DB130	10.72
	×				×				×									3	DB134	10.72
		×								×			×					3	DB167	06.73
				×					×	×								3	DB037	10.71
					×				×	×								3	DB010	09.71
				×					×	×								3	DB065	06.72
					×				×						×			3	DB073	06.72
					×				×				×					3	DB240	08.74
										×			×					2	DB032	09.71
										×							×	2	DB204	09.64
					×				×									2	DB072	07.65
										×		×						2	DB080	09.63
					×				×									2	DB098	08.72
					×				×									2	DB101	08.72
×																×		2	DB228	04.74
										×			×					2	DB241	08.74
					×				×									2	DB102	08.72
					×								×					2	DB104	08.72
				×								×						2	DB199	09.73
	×									×								2	DB003	09.71
					×				×									2	DB107	09.72
				×						×								2	DB109	09.72
		×								×								2	DB110	09.72
	×									×								2	DB117	09.72
	×									×								2	DB118	09.72
×																×		2	DB156	06.73

Appendix 2. (continued)

species																				
Eb	Bl	Bp	Bsb	Sd	Sm	Sse	St	Tm	Tp	Ts	Cs	Ed	Lc	Ec	Et	Lba	Lbe	*N*	code	date
			×			×												2	DB158	06.73
					×					×								2	DB011	09.71
					×				×									2	DB015	10.71
					×				×									2	DB024	08.71
	×												×					2	DB131	10.72
				×					×									2	DB170	06.73
				×							×							2	DB191	08.73
				×					×									2	UA076	07.70
				×					×									2	UA333	07.71
					×				×									2	DB075	06.72
				×	×													2	DB094	07.72
				×						×								2	DB122	09.72
				×				×										2	DB124	09.72
					×				×									2	DB189	07.73
					×			×										2	DB203	09.73
					×			×										2	UA173	08.61
					×					×								2	DB006	09.71
					×				×									2	DB022	09.71
										×					×			2	DB023	09.71
									×						×			2	DB034	09.71
					×				×									2	DB038	10.71
					×				×									2	UA343	10.66
					×					×								2	DB196	08.73
				×						×								2	DB007	10.71
					×				×									2	DB091	06.72
					×				×									2	DB197	08.73
								×	×									2	DB067	04.65
									×						×			2	DB074	06.72
					×			×										2	DB234	07.74
				×				×										2	DB243	09.74
	×								×									2	DB245	11.74

Appendix 3. Other useful references on large branchiopod co-occurrence not mentioned specifically in the text

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