Hydrobiologia **212**: 117–136, 1991.
D. Belk, H. J. Dumont & N. Munuswamy (eds), Studies on Large Branchiopod Biology and Aquaculture.
© 1991 *Kluwer Academic Publishers. Printed in Belgium.*

Multispecies coexistence of branchiopods (Anostraca, Notostraca & Spinicaudata) in temporary ponds of Chaouia plain (western Morocco): sympatry or syntopy between usually allopatric species

Alain Thiéry
Laboratoire de Biologie Animale-Hydrobiologie, Faculté des Sciences, 33 rue Louis Pasteur, F-84000 Avignon, France

Key words: Anostraca, Notostraca, Spinicaudata, temporary ponds, sympatry, coexistence

Abstract

The study of the structure of communities of Crustacean branchiopods Anostraca, Notostraca and Spinicaudata of temporary ponds in Morocco revealed the existence of a geographical area with a particularly diversified number of species. Over a few hectares, 11 species, among the 18 known in Morocco, are present. While most of them are usually allopatric and belong to distinct associations, indicative of particular ecological and climatic conditions, they can coexist in Chaouia plain, either in adjoining ponds (sympatric species) or in the same pond (syntopic species). In one pond we could find up to 10 phyllopods: 6 Anostraca, 2 Notostraca and 2 Spinicaudata.

This faunistic diversity may result from abiotic features (the location of the ponds at the boundary of two climatic areas) and from a heterogeneous geological substratum, creating a patchwork of temporary ponds with various mesologic conditions.

Secondarily, this diversity may result from different life history characteristics of each coexisting species. As all species hatch synchronically, coexistence is only possible if their growth rates and life span are different. This implies that horizontal and vertical distribution, and exploitation of food supplies in the habitat differ for each ecophase of the syntopic species (spatial and trophic exclusion).

Introduction

The pioneering work of Simon (1886), Sars (1896) and Daday (1910, 1914, 1923) addressed the systematics of the Anostraca, Notostraca and Conchostraca (= Spinicaudata and Laevicaudata sensu Fryer, 1987) living in temporary ponds, but their community structure was neglected. Most authors found that rarely more than 2 or 3 anostracans and 1 or 2 conchostracans live together in one biotope (Gauthier, 1928 in North Africa; Dexter, 1946, 1953; Dexter & Kuenhle, 1951; Prophet, 1963; Moore, 1963; Maynard & Romney, 1975; Huggins, 1974; Belk, 1977 and Daborn, 1978 in North America; Alonso, 1981 in Spain; Geddes, 1981 in Australia; Mura, 1985, 1987 and Mura & Cottarelli, 1984 in Italy). The factors determining the composition of these communities are still not well understood. At first, Gauthier (1928, 1930), Rzóska (1961), and Belk (1977), studied populations by a species versus abiotic factors approach. They concluded that a major factor controling the communities was climate, although Horne (1967) stressed the importance of physical and chemical factors. Only Donald (1971), in Canada, stressed that coexistence of congeneric species may result from differences in their reproductive cycle and their food niche. The importance of these biotic factors was recently shown by Hamer & Appleton (1991) in temporary ponds of Natal.

The Notostraca *Triops* and *Lepidurus* are usually allopatric (Williams, 1968: Australia; Thiéry, 1988b: France). Data concerning the coexistence of conchostracan species are limited (Mattox, 1957; Wooton & Mattox, 1958), but in Anostraca, Donald (1983) reported the coexistence of five species. He adds that the percentage of occurrence of three or five anostracan species per pond in the U.S.A. makes up only 1% of the cases, while more than 80% of the ponds are inhabited by one species and 15% by two species. These conclusions confirm Daborn's data (1978) in nearctic regions and Dimentman's (1981) on Israel.

In Morocco, most temporary ponds have communities of one, two or three Anostraca, and often one or two Spinicaudata, and the notostracan *Triops* or *Lepidurus* (Thiéry, 1987). However, in the area of eastern Chaouia, temporary ponds occur which have many coexisting species, particulary in one pond we regularly collected up to

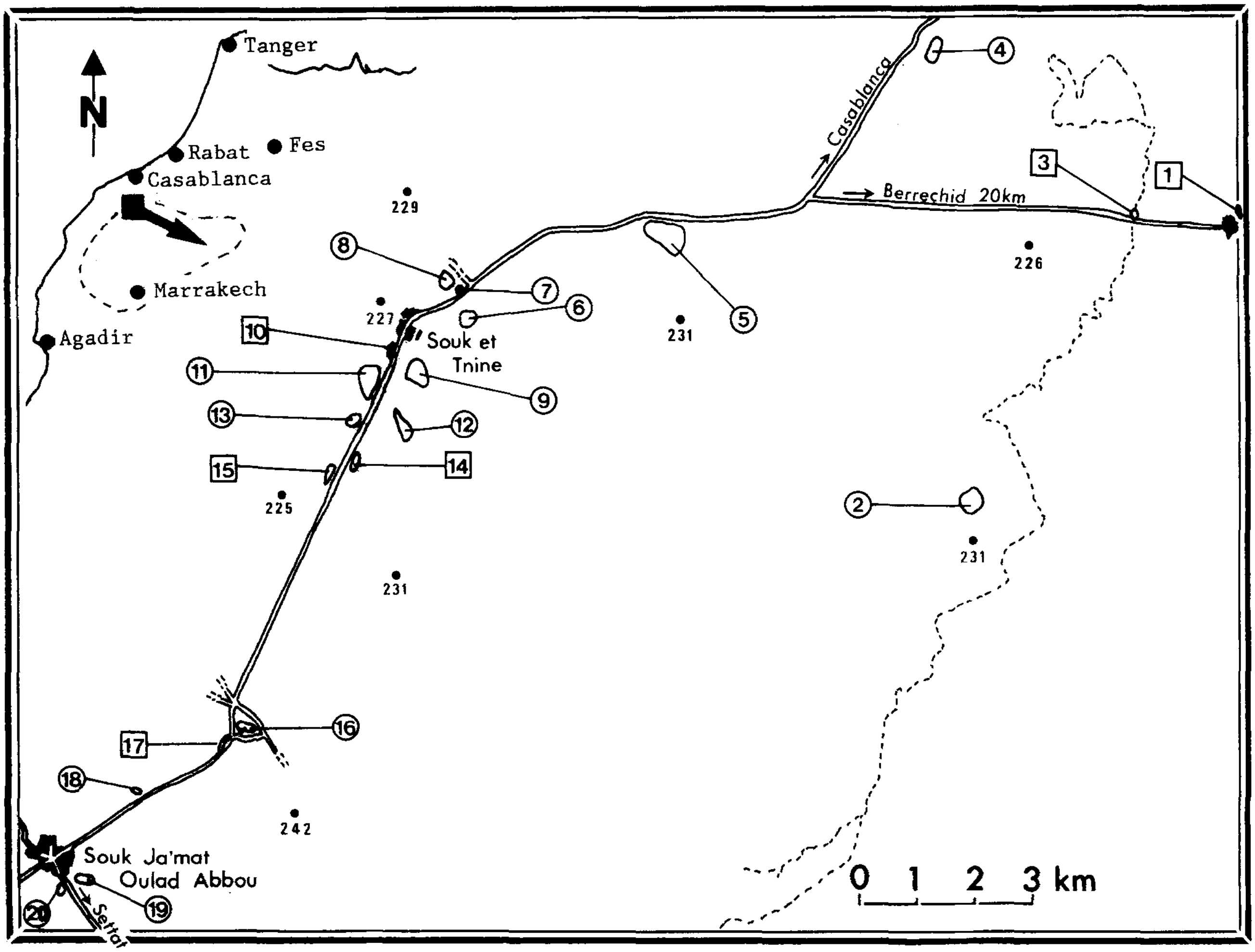

Fig. 1. Map of study area. Insert shows a map of occidental Morocco with location of the semi-arid/arid zone boundary (arid zone inside dotted line). Black points indicate altitude (meters). Numbers encircled are typical temporary ponds (dayas) and numbers in squares are road-ditches.

six anostracans. This situation was never found in the literature (but see Maeda-Martinez, this volume). In the present work, these populations are studied from a biological point of view (body size and feeding ecology), beside the synecological one (species versus abiotic factors), with an aim to determine the importance of specific factors in structuring communities and to explain why Chaouia plain communities differ from others.

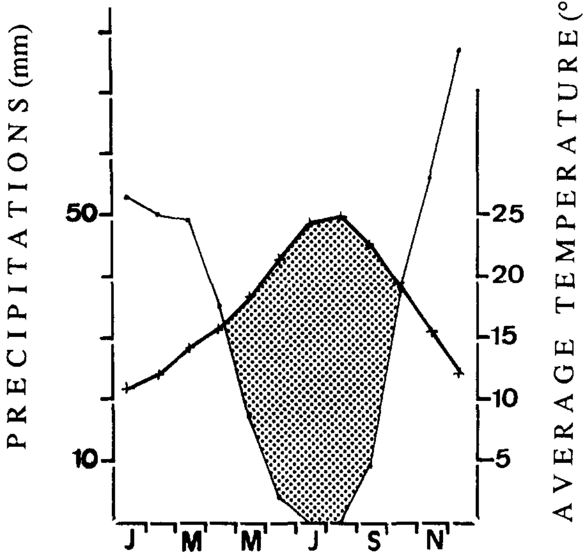

Fig. 2. Ombrothermic diagram at Berrechid-Averroes station (near Casablanca-Nouasser airport). Dry months, in grey on the graph, are characterized by precipitations ≤2 T °C.

Description of study area and habitats

Localisation

The study area is situated in west Morocco, from Souk Jemmaa Oulad Abbou to Berrechid (33° 06′–33° 13′ N; 7° 56′–7° 57′ W) in the eastern Chaouia plain (south of Casablanca), at 240 m above sea level (Fig. 1).

Geology

The temporary ponds of the Chaouia ponds of the Chaouia plain are located on Cretaceous calcareaous marl and clay in a synclinal basin South of Berrechid. The Quaternary period was affected by a succession of wet and dry periods that caused bad draining characteristics for surface water, thus favouring the presence of many temporary ponds (= dayas, Arab term) and road-ditches (Ruhard, 1975). In some cases, a capillary contact with the oligohaline groundwater (Cl^- 1 to 2 $g\,l^{-1}$) salinizes the surface.

Climatic features

The region experiences a thermo-mediterranean climate, with approximately 5–6 dry months (a month is biologicaly dry when precipitation is lower than twice the thermic mean (Fig. 2)). Rain, about 400 mm per year, falls from October to March, and floods the temporary ponds until they dry out between spring and late summer (Fig. 3). Annual average temperature is c. 18 °C. The differences between summer and winter ($\Delta t° = 15.9$ °C) is important in spite of the proximity of the ocean.

Continentality increases rapidly with distance from the ocean (Kutsch, 1978). As shown on the climagram modified after Sauvage (1963) (Fig. 4), the study area forms the boundary of two climatic zones; the oceanic semi-arid climate of the oceanic coast, and the arid zone of the Jbilets mountains of Marrakech (with 7–8 dry months).

Physical properties and water chemistry

When flooded, the ponds cover between many hectares (stations 2, 5, 9, 11) and 250 to 300 m^2, or less (road ditch, station 10, 14, 15, 17, rock-pools, station 18). Their depth does not exceed 1.50 m, and mostly averages 0.30–0.40 m. (Fig. 5). Depth and surface area vary along and across years, in relation with rainfall variability. As in most temporary ponds (Rzóska, 1961, 1984; Prophet, 1962; Moore, 1970; Daborn, 1976b; Williams, 1985), conductivity also varies

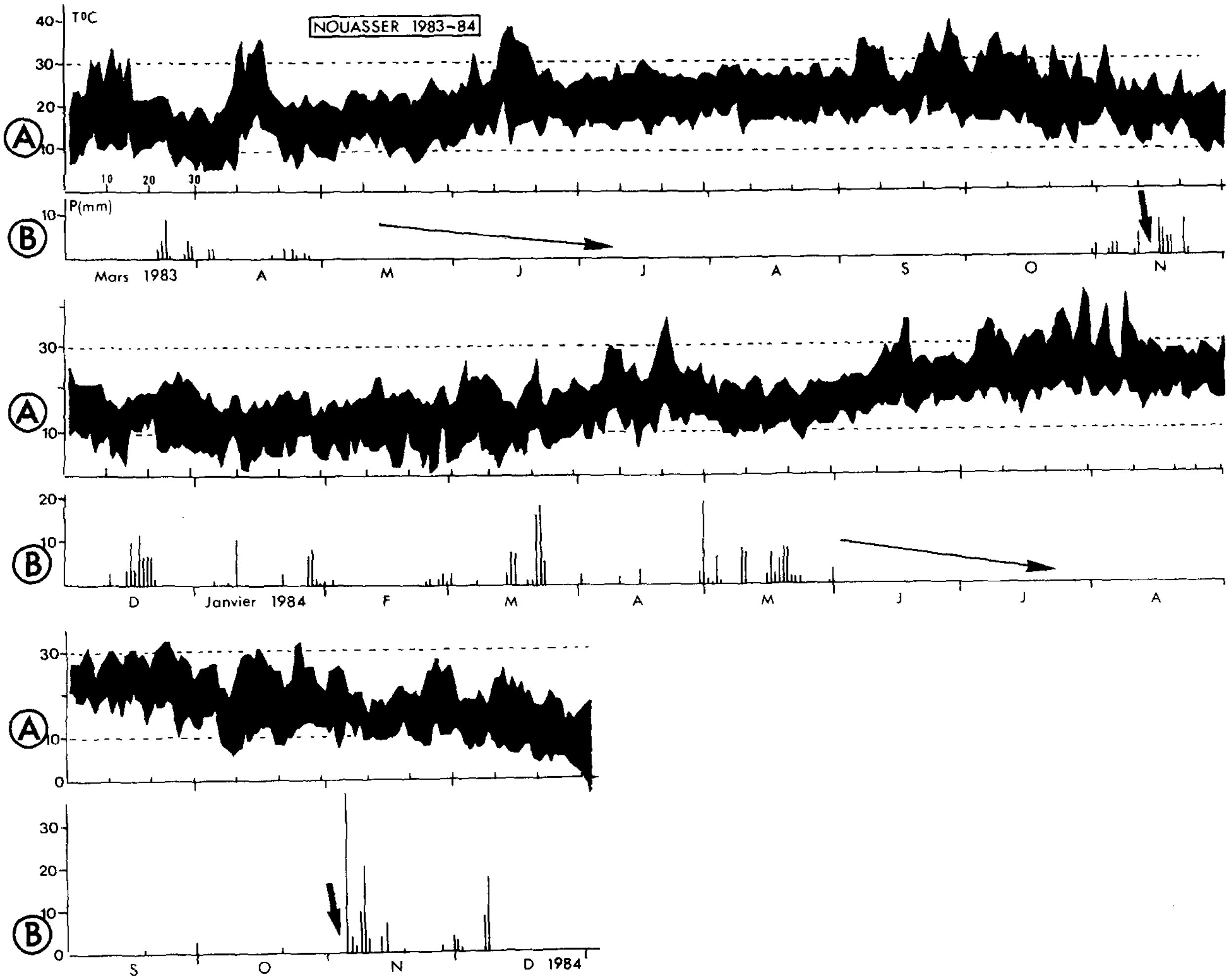

Fig. 3. Climatic features (daily data between march 1983 and december 1984) at Nouasser airport station. A. (Upper): temperatures min and max (°C), b. (lower): rains (mm). Horizontal arrows from May to July indicate the progressive drying of ponds. Vertical arrows in November indicate the flooding of ponds.

through the hydrologic cycle. It is low (30–60 μS cm^{-1}) at flooding and increases (500–800 μS cm^{-1}) as drying up proceeds (Fig. 6). Conductivity is also related to dry residue (Fig. 9), or to transparency, as measured by Secchi disc (Fig. 8). Two distinct salinity types occur: fresh-water ones, not in contact with the groundwater (conductivity 80–600 μS cm^{-1}) and brackish ponds connected to the oligohaline groundwater (conductivity 400–2000 μS cm^{-1}) (Dayas 7, 8 for example). In addition, two types of ponds are distinguishable by substrate type (marl, clay...). Most have a pH between 6.8 and 8.2, but some reach 8.4 to 9.8 (Dayas 2, 5, 8 and 11). In all, much organic matter and clay are in stable suspension (Secchi disc often <5 cm) (Fig. 7a, b, c, d). The suspended colloidal or particulate matter is linked to pH and temperature (Thiéry, 1987). X-ray analysis of the clays shows an almost exclusive presence of Kaolinites and Illites. These clays are the last components of a decaying substratum and result from successive phases of dissolution and erosion, which are characteristic of the genesis of temporary ponds (dayas) in dry areas of North Africa (Thiéry, 1987). They are a suitable substratum for bacterial

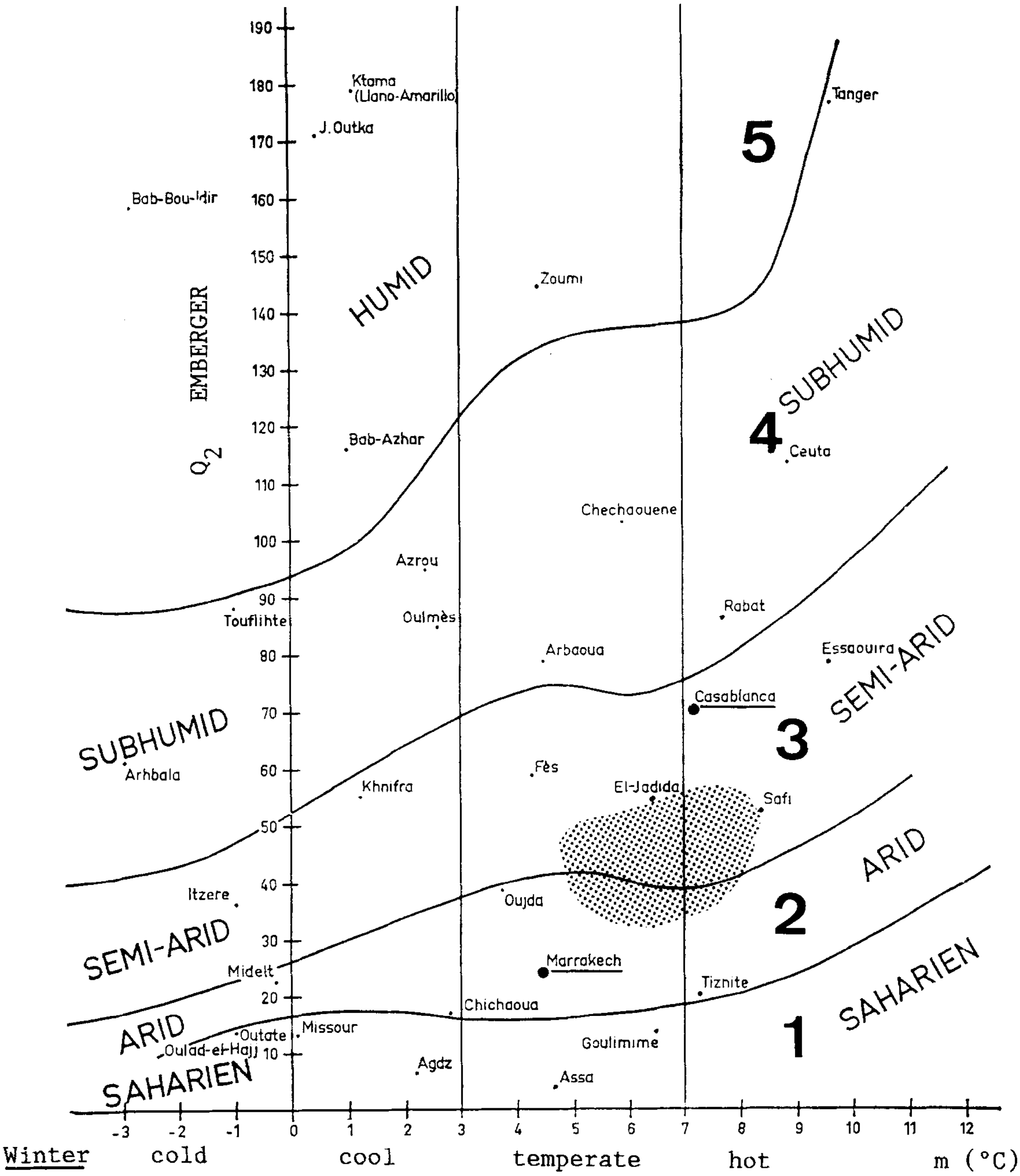

Fig. 4. Situation of the Chaouia plain (grey area) on the climagram of Sauvage (1963), at the interface between semi-arid and arid climates. 1, 2, 3, 4 & 5 are bioclimatic stages.

populations (Felton *et al.*, 1967; Pedrós-Alió & Brock, 1983; Arruda *et al.*, 1983; Melack, 1985). A close relationship exists between total dissolved and particulate organic matter and dry residue (r^2 = 0.904) (Fig. 10). It is low when flooding occurs and increases when ponds dry up. The amount of dry residue evolves inversely to transparency. Waters are well oxygenated with dissolved oxygen at midday from 80% saturation in open water to 180–200% in beds of *Ranunculus*

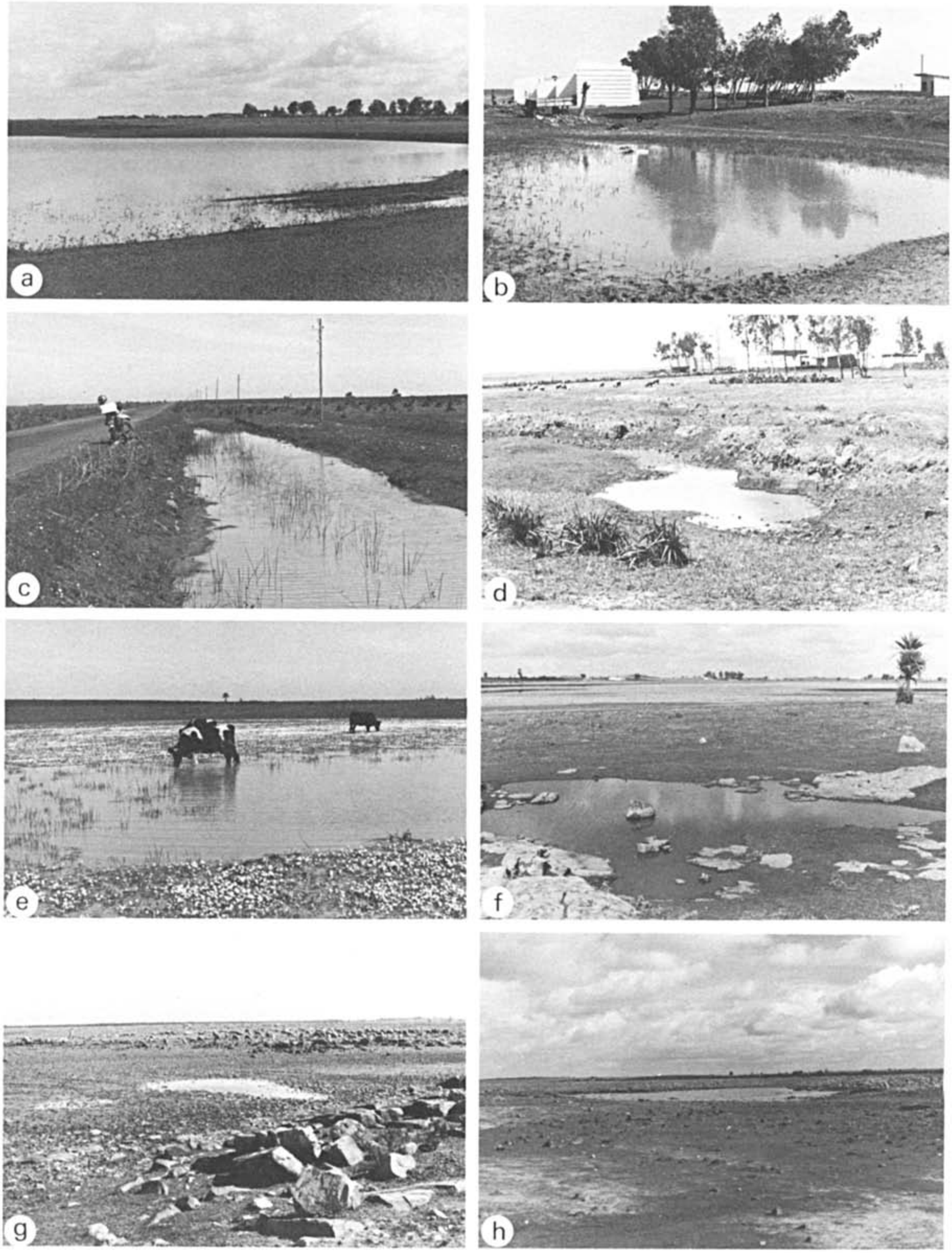

Fig. 5. Height of twenty habitats in which associations of co-occurring species of Branchiopods occur. a) daya 6. b) daya 7. c) road side ditch 14. d) daya 13. e) daya 16. f) rock-pool 18. g) daya 19. h) daya 20. All photographs taken during flood period.

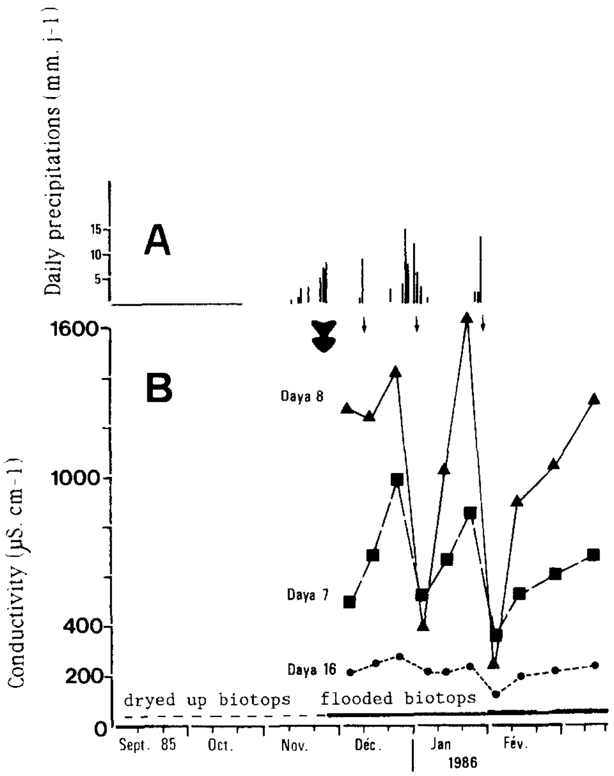

Fig. 6. Evolution of the conductivity -B- in 3 temporary ponds of Chaouia plain during the first 4 months of an hydrologic cycle. Black arrow indicate flooding. Dilutions are linked to rainfalls (daily data upper)-A-. In large daya 16, we noted slighter conductivity changes than in little daya 7, where differences were more important. Daya 8 is sometimes fed by oligohaline groundwater, so its conductivity is high.

and *Spirogyra*. However, during the night, low oxygen concentrations (30–40%) occur in the deepest zones of the ponds.

Vegetation

Many species of macrophytes and algae are present in the dayas. Dense beds of *Ranunculus aquatilis baudotii*, *Eleocharis palustris*, *Glyceria fluitans* occur in the deepest parts, and *Damasonium alisma*, *Isoetes velata* and *Marsilea pubescens* near the shores, entangled with *Spirogyra* spp. and *Chara* spp. (Fig. 7a, b, c). The distribution of *Ranunculus* and *Glyceria* is not homogeneous: zones with dense vegetation and zones with free water are found (Fig. 5e; 7b).

Associated vertebrate fauna

Aquatic vertebrates are mainly composed of the Anoura *Bufo mauritanicus*, *Bufo bufo*, *Hyla meridionalis*, *Rana esculenta* and the Urodele *Pleurodeles waltlii*. Among birds, *Ciconia ciconia*, *Himantopus himantopus* and *Bubulcus ibis* are present but not abundant. Some of these vertebrates (particularly *Pleurodeles*) have a predatory impact on the euphyllopods (Thiéry, 1987). They also dispense eggs among the ponds of one area (amphibians) (Mathias, 1937) or among ponds of distant areas (birds) (Balfour-Browne, 1909; Decksbach, 1924; Proctor *et al.*, 1967; Thiéry & Pont, 1987). The gut contents of *Pleurodeles waltlii* were rich in Anostraca, Notostraca and Spinicaudata. One female from Daya 8, 11 November 1985, contained 1 *Triops cancriformis mauritanicus* (juvenile) and 97 *Tanymastigites brteki*, with numerous ovigerous females and viable eggs in the rectum.

In Daya 8, 24 January 1986: 151 *Tanymastigites brteki* with ovigerous females and viable eggs were found in the digestive tract of one *Pleurodeles* female.

In Daya 9, on December 1985 one female contained 1 *Triops cancriformis mauritanicus* juvenile, 3 *Branchipus schaefferi* of which 2 ovigerous females, 17 *Cyzicus bucheti*, with some Ostracods (*Eucypris virens*) and insect larvae, and in the rectum, many eggs of *Branchipus* and valves of *Cyzicus*.

However, birds and amphibians are not alone involved in cyst dispersal. The transport of eggs between ponds can also be caused by sheep; when they come to drink eggs stick on their feet (Fig. 7e). We scraped feet of five sheep leaving the daya and we counted 7 eggs of *Triops*, 3 eggs of *Branchipus* and 1 egg of *Tanymastigites*.

Methods

Twenty ponds were sampled approximately monthly from March 1983 to June 1986, between 11 a.m. and 2 p.m., except during summer when biotopes were dry. Qualitative samples were col-

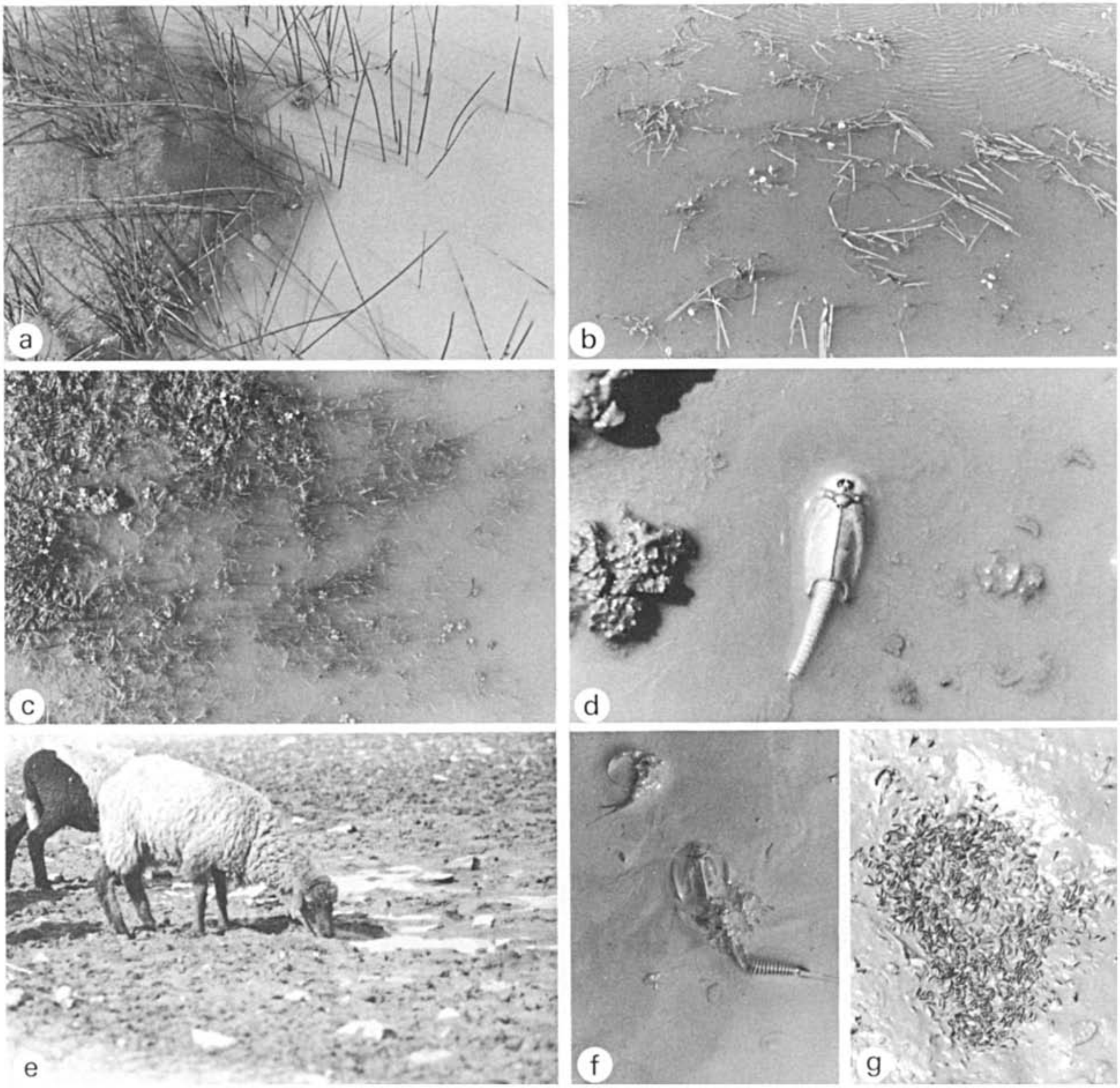

Fig. 7. a) shore of road-ditch 14 with *Spirogyra* entangled in *Eleocharis palustris*. b) *Glyceria fluitans* and *Ranunculus aquatilis* in daya 16. c) *Marsilea pubescens* and *Isoetes velata* at shore of daya 16. d) *Triops granarius* in turbid water during drying period (Secchi disc < 1 cm). e) sheep drinking in a daya with their legs in the mud. f) dead *Triops granarius* in dry daya. g) *Leptestheria mayeti* gathered in deep zone of dry daya.

lected from bottom to surface with a 200 μm net, towed for about 10 minutes across each pond, in and out of the aquatic vegetation. Samples were pooled and preserved in 10% neutralised formalin. At every visit water for analysis of physical and chemical variables of the habitat was collected. Specific Conductance, pH, dissolved Oxygen, temperature, depth and turbidity were measured in the field. Dry residue was evaluated after dehydration at 105 °C for 24 hours. Total organic matter, particulate and in solution, was determined after calcination of dry residue at

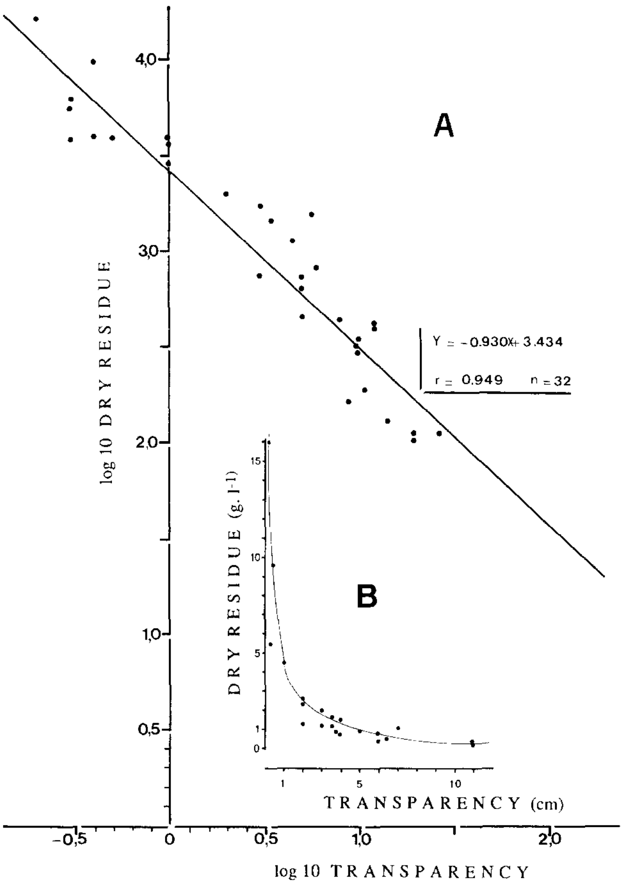

Fig. 8. A. Relation between dry residue and Transparency (log scale): $Y = -0.930\ X + 3.434$ ($r^2 = 0.900$, $n = 32$) B. (Lower), same relation in untransformated data.

525 °C during 6 hours. X-Ray analysis was made with a 600 W powder diffractometer.

Species were determined with the help of Daday (1910, 1914, 1923), Linder (1941), Longhurst (1955), Straskraba (1966), Flössner (1972), and Thiéry (1987, 1988a). Anostraca were measured under a binocular microscope with an eye micrometer. Total length was taken from the front to extremity of the cercopods. Notostraca were measured along the dorsal carina of the cephalothoracic carapace (Longhurst, 1955; Linder, 1952, and Thiéry, 1987). For Spinicaudata the length of the valves was measured. For constructing growth curves, the length of individuals of the three orders were grouped into one millimeter size-classes. Data on rainfall and temperature at Berrechid and Casablanca-Nouasser Airport were provided by the National Meteorologic Department in Casablanca.

For bacterial analysis, samples of water and sediment were stored in ice and brought to the laboratory where they were studied. Enumerations were made after plating out on nutritive gelose (Plate count Agar). All cultures were incubated during 7 days at room temperature (20–25 °C). Bacterial identifications were made by classic staining techniques and using culture medium and identification galeries 'Api System R' 20 E. ref. 2010 & 20 N.E. ref. 2005.

Results

Twelve species were collected: *Chirocephalus diaphanus* Prévost, *Streptocephalus torvicornis bucheti* Daday, *Branchinecta ferox* (Milne-Edw.), *Tanymastigites jbiletica* Thiéry, *Tanymastigites brteki* Thiéry, *Branchipus schaefferi* Fischer, *Tanymastix affinis* Daday, *Triops granarius* (Lucas), *Triops cancriformis mauritanicus* Ghigi, *Cyzicus bucheti* (Daday), *Leptestheria mayeti* Simon, and *Maghrebestheria maroccana* Thiéry (Table 1). Thus, 66.6% of the moroccan euphyllopod fauna is present in the Chaouia plain, much more than in any other geographical and climatic area in Morocco studied (Fig. 13).

The species assemblage of Chaouia ponds is composed of species from two of the bioclimatic areas of Thiéry (1986):

- species from arid areas: *Triops granarius*, *Tanymastigites jbiletica*, *Leptestheria mayeti* and even *Branchipus schaefferi*, although it prefers high continental areas.
- species from semi-arid areas with oceanic influence: *Cyzicus bucheti*, *Maghrebestheria maroccana*, *Streptocephalus torvicornis bucheti*, and *Triops cancriformis mauritanicus*.

The relationship between the two groups of species and the climatic areas is shown on Fig. 11, along a transect between the coastal plain and the Sahara, through the High Atlas. The limits between the various associations are distinct and the transitions are rapid, so their respective species can be considered as allopatric. Only few

Table 1.

Station number	1 (a)			2			3 (a)			4			5			6			7			8			9			10 (a)		
Maximum depth (m)	0.4			0.3			1.5			0.4			0.4			0.6			1.5			0.4			0.3			0.3		
Maximum volume (m³)	20			3.000			6			1.5			10			750			1.980			1.500			1.125			1		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
						(b)						(b)										(b)								
Branchipus schaefferi	●	●	●				●	●	●				●	●	●		●	●	●	●	●				●	●	●	●		●
Tanymastix affinis													●															●	●	●
Streptocephalus torvicornis bucheti													●						●	●										
Chirocephalus diaphanus													●						●	●	●									
Tanymastigites brteki				●	●									●	●	●							●	●						
Tanymastigites jbiletica																														
Branchinecta ferox																							●	●						
Triops cancriformis mauritanicus													●	●			●	●	●	●	●									
Triops grnarius				●	●					●	●		●	●	●	●		●	●	●	●		●	●	●	●	●			
Leptestheria mayeti							●	●	●	●	●					●			●	●			●	●	●	●	●	●		
Cyzicus bucheti							●												●	●										
Maghrebestheria maroccana																														
Richness (S)	1			2			3			2			7			5			7			4			3			3		

Station number	11			12			13			14 (a)			15 (a)			16			17 (a)			18			19			20		
Maximum depth (m)	0.3			0.3			1.2			1.2			0.5			1.5			0.2			0.1			0.3			0.4		
Maximum volume (m³)	7.500			550			45			36			4			5.625			1.5			0.25			190			380		
	A	B	C	A	B	C	A	B	C	A		C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
													(b)						(b)							(b)	(b)			
Branchipus schaefferi							●	●	●		●	●		●	●	●	●	●							●					
Tanymastix affinis											●	●					●	●		●	●	●	●	●						
Streptocephalus torvicornis bucheti				●	●	●				●	●	●		●	●	●	●	●				●			●					
Chirocephalus diaphanus																●	●	●												
Tanymastigites brteki	●	●	●													●	●	●												
Tanymastigites jbiletica																	●	●												
Branchinecta ferox																														
Triops cancriformis mauritanicus										●	●	●		●	●	●	●	●							●			●	●	●
Triops grnarius	●	●		●	●	●	●	●	●							●	●	●												
Leptestheria mayeti					●		●	●	●								●	●												
Cyzicus bucheti										●	●	●				●	●	●										●	●	●
Maghrebestheria maroccana											●	●		●	●													●		●
Richness (S)	2			3			3			6			4			10			1			2			3			3		

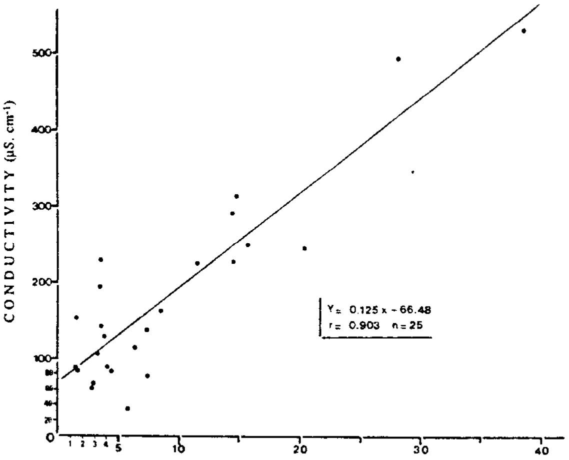

Fig. 9. Relation between conductivity and dry residue: $Y = 0.125\ X + 66.48$ ($r^2 = 0.810$, $n = 25$).

ponds are inhabited by species belonging to arid and semi-arid groups. So, it is clear that the Chaouia region is a particularity. It represents an ecotonic zone wider than most other moroccan transitory zones.

In addition to these two groups we noted the presence of species that have no particular bioclimatic requirement, but are stenotopic, such as *Tanymastix affinis* which is restricted to cupulary ponds, rock-pools, and weedy ditches. The presence of *Tanymastigites brteki* and *Branchinecta ferox* is determined by mineralization of the water (Thiéry & Garcin, 1986).

Table 1 shows the presence of a real patchwork of temporary biotopes inhabited by more or less rich and diversified communities. The richness of the communities is related to biotope surface but also to depth. Figure 12 shows that rich communities always occur in deeper ponds (open circles, maximum depth above 0.6 meter). Here (station 16), up to six Anostraca species, two Notostraca and two Spinicaudata may live together and hatch year after year. This regularity of occurrence was not observed in the species studied by Donald (1983). In the temporary ponds of Chaouia, as in all dayas of Morocco, all species hatch in the few hours or days following flooding (Figs. 14, 15). The study of their respective growth curve (Figs. 14, 15) shows a great diversity in the length of their biological cycle. Species living in arid zones (*T. jbiletica*, *T. granarius*, *L. mayeti* and *B. schaefferi*) grow more rapidly but die earlier than species living in semi-arid zones, even if their feeding mode, habitat and way of moving are homologous (*C. bucheti*, *S. torvicornis bucheti*, *T. cancriformis mauritanicus*, *M. maroccana*). This difference in intrinsic growth between arid and semi-arid zone species is illustrated by the growth curves of *Triops granarius* and *Triops cancriformis cancriformis* in one and the same daya (station 7) (Fig. 14). The growth curves, fitted by the Von Bertalanffy model ($L_t = L\infty\ (1 - e^{-K(t - t0)})$, show that their K coefficients are close ($K_{\textit{Triops granarius}} = 0.039$ and $K_{\textit{Triops cancriformis mauritanicus}} = 0.034$), but maximum length (theoritical value) is different ($L\infty_{\textit{Triops granarius}} = 41.71$ mm and $L\infty_{\textit{Triops cancriformis mauritanicus}} = 30.83$ mm). The Von Bertalanffy equations are: $L_{t \cdot \textit{Triops granarius}}\ _{(\mathrm{mm})} = 41.71\ (1 - e^{-0.039\ T})$ and $L_{t\ \textit{Triops cancriformis mauritanicus}}$ (mm) $= 30.83\ (1 - e^{-0.034\ T})$.

In Daya 16, at the community level, the

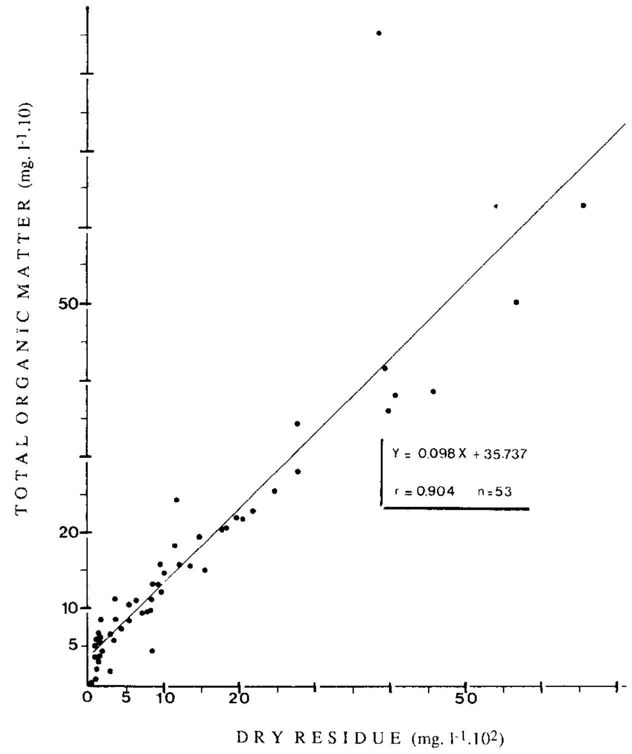

Fig. 10. Relation between total organic matter, and dry residue: $Y = 0.098\ X + 35.74$ ($r^2 = 0.811$, $n = 53$).

sequence for the various species was as follows (Fig. 15): *T. affinis* is adult after a period of six–seven days and disappears around the 16th day; *Tanymastigites jbiletica* completes its biological cycle in 26–30 days. The cycle of *Branchipus schaefferi* and *Streptocephalus torvicornis bucheti* takes 66–75 days and their optimal sizes are similar to each other. The growth curve of *Chirocephalus diaphanus*, in which a gynandromorph has been discovered and described by Thiéry (1983), is not presented because the population was not abundant. *Triops granarius* grows rapidly but disappears after about 56 days, while *Triops cancriformis mauritanicus* grows slowlier but survives for 160–180 days. Similarly, among Spinicaudata *Leptestheria mayeti* grows twice as fast as *Cyzicus bucheti* but disappears after about 66–70 days, while *C. bucheti* only disappears 180 days after of flooding. We found that in Chaouia ponds, species of the arid zone had the same growth as in their typical climatic area.

Predation: as shown by the digestive tract analysis, adults of *Pleurodeles* have an impact on the populations of phyllopods, young feeding on

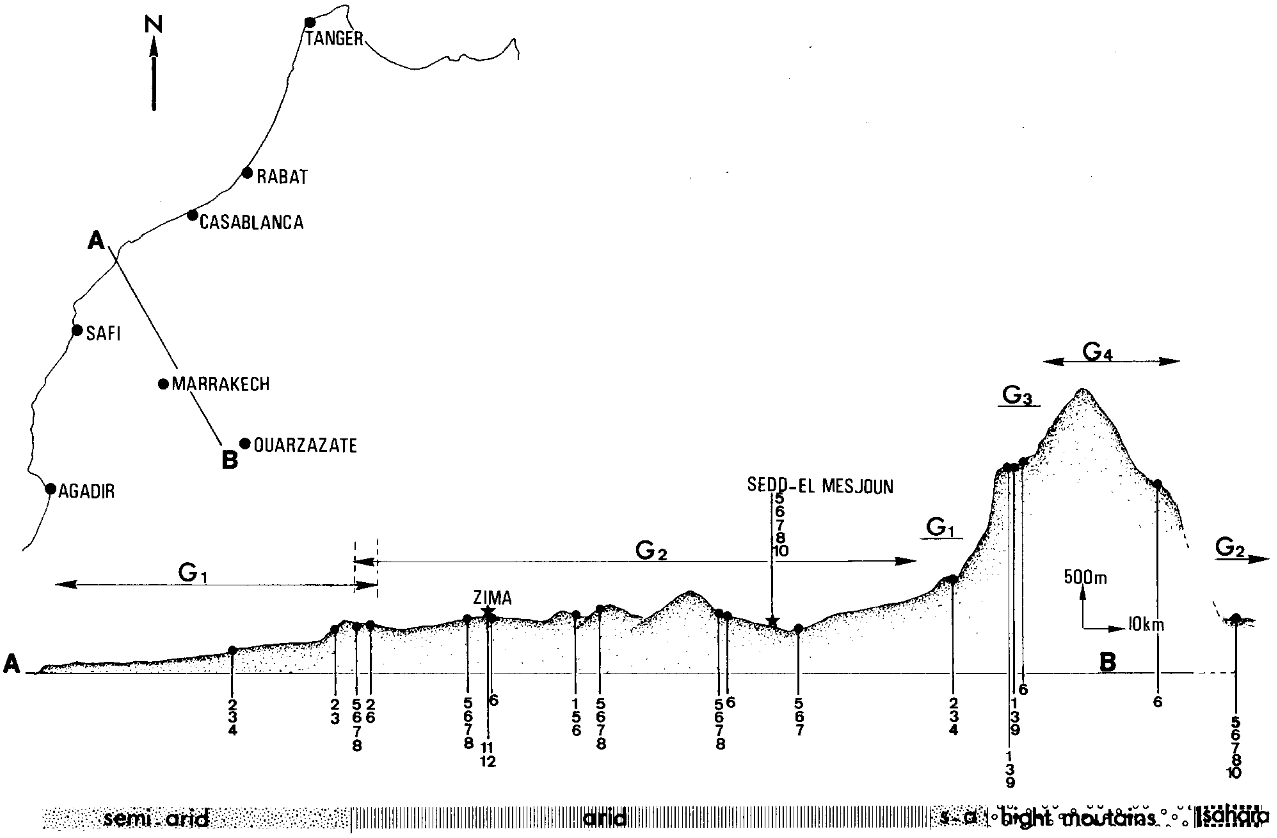

Fig. 11. Altitudinal and bioclimatic transect N. N.W.-S. S.E. showing the zonation of the species groups. 1. *Tanymastix affinis.* (stenotopic of ephemeral ponds), 2. *Streptocephalus torvicornis bucheti*, 3. *Triops cancriformis mauritanicus*, 4. *Cyzicus bucheti* (2–4 species of semi-arid zone), 5. *Tanymastigites jbiletica*, 6. *Branchipus schaefferi*, 7. *Triops granarius*, 8. *Leptestheria mayeti* (5–8 species of arid zone), 9. *Chirocephalus diaphanus*, 10. *Eocyzicus saharicus*, (stenotopic of oligohaline and hot waters), 11. *Artemia* sp, 12. *Branchinella spinosa* (11 & 12 salt waters species).

Black points are temporary ponds along the transect A–B; stars (Zima and Sedd El Mesjoun) are sebkhra's (inland salt waters). Group 1 (G.1.): semi-arid zone; Group 2 (G.2): arid zone; Group 3 (G.3): mountain zone; Group 4 (G.4): high mountain above 2500 m.

Below the transect the semi-arid, arid, high mountain and sub desertic zones are shown. Their borders are according to Sauvage's map (1963). The transition between the different groups, corresponding to bioclimatic stages, are distinct. Only one interpenetration between group 1 and Group 2 was recorded.

benthic Ostracoda and Cladocera. However, as *Pleurodeles* appears only in spring, when phyllopods are in the second half of their growth curve, and that *Pleurodeles waltlii* are low in densities ($< 0.2\ m^{2\,-\,1}$), their predatory impact on phyllopods is not important. Other amphibians, as *Bufo*, eat terrestrial fauna (insects, annelids...) and birds appear only in low densities at the end of hydrological cycle.

Predation by insects (Dytiscidae and Odonata) was not estimated.

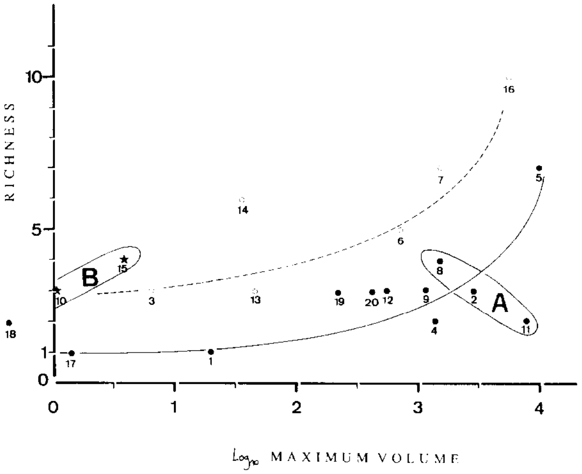

Fig. 12. Relation between species richness and volume of each pond (log transformation). Black points correspond to depths <0.50 m, white circles to depths >0.60 m. A is a group of ponds with brackish water, and B are road-ditches.

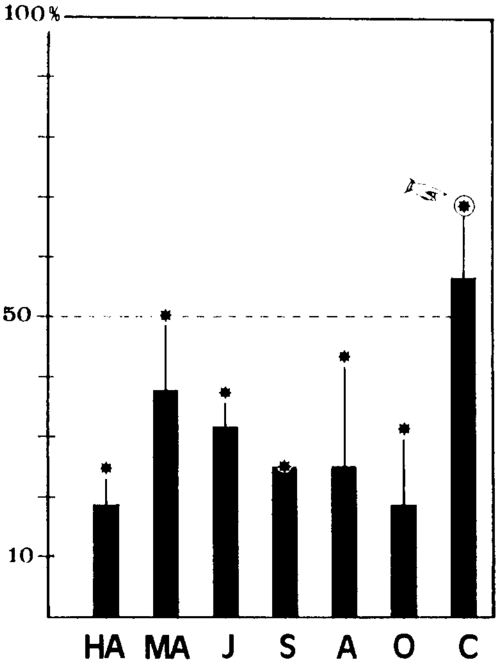

Fig. 13. Species richness of different zones as a percentage of the total freshwater euphyllopods of Morocco (brackish-water species, *Artemia* and *Branchinella* excluded). Black bars: maximum species richness in one pond in %; Stars: maximum richness of each zone, all biotopes together, in %. HA: High Atlas; MA: Middle Atlas; J: Jbilet mountains and Marrakech area; S: Sahara (east of High-Atlas; A: Atlantic coast; O: oriental plateau (east of Middle-Atlas); C: study area, Chaouia plain between Berrechid and Souk Jemma Oulad Abbou, the richest zone.

Discussion

At any point in time all co-occurring species present in a pond showed differences in body-length, resulting from a different neonatal length and a different growth rate. Several authors (Mozley, 1932; Rzóska, 1961; Moore, 1963; Geddes, 1981, 1986; Donald, 1971 and Mura, 1985) observed the same variation in size among sympatric species resulting from different growth speeds. The growth curves obtained from Retallack & Clifford's (1980) data for the pairs *Eubranchipus bundyi* – *E. intricatus*, and for *Lynceus brachyurus* – *L. mucronatus*, also combine different sizes with different growth rates. As well as the anostracans *Eubranchipus bundyi* (life cycle of 2 months) and *E. intricatus* (life cycle of 3–4 months), the life cycle of the Laevicaudata was of two types: *L. mucronatus* grows and lives for 60 days, while *L. brachyurus* lasts 118 days. A third coexisting species, *Cyzicus mexicanus*, persists throughout summer. These results are close to those of Hamer & Appleton (1991) which show the importance of differences between growth rate of phyllopods coexisting in the same temporary pool.

According to Daborn (1976a, 1979) the size range of the individuals belonging to the same or to different species seems to be of major importance. Size variation implies a diversity in feeding behaviour, related to the interspace between filtering setae on the endites of the foliaceous legs. The size of the filtered particles is different for the coexisting species, and filtering segregation may be a major factor permitting coexistence of ento-

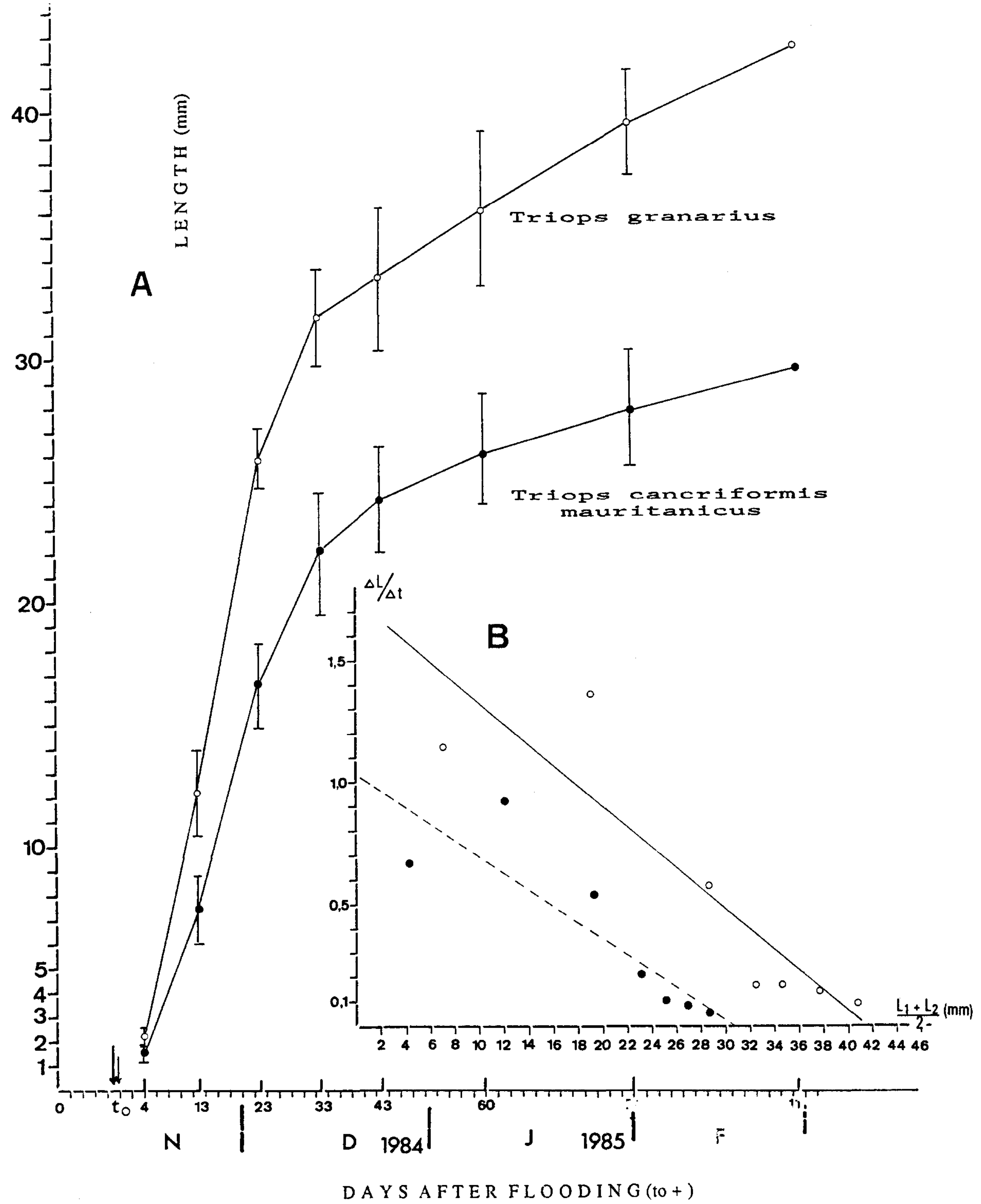

Fig. 14. A: growth-curves of *Triops granarius* (open dots) and *Triops cancriformis mauritanicus* (full points) in Daya 7 between flooding (black arrows) in November 1984 and February 1985. Each average on the growth curves with standard error. *B* (below): graphic determination of $L\infty$ (intersection of with x-axis) and K (slope of regression line).

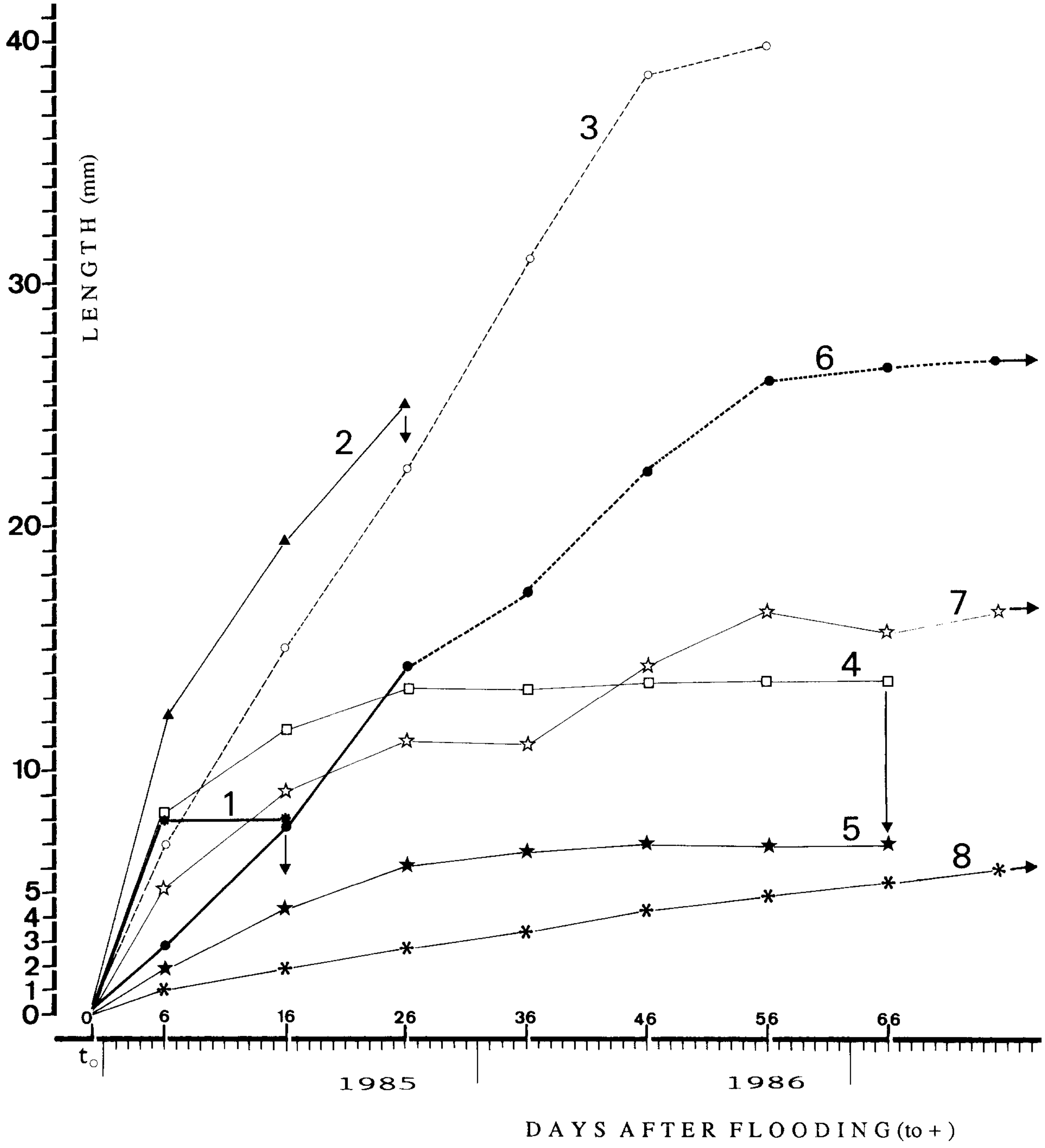

Fig. 15. Growth curves of all co-occurring species of daya 16 from December 1985 (flooding) to March 1986. 1) *Tanymastix affinis* 2) *Tanymastigites jbiletica* 3) *Triops granarius* 4) *Branchipus schaefferi* 5) *Leptestheria mayeti* 6) *Triops cancriformis mauritanicus* 7) *Streptocephalus torvicornis bucheti* 8) *Cyzicus bucheti.* Growth curve of *Chirocephalus diaphanus* not given. Vertical arrows indicate natural extinction of populations (species 1, 2, 3, 4, 5); horizontal arrows indicate that the biological cycle lasts between 2 or 3 months. (species 6, 7, 8).

mostracan species (Walter, 1970; Makarevicz & Likens, 1975; Hebert, 1982; Mertens *et al.*, this volume). In our case, this phenomenon is closely associated with the nature of food supplies. In the turbid water of temporary ponds the production and biomass of phytoplankton is limited (Marzolf & Osborne, 1972; for a review see Stern & Stickle, 1978). In the dayas studied, few phytoplankton cells occur (range 1.2. 10^4 cell l^{-1} - 1.5. 10^6 cell l^{-1}; sometimes 4. 10^8 cells l^{-1}). Moreover these algae have poor nutrient value because of a rapid intestinal transit (less than half an hour) and a low degradation rate. So, bacterial and protist biomass are the main food source for filtering invertebrates (Saunders *et al.*, 1980). As shown by Tezuka (1974) and Berk *et al.* (1976) for Cladocera and Copepods, there is no growth if bacterial concentration is below 10^7 cell ml^{-1}. In turbid dayas the concentration of free-living bacteria (*Micrococcus* represents the dominant biomass) is always lower than 10^7 ml^{-1} (Thiéry, 1987) and therefore the growth of euphyllopods must result from bacteria attached to clay. Many authors (Felton *et al.*, 1967, and Pedrós-Alió & Brock, 1983) have shown that an increase in attachment area stimulates bacterial activities and organic matter fixation (Murphy, 1936). Unlike Montmorillonite clays, Kaolinite and Illite are not toxic to planktonic and benthic animals, even at saturation (Robinson, 1957).

By the continuous rhythmic beat of their thoracic legs branchiopods (Cannon, 1933; Barlow & Asleigh, 1980) create a current which concentrates particles (clays, organic flocks). The ingested bacterial biomass may then be very high.

The distribution of *Triops granarius* inside one pond shows that the individuals do not uniformly occupy all the area. Young individuals are present near the edges of a pond, while older individuals tend to gather in the center (Fig. 16). *Tanymastigites jbiletica*, *Triops cancriformis mauritanicus*, and the Spinicaudata *Leptestheria mayeti* and *Cyzicus bucheti* had a similar distribution inside their ponds. Similar observations are made by Hamer & Appleton (1991) in temporary ponds of Natal. They distinguish two main groups, the 'edge' species and the 'central' species.

Therefore, when two species belonging to various bioclimatic groups live together in the same pond, both differences in growth-speed and spatial spreading may allow these species to occupy distinct micro-habitats.

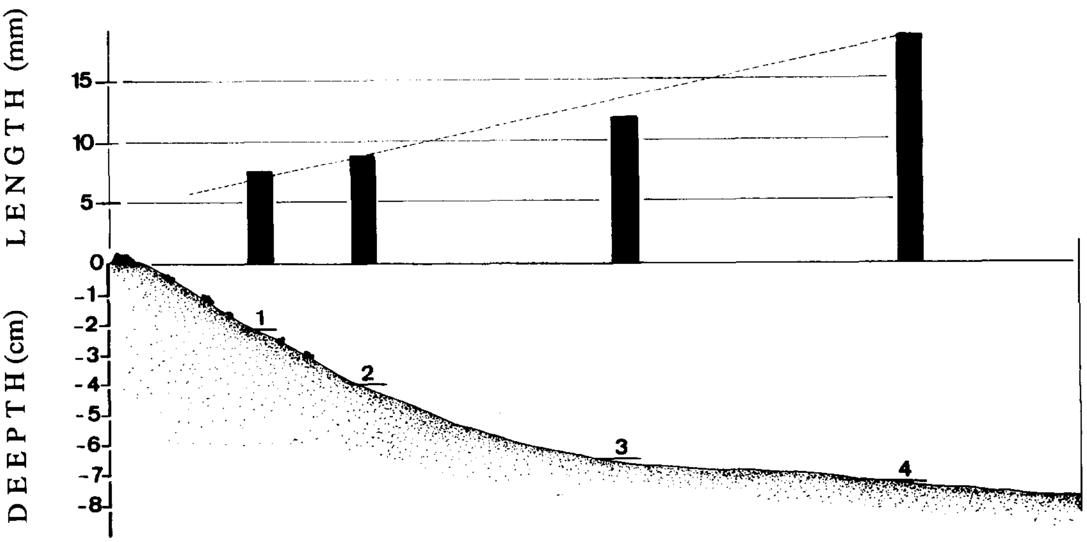

Fig. 16. Differential distribution of one cohort of *Triops granarius* as related to depth in a single pond. Black bars represent average length of cephalothoracic carapace (mm) and numbers (1, 2, 3 and 4) are four stations with different depths (cm) in the pond. The largest *Triops* gather in the deepest zones.

Conclusion

Explanations of the coexistence of otherwise allopatric species of euphyllopods are of four types:

1) Climatic and water characteristics favour the co-occurrence of naturally allopatric species. The concept of a climatic ecotone containing a patchwork of temporary ponds (with or without link with the oligohaline groundwater), some being more, others less temporary, and shallow or deep, may explain the presence of every species in the Chaouia plain. Large and deep ponds allow the biological cycle of more species to get completed than small, ephemeral ponds where only species with short cycles can reach maturity. The former may also develop heterogeneity across the water column. Consequently, their theorical richness should be greater (Table 1), shown also by Bengtsson (1989), and Fryer (1985). Co-occurrence is facilitated by importation of resting eggs by amphibians, birds and sheep (zoochory).

2) In turbid environment a diversity of food types, greatly paired to organic matter attached to clay, may allow a resource partitioning. Anostraca, Notostraca and Spinicaudata, although filtering species, do not exploit the same resources. While Anostraca are principaly microphagous filter-feeders, abstracting particles from suspension in the open water (Fryer, 1987), Notostraca are non-filtering, benthic omnivores, feeding on detritus (Fryer, 1987, 1988). Sometimes Notostraca can also be diggers and sifters of organic bottom material and feed on small animals like Tubificidae (Thiéry, 1987). Spinicaudata are also omnivorous (Royan, 1976) but sometimes obtain food by scraping the periphyton attached to vegetation. As the source of food is diversified (benthic bacterial flocks, planktonic ones, detritus, periphyton, small benthic prey...), an obvious result is that the resources exploited by co-occurring species of these different orders are distinct enough to permit this coexistence. As the nutritional resources based on argillotrophic system are most of the time in excess, this typical characteristic of temporary ponds of arid and semi-arid zones (Yaron, 1964; Brown, 1968; Daborn, 1975; Rzóska, 1984; Thiéry, 1987) seems a major factor regulating the life history of euphyllopods. All branchiopods of semi-arid and arid zones of Morocco could be considered as 'argillotrophobacterivorous' animals.

3) In coexisting Anostraca, Notostraca and Spinicaudata in Chaouia dayas, significant size differences exist between species. These data are close to these of Hutchinson (1951), Cole (1961), Hammer & Sawchyn (1968), Anderson & Fabris (1970) and Champeau (1970) on Copepod populations. As these authors suggest, size differences may result in a difference in food niche. Presumably, larger species will ingest larger food particles than smaller species.

4) Horizontal or vertical distribution of the species of the different orders within the pond seems to be of great importance. Our data on *Triops granarius* show that Notostraca of different length (but also, Anostraca and Spinicaudata) may be separated horizontally and vertically). The vertical and horizontal heterogeneity of the pond, mainly vegetation structure or any other environmental factor correlated with turbidity, like vertical thermic microstratification (Thiéry, 1987), favours the optimal occupation of microhabitats by all the syntopic species.

In consequence, following Mac Arthur & Wilson's (1967) theory, according to which interspecific competition increases local extinction rates and limits the regional richness of species in islands or restricted areas, we could predict that the lack or the low level of interspecies competition between Anostraca, Notostraca and Spinicaudata is an important factor favoring richness of species in pond communities. The results of Bengtsson (1989) on three allotopic *Daphnia* species reinforce this interpretation: while these species, using common food resources and of similar population dynamics, increase their extinction rate when they coexist in experimental conditions, they never occur together in the same habitat (natural rockpools or ponds in Sweden or Finland (trophical exclusion).

Our study suggests that the spatial and temporal distribution of co-occurring species in a temporary pond results, at each time, from differences in body size. Neonatal length and mass, length of juvenile growth period, feeding behaviour, intrinsic growth rates, are major factors in separating ecophases of all species. Occupying optimally all the available microhabitats, these sympatric species, (to the Chaouia plain geographical scale), must be considered as syntopic species in the larger dayas, or allotopic in smaller ones (in the sense of Rivas, 1964).

Although our results, based on natural observations, do not fully explain the coexistence of branchiopod species, they are a first step towards further research which should consider laboratory culture of animals, food types in relation to length, and behaviour under different conditions (vegetation, open water, depth, turbidity, temperature, light....).

Acknowledgements

I am grateful to Dr. H.J. Dumont for useful comments and advice.

References

Alonso, M., 1981. Las comunidades de entomostraceos de las lagunas de Villafafila (Zamora). Actas del Primer Congreso Espanol de Limnologia, Barcelona: 61–67.

Anderson, R. S. & G. L. Fabris, 1970. A new species of diaptomid copepod from Saskatchewan with notes on the crustacean community of the pond. Can. J. Zool. 48: 49–54.

Arruda, J. A., G. R. Marzolf & R. T. Faulk, 1983. The role of suspended sediments in the nutrition of zooplankton in turbid reservoirs. Ecology 64: 1225–1235.

Balfour-Browne, F., 1909. Note on the rediscovery of *Apus cancriformis* in Britain. Ann. Scot. nat. Hist. 1909: 118.

Barlow, D. I. & M. A. Sleigh, 1980. The propulsion and use of water currents for swimming and feeding in larval and adult *Artemia*. In G. Persoone, P. Sorgeloos, O. Roels & E. Jaspers (eds), The Brine shrimp *Artemia*. Vol. I. Morphology, Genetics, Radiobiology, Toxicology. Universa Press, Wetteren, Belgium: 61–73.

Belk, D., 1977. Zoogeography of the Arizona Fairy Shrimps (Crustacea: Anostraca). Arizona Academy of Science 12: 70–78.

Bengtsson, J., 1989. Interspecific competition increases local extinction rate in a metapopulation system. Nature 340: 713–715.

Berk, S. G., R. R. Colwell & E. B. Small, 1976. A study of feeding responses to bacterial prey by estuarine ciliates. Trans. Am. Micros. Soc. 95: 514–520.

Brown, G. W., 1968. Desert biology; Special topics on the physical and biological aspects of arid regions. Academic Press ed., 1: 635 pp.

Cannon, H., 1933. On the feeding mechanism of the Branchiopoda. With an appendix on the mouth parts of the Branchiopoda by Cannon H. & F. M. C. Leak. Phil. Trans. r. Soc. London B 222: 267–352.

Champeau, A., 1970. Recherches sur l'écologie et l'adaptation à la vie latente des Copépodes des eaux temporaires provençales et corses. Thèse Doctorat es Sciences, Université Aix-Marseille I, 360 pp.

Cole, G. A., 1961. Some calanoid copepods from Arizona with notes on congeneric occurrences of *Diaptomus* species. Limnol. Oceanogr. 6: 432–442.

Daborn, G. R., 1975. The argillotrophic lake system. Verh. Int. Ver. Limnol. 19: 580–588.

Daborn, G. R., 1976a. The life history of *Branchinecta mackini* Dexter (Crustacea, Anostraca) in an argillotrophic lake of Alberta. Can. J. Zool. 55: 161–168.

Daborn, G. R., 1976b. Physical and chemical features of a vernal temporary pond in Western Canada. Hydrobiologia 51: 33–38.

Daborn, G. R., 1978. Distribution and biology of some nearctic tundra pool phyllopods. Verh. Int. Ver. Limnol. 20: 2442–2451.

Daborn, G. R., 1979. Limb structure and sexual dimorphism in the Anostraca (Crustacea). Can. J. Zool. 57: 894–900.

Daday, E., 1910. Monographie systématique des Phyllopodes Anostracés. Ann. Sc. Nat. Zool. sér. 9, 9: 91–489.

Daday, E., 1914. Monographie systématique des phyllopodes Conchostracés. Ann. Sc. Nat. Zool. série 9, 20: 39–330.

Daday, E., 1923. Monographie systématique des phyllopodes Conchostracés. Ann. Sc. Nat. Zool. série 10, 6: 255–390.

Decksbach, N. K., 1924. Zür Verbreitung und Biologie der Apusidae in Russland. Russ. Hydrobiol. Zeits. 3: 143–155.

Dexter, R. W., 1946. Further studies on the life history and distribution of *Eubranchipus vernalis* (Verrill). Ohio J. Sci. 46: 31–44.

Dexter, R. W., 1953. Studies of North American fairy shrimps with the description of two new species. Am. Midl. Nat. 49: 751–771.

Dexter, R. W. & C. H. Kuehnle, 1951. Further studies on the fairy shrimp populations of North eastern Ohio. Ohio J. Sci. 51: 73–86.

Dimentman, C., 1981. The rainpool ecosystems of Israel: geographical distribution of freshwater Anostraca (Crustacea). Israel J. Zool. 30: 1–15.

Donald, D. B., 1971. Limnology and plankton of temporary ponds. Thesis, University of Calgary, Alberta, Canada. 135 pp.

Donald, D. B., 1983. Erratic occurrence of Anostracans in a temporary pond: colonization and extinction or adaptation to variations in annual weather? Can. J. Zool. 61: 1492–1498.

Felton, M., J. J. Cooney & W. F. Moore, 1967. A quantitative study of the bacteria of a temporary pond. J. gen. Microbiol. 47: 25–31.

Flössner, D., 1972. Krebstiere, Crustacea, Kiemen- und Blattfusser, Branchiopoda Fischlause, Branchiura. Tierwelt Deutschlands, Veb Gustav Fischer Verlag Jena Ed. 60: 1–501.

Fryer, G., 1985. Crustacean diversity in relation to the size of waterbodies: some facts and problems. Freshwat. Biol. 15: 347–361.

Fryer, G., 1987. A new classification of the branchiopod Crustacea. Zool. J. Linn. Soc. 91: 357–383.

Fryer, G., 1988. Studies on the functional morphology and biology of the Notostraca (Crustacea: Branchiopoda). Phil. Trans. r. Soc., London B, 321: 27–124.

Gauthier, H., 1928. Recherches sur la faune des eaux continentales de l'Algérie et de la Tunisie. Thèse, Lechevallier Ed., Paris, 419 pp. + 4 pl. h. t.

Gauthier, H., 1930. Sur la répartition en Algérie et en Tunisie de certains Entomostracés d'eau douce Européens (Branchipes et *Apus*). C. r. Assoc. fr. Avanc. Sci.: 572–575.

Geddes, M. C., 1981. The Brine shrimps *Artemia* and *Parartemia*. Comparative physiology and distribution in Australia. Hydrobiologia 81: 169–179.

Geddes, M. C., 1986. Understanding Zooplankton communities in Farm Dams: the importance of predation. In P. De Deckker & W. D. Williams (eds), Limnology in Australia, Monographiae Biologicae Vol. 61, Dr W. Junk, Dordrecht: 387–401.

Hamer, M. L. & C. C. Appleton, 1991. Life history adaptations of phyllopods in response to predators, vegetation and habitat duration in north-eastern Natal. In Belk, D., H.J. Dumont & N. Munuswamy (eds), Studies on Large Branchiopod Biology and Aquaculture. Developments in Hydrobiology 64. Kluwer Academic Publishers, Dordrecht: 105–116. Reprinted from Hydrobiologia 212.

Hammer, U. T. & W. W. Sawchyn, 1968. Seasonal succession and congeneric associations of *Diaptomus* spp. (Copepoda) in some Saskatchewan ponds. Limnol. Oceanogr. 13: 476–484.

Hebert, P. D. N., 1982. Competition in zooplankton communities. Ann. Zool. Fenn. 19: 349–356.

Horne, F., 1967. Effects of physical-chemical factors on the distribution and occurrence of some southeastern Wyoming Phyllopods. Ecology 48: 472–477.

Huggins, D. G., 1974. The sympatric occurrence of three species of Eubranchiopoda in Douglas County, Kansas. Southw. Nat. 20: 577–578.

Hutchinson, G. E., 1951. Copepodology for the Ornithologist. Ecology 32: 571–577.

Kutsch, H. G., 1978. Le pouvoir d'évaporation du climat marocain. Ministère de l'Agriculture et de la Réforme Agraire. Direction de la Recherche Agronomique ed., Rabat 378 pp.

Linder, F., 1941. Contributions to the morphology and taxonomy of the Branchiopoda Anostraca. Zoo. Bidr. Uppsala 20: 101–302 + 1 pl. h. t.

Linder, F., 1952. Contributions to the morphology and taxonomy of the Branchiopoda Notostraca, with special reference to the North American species. Proc. U. S. Nat. Mus. 102: 1–69.

Longhurst, A. R., 1955. A review of the Notostraca Bull. Brit. Mus. (Nat. Hist.) Zool. London 3: 1–57.

Mac Arthur, R. H. & E. O. Wilson, 1967. The theory of island biogeography. Princeton University Press ed.

Maeda-Martinez, A., 1991. Distribution of species of Anostraca, Notostraca, Spinicaudata, and Laevicaudata in Mexico. In Belk, D., H.J. Dumont & N. Munuswamy (eds), Studies on Large Branchiopod Biology and Aquaculture. Developments in Hydrobiology 64. Kluwer Academic Publishers, Dordrecht: 209–219. Reprinted from Hydrobiologia 212.

Makarewicz, J. C. & G. E. Likens, 1975. Niche analysis of a zooplankton community. Science 190: 1000–1003.

Marzolf, G. R. & J. A. Osborne, 1972. Primary production in a Great Plains reservoir. Verh. int. Ver. Limnol.: 18: 126–133.

Mathias, P., 1937. Biologie des Crustacés Phyllopodes. Act. Sci. Ind. 447, Hermann Paris, 107 pp.

Mattox, N. T., 1957. A new estheriid conchostracan with a review of other North American forms. Am. Midl. Nat. 58: 367–377.

Maynard, S. S. & S. V. Romney, 1975. The occurrence of four new Anostracan (Crustacea) Phyllopod in Utah, multispecies records, and some notes on their ecology. Utah Acad. Proc. 52: 6–11.

Melack, J. M., 1985. Interactions of detrital particulates and plankton. Hydrobiologia 125: 209–220.

Mertens, J., N. Munuswamy & H. J. Dumont, 1991. The filtration apparatus of Anostraca (Crustacea): species specific setulation in the genus *Streptocephalus*), In Belk, D., H.J. Dumont & N. Munuswamy (eds), Studies on Large Branchiopod Biology and Aquaculture. Developments in Hydrobiology 64. Kluwer Academic Publishers, Dordrecht: 187–193. Reprinted from Hydrobiologia 212.

Moore, W. G., 1963. Some interspecies relationships in Anostraca populations of certain Louisiana ponds. Ecology 44: 131–139.

Moore, W. G., 1970. Limnological studies of temporary ponds in Southeastern Louisiana. Southwest. Nat. 15: 83–110.

Mozley, A., 1932. A biological study of a temporary pond in western Canada. Am. Nat. 66: 235–249.

Mura, G., 1985. Preliminary report on the sympatric occurrence of two species of Fairy shrimps (Crustacea, Anostraca) in some temporary ponds from Italy. Riv. Idrobiol. 24: 73–82.

Mura, G., 1987. Occurrence of *Artemia* in solar saltworks and coastal brine ponds in Sardinia, Italy. J. Crust. Biol. 7: 697–703.

Mura, G. & V. Cottarelli, 1984. Gli Anostraci delle acque temporanee di Castel Porziano (Roma). Riv. Idrobiol. 23: 165–171.

Murphy, H. F., 1936. The role of Kaolinite in phosphate fixation. Hilgardie 12: 343–382.

Pedrós-Alió, C. & T. D. Brock, 1983. The importance of attachment to particles for planktonic bacteria. Arch. Hydrobiol. 98: 354–379.

Proctor, V. W., E. R. Malone & V. L. De Vlaming, 1967. Dispersal of aquatic organisms: viability of disseminules recovered from the intestinal tract of captive killdeer. Ecology 48: 672–676.

Prophet, C. W., 1962. Ecology and reproduction of five species of Anostraca in Oklahoma. Dissert. Abs. USA 23: 1129.

Prophet, C. W., 1963. Physical-chemical characteristics of habitats and seasonal occurrence of some Anostraca in Oklahoma and Kansas. Ecology 44: 798–801.

Retallack, J. T. & H. F. Clifford, 1980. Periodicity of Crustaceans in a saline Prairie Stream of Alberta, Canada. Am. Midl. Nat. 103: 123–132.

Rivas, L. R., 1964. A reinterpretation of the concepts 'Sympatric' and 'Allopatric' with proposal of the additional terms 'Syntopic' and 'Allotopic'. Syst. Zool. 13: 42–44.

Robinson, M., 1957. The effects of suspended materials on the reproductive rate of *Daphnia magna*. Pub. Inst. mar. Sci. 4: 265–277.

Royan, J. P., 1976. Studies on the gut contents of *Leptestheriella maduraiensis* (Conchostraca: Branchiopoda) Nayar and Nair. Hydrobiologia 51: 209–212.

Ruhard, J. P., 1975. Chaouia et plaine de Berrechid. In Ressources en eau du Maroc. Tome 2. Plaines et bassin du Maroc atlantique. Notes et Mémoires du service géologique n° 231. Service Géologique du Maroc, Rabat, pp. 185–221.

Rzóska, J., 1961. Observations on tropical rainpools and general remarks on temporary waters. Hydrobiologia 17: 265–286.

Rzóska, J., 1984. Temporary and other waters. In L. L. Cloudsley-Thompson (ed.), Key environments: Sahara desert, Pergamon Press, pp. 105–114.

Sars, G. O., 1896. Phyllocarida and Phyllopoda. In Fauna Norvegiae Vol. I. 140 pp.

Saunders, G. W., K. W. Cummins, D. Z. Gak, E. Pieczynska, V. Straskrabova & R. G. Wetzel, 1980. Organic matter and decomposers. In E. D. Le Cren & R. H. Lowe-McConnell (eds), The functioning of freshwater ecosystems. I. B. P. 22, Cambridge University Press pp. 341–392.

Sauvage, C., 1963. Etages bioclimatiques. In Atlas du Maroc. Comité National de Géographie du Maroc, Section II. Physique du Globe et Météorologie: 44 pp.

Simon, E., 1886. Etude sur les Crustacés du sous Ordre des Phyllopodes. Ann. Soc. ent. Fr., S6, 6: 393–460.

Stern, E. M. & W. B. Stickle, 1978. Effects of turbidity and suspended material in aquatic environments litterature review. Technical Report D-78-21, United States Army Corps of Engineers Waterways Experiment Station, Vicksburg, Mississippi, USA.

Straskraba, M., 1966. Taxonomical studies on Czechoslovak Conchostraca III. Family Leptestheriidae; with some remarks on the variability and distribution of Conchostraca and a key to the Middle-European species. Hydrobiologia 27: 571–589.

Tezuka, Y., 1974. An experimental study on the food chain among Bacteria, *Paramecium* and *Daphnia*. Int. Revue ges. Hydrobiol. 59: 31–37.

Thiéry, A., 1983. Un cas de gynandromorphisme naturel chez *Chirocephalus diaphanus* Prévost (Crustacea, Anostraca). Riv. Idrobiol. 22: 84–87.

Thiéry, A., 1986. Les Crustacés Branchiopodes Anostracés, Notostracés et Conchostracés du Maroc occidental: I. Inventaire et répartition. Bull. Soc. Hist. nat. Toulouse 122: 145–155.

Thiéry, A. & C. Garcin, 1986. Les Crustacés Branchiopodes (Anostraca, Notostraca, Conchostraca) du Maroc occidental. II: caractérisation de la structure du peuplement par l'analyse factorielle des correspondances. 1st Colloque interuniversitaire Maroco-français, Fes, 5 pp. (unpublished).

Thiéry, A., 1987. Les crustacés Branchiopodes Anostraca, Notostraca & Conchostraca des milieux limniques temporaires (Dayas) au Maroc. Taxonomie, Biogéographie, Ecologie. Thèse Doctorat es Sciences, Université Aix-Marseille III, 405 pp.

Thiéry, A., 1988a. *Maghrebestheria maroccana* n. Gen., n. sp., nouveau représentant des Leptestheriidae au Maroc (Conchostraca). Crustaceana 54: 43–56.

Thiéry, A., 1988b. *Triops* Schrank, 1903 et *Lepidurus* Leach, 1816, Crustaces Branchiopodes Notostracés. In Documents pour un Atlas Zoogéographique du Languedoc-Roussillon, Univeristé Paul Valéry, Montpellier ed., n° 33 pp. 1–4.

Thiéry, A. & D. Pont, 1987. *Eoleptestheria ticinensis* (Balsamo-Crivelli, 1859). Conchostracé nouveau pour la faune de France (Crustacea, Branchiopoda). Vie Milieu 37: 115–121.

Walter, G. M., 1970. Limnological studies of temporary ponds in southeastern Louisiana. Southwest. Nat. 15: 83–110.

Williams, W. D., 1968. The distribution of *Triops* and *Lepidurus* (Branchiopoda) in Australia. Crustaceana 14: 119–126.

Williams, W. D., 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. Hydrobiologia 125: 85–110.

Wootton, D. M. & N. T. Mattox, 1958. Notes on the distribution of conchostracans in California. Bull. South. Calif. Acad. Sci. 57: 122–124.

Yaron, Z., 1964. Notes on the ecology and Entomostracan fauna of temporary rainpools of Israel. Hydrobiologia 24: 489–513.