THE ECOLOGY OF *DAPHNIA CHEVREUXI* RICHARD
IN NORTHEAST ALGERIA (CRUSTACEA: ANOMOPODA)

Abstract

Seasonal dynamics and life history traits of one population of the cladoceran *Daphnia chevreuxi* Richard were monitored under field and laboratory conditions. Temperature dependent demographic traits (birth, size, longevity and development rates) were followed throughout the year. The influence of predation, through the use of fish kairomones, on life history traits has been investigated and the main response to fish chemicals has been shown to be a decrease in size at first reproduction (S.F.R.).

Key Words: Daphnia, population dynamics, life history, fish predation, Algeria.

Résumé

La dynamique saisonnière et les caractères de l'histoire de vie d'une population du cladocère *Daphnia chevreuxi* Richard ont été suivis au laboratoire et dans des conditions naturelles. Les traits démographiques qui dépendent de la température (naissance, taille, longévité et taux de développement) ont été suivis sur une année. L'influence de la prédation, à travers l'utilisation de kairomones de poissons, sur les caractères de l'histoire de vie a été explorée et la réponse majeure de *D. chevreuxi* à la présence de poissons, a été une diminution de la taille à la première reproduction (SFR).

Mots clés: Daphnia, dynamique des populations, histoire de vie, prédation de poissons, Algérie.

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ملخص

تمت دراسة الديناميكية الفصلية وخصائص دورة حياة عشيرة براغيث الماء للنوع *Daphnia chevreuxi* Richard في ظروف المخبر وتحت الظروف الطبيعية.

اتبعت الخصائص الديموغرافية التي تعتمد على درجة الحرارة (الولادة، الطول، العمر، سرعة النمو) لمدة سنة كاملة كما تمت دراسة تأثير الافتراس من الماد المفرزة Kairomones على خصائص دورة الحياة و كانت الاستجابة لوجود السمك بتصغير الطول عند أول تكاثر.

الكلمات المفتاحية: *Daphnia،* دورة الحياة — الافتراس (الأسماك)- ديناميكية العشيرات- الجزائر.

Despite taxonomical difficulties, the widespread and cosmopolitan genus *Daphnia* Müller, 1785 has been the focus of many studies [1, 2], an acknowledgement of its critical role in food webs in both brackish and freshwater ecosystems. Its size and ease of breeding have made it a good model to elucidate complex ecological problems like competition, predation, life history strategy, community structure and genetic differentiation [3-10].

Problems concerning the geographic variation in life histories remain central to life history theory. Indeed, in spite of the enormous body of knowledge accumulated, the ecology of several species occurring outside the temperate regions and the variability of distinct populations of a single species across a latitudinal gradient have been poorly documented. More data on the life history of subtropical and tropical species of *Daphnia* are needed [11] before we can understand how species respond to their environment and explain the « case of the vanishing *Daphnia* » in the tropics [12]. In this respect, data on the ecology of North African species of *Daphnia* and in particular those of N.E. Algeria, where a subtropical climate prevails [13, 14], have more than a local significance.

Four species of *Daphnia* are known to occur in Northeast Algeria : *D. chevreuxi* Richard 1896, *D. longispina* (O.F. Müller, 1785), *D. magna* Straus, 1820, and *D. pulex* Leydig, 1758 [15-17], but the taxonomical status of the local populations of *D. pulex* deserves clarification. We have monitored one population of the Mediterranean species *Daphnia chevreuxi* Richard inhabiting a temporary pool and compared our observations with life history traits displayed by clones from the same population reared under laboratory conditions. This work is part of a larger comparative study of life history characteristics of local species of *Daphnia*.

METHODS

The study was carried out at the Laboratoire de Recherche des Zones Humides (University of Annaba, Algeria) between December 1995 and August 1996. Field data were collected from a seasonal pool, Mare aux Frênes (36°51'652 N, 8°15'065 E) of about 0.1ha. This freshwater depression is situated amidst an Ash (*Fraxinus excelcior* L.) plantation and its substrate is clayish with water depth rarely exceeding 1m. Water conductivity ranged between 270 μS cm^{-1} and 500 μS cm^{-1}. The habitat was devoid of fish but housed newts *Pleurodeles poireti* (Gervais, 1835) and a small number of aquatic insects. Crustacean were abundant and they included large branchiopods like *Chirocephalus diaphanus* Prévost, 1803 and *Lepidurus apus lubbocki* (Brauer, 1873). Another daphniid, *Daphnia pulex,* has sporadically been recorded within the site.

Irregularity characterizes patterns of rainfall in North Africa and in 1997, rainfall came late in the season and the amount of rain was moderate. Mare aux Frênes filled up a few days before the first sampling date (January 13) and dried up in mid-April. Exceptionnally, it refilled in May with water that lasted for another month.

Zooplankton was sampled with a plankton net (mesh size = 0.05 mm) at weekly intervals between January 13 and March 31, 1997. The net was trailed for a fixed distance of 10 m and a volume of 100 ml was collected and fixed in 5% formaldehyde. Data was obtained from a standard volume of 25 ml.

Laboratory cultures of *D. cheveuxi* were initiated with females obtained from the study pond. Experiments were carried out using offspring of females previously acclimated to laboratory conditions for several generations. All laboratory animals were cultured individually in aged tap water at room temperature in 75 ml tubes and were fed commercial yeast every other day and daily extracts of *Beta vulgaris maritima*. The extract was prepared by boiling 1 kg of *Beta vulgaris maritima*, homogeneizing it in a mixer and filtering it. At least ten replicates were monitored throughout the study period. Room temperature was measured daily at 12 am.

Body length was measured, under a microscope, to the nearest 0.05mm from the top of the head to the base of the tail spine. The following life history traits were measured : age at maturity, interval between clutches, life span (longevity in days); number of offspring in the first and subsequent clutches; number of clutches; total number of offspring produced; size of the first adult instar and of subsequent instars; size of neonates from the first clutch.

In a separate and parallel experiment, clones from Mare aux Frênes were raised in water coming from aquaria containing the mosquitofish *Gambusia affinis* (Baird & Girard, 1853) at a density of 1fish/l. Measures of life history characteristics were carried out under an identical environment as controls.

SFR (size at first reproduction) and SN (size of neonates) were compared between females raised in water with fish kairomones and females used as controls using one-way and two-way ANOVA's [19]. Tukey tests were applied to determine whether differences in means are significantly different. Spearman Rank Correlation Coefficients were calculated to identify relationships between variables (temperature, life history traits).

RESULTS

Life table experiment

Age at maturity and clutch interval declined when room temperature approached and overshot 15°C (Fig.1). It took females 5 to 7 days to mature in spring and summer while this process lasted between 13 and 17 days in winter. Longevity displayed two peaks (end of February and June). The number of females surviving decreased exponentially with time (Fig.2). Some individuals were observed to survive for up to 51 days.

Size of neonates and size at first reproduction were also negatively correlated with temperature (SN: r= -0.66 (N=72), P<0.001; SFR: r= -0.93 (N=72), P<0.001) (Fig.3). A drop in SFR was initiated after temperature rose above ~15°C. The size of females at maturity varied between 1.1 mm and 3.0 mm, with the largest size attaining 3.65mm.

Brood size tended to decrease with increasing temperature, and fluctuated around 7 neonates per clutch in the temperature range of 12-15°C (Fig.4). The average number of broods per female increased with temperature, probably because brood interval dropped. Most females produced less than 30 offspring (Fig.5) and while the maximum number of broods/female was twelve (Fig.6), most females (>80%) had a number of broods between 0 and 6. There was an increase in the size of the brood with increasing brood number for the first three clutches (Fig.7). The size of neonates from the first clutch were smaller (0.53 ± 0.23 mm) than that of neonates of subsequent clutches (0.55 ± 0.18 mm and 0.67 ± 0.31 mm, for the second and eighth clutch, respectively). The difference in the means of the first three clutches, where N=40 in each case, is highly significant ($F_{2, 127}$ = 12.417, P<0.001). Tukey tests confirmed that the first clutch is significantly smaller than the subsequent two clutches (P<0.001).

It is of interest to note that the number of young produced per brood seemed to fluctuate throughout life but with no apparent trend (Fig.8). The largest number of offspring produced in a single clutch totalled 25. Two peaks of male production were recorded : a minor one at the end of February and a major one in the first half of May (Fig.9).

The effect of fish kairomones

Size at first reproduction was significantly smaller for females exposed to fish kairomones (Table 1). Size of neonates (positively correlated with S.F.R. with r = 0.71 (N=82), P<0.001) was not affected by fish kairomones (Table 2), but showed a fish x temperature effect (Table 2; Fig.10).

Results of the two-way ANOVAs show a highly significant temperature x fish interaction effect on both SFR and size of neonates (Tables 1 & 2).

Population dynamics in the field

The first specimens of *Daphnia* were collected on January 27. Almost half of the females were ovigerous (Fig.11). The first ephippial females appeared synchro-
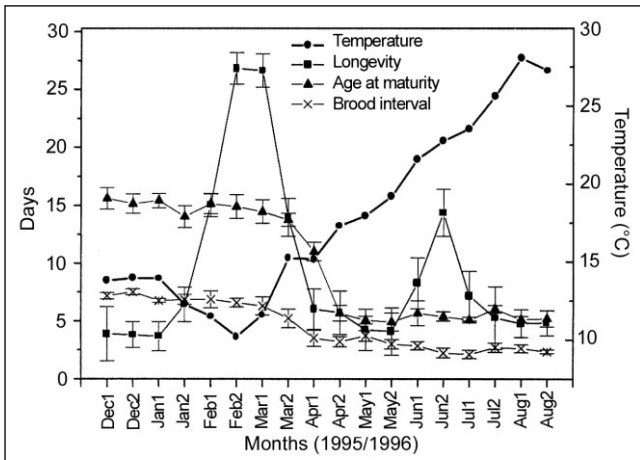
Figure 1: Changes in temperature and in seasonal mean longevity, age at maturity, brood interval of reared females during the course of the study. Changes are shown half-monthly. Error bars, when present, indicate one standard deviation.
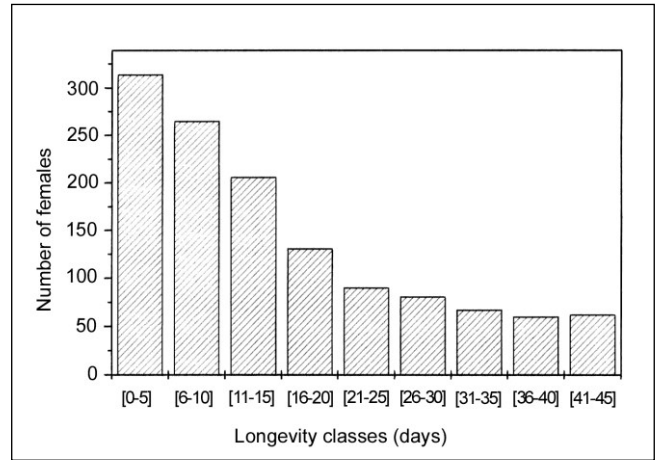

Figure 2: Distribution of longevity classes among reared females.
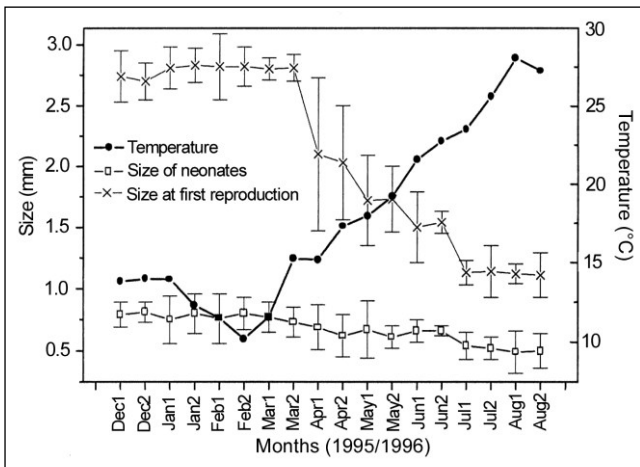

Figure 3: Changes in mean water temperature, size of neonates (S.N.) and size at first reproduction (S.F.R.) during the course of the study.
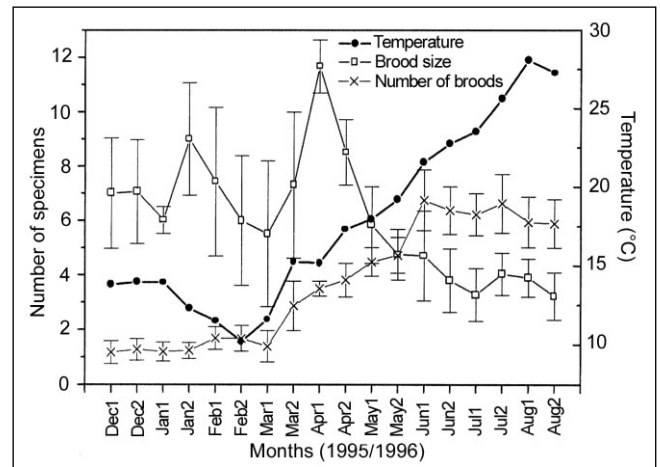

Figure 4: Changes in mean water temperature, number of broods (N.B.) and brood size (B.S.) of reared females during the course of the study.
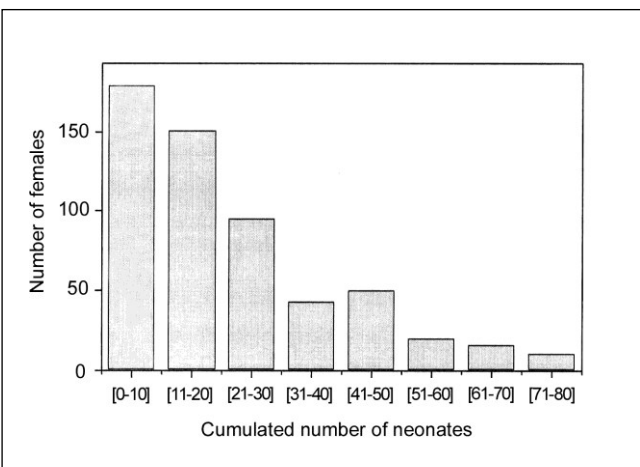

Figure 5: Frequency distribution of females according to total number of neonates produced.
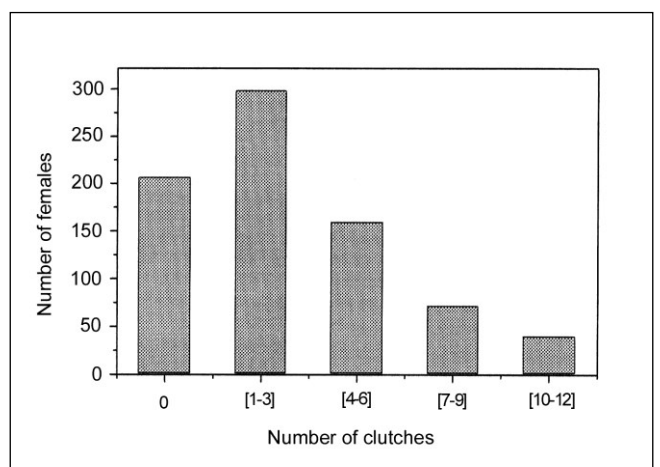

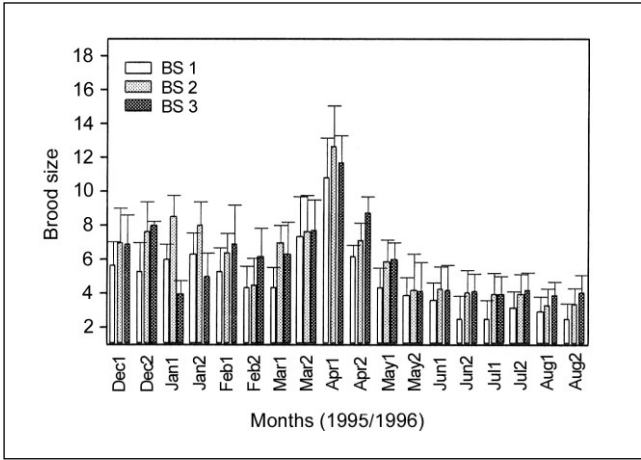**Figure 6:** Distribution of the number of clutches among reared females.

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Figure 7: Seasonal changes in the clutch size of the first three clutches of reared females. BS stands for brood size.
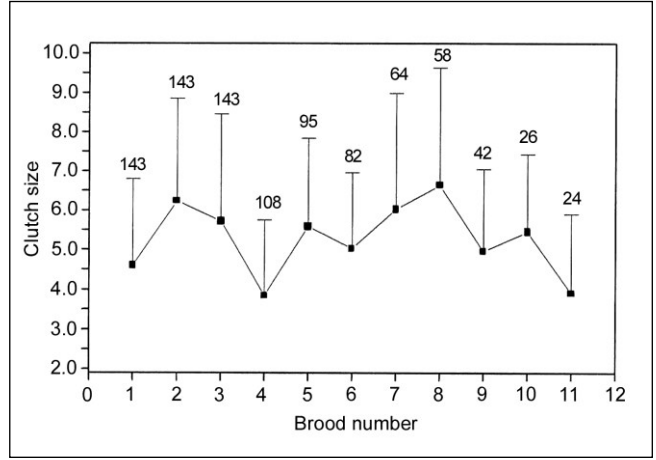
Figure 8: Variation in clutch size throughout the life cycle of reared females.
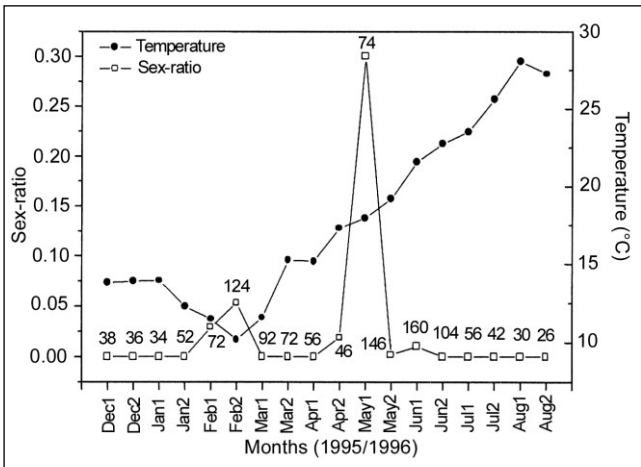
Figure 9: Seasonal variation in the sex ratio (fraction of males) of neonates produced by reared females.
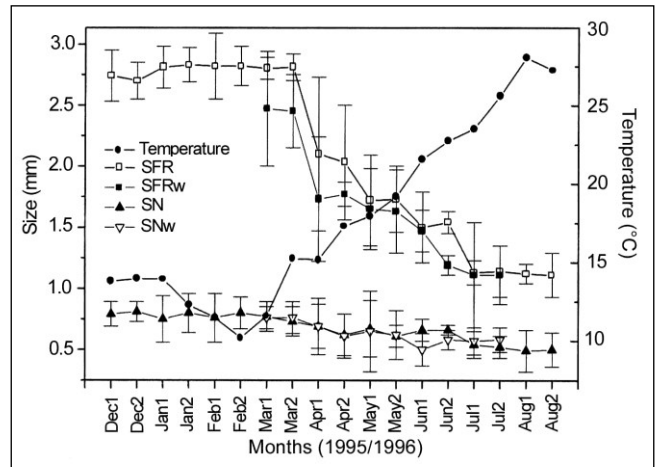
Figure 10: Seasonal changes in temperature, SFR and size of the neonates for controls (SN) and for females exposed to fish kairomones (SFRw, SNw).

Figure 11: Population dynamics of *D. chevreuxi* in Mare aux Frênes: seasonal changes in the total number of specimens, the number of ovigerous females, ephippial females and males.

Figure 12: Population dynamics of *D. chevreuxi* in Mare aux Frênes: seasonal changes in brood size.

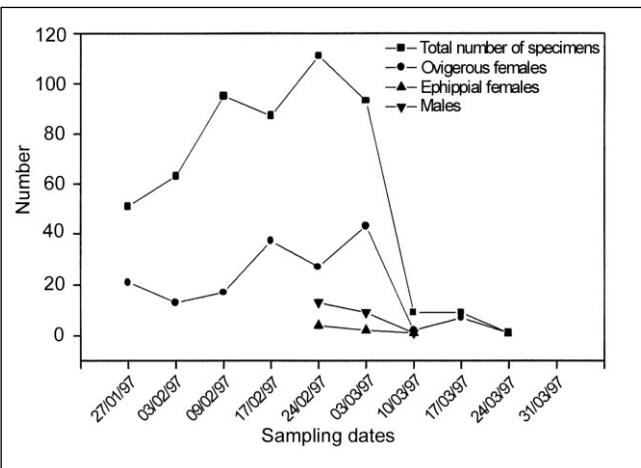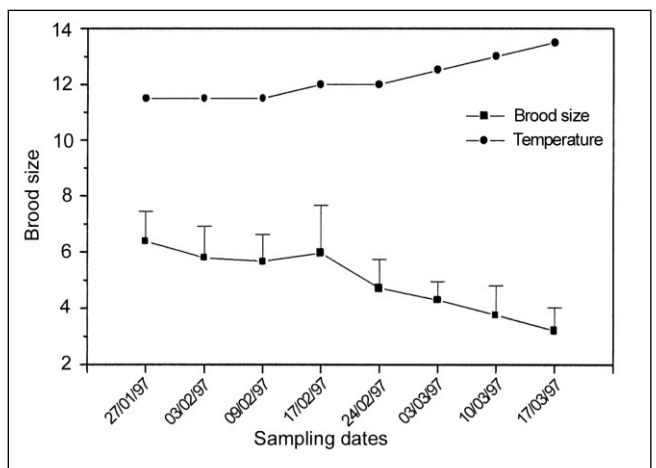nously with the first males when the density of the population was at its highest (end of February). The population peaked then before crashing and disappearing in March. The maximum recorded brood size was 13 and the average brood size declined steadily with time (Fig. 12). The mean brood size recorded in the field was 4.97 ± 1.04 (N=150) compared to a mean brood size of 6.09± 1.53 (N=738) when recorded under laboratory conditions.

$[R^2 = 0.672]$

Source of variation	df	Sum of squares	F	P
Fish	1	1.190	12.791	< 0.01
Temperature	3	27.010	96.756	< 0.01
Fish *Temp.	3	0.815	2.920	0.036
Error	152	14.144		

Table 1: Results from two-way ANOVA testing for the effects of fish kairomones on SFR.

$[R^2 = 0.582]$

Source of variation	df	Sum of squares	F	P
Fish	1	0.002	0.250	0.618
Temperature	3	1.245	66.348	<0.001
Fish *Temp.	3	0.078	4.168	0.007
Error	152	0.951		

Table 2: Results from two-way ANOVA testing for the effects of fish kairomones on size of the neonates.

DISCUSSION

Within Northeast Algeria, most waterbodies are seasonal, and *Daphnia chevreuxi* has only been found in such seasonal habitats [16, 17]. During the study period, the aquatic phase of Mare aux Frênes lasted roughly five months. Like the rest of the aquatic fauna, *D. chevreuxi* is adapted to the local environmental conditions characterized by high fluctuations of temperature and water level and the studied population which reproduces by cyclical parthenogenesis during the wet phase is regularly refounded anew from sexual eggs after the dry phase.

Several workers [11, 20, 21] have shown the importance of temperature and food on the life history of *Daphnia*. In response to mild food limitation, *Daphnia* reduce growth and reproduction and as food shortage becomes acute, they produce resistant diapausing eggs [22-24]. The importance of temperature is also highlighted by seasonal changes in the clonal structure of a natural population [25]. While our study does not address food as a factor, our results confirm the influence of temperature on several life history traits of *D. chevreuxi* (clutch size, SN, age at maturity and SFR).

Species of *Daphnia* have an optimal temperature range [26, 27] although intraspecific thermal differentiation among seasonal clones has been described [28]. For the studied population, beyond a threshold of around 15°C, we note a shift in the pattern of energy allocation marked by a clear trade-off [29, 30]: shorter clutch intervals resulting in an increase of the number of broods per female were coupled with smaller brood and neonate sizes as well as shorter age and size at maturity. Egg development time is temperature-dependent and has been shown to be positively correlated with the size of eggs and neonates [31].

Several of these features : shorter maturation periods, smaller sizes of females and clutch sizes are sequentially and intrically bound. Brood size has been reported to be temperature-independent but this may be true for arctic species and for the range of temperature tested [6, 32] as fecundity differences between clones under natural conditions has been reported (Carvalho, 1985 in [28]). Another trait, longevity, is predicted to be temperature-dependent but the pattern displayed by *D. chevreuxi* is difficult to interpret as the smaller peak (Fig. 1) is achieved when in the field the species is normally in a dormant state as sexual eggs, enclosed in ephippia. Survivorship is known to decrease at increasing temperature for several daphniids [11]. A puzzling fact is the pattern of egg production throughout life which differs markedly from that of *Daphnia magna* [33]. However, data from Green [33] and other workers [34-37] seem to suggest that there are significant differences in this pattern for geographically distinct populations.

Brood size obtained from females in the field (Fig. 12) responded to temperature in a similar way to that of cultured females. There may be a high metabolic cost linked to high temperatures which may act in a direct (food disponibility) or indirect ways (predation, competition). However, caution is needed when comparing between field and laboratory results and among the many factors which may impinge on life history traits, density has been shown to affect the age at which females reproduce [38].

The phenology displayed by Italian populations of *D. chevreuxi* [39] is similar to their Algerian counterparts. Crosetti & Margaritora [39] also report that males appeared at the end of February with concommitant production of ephippia. The Algerian population, however, crashed by late March as opposed to late April.

What are the proximal factors prompting the disappearance of *Daphnia* before the onset of drought, while clones of the same population can be kept throughout the year in the laboratory? "Bottom up" and "Top down" controls have been shown to influence Daphnia's abundance [40] and in particular biotic factors like predation and food limitation have both been associated with the decline of cladoceran populations [41, 42]. In the region, predation is noticeably higher, from early spring, with recruitment of fish, especially *Gambusia affinis* which are able to invade a large number of temporary ponds during episodic floodings, and cohorts of insect larvae (notonectidae, odonata, *Chaoborus*, *Cybister*). All four insect taxa are important predators of daphniids [43-45]. However, the production of males and ephippial females is rather suggestive of food shortage [22-24] and the fact that the population size declined immediatly after its density peaked may well be indicative of environmental deterioration (food limitation). Although data on freshwater algae have not been monitored, the disappearance of *Daphnia* coincided also with the expansion of filamentous algae.

During the study period, the daphniid population has not been in contact with fish but it is likely that it had in the past. Some studies [46-49] have shown that *Daphnia* clones tend to differ in their response to the presence of chemicals released by predators depending on whether these were invertebrates (*Notonecta*, *Chaoborus*) or vertebrates (fish) and whether or not the prey originated from populations exposed to these predators. *D. chevreuxi,* in general, do not coexist with fish but occasionally most populations are exposed to fish. Under some circumstances, involving both specific behaviour and the availability of refuges, certain species of *Daphnia* are able to coexiste with fish [50]. There is also a range of responses to the presence of predators and these changes can be morphological [51-53], behavioural [54] or involve life history strategies [47, 55].

CONCLUSION

The response to fish kairomones in the *Daphnia* studied was mediated through a reduced size of neonates and S.F.R. The adaptive significance of this answer is in agreement with life history theory which predicts that in the event of reduced adult survival, natural selection will select for earlier maturation (smaller individuals) and increased reproductive effort [30]. Following Brooks & Dodson [56], many workers have gathered more data in support of the size-selection hypothesis [57-60].

Our results indicate that both temperature (through seasonal variability) and size-selective predation are able to exert a significant influence on *Daphnia* populations by shifting the size structure of populations.

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