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# The effects of ploidy level on the thermal distributions of brine shrimp *Artemia parthenogenetica* and its ecological implications

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The responses to temperature change of sympatric diploid and pentaploid brine shrimp *Artemia parthenogenetica* were studied. Pentaploids survive better at extremes of both cold (0°C) and heat (37.5°C). When placed in a thermal gradient ranging from 12.5 to 35.1°C, diploids generally located at temperatures above 19°C while pentaploids were more evently distributed along the gradient. These results suggest that pentaploids may be better suited to temperature extremes than sympatric diploids. Our study provides the first experimental evidence in animals of differential temperature use by conspecific sympatric diploid and polyploid organisms.

Our literature review indicates that polyploid *Artemia* are found with greater frequency in low and high latitudes (i.e. $<25$°N and $>40$°N) than in temperate regions (latitudes 35–40°N). The ecological implications of the physiological and behavioural differences between diploids and pentaploids are discussed as they relate to the latitudinal distributions of sexual and parthenogenetic *Artemia* in the Old World.

**Keywords:** *Artemia*, diploid, polyploid, thermal distributions.

## Introduction

Levin (1983) hypothesized that polyploidy in plants may '... greatly alter the cytological, biochemical, physiological, and developmental character of organisms ... which could suit them to conditions which are beyond the limits of their diploid progenitors'. It has been recognized in many plant species and several animal species that polyploids do tend to be found at high latitudes, high altitudes or at the boundary of a species' distributions (Bierzychudek, 1985; Suomalainen *et al.*, 1987; Beaton & Hebert, 1988). Coexistence of conspecific diploids and polyploids has been reported in many plant species (reviewed by Lumaret, 1988) and several animal species (Goldschmidt, 1952; Schultz, 1982; Suomalainen *et al.*, 1987; Beaton & Hebert, 1988). Despite this, the dynamics of the shift from the coexistence of diploids and polyploids in some habitats, to the exclusion of one cytotype by the other in other habitats, has received little attention.

It has also been noted, both in plants and in animals, that parthenogenetic forms have different geographical distributions from sexual relatives, and they generally tend to be found at higher latitudes and altitudes (reviewed by Suomalainen *et al.*, 1987). This distribution pattern of parthenogens has been termed 'geographic parthenogenesis' (Vandel, 1928; reviewed by Suomalainen *et al.*, 1987). The cause of geographic parthenogenesis has been debated (reviewed by Bierzychidet, 1985). Most recent authors (Glesener & Tilman, 1978; Bell, 1982; Browne & MacDonald, 1982) attribute the geographical parthenogenic trend to direct selection for breeding systems. That is, an asexual reproduction mode is selected for in situations when physical, rather than biotic, factors are important, these situations usually correspond to habitats in high altitudes, high elevations or arid regions. Sexual forms with the potential for rapid genetic change are dominant in situations when biological interactions are important.

Correlated with parthenogenesis is the occurrence of polyploidy (Bierzychudek, 1985; Suomalainen *et al.*, 1987). Suomalainen (1962; 1969) argues that geographical parthenogenesis arises indirectly, as a result of selection for elevated ploidy level in some habitats.

This hypothesis has gained some support (Bierzychudek, 1985; Beaton & Hebert, 1988). More knowledge of the physiological differences and distribution patterns of diploids and polyploids are necessary in order to evaluate Suomalainen's hypothesis and the role of polyploidy in animal evolution.

It has been suggested that the increased frequency of polyploids in many animal species at higher latitudes is due to their greater tolerance of cold stress and better colonizing abilities (reviewed by Suomalainen *et al.*, 1987). However, the evidence to support the distributions of diploids and polyploids and their temperature requirements, is tenuous. First, as most comparisons involve geographically isolated populations, the variability in tolerance may reflect environmental differences to which the populations have become adapted. Few comparisons have been made of physiological differences between sympatric diploid and polyploid populations. The best studied case is that of the unisexual fish *Poeciliopsis monacha-lucida* (Schultz, 1982). In this system, compared with sympatric diploids, triploids have a higher tolerance of cold, but a lower tolerance of high temperature. Furthermore, neither the observed high survival of polyploids at low temperatures under laboratory conditions nor the existing distribution patterns of diploids and polyploids necessarily indicate that polyploids have a greater colonizing ability than sympatric diploids. It is also unclear whether the more northerly distributions of polyploids, in relation to diploids, result from different temperature requirements of the two cytotypes. In order to understand the role of polyploidy in animal evolution, it is essential to know both if, and how, polyploids are preadapted to stressful temperatures than sympatric conspecific diploids.

Previous studies of temperature optima of aquatic invertebrates have concentrated on examining the life-history characteristics under a series of different temperatures (King, 1972; Vanhaecke *et al.*, 1984; Browne *et al.*, 1988). However, the physiologically optimal temperatures of an ectotherm are not necessarily ecologically optimum temperatures (Huey & Slatkin, 1976; Huey & Bennett, 1987). That is, optimal for growth and reproduction may differ from temperatures chosen by the animal when confronted with a variety of possible choices. This assumes that animals in laboratory situations choose ecologically optimal temperatures. One approach to studying the selected temperatures of ectotherms is to permit them to choose their locations in an environment with a gradient of temperatures.

Brine shrimp of the genus *Artemia* (Branchiopoda, Anostraca) occur on every continent except Antarctica (Browne & MacDonald, 1982). Some species reproduce sexually, others by obligate parthenogenesis. Cyclic parthenogenesis has never been found. Members of the genes *Artemia* are usually the competitive dominant animals in inland salt lakes and solar salt works where high salinity excludes most predators (Browne, 1988). In the Old World, the genus *Artemia* consists of a number of sibling species that can be divided into sexual diploid groups (*A. tunisiana* and *A. urmiana*) and obligate parthenogenetic species (*A. parthenogenetica*) composed of both diploid and polyploid individuals (Browne & Bowen, 1990; Lenz & Browne, 1990). Polyploidy has only been found in parthenogenetic *Artemia*. In the western hemisphere, *Artemia* reproduced solely by sexual reproduction, while in the Old World, *A. parthenogenetica* is the most common form and sexual forms are found in relatively fewer habitats (Browne & MacDonald, 1982). Parthenogenetic and sexual forms, as well as individuals of different ploidy levels, have been reported to co-occur in many *Artemia* populations. Our preliminary literature review (see results) revealed that polyploid *Artemia* are found with increasing frequency in the low and high latitudes (i.e. $<25°N$ and $>40°N$) in the northern hemisphere of the Old World, which may correspond to high and low temperature habitats. This led us to wonder if diploid and polyploid *Artemia* have different temperature requirements.

Diploid and pentaploid *A. parthenogenetica* are sympatric in the north-east salterns (between latitudes of 35–41°N) of the People's Republic of China, with diploids as the most common form (Wang, 1986). Pentaploids from this population have lower fecundity and tolerance of semi-starvation conditions than sympatric diploids (L. Zhang & C. E. King, unpublished data).

In this study, we examine the responses of sympatric diploid and pentaploid *A. parthenogenetica* to extreme temperatures. Furthermore, the behaviour of the two groups is investigated using an aquatic thermal gradient ranging from 12.5 to 35.1°C.

## Materials and methods

Diploid and pentaploid *A. parthenogenetica* cysts were collected from the Dong Fang Hong saltern in north-east China by Dr Charles E. King in July 1985 and hatched in Dr King's laboratory at Oregon State University. Three diploid clones and three pentaploid clones were isolated. These clones were maintained at a temperature of $25 \pm 0.5°C$ in natural sea-water with a salinity of approximately 35 p.p.t. under 24-h cool white fluorescent lighting at an intensity of 4,000–5,000 lux. The unicellular green alga *Dunaliella tertiolecta* was grown on $2 \times F$ medium at $25 \pm 0.5°C$

and used as food. The *Dunaliella* were raised under a 16L/8D light cycle, with a light intensity of 8,000–10,000 lux. Food was added daily at a concentration of approximately 17,090,000 cells/ml.

To determine the thermal responses of diploids and pentaploids, equal numbers of 15-day-old juveniles from each of three diploid clones were mixed to obtain diploid mixtures. Pentaploid mixtures were obtained in a similar manner. The animals were placed in a grey epoxy-painted wooden container. The container measured 273 × 27 × 46 cm and was filled with natural sea-water to a depth of 1.5 cm. The warm end of the thermal gradient was created by placing a 0.5 litre beaker of water containing two 200 W immersion coils at one end. The cold end was created by immersing a cooling coil at the opposite end. Both the hot and cold elements were separated from the animals by closely spaced layers of 6 $cm^2$ plastic mesh placed 19 cm from the container ends. The length of the chamber available to the animals was therefore 234 cm. Temperatures, to the nearest tenth of a degree, were recorded at 10 zones spaced 23.4 cm apart along the midline of the chamber. No vertical stratification of temperature was observed. Temperatures ranged from an average of $12.1 \pm 1.1$°C in zone 1 to an average of $35.1 \pm 1.6$°C in zone 10. The temperature of each zone varied by less than 2°C throughout. To avoid the confounding effect of light all tests were conducted in darkness. Once the gradient had been established, groups of 5 diploid and 5 pentaploid animals from the mixtures were added to each of the 10 zones. Preliminary results indicated that the distribution of the animals after 1 h in the gradient did not differ systematically from distributions after 2 and 4 h. Therefore, at the end of 1 h, barriers were placed between the zones and the number of animals of each cytotype present and the temperature of each zone were recorded (diploids and pentaploids are morphologically distinguishable). Temperatures were recorded using a K type thermocouple connected to an Omega HH 82 digital thermometer. Five trials of 50 diploids and 50 pentaploids each were run. Each trail involved different animals. To explore whether or not the density of animals played a factor in thermoregulatory behaviour, trials using both 15 and 150 animals of each ploidy were conducted. The possible effect of interaction between the two cytotypes was explored by testing 100 animals of each cytotype separately in the container.

To examine the survival of diploid and pentaploid *Artemia* under extreme temperatures, both newly produced nauplii and 10-day-old juveniles were tested. Three replicates of 20 individuals each were used for each clone. As *Artemia* from north-east China have been reported to have low survival in 18°C and 32°C water (Vanhaecke *et al.*, 1984), 0 and 37.5°C were used to produce extreme cold and heat. The control was 25°C. Survival of individuals was recorded at hourly intervals except for the survival of nauplii at 0°C. Because they were inactive at 0°C it was difficult to determine if nauplii were alive without microscopic examination, but this entailed illuminating and therefore possibly heating. To avoid this problem, we selected 4 days as experimental duration because in a preliminary experiment more than half (on average) of the diploids had died at 0°C. At the end of the experiment the nauplii were transferred to a rearing regime at 25°C. After 2 h, their survival was recorded and analysed using one-way analysis of variance (one-way ANOVA). Clonal survival data at each time interval for all juveniles were analysed using one-way analysis of variance (one-way ANOVA) to examine within-cytotype variations and between-cytotype variations.

## Results

### *Gradient*

Trials using control animals in the chamber without a gradient at a constant temperature of 21.1°C indicated a preference of both cytotypes for the ends of the chamber. No preference was noticed for one end over the other (diploid $\chi^2 = 0.80$, $P = 0.37$, pentaploid $\chi^2 = 0.25$, $P = 0.62$). In the presence of a thermal gradient there was heterogeneity between trials, but chi-squared values showed a significant difference in the distribution of diploids when compared to polyploids in each trial ($\chi^2 > 18.23$, $P < 0.05$ in each replicate). The temperatures of the two cytotypes were normally distributed. Figure 1a indicates the average frequencies of diploids and pentaploids in each zone along the gradient. The mean temperature of diploids ($23.87 \pm 0.4$°C) is significantly higher than that of pentaploids ($22.18 \pm 0.4$°C, pooled *t*-test, $P < 0.01$). While the variance of the individual temperatures of the pentaploids was greater than that of the diploids, which suggests that pentaploids were more evenly distributed along the thermal gradient than diploids, the two variances were not significantly different (*F*-test, $P < 0.05$). As both cytotypes had been cultured for more than 30 generations at a constant temperature of $25 \pm 0.5$°C, acclimation is an unlikely cause of the different temperature distributions.

The median temperature was 19.0°C for pentaploids and 23.2°C for diploids. Figure 1b indicates the percentage of total animal after 1 h in zones with temperatures below 17°C (non-optimal growth temperatures) compared to controls (animals tested at a water temperature of 21.1°C in all zones). The majority of the

diploids left low temperature zones (i.e. zones 1–3) and moved to warmer zones, while a greater percentage of the pentaploids remained in low temperature zones (paired $t$-test, $P=0.003$; Bonferroni adjusted $P=0.009$). Significant differences in the mean temperatures of the two cytotypes were also observed when animals were tested at both a lower density (15 diploids mixed with 15 pentaploids, pooled $t$-test, $P<0.05$), at a higher density (150 diploids with 150 pentaploids, $P<0.05$), and when 100 diploids or 100 pentaploids were tested in the absence of the other cytotype ($P<0.01$). In all cases the mean temperature of the diploids was significantly higher than that of the pentaploids, and the variance of pentaploids was higher, but not significantly so, than that of diploids ($F$-test, $P<0.05$ in all cases).

## Survival

Under both 0 and 37.5°C, at each time interval examined, the mean survival of pentaploids was significantly higher than that of diploids (one-way ANOVA, $P<0.01$). At 0°C the mean 50 per cent-survival (the time at which 50 per cent of the individuals in a cohort were alive) of pentaploids is over five times longer than that of diploids (Fig. 2a). Furthermore, after exposure to 0°C for 11 h, more than 90 per cent of the diploid juveniles had died while more than 90 per cent of the pentaploid juveniles were still alive. At 37.5°C, the mean 50 per cent-survival of pentaploids are nearly twice that of diploids (Fig. 2b). The results were also consistent for comparisons among newly hatched nauplii (one-way ANOVA, $P<0.01$, L. Zhang & H. Lefcort, unpublished data).

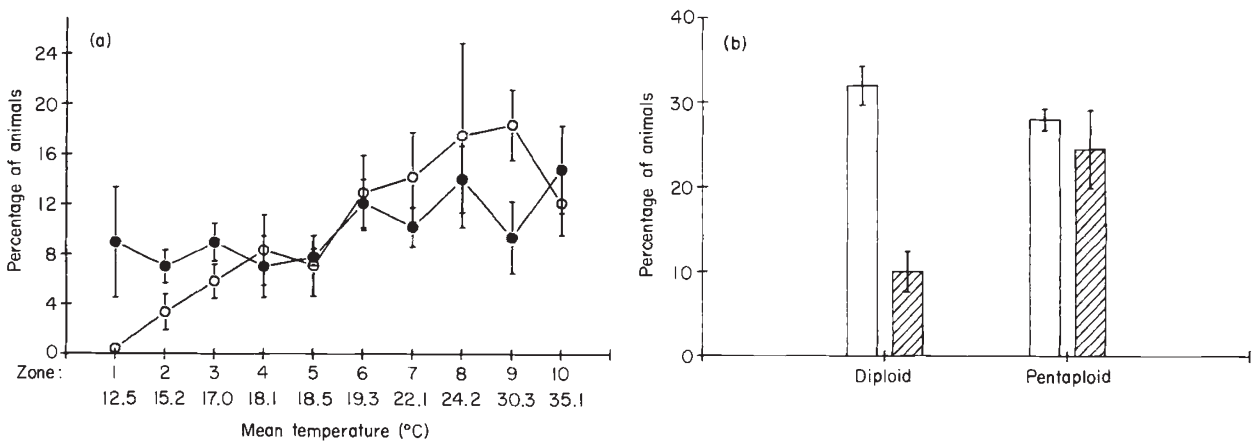


**Fig. 1** (a) Percentage (± SE) of diploids (○) and pentaploids (●) in each zone along a thermal gradient. Data are pooled from five trials. (b) Percentage (± SE) of total animals in zones with temperatures below 17°C (□), compared to controls (□) in these zones. Data are pooled from five trials.

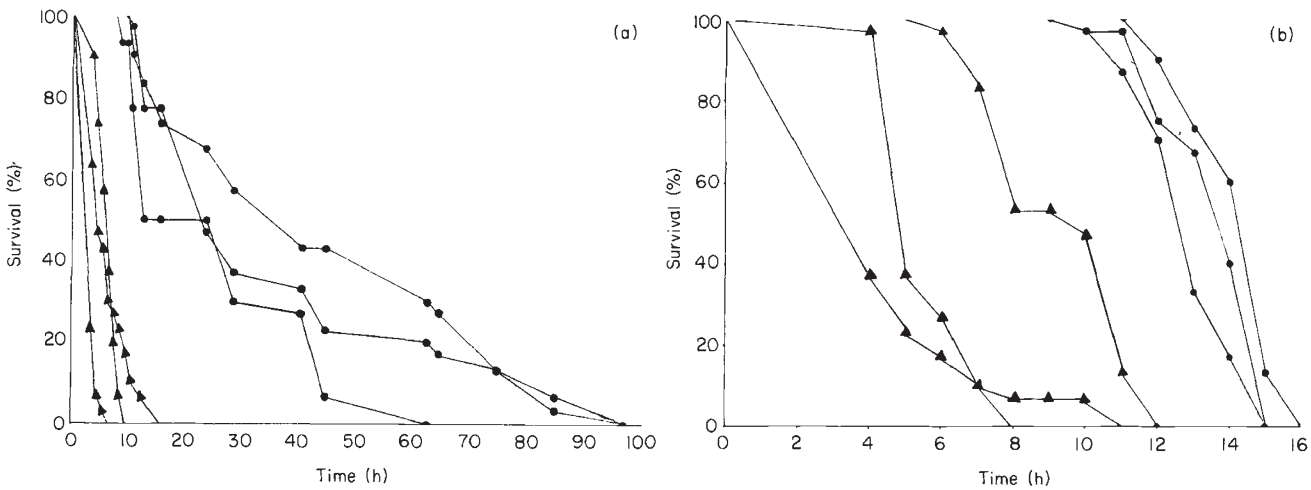


**Fig. 2** Survival (%) of 10-day-old juveniles for three diploid clones (2N, ▲) and three pentaploid clones (5N, ●) under (a) cold stress (0°C) and (b) heat stress (37.5°C). Three replicates of 20 individuals each were used for each clone.

**Table 1** Locations, ploidy number (where reported) and the approximate latitudes of sexual and parthenogenetic *Artemia* in the Old World

| Locality | Dominant cytotype (estimate) | Latitude (degree) | Reference | Locality | Dominant cytotype (estimate) | Latitude (degree) | Reference |
|---|---|---|---|---|---|---|---|
| India | | | | Bras de Port | pd | 35–40 | 3 |
| Tuticorin | pp | 0–10 | 12 | Bonmati | pd | 35–40 | 3 |
| Madras | pp | 10–15 | 10 | Caple | pd | 35–40 | 3 |
| Kutch | pp | 20–25 | 6 | Gerri de la Sal | pd | 40–45 | 3 |
| Israel | | | | San Felix | sd | 35–40 | 3 |
| Elit | pp | 25–30 | 7, 11 | San Fernando | sd | 35–40 | 3 |
| Athlit | pp | 30–35 | 7, 11 | San Pedro del Pinatar | sd | 35–40 | 3 |
| Turkey | | | | Bras de Port | sd | 35–40 | 3 |
| Izmir | pp | 35–40 | 2 | Salinera Espanola | sd | 35–40 | 3 |
| Iran | | | | Ibiza | sd | 35–40 | 3 |
| Lake Urmia | sd | 35–40 | 7 | San Antonio | pp | 40–45 | 3 |
| Cyprus | | | | Medinaceli | pp | 40–45 | 3 |
| Larnaca Lake | sd | 30–35 | 7 | Rienda | pp | 40–45 | 3 |
| Tunisia | | | | Imon | pp | 40–45 | 3 |
| Megrine | sd | 30–35 | 8, 9 | Saelices | pp | 40–45 | 3 |
| Chott Ariana | sd | 35–40 | 7 | Armalla | pp | 40–45 | 3 |
| Bekalta | sd | 35–40 | 16 | Peralta | pp | 40–45 | 3 |
| Sebket mta Moknine | sd | 35–40 | 16 | Laguna de la | pp | 40–45 | 3 |
| Sfax | sd | 35–40 | 16 | Playa Tierzo | pp | 40–45 | 3 |
| Egypt | | | | Delta del Ebro | pp | 40–45 | 2 |
| Wadi Natrun | sd | 30–35 | 8, 9 | Portugal | | | |
| Libya | | | | Alcochete | pp | 35–40 | 3 |
| Mandara | sd | 25–30 | 16 | Itlay | | | |
| China | | | | Trapani | sd | 35–40 | 16 |
| Gao Dao | pd | 35–40 | 14 | San Bartollomeo | sd | 35–40 | 7 |
| Xiao Tan | pd | 35–40 | 14 | Santa Gilla | pd | 35–40 | 2 |
| Dongfeng | pd | 35–40 | 13 | Comachio | pp | 40–45 | 7 |
| Nanwan | pd | 35–40 | 13 | France | | | |
| Jime | pd | 35–40 | 13 | Sete | pd | 40–45 | 5 |
| Yangkou | pd | 35–40 | 13 | Salin de Giraud | pd | 40–45 | 2 |
| Huanghuai | pd | 35–40 | 13 | La Plame | pd | 40–45 | 15 |
| Hangu | pd | 35–40 | 13 | Greece | | | |
| Daqing He | pd | 35–40 | 13 | Citros, Pieria | pp | 40–45 | 1 |
| Yengko | pd | 40–45 | 13 | M. Embolon | pp | 40–45 | 1 |
| Spain | | | | Yogoslavia | | | |
| Janubio | pd | 25–30 | 3 | Istria | pp | > 45 | 5 |
| Ayamonte | pd | 35–40 | 3 | Sovient Union | | | |
| Isla Cristina | pd | 35–40 | 3 | Odessa | pp | > 45 | 5 |
| San Fernando | pd | 35–40 | 3 | Kalator Lake | pp | > 45 | 4 |
| Cabo de Gata | pd | 35–40 | 3 | Burlju Lake | pd | > 45 | 4 |
| San Pedro del Pinter | pd | 35–40 | 3 | | | | |

pd = parthenogenetic diploid. pp = parthenogenetic polyploid. sd = sexual diploid. Populations which are considered to be transplanted are not included. Reference code: 1, Abatzopoulos *et al.* (1986); 2, Abreu-Grobois & Beardmore (1982); 3, Amat Domenech (1980; 4, Badaracco *et al.* (1987); 5, Barigozzi (1980); 6, Browne (1980); 7, Browne & Macdonald (1982); 8, Browne (1988); 9, Browne & Bowen (1990); 10, Browne, R.A. personal communication; 11, Goldschmidt (1952); 12, Vanhaecke *et al.* (1984); 13, Wang (1986); 14, Zhang, L. (unpublished data); 15, Gilchrist (1960); 16, Vanhaecke *et al.* (1987).

**Table 2** Summary of Table 1. Distribution patterns of sexual diploid, asexual diploid and polyploid *Artemia* populations in the Old World

| Latitude (degree) | Number of sexual populations | Number of asexual populations | | Percentage polyploid populations |
|---|---|---|---|---|
| | | Diploid | Polyploid | |
| 0–10 | 0 | 0 | 1 | 100 |
| 10–15 | 0 | 0 | 1 | 100 |
| 15–20 | 0 | 0 | 0 | 0 |
| 20–25 | 0 | 0 | 1 | 100 |
| 25–30 | 1 | 1 | 1 | 50 |
| 30–35 | 3 | 0 | 1 | 100 |
| 35–40 | 13 | 18 | 2 | 10 |
| 40–45 | 0 | 5 | 13 | 72 |
| > 45 | 0 | 1 | 3 | 75 |

Populations with unknown ploidy compositions are not included.

### *Literature review of Old World asexual diploid and polyploid* Artemia

Our literature review (Tables 1 and 2) reveals that asexual diploid and ploypoid *Artemia* in the Old World differ in their distribution patterns. Table 1 is based on populations of *Artemia* in which both the mode of reproduction and the chromosome number of the dominant cytotypes have been reported. Table 2 indicates that polyploids are found with increasing frequency at both low and high latitudes. In populations known to experience high temperatures (latitudes 0–35°N), the majority of populations reported are chiefly composed of polyploids. In milder temperate regions (latitudes 35–40°N), diploids are the most common cytotype. At relatively higher and colder latitudes (40–45°N and >45°N), polyploids are found with increasing frequency.

## Discussion

### *Thermal distribution*

The responses differed when diploids and pentaploids were placed in the thermal gradient. Diploid thermal distributions suggest a preferred temperature above 17°C, while pentaploids were relatively more evenly distributed along the thermal gradient. The mean temperatures for diploids (23.87 ± 0.4°C) and pentaploids (22.18 ± 0.4°C) are concordant with the study of Vanhaecke *et al.* (1984) which predicted that the common temperature optimum for survival would be between 20 and 25 for *A. parthenogenetica* from the People's Republic of China.

Our study provides the first experimental evidence of conspecific sympatric diploid and polyploid animals choosing different temperatures. Furthermore, polyploid *Artemia* are more tolerant of both low and higher temperatures than conspecific sympatric diploids. These differences may substantially contribute to the ability of pentaploid *Artemia* to outcompete diploid *Artemia* in low temperature habitats or during colder seasons. Our data support the suggestion made by Levin (1983) regarding the colonizing ablilties of polyploids versus diploids in plants; i.e. polyploids may occupy habitats which are beyond the tolerance limits of their diploid progenitors.

Our results suggest that when compared with sympatric diploids, polyploid animals not only have higher survival rates under extreme temperatures, but may also use more ecologically relevant (< 17°C) low temperature regions. this would allow pentaploid *Artemia* to exploit a wider range of temperature habitats, both spatially and temporally.

In the salterns of north-east China (between latitudes of 35 and 41°N), diploids are the most common form, making up an average of 85 per cent in the cyst population (Wang, 1986). Pentaploids may be disadvantaged during the middle of the *Artemia* population growth season when intraspecific competition is important, because they have lower fecundity and lower tolerance of semi-starvation conditions when compared to sympatric diploids (L. Zhang & C. E. King, unpublished data). By contrast, the robustness of pentaploids to temperature extremes may afford them an ability to exploit a wider range of temperature microhabitats than diploids during less optimal months, thereby reducing intraspecific competition.

### *Polyploidy and temperature extremes in* Artemia

The difference in temperature requirements for diploids and pentaploids could be related to chromosome doubling. Polyploid *Artemia* populations have been found to have a higher level of average heterozygosity than parthenogenetic diploid *Artemia* populations (Abreu-Grobois & Beardmore, 1982). This has also been documented in many polyploid populations of other species (reviewed by Suomalainen *et al.*, 1987). In the population we studied, pentaploids showed a higher level of average heterozygosity than diploids, as measured by eight polymorphic isozymes and 50 clones for each ploidy (L. Zhang & C. E. King, unpublished data). The high level of average heterozygosity and the increased gene dosage for each locus may provide polyploid *Artemia* with a general-purpose

genotype and, therefore, fit them to environmental extremes better than sympatric diploids. The occurrence of polyploidy at low and high latitudes fits with our laboratory observations. Experiments on sympatric diploids and polyploids from additional *Artemia* populations are needed to test if our findings of Chinese *Artemia* apply to other parthenogenetic *Artemia* populations.

### *Geographical parthenogenesis in* Artemia

The knowledege of geographical distributions of sexual and asexual diploids and of polyploids, and of their phylogenetic relationships, is necessary in order to understand the distributions of parthenogenic and sexual forms. Such information is available for Old World *Artemia*. Evidence of geographical parthenogenesis in *Artemia* is present in the Old World (Browne & MacDonald, 1982; Browne, 1988).

It has been generally accepted that the genus *Artemia* originated from the Mediterranean Sea (Badaracco *et al.*, 1987; reviewed by Browne & Bowen 1990). There is strong evidence to show that asexual polyploid *Artemia* evolved from asexual diploid *Artemia*, which themselves branched from ancestral sexual *Artemia tunisiana* (Abreu-Grobois & Beardmore, 1982; Browne & Bowen, 1990). Although *A. tunisiana* (sexual form) have ecological advantages at low temperatures (Browne *et al.*, 1988; Browne & Halanych, 1989; Lenz & Browne, 1990), and are the dominant form in winter when they are sympatric with *A. parthenogenetica* in Spanish salinas (Perez, 1987), they have never been found north of 40°N (Browne & MacDonald, 1982; Browne, 1988; Lenz & Browne, 1990). In the Old World, sexual populations are only found in the centre of *Artemia*'s distribution (between latitudes of 25 and 40°N) while their parthenogenetic relatives are distributed far beyond this range (Table 2). Sexual forms may be at a selective disadvantage when compared to parthenogenetic forms at low and high latitudes in the Old World. The distributions of parthenogenetic population of different ploidy levels indicates that polyploid *Artemia* have a wider latitudinal distribution than diploid *Artemia*. This may be a result of polyploids having greater colonizing abilities than diploid *Artemia* due to a robust phenotype. Thus, the geographical distributions of sexual, asexual diploid and polyploid *Artemia* and their phylogenetic relationships in the Old World support Suomalainen's (1962; 1969) hypothesis that geographical parthenogenesis arises indirectly as a result of selection for elevated ploidy level in some habitats.

An accompanying question is: why are *Artemia* exclusively sexual in north America? It has been generally accepted that sexual *Artemia* in the Western World evolved from the ancestral sexual forms from the Old World (Abreu-Grobois & Beardmore, 1982; Badaracco *et al.*, 1987). In North America, *Artemia* are distributed from 10 to 50°N latitude (Browne & MacDonald, 1982). Although Suomalainen's hypothesis may explain the geographical parthenogenesis of *Artemia* in the Old World, it cannot explain the distribution of sexual *Artemia* in the Western World. *Artemia* are found at extremes of temperature and latitude, yet all forms are sexual.

The success of polyploids at environmental extremes seems to depend on their acquisition of duplicated genes. Both the high levels of heterozygosity and extra gene dosage of polyploids may provide them with a greater genetic buffering ability against drastic environmental change (Levin, 1983). Localized gene duplication may also confer on an organism a better genetic buffering ability for specific enzymes; these have been found in many animals and may contribute greatly to the evolution of increasingly complex organisms (Ohno, 1970). A comparision of DNA content (which may provide information about duplicated genes) of sexual *Artemia* in north America, and its correlation with latitude and altitude, is needed in order to test fully Suomalainen's hypothesis in *Artemia*.

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## References

ABATZOPOULOS, T. J., KASTRITSIS, C. D. & TRIANTAPHYLLIDIS, C. D. 1986. A study of karyotypes and heterochromatic associations in *Artemia*, with special reference to two Greek populations. *Genetica*, **71**, 3–10.

ABREU-GROBOIS, F. AND BEARDMORE, J. 1982. Genetic differentiation and speciation in the brine shrimp, *Artemia*. pp. 221–252. In: Barigozzi, C. (ed.), *Mechanisms of Speciation*. Alan R. Liss, New York.

AMAT DOMENECH, F. 1980. Differentiation in *Artemia* strains from Spain. In: Persoone, G., Sorgeloos, P., Roels, O. & Jaspers, E. (eds), *The Brine Shrimp Artemia*. Vol. 1. Universa Press, Wetteren, Belgium, pp. 19–40.

BADARACCO, G., BARATELLI, L., GINELLI, E., MENEVERI, R., PLEVANI, P., VALSASNINI P. AND BARIGOZZI, C. 1987. Variation in repetitive DNA and heterochromatin in a genus *Artemia*. *Chromosoma*, **95**, 71–75.

BARIGOZZI, C. 1980. Genus *Artemia*: Problems of systematics. In: Persoone, G., Sorgeloos, P., Roels, O. & Jaspers, E. (eds), *The Brine Shrimp Artemia*. Vol. 1. Universa Press, Wetteren, Belgium, pp. 147–153.

BEATON, M. J. AND HERBERT, D. N. 1988. Geographical parthenogenesis and polyploidy in *Daphnia pulex*. *Am. Nat.*, **132**, 837–845.

BELL, G. 1982. *The Masterpiece of Nature*. Croom Helm, London.

BIERZYCHUDEK, P. 1985. Patterns in plant parthenogenesis. *Experimentia*, **41**, 1255–1263.

BROWNE, R. A. 1980. Reproductive pattern and mode in the brine shrimp. *Ecology*, **61**, 466–470.

BROWNE, R. A. AND MACDONALD, G. H. 1982. Biogeography of the brine shrimp, *Artemia*: distribution of parthenogenetic and sexual populations. *J. Biogeogr.*, **9**, 331–338.

BROWNE, R. A. 1988. Ecological and genetic divergence of sexual and asexual brine shrimp (*Artemia*) from the Mediterranean Basin. *National Geographic Research*, **4**, 548–554.

BROWNE, R. A., DAVIS L. E. AND SALLEE. S. E. 1988. Effects of temperature and relative fitness of sexual and asexual brine shrimp *Artemia*. *J. Exp. Mar. Biol. Ecol.*, **124**, 1–20.

BROWNE, R. A AND HALANYCH, K. M. 1989. Competition between sexual and parthenogenetic *Artemia*: a re-evaluation (Branchiopoda, Anostraca). *Crustaceana*, **57**, 57–71.

BROWNE, R. A. AND BOWEN, S. T. 1990. Taxonomy and population genetics of *Artemia*. In: Browne, R. A., Sorgeloos, P. & Trotman, C. N. (eds), *Aetemia Biology*. CRC Press, Boca Raton, FL (in press).

GILCHRIST, B. 1960. Growth and form in the brine shrimp *Artemia salin* (L). *Proc. Zool. Soc.*, **134**, 221–235

GLESENER, R. R. AND TILMAN, D. 1978. Sexuality and the components of enviromental uncertainty: clues from geographic parthenogensis in terrestrial animals. *Am. Nat.*, **112**, 659–673.

GOLDSCHMIDT, E. 1952. Fluctuation in chromosome number in *Artemia salina*. *J. Morphol.*, **91**, 111–134.

HUEY, R. B. AND BENNETT, A. F. 1987. Phylogenetic studies of coadaptation: preferred temperatures, versus optimum performance temperatures in lizards. *Evolution*, **41**, 1098–1115.

HUEY, R. B. AND SLATKIN, M. 1976. Cost and benefit of lizard thermoregulation. *Quart. Rev. Biol.*, **51**, 363–384

KING, C. E. 1972. Adaptation of rotifers to seasonal variation. *Ecology*, **53** 408–418.

LENZ, P. H. AND BROWNE, R. A. 1990. Ecology of *Artemia*. In: Browne, R. A., Sorgeloos, P. & Trotman, C. N. (eds), *Artemia Biology*, CRC Press, Boca Raton, FL (in press).

LEVIN, D. A. 1983. Polyploidy and novelty in flowering plants. *Am. Nat.*, **123**, 1–25.

LUMARET, R. 1988. Adaptive strategies and ploidy levels. *Acta CEcologica/CEcol. Plant.*, **9**, 83–93

OHNO, S. 1970. *Evolution by Gene Duplication*. Springer-Verlag, New York.

PEREZ, R. 1987. Cysts production of *Artemia* in salt ponds in south-eastern Spain. In: Sorgelous, P., Bengtson, D. A., Decleir, W. & Jaspers, E. (eds), *Artemia Research and its Applications*. Vol. 3. Universa Press, Wetteran, Belgium, p. 215.

SCHULTZ, R. J. 1982. Competition and adaptation among diploid and polyploid clones of unisexual fishes. In: Dingle, H. & Hegmann, J. P. (eds), *Evolution and Genetics of Life Histories*. Springer-Verlag, New York, pp. 103–119.

SOUMALAINEN, E. 1962. Significance of parthenogenesis in the evolution of insects. *Ann. Rev. Entomol.*, **7**, 349–365.

SUOMALAINEN, E. 1969. Evolution in parthenogenetic *Curculionidae*. *Evol. Biol.*, **3**, 261–296.

SUOMALAINEN, E., SAURA, A. AND LOKKI, J. 1987. Polyploidy in association with parthenogenesis. In: Suomalainen, E., Saura, A. and Lokki, J. (eds), *Cytology and Evolution in Parthenogenesis*. CRC Press, Inc. Florida, pp. 71–112.

VANDEL, A. 1928. La parthenogenese geographique. Contribution a l'etude biologique et cytologique de la parthenogenese naturelle. *Bull. Biol. Fr. Belg.*, **62**, 164–281.

VANHAECKE, P., SIDDALL, S. E. AND SORGELOOS, P. 1984. International study on *Artemia*. XXXII. Combined effects of temperature and salinity on the survival of *Artemia* of various geographical origin. *J. Exp. Mar. Biol. Ecol.*, **80**, 259–275.

VANHAECKE, P., TACKAERT, W AND SORGELOOS, P. 1987. the biogeography of *Artemia*: an updated review. In: Sorgeloos, P., Bengtson, D. A., Decleir, W. & Jaspers, E. (eds), *Artemia Research and its Applications*. Vol. 1. Universa Press, Wetteren, Belgium, pp. 129–155.

WANG, Y. X. 1986. *A cytological study of* Artemia parthenogenetica *clones from the salterns of northeast China*. Masters Thesis. Shandong College of Oceanography, China.