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Importance of longevity, growth, and diapause in the evolution of *Asellus aquaticus*

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INTRODUCTION

When a species, split into isolated populations, occupies a whole continent, it is reasonable to wonder to what extent local adaptation led to genetic divergence or whether, instead, the gene flow opposed this divergence (Chow *et al.*, 1988). In order to shed light on these problems, we studied three populations of *Asellus aquaticus* collected from three localities sharply differing from each other for winter duration and hypooxygenation of waters: Naples (Italy), St. Andrews (Scotland), and Utrecht (Holland).

A. aquaticus was chosen because of its low vagility and preference for living in beta-mesosaprobic waters which cause habitat isolation.

The three populations are morphologically similar and have an identical chromosome number, that is $2n = 16$. However, they differ in physiological characters, some of which may be considered clinal. For instance, maximal longevity is 9, 13, and 20 months for the Naples, Utrecht, and St. Andrews population, respectively (Vitagliano *et al.*, 1988).

We investigated: (1) the degree of divergence of the three populations on the basis of their reproductive isolation; (2) the presence in one of the three populations of characters typical of the other two, such as reproductive diapause and the resistance of embryonal and larval stages to 4°C; (3) the influence of environmental factors, such as temperature and photoperiod, on life span and reproductive diapause; (4) the genetics of the body size and reproductive diapause. In this context, it is worth recalling that in a previous study (Vitagliano *et al.*, 1988) life span and indeterminate growth were regarded as «enabling» characters, as they allowed *A. aquaticus* to invade almost all Eurasia (Williams, 1962). On the other hand, reproductive diapause was considered a «shielding» character, as it links the population to a specific genetic pool and hinders gene flow for many months.

MATERIALS AND METHODS

The three *Asellus aquaticus* populations were collected from the following sites: (1) the St. Andrews population from a canal near the Institute of Zoology of the local University; (2) the Utrecht population from the northern outskirts of the town; (3) the Naples population from a back-water of Sarno river.

The animals were exposed to artificial light/dark (L/D) cycle of either 16/8 h or 8/16 h, in thermostatic chambers set at 4°C, 12°C, 16°C, and 30°C, and equipped with fluorescent tubes «F 72PG17CW Power Groove cool G. E. White». The chambers exposed to a natural photoperiod (Rome latitude) were illuminated by daylight streaming through very large windows set south-westwards; thus light intensity was higher in the afternoon and depended upon the daily cloudiness.

The same standard food was given to all the animals and consisted of leached plant detritus.

A part of F1 larvae of the last stage, of the three populations raised at 16°C was gradually (over 30 days) cooled to 4°C or 12°C (under natural photoperiod) until the juvenile stage was reached. Other lar-

ABSTRACT

In *Asellus aquaticus* it was shown that: (1) populations of South Europe have embryos/larvae resistant to 4°C, a life span of 9 months, small body size, and lack of reproductive diapause; (2) populations of North Europe have a life span of 20 months, large body size, long reproductive diapause, and embryos/larvae not resistant to 4°C; (3) life span and reproductive diapause are genetic characters; and (4) body size is determined by indeterminate growth.

KEY WORDS: Adaptation - Gene flow - Life span - Reproductive diapause - Isopods.

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vae of St. Andrews population were bred at 16° C and under two different L/D photoperiods (16/8 h and 8/16 h) to evaluate the influence of reproductive activity on longevity. Some individuals were acclimatized from 16° C to 30° C, during one week. All animals were observed each third day for their entire life span.

Embryos and larvae born in laboratory at 4° C and developed beyond the final larval stage within 60 days were defined as «resistant», albeit taking double the time taken by the control at 16° C. Embryos and larvae which did not progress beyond a stage of embryonal/larval development, and died without reaching the final larval stage, were defined as «non-resistant».

Adults were 45-days old at the start of the experiments. In order to estimate the duration of the reproductive diapause, females and males were bred in single pairs, maintained in 25x25x10 cm bowls containing 1000 ml of natural water filtered through Whatman paper. Population 1 of 25 females and 25 males were also bred.

Fertility rates in the diapausing period (October-December) and fertile period (February-July) were evaluated in: (1) crosses between Utrecht females and males and Naples males and females; (2) hybrids and backcrosses. Females and males were considered in reproductive diapause if, when maintained isolated in single pairs and/or in population, they did not produce embryos within 60 days. In the reproductive period, about 95% of females were fertilized in this time span.

Body size measurements, taken from head to telson (antennae and furca excluded), were made on F₁ and also on hybrid F₁ specimens in the various age classes until the 75th day of life. Larvae of the last stage emerged at the same length (0.8 mm) from the brood pouch. The experiments were made in absence of competition (10 larvae/bowl) and in standard conditions for food and water.

To evaluate the genetic divergence among the three populations studied, we calculated the reproductive isolation rate by means of intrapopulation crosses, interbreeding, hybrid crosses, and backcrosses. For all crosses the individuals were chosen at random. Calculations were made: (1) of the number of females that in single pairs or in populations did not mate in the fertile period (Spring-Summer); (2) of those that did not lay embryos in the brood pouch, or that laid embryos which died during embryonal development; (3) of those that produced offspring which proved to be sterile in interbreeding and backcrosses. The age class of parental females was unknown. The age class of F₁ (also F₁ hybrids) was between 90 and 150 days. As a correlation exists between the mother body dimensions and the number of newborns, females with the most similar body dimensions were chosen for a better evaluation of the reproductive isolation.

RESULTS

Periods of more than 30 days at 16° C were well tolerated by every stage of *A. aquaticus* examined and survival rates were very high (Fig. 1). At 4° C and 30° C, all embryos and larvae of St. Andrews and Utrecht populations died, while only 6-16% of embryos and larvae of Naples population survived and reached sexual maturity. Adults of all three populations survived at 4° C, while at 30° C their survival was 15%, 5%, and 12% for the Naples, Utrecht, and St. Andrews populations, respectively.

The mean and maximal life span of the two populations exposed to different temperatures and natural photoperiods are given in Table I. As can be seen, the mean life span is significantly different among individuals of Naples population and St. Andrews population growing up at different temperatures, whereas it is not significantly different among individuals of St. Andrews

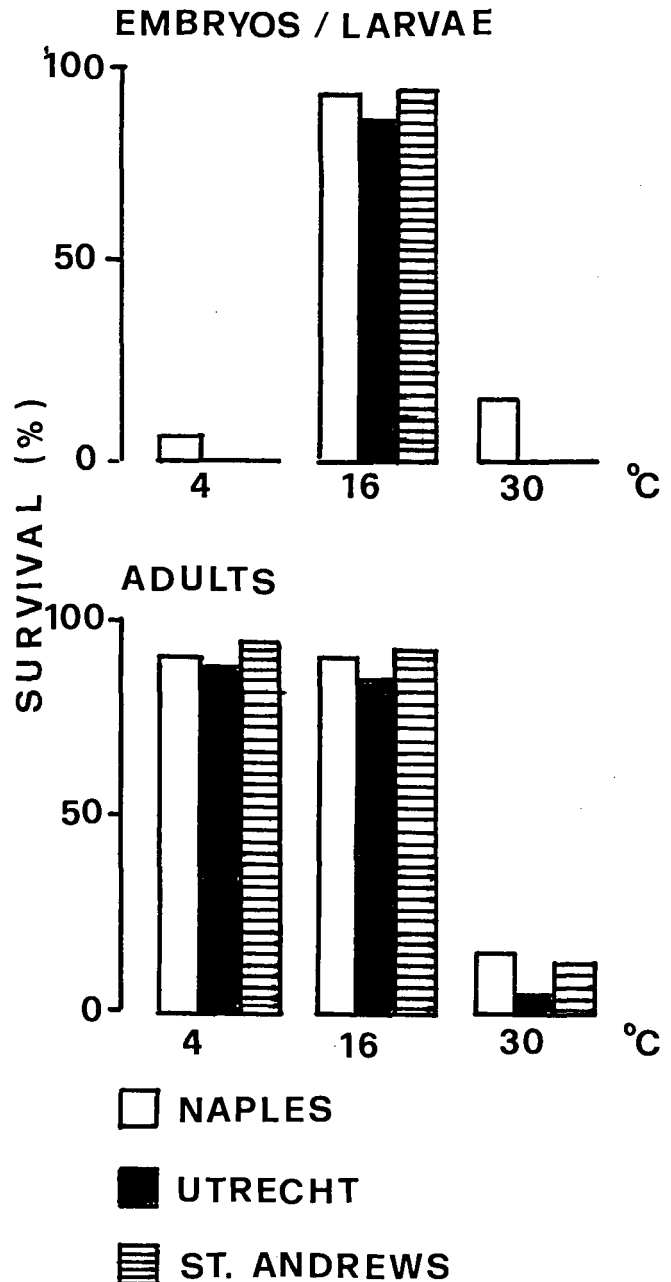


Fig. 1 - Survival of 400 females, 400 males, and 1500 embryos bred for 60 days at 4, 16, and 30° C, under natural photoperiod. At the start of the experiment the adults were 45 days old.

population growing at different photoperiods (ANOVA test, one-way). Also the mean life span of Naples and St. Andrews populations is significantly different. Maximal life span is markedly different. The individuals of Naples population in the three breeding conditions have a maximal longevity of 270 days. At the same temperature maximal longevity of the St. Andrews individuals is remarkably higher, as it is 600 days (Table I).

An uninterrupted sexual activity, under a L/D cycle of 16/8 h, does not shorten the life span. This becomes of 570 days in individuals entering the reproductive diapause at a L/D cycle of 8/16 h, (Table I).

TABLE I - Mean and maximum life span of individuals of *Asellus aquaticus* born in laboratory and exposed at different temperatures and photoperiods.

Population	Individuals (n)	Temperature (°C)	Photoperiod	Days of life	
				$\bar{X} \pm S.E.$	maximum
St. Andrews	480	16	natural	205.50 \pm 12.33	600
	360	16	16/8 (L/D)	230.10 \pm 12.63	600
	440	16	8/16 (L/D)	239.70 \pm 16.13	570
	360	12	natural	259.80 \pm 13.45	600
	400	4	natural	444.60 \pm 14.19	600
Naples	540	16	natural	166.80 \pm 5.10	270
	480	12	natural	190.50 \pm 5.08	270
	500	4	natural	212.70 \pm 5.07	270

TABLE II - Body size till the 75th day of life of *Asellus aquaticus* hybrids bred at 16° C under natural photoperiod.

Parental crosses females	Parental crosses males	Larvae (n)	Body size ^a ($\bar{X} \pm 2 S.E.$)				
			1st day larvae	50th days		75th days	
				females	males	females	males
N ^b	N	400	0.8 \pm 0.1	3.2 \pm 0.5	4.4 \pm 0.6	8.0 \pm 0.9	12.0 \pm 1.0
S ^c	S	350	0.8 \pm 0.1	3.2 \pm 0.5	4.4 \pm 0.5	8.4 \pm 0.8	13.2 \pm 1.2
N	S	200	0.8 \pm 0.1	3.2 \pm 0.5	3.6 \pm 0.5	3.6 \pm 0.4	4.8 \pm 0.5
S	N	200	0.8 \pm 0.1	5.6 \pm 0.8	6.4 \pm 0.7	8.4 \pm 0.6	13.2 \pm 0.8

^a Measures are in mm^b Naples population^c St. Andrews population

The body sizes in successive age classes (till the 75th day of life) of Naples and St. Andrews F_1 individuals and of their hybrids are reported in Table II. As can be seen, the differences are mainly due to sexual dimorphism and underdevelopment of the hybrids born from crossing Naples females and St. Andrews males.

In Table III, the data of the fertility rate of two periods for F_1 hybrids, and backcross offspring, carried out either between different populations or within the same population, are reported. In the period February-July, the percentage of fertilized females is maximal (i. e., 100% in the cross between Utrecht females and males, and 90% in the cross between Naples females and males), while it is lower in crosses between different populations. In the period October-December, the reproductive diapause of Utrecht individuals appears to be an obstacle to mating. The offspring show a marked reproductive diapause in the period October-December, in the case of Naples/Utrecht hybrids backcrossed to Naples parents, as well as in the crosses between Naples-Utrecht hybrids. In the

same period, all Naples parents appear capable of mating.

In Table IV, the results obtained on the reproductive isolation are reported. As can be seen, the mean numbers of newborns from each female differs in the three populations studied, for both parents and F_1 offspring yielded in the laboratory. The number of newborns from F_1 females is lower than that from parental females, most likely due to the fact that F_1 females were relatively small for their age (90-150 days), while parental females had larger body size. All the crosses carried out between different populations showed a very high degree of reproductive isolation; the lowest number of newborns was observed in some backcrosses.

DISCUSSION

Every species extends its own area of distribution until it encounters barriers to further dispersal. Geographical distance does not necessarily lead to divergence among

TABLE III - Fertility in different generations of *Asellus aquaticus* bred at 16°C under natural photoperiod, during fertile period and reproductive diapause.

Crosses		Pairs <i>n</i>	Fertilized females (%)	
females	males		February- July*	October- December**
U ^a parent	× U parent	100	100	14
N ^b parent	× N parent	100	90	100
U parent	× N parent	80	86	0
N parent	× U parent	80	40	8
NU hybrid	× NU hybrid	70	75	10
N parent	× NU hybrid	70	50	0

^a Utrecht population

^b Naples population

* Fertile period

** diapause period

distinct populations if gene flow allows interbreeding (Slatkin, 1987; Baur & Raboud, 1988). Species lacking in vagility, subjected only to passive dispersal are particularly liable to speciation due to local adaptation (Dingle & Hegman, 1982). *Asellus aquaticus* may be considered one of these species, as it is present, through passive dispersal in almost all Eurasia and so has had to overcome many geographical and ecological barriers. These barriers certainly include sea, and exposure to long periods of low temperature and water hypooxygenation. Our findings show that: (1) embryos/larvae resistant to 4° C are present only in Naples population; (2) maximal life span and reproductive diapause are most probably genetically determined; (3) the three populations studied have a high degree of reproductive isolation. From the following discussion of these findings it will appear that life span and indeterminate growth of *Asellus* are enabling characters and that the reproductive diapause is a shielding character.

Embryos/larvae resistant to 4° C are present only in Naples population of *A. aquaticus*; in fact, the diapausing Utrecht and St. Andrews populations of *A. aquaticus* are not under selection form embryos/larvae resistant to 4° C, whereas non-diapausing *A. aquaticus* of Naples population are exposed to this selection. The result is that animals from warmer climates have embryos/larvae more resistant to lower temperature than specimens from colder climates. Also in a population of *A. aquaticus* from Sweden, it has been found that embryos/larvae are die at a temperature of 4° C (Andersson, 1969). This finding is counterintuitive, but interesting.

The mean life spans of St. Andrews and Naples populations are significantly different from each other, the members of former being more long living in every

breeding condition. However, the mean life span does not differ as much as the maximal life span of St. Andrews *A. aquaticus*, that lasts for 600 days versus a maximum of 270 days (at every temperature) for Naples individuals. This doubling of the life span in St. Andrews individuals compared with that shown by Naples individuals may be explained only by assuming a genetic determination for longer, or shorter, life span. Moreover, the survival rates lead us to suppose that the determination is probably polygenic, as in *Drosophila* (Luckinbill *et al.*, 1988). We can also exclude that the shorter life span of Naples individuals is due to lack of reproductive diapause, as previously assumed (Vitagliano & Vitagliano, 1965), and as shown by Curio (1988) for the coleopterous *Speonomus delarouzei* and by Neal & Douglass (1988) for the heteropterous *Stephanitis pyrioides*. Indeed, St. Andrews individuals artificially maintained in uninterrupted sexual activity showed a life span equal to that of diapausing individuals. It can thus be reinforced the hypothesis that the life span has «enabled» *A. aquaticus* to invade almost all Eurasia. The populations with long life span may in fact overcome the winter reproductive diapause; on the other hand, the populations with short life span may avoid overlapping of the autumnal generation with the summer generation, which is exposed to the risk of a high population density.

None of the Naples pairs of *A. aquaticus* showed a reproductive diapause; indeed, the number of autumnal mating was higher than that of the Spring-Summer months. The Naples × Utrecht hybrids, which mate during Summer, enter the reproductive diapause at the same time, and for the same duration as the Utrecht parents. It appears, therefore, that the reproductive diapause has most likely linked the populations to a particular environment, reducing the gene flow by means of a «chronocline isolation». This hypothesis was formerly put forward by Marcus (1984) in relation to the embryonal diapause of the copepod *Labidocera aestiva*.

Hybrids showed body underdevelopment, and this suggests that the body size is somehow regulated by a genetic component (maternal effect?). The body size, because of its plasticity and dependence on life span, has been defined an «enabling» character. The development of a large body in fact, as in individuals of northern populations, may allow the production of a large number of newborns when the reproductive diapause ends. Andersson (1969) gives a size of 20 mm for Danish *Asellus* in Spring. On the other hand, a small body size, due to a short life span, allows the hatching of only a few newborns and this, in the presence of high population densities and with hypooxygenation, appears to be of great advantage.

No gene flow has probably occurred among the three populations examined or, if gene flow did occur, it was selected against. In fact, reproductive isolation is very high, as especially seen in the crosses between hybrids and in backcrosses. The crosses between Utrecht females and St. Andrews males shows a higher value of mating

TABLE IV - Mean number of newborns per female in different crosses raised at 16°C under a natural photoperiod of *Asellus aquaticus* populations.

Crosses		Pairs (n)	Newborns per female ($\bar{X} \pm 2$ S.E.)
females	males		
S ^a parent	× S parent	100	60.81 ± 2.50
U ^b parent	× U parent	100	54.15 ± 1.67
N ^c parent	× N parent	100	39.98 ± 1.70
S parent	× U parent	66	10.41 ± 1.94
S parent	× N parent	65	22.49 ± 0.23
U parent	× S parent	67	5.00 ± 0.90
U parent	× N parent	65	17.49 ± 2.56
N parent	× S parent	68	14.16 ± 1.68
N parent	× U parent	66	15.41 ± 1.25
S F ₁	× S F ₁	100	35.07 ± 1.25
U F ₁	× U F ₁	100	29.99 ± 1.70
N F ₁	× N F ₁	100	24.99 ± 3.33
SN hybrid	× SN hybrid	50	10.41 ± 1.87
NS hybrid	× NS hybrid	50	7.50 ± 1.80
SU hybrid	× SU hybrid	50	7.45 ± 1.65
SN hybrid	× S parent	70	14.16 ± 1.67
SN hybrid	× N parent	70	4.17 ± 1.25
NS hybrid	× S parent	70	9.16 ± 2.08
NS hybrid	× N parent	70	2.50 ± 1.70
NU hybrid	× N parent	70	2.49 ± 1.66
S parent	× SN hybrid	70	2.52 ± 1.67
S parent	× NS hybrid	70	1.83 ± 0.84
N parent	× SN hybrid	70	14.99 ± 1.70
N parent	× NS hybrid	70	14.11 ± 2.08
N parent	× NU hybrid	70	7.50 ± 2.10

^a St. Andrew population^b Utrecht population^c Naples population

isolation than those between Utrecht females and Naples males. This suggests that the local adaptation and not the distance may cause a reproductive isolation between St. Andrews and Utrecht populations. Both these populations have a reproductive diapause which reduces a possible overcoming of gene flow for many months, as well as a selection of embryos/larvae resistant to 4° C, thus reducing exposure to natural selection.

In conclusion, the reproductive diapause is held to reduce for many months the gene flow by means of a «chronocline isolation». Accordingly, we defined it as a shielding character to emphasize its influence in hindering the selection of the other adaptive characters. The

reproductive diapause links the population to a defined gene pool. The genetically determined long and short life spans (i. e., 20 and 9 months in St. Andrews and Naples populations, respectively) are defined enabling characters, because they have enabled *A. aquaticus* to invade almost all Eurasia, by (1) overcoming the long period of reproductive diapause and (2) halving the population density by means of a reduced life span. Also indeterminate growth is defined as enabling character, because it allows 13- (Utrecht) (Vitagliano *et al.*, 1988) or 20- (St. Andrews) month-old females to attain a large body size, thus allowing the production of a large number of newborns when the reproductive diapause ends. On the contrary, a small body size in the 9-month-old females allows the hatching of only a small number of larvae, when the water level drops in summer.

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