

Growth, size and shape of *Daphnia longispina*, *D. magna* and *D. pulex*

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We cultured *Daphnia magna*, *D. pulex* and *D. longispina* at 15°C and 20°C at low and high food levels. Individuals of different ages were measured for body size and body shape. Growth of the three *Daphnia* species was linear. Both food level and ambient temperature affected daily growth rate. Variation in shape was mainly due to species-specific differences and age(body size)-related differences in relative head and caudal spine length. Although temperature affected *Daphnia* body shape, food density did not. *D. magna* had the shortest caudal spine relative to core body length. It was also more spherical in body shape than the two other species. The length of the caudal spine increased with body length both in *D. pulex* and *D. longispina*, but *D. magna* showed a weak negative correlation between the two variables. Newborn individuals tended to have a longer caudal spine and longer head than mature individuals. The core body was spherical in mature individuals, whilst newborns of the three species were thin and elongated.

1. Introduction

Variation in size and shape among and within *Daphnia* species has generally been considered to be adaptive (Zaret 1980, Jacobs 1987, Dodson 1989a). As individuals grow and mature, they

may experience different selective pressures and adjust their morphology accordingly. For example, it has been argued that predators selecting *Daphnia* of different sizes may induce various morphological defenses such as spines, helmets and neck teeth (Dodson 1974, 1989a, b, Jacobs 1987, Walls & Ketola 1989). As such defenses may entail energetic costs, defensive structures could be expected to be differentially expressed in animals of different sizes. On the other hand,

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variation in shape between different-sized animals or under different environmental conditions may also be a consequence of the morphological or physiological processes involved in growth, without any direct adaptive significance (cf., Gould & Lewontin 1979).

Gradual responses of organisms to different environmental conditions, e.g., variations in predation pressure, have been termed "reaction norms" (Woltereck 1909, Levins & Lewontin 1986, Stearns 1989, Dodson 1989a). Such responses can either be morphological or can involve changes in life-history traits. It has been argued that the chief objects of natural selection are not particular traits, but rather the set of reaction norms of an organism (see, Gebhardt & Stearns 1988, Stearns 1989). Although an old topic of discussion, interest in reaction norms has increased greatly in recent years (e.g., Stearns 1989, Dodson 1989a for reviews).

Three *Daphnia* species, *D. magna* (Straus), *D. pulex* (de Geer) and *D. longispina* (O.F. Müller) commonly inhabit ponds, rock-pools and other small freshwater habitats (Ranta 1979, Fryer 1985, Bengtsson 1988). Along the Baltic Sea, the species are the commonest cladocerans in rock-pools, i.e., small water-filled bed-rock depressions (Lagerspetz 1955, Ranta 1979, 1982, Bengtsson 1986, 1988, Pajunen 1986). The three species differ in size, *D. magna* being the largest and *D. longispina* the smallest, and they have highly overlapping niches along several physico-chemical axes, as well as the food axis (Ranta 1979, Bengtsson 1988).

Insect predators are common in rock-pools, while vertebrate predators usually are lacking (Ranta 1982, Ranta & Espo 1989, Bengtsson 1988). However, large rock-pools may harbour newts or sticklebacks (Ranta & Nuutinen 1984, 1985, Bengtsson 1988), which feed preferentially on the larger zooplankton. Thus *D. magna* is not found in rock-pools with these predators, while *D. longispina* and *D. pulex* may coexist with newts (Ranta & Nuutinen 1985, Ranta & Tjossem 1987, Bengtsson 1988). Invertebrate predators, on the other hand, frequently show a preference for smaller-sized zooplankton (Ranta & Espo 1989), although some large insects such as *Notonecta* usually have a prey choice more similar to that of vertebrates (Scott & Murdoch 1983).

Thus, depending on planktivore composition, *Daphnia* in rock-pools experience differing selective factors, which, in addition, may vary throughout the year depending on predator phenology. Ranta & Tjossem (1987) found that for rock-pool inhabiting *D. longispina*, body length decreased during the summer, while caudal spines were longer and heads more pointed than in early summer. This is a typical example of cyclomorphosis. It may be driven by vertebrate predators or by changes in environmental conditions (Jacobs 1987). Moreover, individuals in large rock-pools with vertebrate predators had larger body exuberances than did those from smaller rock-pools. This was accounted for by differences in planktivore composition.

Predation often has been argued to be the ultimate cause of cyclomorphosis and changes in body shape of cladocerans (Jacobs 1987, Dodson 1989a for reviews). Considerably fewer studies have analyzed the effects of other environmental conditions such as temperature or food density on body shape, although such factors were earlier invoked to explain cyclomorphosis (see Jacobs 1987). For example, in the above case of *D. longispina* in rock-pools, one would need to examine the effects of other environmental variables on size and shape before properly evaluating the hypothesis that the differences observed are adaptive responses to avoid predation. The present laboratory study examines the effects of two levels of food and temperature on growth and body shape in the three rock-pool *Daphnia* species. This will allow us to compare their responses to the same environmental factors, to analyze whether reaction norms for shape characteristics exist, and to provide a base-line for evaluating possible additional effects of predators.

2. Material and methods

2.1. *Daphnia* cultures

Individuals of the three *Daphnia* species were reared in 100 ml jars at two food-levels (low, high; details below) and temperature (low = 15°C, high = 20°C). The rearing conditions are explained in detail by Bengtsson (1986). The animals originated from the Ångskär islands in the

northern part of the Stockholm archipelago (N59°33', E19°17'), and the clones were *D. magna* (RB), *D. pulex* (MA) and *D. longispina* (RH) (Table 1; see Bengtsson 1986, 1988, for details). A single rock-pool clone of each species was used in the experiments. Limiting the choice to these clones was done, first of all, because much other experimental research has involved them (Bengtsson 1986, 1987a,b, 1988, 1989, 1991, 1992, Milbrink & Bengtsson 1991). Second, as Stearns (1992: 41) puts it: "If an organism is cloned and the genetically identical offspring are tested across a range of environments, we can measure the reaction norm, for example, of body size as a function of temperature. When a single genotype is cloned and tested in many environments, the reaction norms transform environmental variation into phenotypic variation". In an ideal world, a more feasible strategy would have been to use as many clones as possible. However, logistic reasons set physical limits to the number of factor level combinations feasible.

The experiments were run from the end of January to the end of May, 1986, at the Department of Zoology, Uppsala University. Four separate cultures of each species were started under each set of conditions. Each culture originally consisted of 10 to 25 newly born (0–24 h old) individuals that were obtained from females that had been isolated from stock cultures for this purpose and kept under the conditions at which their progeny would then be raised. *Daphnia* were removed from the cultures every two days at 20°C and every three days at 15°C. The sampling continued for two sampling occasions after the first young had been produced in the culture. A sample of about 12 *Daphnia* were removed on each occasion. The actual number removed for

each culture was randomized and followed a scheme worked out in advance. This allowed the four cultures that constituted one experiment to be run at different times. This was necessary especially in the case of *D. magna* due to the low number of young available, and in cases in which experiments had to be terminated or interrupted.

The food used was the green alga *Scenedesmus quadricauda* Turpin, cultured according to Bengtsson (1986). The algae used were 5–8 days old. The water of the cultures was changed every 3–4 days. At this time low-food cultures received about 0.2 ml of *Scenedesmus* suspension, and high-food cultures about 1 ml. The exact amount was calculated so as to achieve an algal density of 1×10^4 cells/ml in low-food and 5×10^4 cells/ml in high-food experiments. Between water changes, algae were added daily to compensate for the approximate amount grazed by the animals (calculated from J. Bengtsson, G. Milbrink & A. Claesson, unpublished data).

2.2. Measurements

The *Daphnia* were killed and preserved in 70% ethanol. When all the cultures were terminated the *Daphnia* collected were measured under a microscope to an accuracy of 0.025 mm. The following six dimensions of the body were measured: (A) core body length, (B) caudal spine length, (C) body width, (D) head width, (E) head length, and (F) body breadth (Fig. 1).

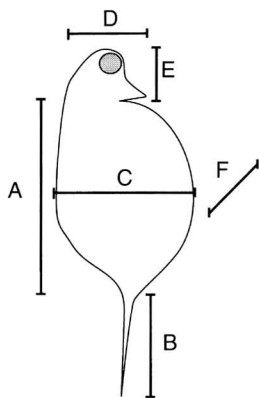
The size variables were further used in deriving the following body shape variables:

- 1) relative caudal spine length, caudal spine length divided by core body length, B/A,

Table 1. Life-history characteristics of three *Daphnia* species under four sets of experimental conditions. Age is age at first reproduction, size refers to core body length at first reproduction, LF and HF refer to low and high food levels (modified from Bengtsson 1986).

	<i>D. magna</i>				<i>D. pulex</i>				<i>D. longispina</i>			
	15°C		20°C		15°C		20°C		15°C		20°C	
	LF	HF	LF	HF	LF	HF	LF	HF	LF	HF	LF	HF
Age (days)	16	18	12	10	14	12	11	9	15	16	13	10
Size (mm)	1.3	1.5	1.6	1.5	1.0	1.2	1.1	1.0	1.0	1.2	1.3	1.1
Life span (days)	52	69	35	35	44	56	38	42	62	38	45	40

Fig. 1. Size and shape characteristics of *Daphnia* body measured: (A) core body length, (B) caudal spine length, (C) body height, (D) head width, (E) head length (F) body breadth.



- 2) relative body width, body width divided by body length, C/A ,
- 3) relative head width, head width divided by body length, D/A ,
- 4) relative head length, head length divided by body length, E/A ,
- 5) relative body breadth, body breadth divided by body length, F/A ,
- 6) body breadth divided by body width, F/C , and
- 7) head pointedness, head length divided by head width, E/D .

In the numerical analyses we used both the original and the derived measures. Justification for such derived variables in shape analysis can be found, such as in James (1982). Characterization of the data collected is given in the Appendix. In the following, body

size always refers to the original variables and body shape or relative measures to the derived variables. These variables are kept separate in the analyses. In addition to basic statistical methods we also used principal component analysis. This method is especially suited for morphometric data where many of the variables are intercorrelated (Pimentel 1979). Separate runs were done for the two variable types, size and shape.

3. Results

3.1. Growth and size

In statistical terms, a linear regression model yields the best fit between age and body length of the three *Daphnia* species in all the four treatments (Fig. 2). Therefore, the daily growth rate is best characterized by the slope of the linear regression model; when slopes are compared, a clear pattern emerges (Fig. 3). The daily growth rate is lower in the cultures at 15°C than at 20°C. Also, a low food ration makes *Daphnia* grow slower than with a high ration. Ranking the species according to their growth rate results in the following order at 20°C with high food, from the fastest to the slowest rate: *magna*, *pulex*, *longispina*. With low food we obtain *magna*, *longispina*, *pulex*. At 15°C under both food conditions the corresponding order is *pulex*, *magna*, *longispina* (Fig. 3).

The differences in growth rates within a species, as expressed in the regression slopes, are

Table 2. Results of principal component analyses run with the size data and shape data: size variable names refer to Fig. 1. Shape variables are derived from size variables as shown, variable-specific loadings on extracted principal components, eigenvalues and corresponding percentages of total variance.

	Size			Shape		
	PC1	PC2		PC1	PC2	PC3
A core body length	-0.453	0.043	B/A	-0.422	-0.109	0.258
B caudal spine length	-0.058	0.985	C/A	0.497	-0.065	0.297
C body width	-0.454	-0.048	D/A	0.353	-0.314	0.496
D head width	-0.449	-0.080	E/A	-0.307	-0.344	0.572
E head length	-0.431	0.074	F/A	0.223	-0.645	-0.218
F body breadth	-0.441	-0.116	F/C	-0.164	-0.586	-0.459
			E/D	0.526	-0.082	0.120
Eigenvalue	4.677	1.011		2.816	1.781	1.394
% of total variance	77.9	16.9		40.2	25.4	19.9

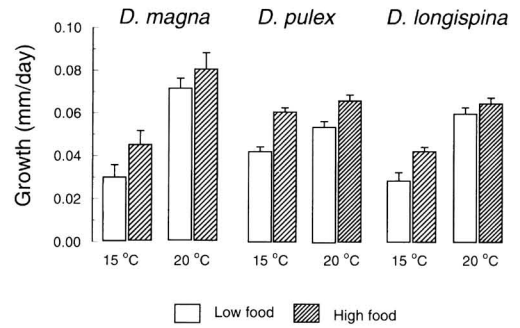
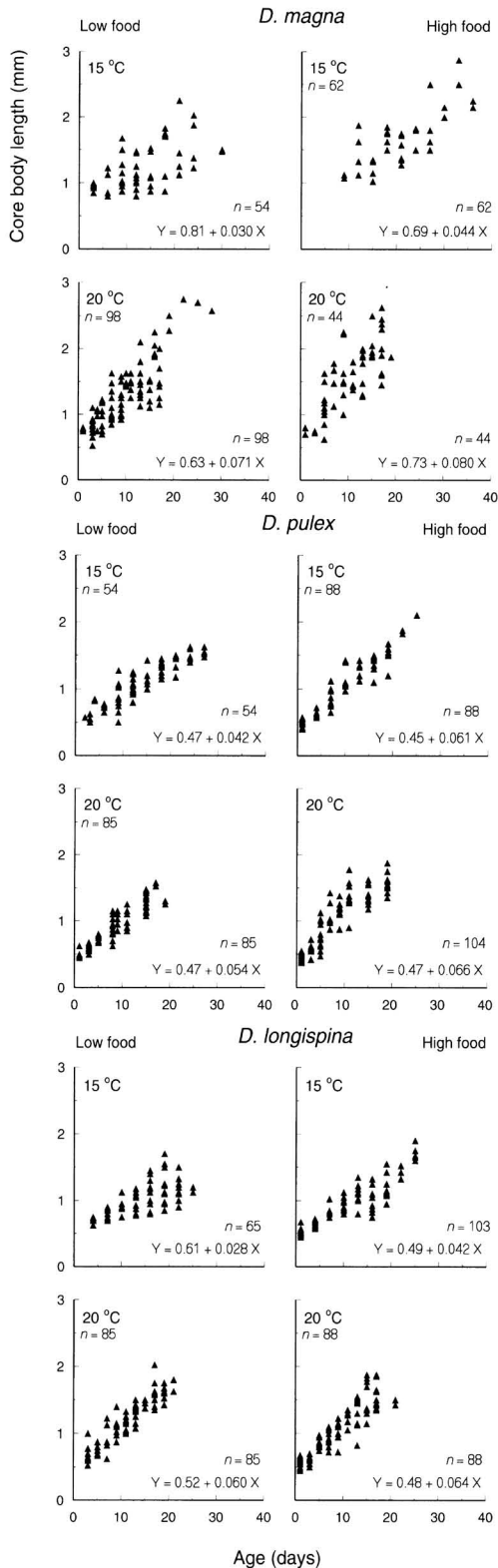


Fig. 3. Daily growth rate of three *Daphnia* species reared at low and high food levels at 15°C (open bars) and 20°C (hatched bars). Growth rate expressed as slope of regression equation (with standard error) in Fig. 2.

significant in statistical terms (ANCOVA, test for homogeneity of slopes: *D. magna*, $F_{3,240} = 15.12$, $P < 0.001$; *D. pulex*, $F_{3,321} = 19.02$, $P < 0.001$; *D. longispina*, $F_{3,336} = 30.75$, $P < 0.001$). This finding makes problematical further statistical comparisons (with the analysis of covariance) of the effects of the factors food and temperature on the growth of the three species.

Results of the principal component analysis run with the size variables are clear-cut: Two components are needed to encompass 95% of the total variation in the original variables. The caudal spine is the only character scoring high on the second component (Table 2).

3.2. Shape

Examination of *Daphnia* body shape began by running a principal component analysis on the seven derived variables (Table 2). The three first principal components explained about 85% of the total variation in the shape variables (Table 2). For the first component (PC1) *Daphnia* with a short caudal spine (relative to body length)

Fig. 2. Growth of three *Daphnia* species reared under low (LF) and high food (HF) regimes at 15°C and 20°C. Regression equations inserted (e.g., for *D. magna* at 15°C with low food body length equals to $0.81+0.0030$ Age).

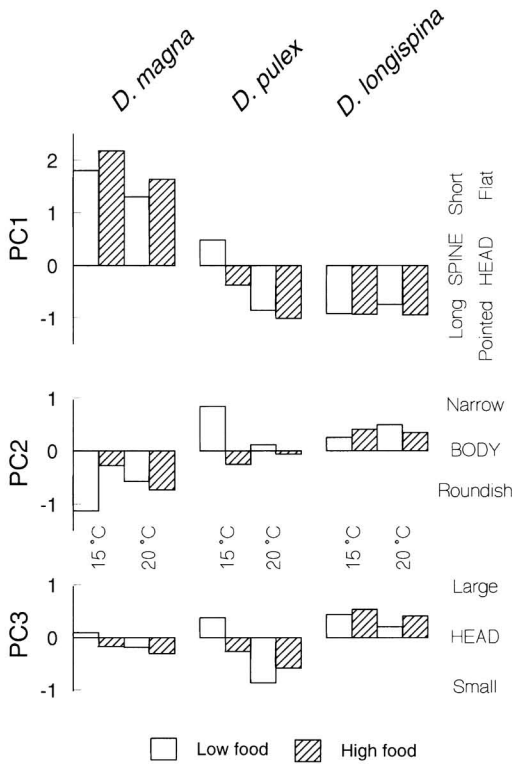


Fig. 4. Principal component score values for three *Daphnia* species reared at low (open bars) and high (hatched bars) food levels at 15°C and 20°C. First three principal components (PC1, PC2 and PC3; Table 2) are graphed (right-hand side giving verbal reading for each of the three components). Values drawn corrected for age.

score positive values. They also have a relatively high ratio of body width to body length (relative body width), and their head pointedness is rather low (low values for head length/head width). The second principal component (PC2) scores high positive values for *Daphnia* having narrow bodies (low ratios for body breadth divided by body length or by body width). *Daphnia* with wide (a high ratio between head width and body length) and relatively long heads (a high ratio between head length and body length) score high positive values for the third principal component (PC3).

Thus PC1 can be interpreted as mainly describing differences in relative caudal spine length and head shape, PC2 as describing core body

shape dimension, and PC3 as describing head shape in relation to body size. A summary of the principal component scores of the shape variables for each of the three species in the four treatments is given in Fig. 4.

Our next step is to examine the significance of the main factors (species, temperature, food) affecting *Daphnia* body shape. To do this we apply a factorial design in the analysis of variance. However, as body shape changes throughout growth we take age (in days) as a covariate. First, the three species are different in shape (Table 3). The data also suggest that *Daphnia* shape is affected by water temperature but not by food level (Table 3). This conclusion is strengthened by the finding that there is no interaction between the factors *food* and *temperature* (Table 3). In the ANOVA results (Table 3) interaction terms with species included reflect mostly the key significance of species as a discriminating factor. Therefore, not too much weight should be put on interpretation of these interaction terms. When examined at the species level one can note that ambient temperature is a significant main factor in all species and in all three principal components (PC2 with *D. pulex* and *D. magna* as exceptions; Table 3).

An examination of the relationship between body length vs. caudal spine length in the three species reveals that there were strong positive correlations between the two variables both in *D. pulex* and *D. longispina*, but negative correlations in *D. magna* (Fig. 5). However, when the relative caudal spine length is graphed against age, the three species match. In all cases there is a strong negative correlation (Fig. 6). Thus, smaller *Daphnia* have a longer caudal spine proportional to their body length than larger *Daphnia* have. Taking age again as a covariate and running an analysis of covariance results in the following tabulation (note that only the main effects are listed; moreover, the criterion of homogeneity of slopes is fulfilled):

Source	df	F	P
Age (covariate)	1	1138.94	< 0.001
Species	2	212.92	< 0.001
Food	1	0.45	0.508
Temperature	1	24.72	< 0.001
Error	908		

We conclude that food level has no effect on relative length of the caudal spine in the three *Daphnia* species. Although the effect of temperature is significant, the covariate age and the factor species contribute most of the documented variance.

Further to examine body shape differences between the three species we made the following analysis: First we selected four variables characterizing *Daphnia* body shape: caudal spine length, head length, body width and body breadth (all divided by body length). All these variables exhibit a linear relationship with the age of an individual. Therefore the selected shape variables were regressed on age. The equations were first solved for newborn size *Daphnia*. Second, we took the age at the first reproduction of each of

the species at the two food and temperature levels (Table 1; Bengtsson 1986) and applied regression equations to estimate the shape of mature *Daphnia*.

The results are straightforward (Fig. 7): The newborn of all species have caudal spines which are longer relative to body length than are spines of mature *Daphnia*. This holds also for the ratio of head length over body length (Fig. 7). The core body shape, however, is consistently the opposite, viz., mature *Daphnia* are more spherical than are newborn individuals (Fig. 7). The three species differ to some extent, though. Not unexpectedly, *D. magna* is more oval than the two other species, and the difference in its relative caudal spine length between newborn and mature individuals is much more pronounced

Table 3. Summary of analyses of covariance for principal components (PC1, PC2, PC3) based on shape variables (age as a covariate, *df* = degrees of freedom, *F*-ratio and *P* = corresponding statistical significance).

Source	<i>df</i>	PC1		PC2		PC3	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
All species							
Cov: Age	1	327.10	0.000	130.74	0.000	53.29	0.000
S: Species	2	256.26	0.000	88.98	0.000	43.20	0.000
F: Food	1	0.49	0.489	0.01	0.878	2.68	0.097
T: Temperature	1	5.03	0.023	15.10	0.000	60.34	0.000
S × F	2	0.05	0.933	3.82	0.021	3.70	0.024
S × T	2	31.65	0.000	4.44	0.011	7.75	0.000
F × T	1	0.13	0.712	0.61	0.439	3.01	0.078
S × F × T	2	6.61	0.001	3.32	0.035	6.09	0.002
Error	908						
<i>D. magna</i>							
Cov: Age	1	97.55	0.000	3.41	0.062	20.53	0.000
Food	1	0.001	0.923	1.67	0.194	0.03	0.830
Temperature	1	5.32	0.020	1.56	0.213	13.79	0.000
F × T	1	6.70	0.009	6.82	0.009	0.94	0.332
Error	243						
<i>D. pulex</i>							
Cov: Age	1	112.23	0.000	112.01	0.000	11.66	0.001
Food	1	0.01	0.872	0.46	0.501	7.53	0.006
Temperature	1	14.56	0.000	1.74	0.184	49.67	0.000
F × T	1	0.00	0.908	0.65	0.421	12.83	0.000
Error	324						
<i>D. longispina</i>							
Cov: Age	1	122.76	0.000	52.10	0.000	24.06	0.000
Food	1	0.98	0.323	3.79	0.049	0.10	0.738
Temperature	1	39.26	0.000	7.36	0.007	7.98	0.005
F × T	1	8.36	0.004	1.65	0.196	0.01	0.861
Error	339						

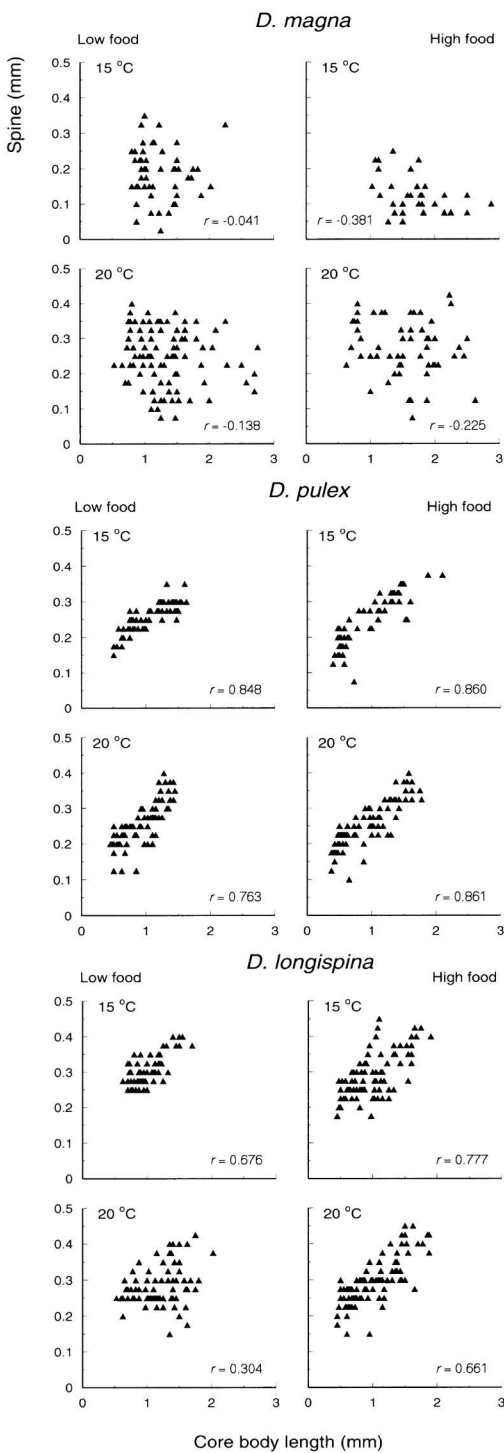


Fig. 5. Relationship between body length and caudal spine length in three *Daphnia* species reared at low and high food levels at 15°C and 20°C (correlation coefficients inserted).

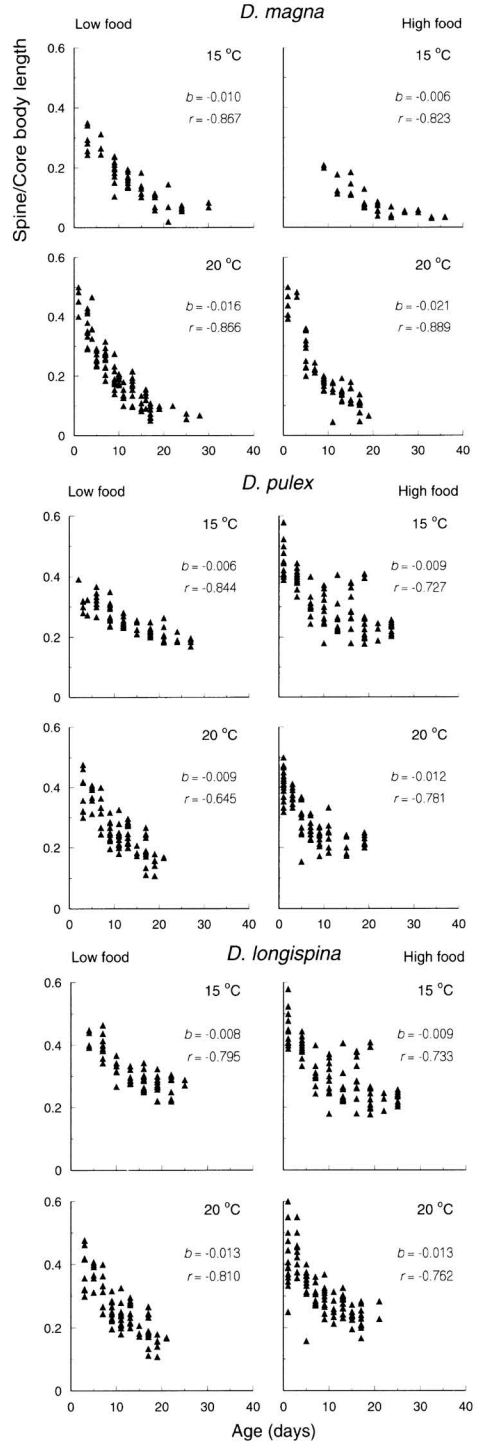


Fig. 6. Relationship between relative caudal spine length (caudal spine length divided by body length) and age in three *Daphnia* species reared at low and high food levels at 15°C and 20°C (b = slope of regression line, r = correlation coefficient).

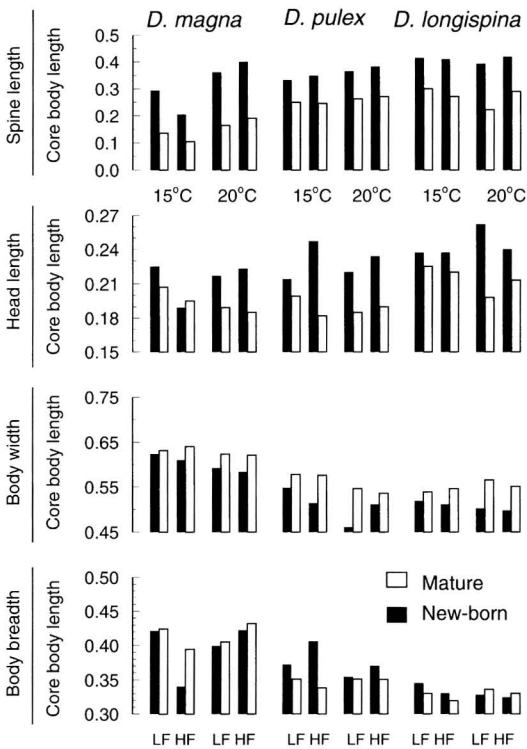


Fig. 7. Graphs of body shape for three *Daphnia* species reared at low (LF) and high food (HF) levels at 15°C and 20°C. New-born and mature individuals treated separately.

than for *D. pulex* and *D. longispina*. In the latter two species the length of the caudal spine is always more than 25% of body length (Fig. 7).

4. Discussion

4.1. Growth

In cladocerans, juvenile growth in body length is generally linear over time (see the review in Frey & Hann 1985, Taylor 1985, Tessier & Goulden 1987, Perrin 1989). When individuals reach maturity, growth slows as resources are allocated to reproduction. As animals become older, growth rates usually decline with size, and they may eventually reach a stable size (Frey & Hann 1985). In our experiments, growth could — reliably

enough — be described by linear regressions. Since the experiments were terminated 4–6 days after the initiation of reproduction, this is in agreement with previous studies.

Both temperature and food level affected growth rates of the three species. In *D. magna* and *D. longispina*, growth rates were higher in 20°C low-food regimes than in 15°C high-food experiments, whereas growth in *D. pulex* was fastest in the two high-food treatments. Food quantity generally has a large effect on *Daphnia* growth rates (Hrbáková & Hrbáček 1978, Frey & Hann 1985, Taylor 1985, Tessier & Goulden 1987, Lampert 1987). In many cases, low food levels result in increased duration of instars and reduced size increments at each moult. Our experimental design did not allow us, however, to examine the contributions of these factors to the observed growth rates. Temperature generally influences growth rates by affecting the physiological processes involved (e.g., Frey & Hann 1985). Several other factors, not investigated in the present study have also been shown to influence growth rates of cladocerans, e.g., food quality and length of photoperiod (Frey & Hann 1985, Lampert 1987).

At 15°C as well as at 20°C, the large *D. magna* had a higher growth rate than *D. longispina* in both high-food and low-food experiments. *D. pulex* had a higher growth rate than *D. magna* at 15°C, whereas the reverse was found at 20°C. *D. pulex* had a higher growth rate than *D. longispina* in all cases except under 20°C with low-food conditions. These results might suggest that *D. magna* and *D. pulex* generally are competitors superior to *D. longispina* (cf., Tessier & Goulden 1987), whereas *D. pulex* would outcompete *D. magna* at lower temperatures but not at higher. As regards *D. pulex* vs. *D. longispina*, this is consistent with competition experiments in the laboratory (Bengtsson 1987a). However, in the other two-species combinations, growth rate does not appear to be a good predictor of competitive dominance. Bengtsson (1987a) found that *D. magna* was generally a better competitor at 15°C than at 20°C, and at higher food levels, whereas it was outcompeted by *D. pulex* as well as by *D. longispina* in low-food experiments at 20°C. Obviously, other factors than growth rate may be important for the competitive ability of these

species. Some good examples of such a factor are resistance to starvation (Tessier *et al.* 1983), ability to grow with food densities lower than in the present experiments (e.g., fig. 3 in Tessier & Goulden 1987), or a high population growth rate (cf., Bengtsson 1987a, b, Tessier & Goulden 1987).

4.2. Body shape

We found that, whereas there were significant temperature effects on *Daphnia* body shape, food abundance had little effect on it. The major effects on shape in the analyses of covariance were age and species. Thus, differences between the species were more pronounced than were the treatment differences. The age differences in shape are presumably related to body size, and will be discussed below. Some of the variation accounted for by temperature may be associated with the lower growth rates and smaller body sizes at any given age at 15°C.

As expected, *D. magna* differs in shape from the other two species in several respects. It has a more spherical body, relatively shorter caudal spines and a flatter, less pointed head. *D. longispina* usually has a relatively larger head than the other two species, and a more pronounced helmet formation.

The present results can be viewed in relation to those by Ranta & Tjossen (1985) in an investigation on rock-pool *D. longispina*. In their data body length decreased during the summer, and caudal spines were longer and heads more pointed in late than in early summer. Since relative caudal spine length as well as head length both decrease with age (and hence also body size), the differences they observed were probably partly due to differences in body size between early and late summer. Differences in food availability and temperature conditions probably played a minor role.

Shape differences among *Daphnia* have traditionally been discussed under the heading of cyclomorphosis, i.e., seasonal differences in body protuberances. In a review, Jacobs (1987) discussed a number of hypotheses proposed to explain the adaptive significance of cyclomorphosis. Those included the view that spines and helmets

enlarge the animals and are devices for escaping invertebrate predators such as phantom midges and copepods (Zaret 1980, Dodson 1974); and that such devices might enhance gas exchange in warmer waters (Hebert 1978). As we generally did not find that higher temperature led to larger heads or longer caudal spines, the latter suggestion is not supported by our data.

Longer caudal spines, helmets and other protuberances often make individual prey less susceptible to predation by invertebrates such as copepods and *Chaoborus* larvae (Zaret 1980, Jacobs 1987, Dodson 1989a). Invertebrate predation is usually heavier on smaller-sized individuals, while individuals above 1.5 to 2 mm are usually not preyed upon by invertebrate planktivores (Zaret 1980). Thus, if invertebrate predators are important mortality agents, one might expect smaller, immature individual *Daphnia* to have longer spines and larger helmets than larger, older ones. In all three species relative caudal spine length (and also the relative head length) decreased with age, indicating that investment in caudal spine mass decreases with size. In *D. longispina* and *D. pulex*, absolute caudal spine length increased with size. However, this was not the case in *D. magna*, where caudal spine length decreased or did not change at all with body size. This indicates that longer caudal spines are not needed when body length exceeds about 2 mm. If these patterns have any adaptive significance, invertebrate predators are a likely selective agent. Indeed, Ranta & Espo (1989) demonstrated that all instars of the three species of common and abundant rock-pool insects preferred *Daphnia* of about 1.7 mm to larger *Daphnia*.

Invertebrate predators are common in rock-pools, but their impact on *Daphnia* populations is not so well documented. Corixid bugs (Ranta & Espo 1989) and facultatively predaceous copepods belong to this type of predator, but relatively little is known concerning their feeding habits. Corixids and copepods do not appear to have an effect on the distribution of rock-pool *Daphnia* species (Bengtsson 1988, cf., Ranta *et al.* 1987), although they may contribute to the scarcity of smaller cladocerans in rock-pools (Ranta & Espo 1989). In the laboratory, *Daphnia* populations can withstand high predation rates of the invertebrate type without going extinct (Milbrink & Bengtsson

1991). However, because of their commonness, these predators may be important selective agents to which *Daphnia* must be adapted to be able to survive in the rock-pool environment.

In all three species relative body width and partly also relative body breadth increased in mature individuals relative to neonates. This can probably be attributed to the fact that egg-bearing female *Daphnia* need more space under the carapace than immature ones (cf., Frey & Hann 1985). Although this inevitable change in morphology associated with maturity might possibly alter such factors as swimming ability, additional adaptive explanations for this difference in shape between neonates and mature individuals are probably not needed.

Although few similar analyses of body shape in *Daphnia* have been made (Frey & Hann 1985), our results are often in agreement with previous studies. Dodson (1989b; tables 1–8) reported that in seven *Daphnia* species (*D. pulex* among them), relative head length as well as tail length decreased in adults compared to neonates. Fryer (1985) noted that juvenile *D. magna* have longer caudal spines than do adults. Anderson (1931) found that in *D. magna* the ratio of carapace length to total length increased from birth to sexual maturity, i.e., a decrease in relative head length with age.

In other respects, however, ours and previous findings seem dissimilar. We did not find that food availability influenced shape, as has been shown for helmet growth in some species (Jacobs 1987, Dodson 1988, 1989a). One reason for this may be that the differences in head shape found among our species are not as pronounced as those described by the above authors. In fact, it may be questionable to ascribe the term "true helmet" to what we have observed in our study. Nonetheless we suggest that the differences in head shape that we found may have a similar function.

To conclude, we found that variation in shape among rock-pool *Daphnia* was mainly due to species-specific differences, and age and/or body size-related differences in relative head and caudal spine length. Of the environmental conditions examined, food density appeared to play no role at all, whereas temperature did affect body shape in a way that — presumably in large part — was a consequence of its effect on growth

rate. Hence, the shape of *Daphnia* seems to be quite inflexible as a response to imposed environmental changes, at least within the limits of the present study. We have not explicitly examined the hypothesis that the differences observed are adaptive responses to invertebrate predation. Nonetheless, our results are consistent with this explanation for differences in relative caudal spine and head length between newborn and mature individuals.

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Appendix. Characterization of morphometric data by size variables (A= core body length, B= caudal spine length, C= body width, D= head width, E= head length, F= body breadth) and shape variables (B/A = caudal spine length divided by core body length, C/A = body width divided by body length, D/A = head width divided by body length, E/A = head length divided by body length, F/A = body breadth divided by body length, F/C = body breadth divided by body width, E/D = head length divided by head width). Minimum, median and maximum values indicated for species cultured at 15°C and 20°C with low (LF) and high food (HF) levels (age in days and A – F in mm).

	15°C						20°C					
	LF			HF			LF			HF		
	min	med	max	min	med	max	min	med	max	min	med	max
<i>D. magna</i>												
Age	4	13	31	10	22	37	1	9	28	1	10	19
A	0.80	1.12	2.25	1.02	1.62	2.87	0.52	1.25	2.75	0.62	1.50	2.62
B	0.02	0.18	0.35	0.05	0.12	0.25	0.07	0.25	0.40	0.07	0.27	0.42
C	0.50	0.73	1.37	0.62	1.10	1.82	0.32	0.77	1.97	0.42	1.00	1.62
D	0.40	0.55	0.95	0.40	0.75	1.25	0.25	0.56	1.32	0.30	0.71	1.12
E	0.17	0.25	0.40	0.20	0.30	0.55	0.12	0.25	0.50	0.12	0.27	0.40
F	0.25	0.50	1.00	0.37	0.62	1.25	0.17	0.50	1.15	0.25	0.62	1.12
B/A	0.02	0.15	0.35	0.03	0.06	0.20	0.05	0.19	0.50	0.04	0.17	0.50
C/A	0.54	0.61	0.75	0.55	0.65	0.73	0.46	0.61	0.79	0.50	0.61	0.69
D/A	0.36	0.47	0.58	0.37	0.44	0.55	0.32	0.43	0.56	0.30	0.45	0.55
E/A	0.14	0.21	0.31	0.13	0.19	0.26	0.11	0.19	0.29	0.12	0.19	0.26
F/A	0.29	0.42	0.55	0.28	0.40	0.52	0.21	0.40	0.51	0.32	0.42	0.59
F/C	0.50	0.68	0.88	0.44	0.62	0.75	0.38	0.66	1.05	0.52	0.68	0.86
E/D	0.34	0.44	0.57	0.33	0.43	0.58	0.25	0.43	0.66	0.28	0.40	0.61
<i>D. pulex</i>												
Age	3	13	28	1	7	25	1	9	19	1	7	19
A	0.50	1.12	1.62	0.40	1.02	2.10	0.45	0.97	1.57	0.37	0.98	1.87
B	0.15	0.27	0.35	0.07	0.22	0.37	0.12	0.25	0.40	0.10	0.25	0.40
C	0.27	0.70	1.00	0.17	0.55	1.15	0.22	0.50	0.92	0.17	0.47	1.07
D	0.20	0.47	0.70	0.12	0.37	0.75	0.15	0.32	0.67	0.12	0.32	0.70
E	0.10	0.22	0.35	0.10	0.17	0.37	0.10	0.17	0.30	0.10	0.17	0.35
F	0.15	0.37	0.70	0.15	0.33	0.65	0.15	0.32	0.67	0.12	0.35	0.60
B/A	0.16	0.25	0.39	0.10	0.28	0.47	0.14	0.27	0.50	0.15	0.30	0.50
C/A	0.40	0.58	0.71	0.34	0.56	0.65	0.36	0.51	0.71	0.36	0.52	0.75
D/A	0.26	0.42	0.54	0.24	0.40	0.58	0.26	0.36	0.51	0.20	0.36	0.50
E/A	0.14	0.20	0.27	0.11	0.18	0.34	0.13	0.18	0.31	0.12	0.19	0.33
F/A	0.23	0.33	0.45	0.25	0.34	0.52	0.26	0.34	0.56	0.21	0.35	0.47
F/C	0.38	0.56	0.72	0.42	0.65	1.00	0.44	0.69	1.18	0.38	0.66	1.00
E/D	0.35	0.45	0.70	0.31	0.47	1.00	0.33	0.50	1.00	0.36	0.55	1.00
<i>D. longispina</i>												
Age	4	16	25	1	10	25	3	11	21	1	7	21
A	0.62	1.00	1.70	0.45	0.96	1.90	0.52	1.25	2.02	0.45	0.97	1.87
B	0.25	0.30	0.40	0.17	0.27	0.45	0.15	0.27	0.42	0.15	0.30	0.45
C	0.32	0.50	0.87	0.22	0.50	1.20	0.27	0.65	1.12	0.22	0.51	1.12
D	0.22	0.40	0.62	0.17	0.37	0.85	0.22	0.48	0.75	0.15	0.37	0.80
E	0.15	0.22	0.37	0.07	0.20	0.42	0.15	0.25	0.37	0.10	0.22	0.40
F	0.22	0.32	0.57	0.15	0.27	0.70	0.17	0.40	0.72	0.10	0.28	0.80
B/A	0.22	0.29	0.46	0.17	0.30	0.57	0.10	0.24	0.47	0.15	0.31	0.60
C/A	0.44	0.53	0.64	0.44	0.53	0.64	0.42	0.55	0.67	0.38	0.53	0.71
D/A	0.28	0.40	0.50	0.31	0.40	0.50	0.31	0.40	0.58	0.28	0.40	0.62
E/A	0.18	0.22	0.28	0.16	0.22	0.33	0.15	0.20	0.40	0.14	0.22	0.30
F/A	0.25	0.32	0.43	0.25	0.32	0.45	0.25	0.33	0.44	0.22	0.31	0.45
F/C	0.44	0.63	0.80	0.44	0.60	0.81	0.48	0.60	0.77	0.44	0.60	0.90
E/D	0.45	0.55	0.72	0.37	0.55	0.83	0.38	0.51	0.93	0.35	0.55	0.77