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Variation in sexual size dimorphism in the calanoid copepod *Diaptomus leptopus*: a test of 2 hypotheses

Timothy S. Nishikawa

A Thesis

in

The Department

of

Biology

Presented in Partial Fulfillment of the Requirements
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March 1995

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ABSTRACT

Variation in sexual size dimorphism in the calanoid copepod *Diaptomus leptopus*: a test of two hypotheses

Timothy S. Nishikawa

The calanoid copepod, *Diaptomus leptopus*, shows greater sexual size dimorphism in temporary ponds than in permanent ponds. I examined whether this intraspecific variation in dimorphism could be explained by variation in body size or variation in developmental constraints. Allometry did not explain variation in sexual dimorphism within populations or among populations. Individuals from four locations were mated and their offspring were raised under identical laboratory conditions. Significant differences in development time were found between the sexes and between the two pond types, temporary and permanent: males matured before females and individuals from permanent ponds matured before those from temporary ponds. There was no significant difference in protandry between permanent and temporary habitats. Development time was not correlated with body size, and laboratory reared populations with large sexual differences in length had a low degree of protandry. These results suggest that allometry and developmental constraints have no affect on the observed differences in sexual size dimorphism among ponds. Potential adaptive hypotheses to explain the population characteristics are discussed.

ACKNOWLEDGEMENTS

I would like to thank Dr.'s Daphne Fairbairn and Jim Grant for their assistance and professionalism in being my committee members. Thanks also go to Dr. Stewart Anderson for supplying copepod samples from the Canadian Rocky Mountains; to Dr. Perry Anderson for allowing me to use equipment and space in his laboratory and to Dr.'s Catherine Potvin and Mary Maly for their statistical acumen. In addition, I thank Mike Bryant, Dr. Paul Albert and his students for use of their computing knowledge and equipment. I would also like to thank Dr. Caroline Beckman and countless genetics students for keeping me financially solvent in the dark years of this thesis.

Finally, there are the numerous personal thanks that one accumulates over a length of time such as this and the question becomes "Do they deserve to be placed in a separate appendix?". An overwhelming portion of these thanks goes to the multiple generations of Maly Mobs which I have had the pleasure of experiencing. Thus, there is really only one person to thank. Thank you Ed Maly.

DEDICATION

This thesis is dedicated to those members of my family and friends who have had to put up with me through these oh so eventful years.

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INTRODUCTION

Sexual size dimorphism, or body size differences between the sexes, has been the subject of several studies (see reviews by Gilbert & Williamson 1983, Hedrick & Temeles 1989 and Fairbairn 1990). Variation in sexual size dimorphism within and among taxa has been explained by a number of hypotheses including sexual selection (Darwin 1871, Gould & Gould 1989) and intraspecific competition for food (Slatkin 1984, see review by Shine 1989). Some studies have found allometric correlations between sexual size dimorphism and body size (Cheverud et al. 1985, Fairbairn 1990). Others have hypothesized that body size, and thus also sexual size dimorphism, may be indirectly influenced by selection on development time (Thornhill & Alcock 1983). This study examines variation in sexual size dimorphism among several populations of the calanoid copepod, *Diaptomus leptopus* Forbes, to determine if it can be explained by allometry, variation in body size among populations, or variation in selection for development time in habitats with varying degrees of permanence.

Allometry

Allometry is the relation between a particular trait and absolute body size. In terms of sexual size dimorphism, two trends have been recognized. Fairbairn & Preziosi (1994) reported that in species with male-biased dimorphism, hyperallometry or increasing sexual size dimorphism with increasing body size occurred whereas hypoallometry or decreasing size dimorphism with increasing body size occurred in species with female-biased size ratios. Thus, the degree of dimorphism in a taxon may simply be the result of a function of absolute body size.

Body size accounts for 36% of the variation in male-biased dimorphism among primate species (Cheverud et al. 1985). Similarly, scaling for body size has been shown to remove the difference in male-biased dimorphism between monogamous and polygynous species of two families of birds, the Fringillidae and the Emberizidae (Bjorklund 1990).

Body size may also account for a significant portion of the variation in female-biased dimorphism. In birds of prey, large female-biased dimorphism occurs in species with large proportional breeding increments in females (Wheeler & Greenwood 1983). In other words, smaller species were observed to be more sexually dimorphic than larger species. In a study of 12 species of waterstriders, Fairbairn (1990) also observed greater female-biased sexual size ratios in smaller species.

Developmental constraints

If there is a physiological relationship between development time and body size, then the degree of sexual size dimorphism may be indirectly influenced by selection for a shortened or extended juvenile growth period

(Thornhill & Alcock 1983). In many species (e.g. zooplankton, insects & fishes), large females are more fecund (Shine 1988). However, there may be no corresponding selection for large male size and perhaps even selection for small male body size. For example, early emergence by males (protandry) may increase reproductive success through greater access to females. This strategy may be advantageous if females only mate once in a season, if sperm competition favours early matings or if older females have lower reproductive potential. Selection for early maturation may also occur if there is high juvenile mortality (Thornhill & Alcock 1983).

Wiklund & Forsberg (1991) observed a relationship between sexual size dimorphism and protandry in species from two families of butterflies. Males usually emerge as adults before females and there is interspecific variability in sexual dimorphism. As the developmental constraints hypothesis predicts, in species with a large male-biased dimorphism, there is a lower degree of protandry. This observation suggests that early male emergence remains important even in species with large male-biased size dimorphisms and illustrates the trade off between early development and large body size (Wiklund & Forsberg 1991).

Wiklund et al. (1991) studied selection for large size and protandry in a polyandrous butterfly *Pieris napi*. Males are selected for large size and are selected to mature before females. In the spring, some individuals mature and produce offspring that diapause while others produce offspring that develop and produce a second generation. Individuals that follow the latter developmental pathway are under more extreme time constraints since they must complete another generation cycle before the winter season. The size dimorphism is similar for both pathways since males under the time constrained pathway achieve large body size by increasing their growth rate. There is still evidence for the compromise between early development and large body size since there is lower protandry in these individuals that produce direct developing offspring when compared to individuals that produce diapausing offspring.

Sexual Size Dimorphism In Copepods

There are a number of conflicting observations and hypotheses that try to explain the variation in sexual size dimorphism among copepod taxa in which females are generally larger than males. In some calanoid species, sexual size ratios remain constant among populations (Bayly 1978, Maly 1978). Grad & Maly (1988) suggest a species-specific relationship between sexual size dimorphism and mating success. In other species, there is considerable intraspecific variation in dimorphism both among populations (DeFrenza et al. 1986) and seasonally within populations (Geddes & Cole 1981).

Allometric relationships in copepod sexual size dimorphism have received little attention. In a study of three benthic cyclopoid copepods, Abdullahi & Laybourn-Parry (1985) noted that the smallest species was more sexually dimorphic than the larger species. Maier (1994) found increasing dimorphism with increasing body size among nineteen species of cyclopoid copepods and similarly, Geddes & Cole (1981) found intraspecific increases in dimorphism with increases in body size for six species of calanoid copepod. The latter two observations are contrary to the hypoallometric trend observed in species with female-biased size ratios (Fairbairn & Preziosi 1994).

Bayly (1978) observed extreme dimorphism in centropagid calanoid copepods inhabiting temporary ponds. He suggested that a lack of predation in temporary habitats would select for greater dimorphism to reduce within species competition for limited food resources.

In contrast, Maier (1992) observed a low sexual size dimorphism in the cyclopoid copepod *Metacyclops minutus* inhabiting a temporary pond in Germany. He argued that mating success was a function of size dimorphism and therefore the need to reduce copulation errors in a temporary pond would select for lower sexual dimorphism. Grad & Maly (1992) also proposed that size-selective predation on small individuals (males) may result in selection for lower sexual size dimorphism.

Rodriguez & Jimenez (1990) suggest that the large degree of sexual dimorphism in the marine copepod *Acartia grani* is a characteristic of temporary populations.

Consistent with the developmental constraints hypothesis, they suggest that fecundity selection favours large female size but the need to develop quickly may select for smaller fast developing males. This same strategy may also occur in temporary ponds.

Studies of copepod development have generally focused on marine calanoid species. Evidence of protandry has been found in *Eurytemora herdmani* (McLaren et al. 1989, Escribano & McLaren 1992). Landry (1983) also observed that males generally develop before females in marine calanoid copepods and suggests the importance of mating with virgin females as the selective force behind this protandry.

Geddes & Cole (1981) question the ecological significance of varying degrees of sexual size dimorphism in North American diaptomid copepods. They found that sexual dimorphism did not vary with habitat permanence. They argue that variation in intraspecific sexual size dimorphism and the occurrence of most species in both temporary and permanent habitats are reasons for the lack of adaptive patterns of sexual dimorphism.

Diaptomus leptopus is a calanoid copepod species with variable female-biased sexual size dimorphism among different populations in the Montreal region (DeFrenza et al. 1986). Two populations from permanent ponds are less sexually dimorphic than two populations from temporary ponds that either dry up during the summer or freeze to the bottom in winter. Geddes & Cole (1981) also report variation in sexual dimorphism within one *D. leptopus* population over 13 sampling dates.

In this study, I examine variation in sexual size dimorphism within and among 18 *D. leptopus* populations. I examine whether the dimorphism is variable within populations with respect to body size and season. I also examine whether the variation in dimorphism among the 18 populations can be explained by body size. In addition, studies were designed to determine if the trend between the dimorphism of the population and the permanence of the habitat is valid among the 18 *D. leptopus* populations.

In addition, I examine whether these trends are valid in reported data of calanoid copepods from North America (Geddes & Cole 1981) and from Australia (Bayly 1978). I re-analyzed each data set to examine possible allometric relationships in sexual size dimorphism among calanoid species. And, I also determined whether variation in sexual size dimorphism among species is related to the degree of permanence of the habitat.

I also performed experiments to determine whether differences in sexual size dimorphism between ponds can be explained by the developmental constraints hypothesis. Development times of individuals from both temporary and permanent ponds were determined from laboratory rearing experiments. Early maturation might be particularly important in temporary ponds where eggs must be produced before the pond becomes inhospitable and where invertebrate predators may cause high juvenile mortality. Fecundity selection for large female size would constrain their early development time and hence, I expect greater protandry in the more dimorphic temporary populations. This expectation is contrary to that of Wiklund et al. (1991) since they observed less protandry in the more time constrained pathway. In their study animal, *Pieris napi*, they expected selection for large male body size and this constrained the early development of males and created the lower protandry. I do not expect the same selection for large male size in *D. leptopus* since Grad & Maly (1992) observed similar mating success across a range of sexual size ratios in mated pairs.

MATERIALS AND METHODS

Diaptomus leptopus is a freshwater North American calanoid copepod that occurs in a range of habitats from temporary ponds to permanent lakes at all altitudes from eastern Alaska south to Virginia on the east coast and to Oregon on the west coast (Ward & Whipple 1959). The life cycle involves eggs developing through six naupliar stages and five copepodite stages before the final determinate moult into adulthood (Ward & Whipple 1959). *Diaptomus leptopus* are obliged to mate before a clutch of eggs can be extruded (Watras & Haney 1980) and these clutches are then carried by females in egg sacs. Voltinism among populations is variable. Temporary habitats can support univoltine populations (O'Brien et al. 1973) while permanent habitats can support overlapping generations throughout the year. In inhospitable habitats, copepods survive pond dessication or winter freezing as diapausing eggs in the sediments.

Allometry

This study tested for allometry in sexual size dimorphism in *D. leptopus*. Individuals were sampled and measured from 18 populations: ten Montreal region populations and eight western Canadian populations, provided by R. Stewart Anderson. Montreal region lakes and ponds were sampled using an 80 µm Wisconsin tow net. Animals were concentrated into 25 ml plastic vials and were killed on site with 30% formalin solution. Western Canadian lakes were sampled using a 65-70 µm conical plankton net with mouth diameter of 25 cm; samples were also preserved in formalin (Anderson 1974).

Preserved *D. leptopus* adults were isolated on a depression slide and their size was measured as prosome length (Figure 1). Prosome length is a commonly used estimate of copepod body size (Bayly 1978, Geddes & Cole 1981, McLaren & Corkett 1981). With the aid of a Wild inverted microscope (6x magnification) fitted with a Hitachi closed circuit camera, prosome lengths were measured to the nearest 0.01 mm from a Hitachi 9" monitor. For each population, a minimum of 10 individuals of each sex were measured for any given sampling date. Lake locations, number of sampling dates, and minimum number of individuals of each sex per sample are summarized in Table 1.

To examine possible allometry in sexual size dimorphism, log-transformed average female prosome length was regressed against log-transformed average male prosome length. A slope of one indicates that as absolute size increases, the ratio of female to male size or the size dimorphism is unchanging (Fairbairn 1990). Body lengths were log-transformed to normalize the data and since both axes have sampling error, model II regressions were performed according to Ricker (1984). Confidence limits were calculated for comparisons with a slope of one.

Figure 1: Diagram of copepod measurements. Distance A is the prosome length, from the head to tip of the metasomal wings. Distance B is the length to the base of the furcal rami. Distance C is the length to the end of the furcal rami. Distance D is the total copepod length to the end of the longest furcal setae. (Distances B, C, & D are measures cited in Bayly (1978) and Geddes & Cole (1981) and are referred to in subsequent sections) Original calanoid copepod drawing was taken from Ward & Whipple (1959, p.736).

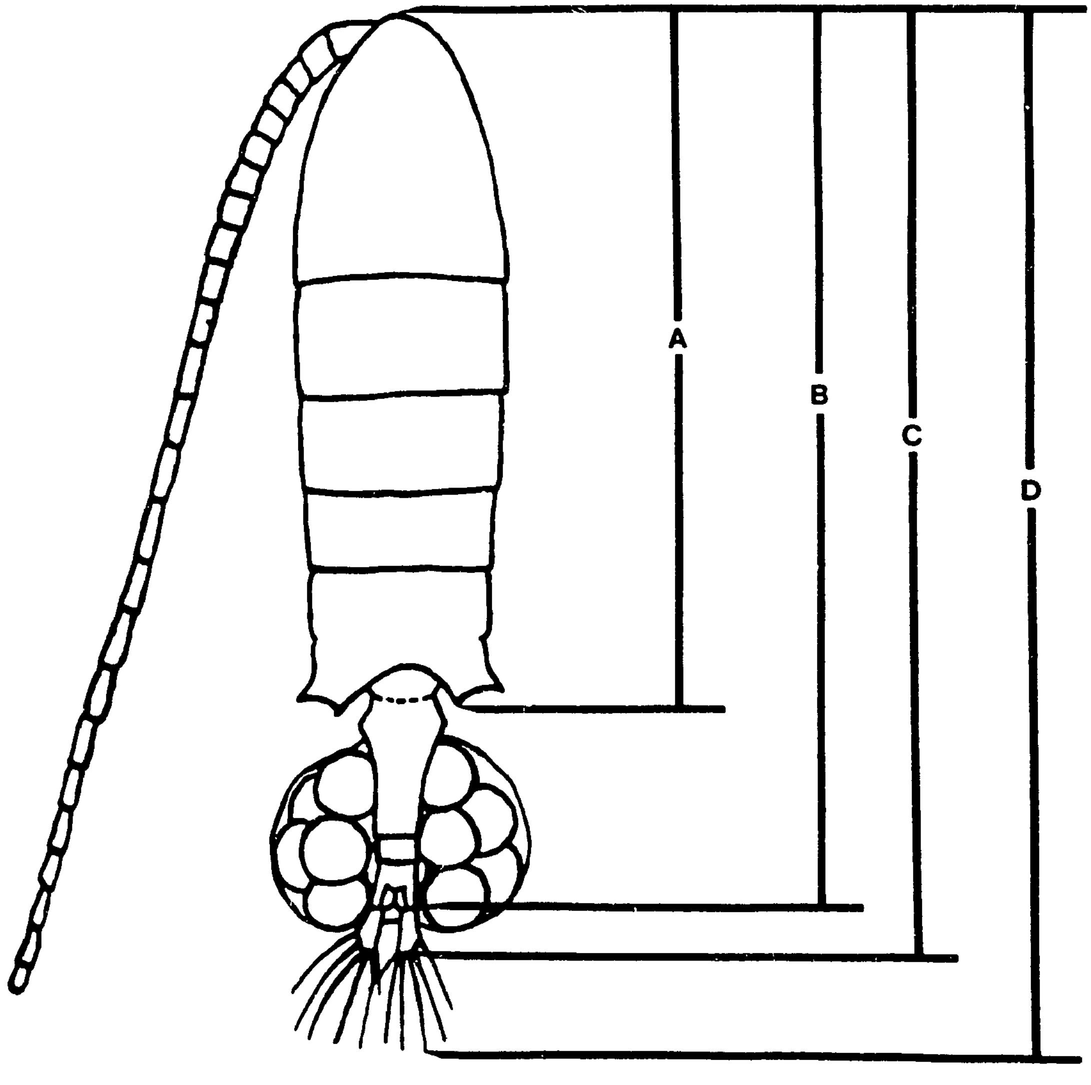

A
B
C
D

Table 1: Summary of 18 *Diaptomus leptopus* populations used in allometric analyses of sexual size dimorphism. Ponds are arranged according to maximum known depth and pondtypes are T = Temporary, P = Permanent and u = unknown.

POND	Location	max. known depth (m)	pond type	no. of sampling dates	min. no. of adults per date per sex
Quarry	45^{0}25'45" N 73^{0}52'30" W	0.6	T	1	20
Malloy 3	45^{0}43'28" N 74^{0}28'40" W	0.8	T	1	20
Stonycroft	45^{0}25'44" N 73^{0}56'22" W	0.8	T	1	20
Malloy 2	45^{0}43'22" N 74^{0}28'43" W	1.0	T	1	20
Nixon	50^{0}44'19" N 115^{0}55'53" W	1.0	u	1	31
Malloy 1	45^{0}43'12" N 74^{0}29'02" W	1.8	T	1	18
Malloy 0	45^{0}43'16" N 74^{0}28'55" W	2.1	T	1	20
Hill	45^{0}25'50" N 73^{0}56'45" W	2.4	T	14	17
Barbotte #3	46^{0}05'21" N 73^{0}52'07" W	3.2	P	10	20
Bear	50^{0}13'04" N 114^{0}25'44" W	4.0	u	1	28
Linnett	49^{0}03'46" N 113^{0}54'16" W	4.7	u	1	18
Virl	52^{0}52'36" N 118^{0}13'58" W	6.0	u	1	28
Truite Rouge	46^{0}27'30" N 74^{0}15'30" W	7.6	P	2	24
Christine	52^{0}53'09" N 118^{0}14'30" W	8.4	P	1	12
Hibernia	52^{0}52'14" N 118^{0}08'30" W	9.0	P	1	28
Lac aux Rats	46^{0}26' N 74^{0}19' W	9.1	P	1	20
Caledonia	52^{0}51'58" N 118^{0}09'40" W	10.5	P	1	10
Dorothy	52^{0}52'56" N 118^{0}13'47" W	16.0	P	1	10

Allometry in sexual size dimorphism was examined within two populations: Hill pond with 14 sampling dates over a three year period, and Barbotte #3 pond with 10 sampling dates over an eight year period (Table 1). Samples of 17-36 animals per sex from Hill Pond and 20-33 animals per sex from Barbotte #3 pond were measured to obtain average prosome length on each date of sampling.

For these two populations, tests were also performed to determine whether the sexual size dimorphism within ponds varied with time. For each pond, sexual differences in length and Julian calendar dates were fitted to linear and quadratic regression models. A two-way analysis of variance was also performed for each pond to determine whether log-transformed prosome length varied between the sexes and/or between the seasons.

Allometry in *D. leptopus* sexual size dimorphism was also examined among the 18 populations. Average prosome lengths were used when more than one sampling date was available. A model II regression of log-transformed female length with log-transformed male length was performed to determine whether absolute body size explains variation in sexual size dimorphism among populations.

Allometric tests were performed on sexual dimorphism data of Australian calanoids (Bayly 1978) and of North American calanoids (Geddes & Cole 1981). Bayly (1978) presented average male and female size for three copepod measurements: total body length, length to the end of the furcal rami and prosome length, while Geddes & Cole (1981) presented two measurements of body size: length to the base of the furcal rami and prosome length (Figure 1). Model II regressions of log-transformed female length with log-transformed male length were performed on the five sets of data to determine if body size explains variation in sexual size dimorphism among calanoid species.

Populations from temporary and permanent habitats

The eighteen populations were examined to determine whether variation in sexual size dimorphism was related to the degree of permanence of the pond or lake. Sexual dimorphism was measured as the difference between the average female and average male prosome length. Maximum known depth of the habitat was used as an estimate of permanence since it accounts for the likelihood of the pond drying up or freezing to the bottom. A model II regression was performed since both axes have sampling error, and confidence limits were calculated according to Ricker (1984) to test the significance of the regressed slope.

Similar tests were performed on data from Australian calanoids (Bayly 1978), and from North American calanoids (Geddes & Cole 1981). Both studies reported the tendency for species to inhabit permanent or temporary habitats. For each of the three measures reported by Bayly (1978) and for one of the measures reported by Geddes & Cole (1981), an analysis of covariance was performed to determine whether the regression of log-transformed female length onto log-transformed male length was similar for species found in permanent habitats and for species found in temporary habitats. Species that were not clearly classified as either permanent or temporary pond inhabitants were ignored.

Developmental constraints

Diaptomus leptopus was collected from the field to permit matings in the laboratory. Adults were sampled in oblique tows with an 80 µm Wisconsin tow net and were transported back to the laboratory in 20 litre plastic carboys. Copepods from three temporary ponds (Malloy 0, Malloy 2 and Malloy 3) and one permanent pond (Barbotte #3) were used in this development time experiment.

Adults from each pond were mated in the laboratory so that date of clutch extrusion could be observed. Copepods of each sex were first separated into 500 ml beakers filled with their pond water filtered with an 80 µm mesh. For each pond, ten males and ten females without clutches were allowed to mate in four litre pickle jars filled with filtered pond water. Copepods were fed on alternating days with *Cryptomonas erosa* var. *reflexa* in concentrations greater than 5000 cells/ml. Isolated adults and mating adults were kept at ambient room temperature (20-22°C) and a 16:8 light:dark photoperiod. The copepod mating jars were observed daily so that newly clutched females could be removed and replaced with unclutched females. Dead adults were also removed and replaced.

Cryptomonas erosa var. *reflexa* was cultured in 4 litre jars filled with modified Guillard's Woods Hole MBL medium modified from Stemberger (1981). Cell concentrations were determined with a haemocytometer. To concoct the sterile medium, individual nutrient stocks were sterile filtered before these were added to autoclave-sterilized distilled water (Appendix). One ml of each of the 15 nutrient stocks and the one vitamin stock was added to one litre of sterilized water. Cultures used to feed copepods in all parts of this experiment were at concentrations greater than 5000 cells/ml

Clutches from newly mated females were removed and placed under common laboratory conditions. Clutches were removed from females with dissecting probes. Individual clutches were rinsed with charcoal filtered City of Montreal tap water and placed in 25 ml plastic vials filled with equal parts filtered tap water and *Cryptomonas* food culture. Vials were capped and labelled according to pond and date of egg extrusion. Vials were then transferred to 56 x 116 x 40mm plastic flow through water baths that were maintained at a constant temperature (28.5°C, SD = 0.7°C) and at a 16:8 light:dark photoperiod.

Observations were made each morning to determine the egg to adult development time for each pond. Egg clutches were monitored daily to determine the egg extrusion to egg hatching development time. Once the eggs hatched, nauplii were transferred into a 4 litre jar containing charcoal filtered tap water and 500 ml of *Cryptomonas* food culture. Each 4 litre jar contained a maximum of four clutches from the same population that hatched on the same day. One jar for each of the three temporary ponds and two jars for the one permanent pond were used in this experiment. Jars were maintained under the same conditions as the egg clutch vials and were fed on alternating days 500 ml of *Cryptomonas* food culture. Once adults emerged, they were preserved in 30% formalin solution and were later measured for prosome length.

The SAS statistical package was used to test for development time differences between the sexes, between the temporary and permanent ponds and between the individual pond replicates. Time to develop from egg hatching to adult or "post-hatching development time" was used in the analyses. The GLM procedure is appropriate for unbalanced ANOVA designs and it assumes all effects are fixed. Since the experimental design includes a nested effect, to test for differences between the two pond types: permanent and temporary, the individual pond sum of squares was used as the error sum of squares. Furthermore, type III estimable functions were used since they are the most appropriate tests for unbalanced designs (SAS User's Guide 1985).

An assumption and a prediction of the developmental constraints hypothesis were also tested. A linear regression model was fitted between body size and development time to determine if larger animals take longer to develop. This test was repeated separately for male and female data sets. The prediction that populations with greater protandry will have greater sexual size dimorphism was tested by correlating these two measures from the average values for each replicate from the development time experiment. Protandry was measured as the difference between average female development time and average male development time. Sexual size dimorphism was measured as the difference between average female prosome length and average male prosome length.

RESULTS

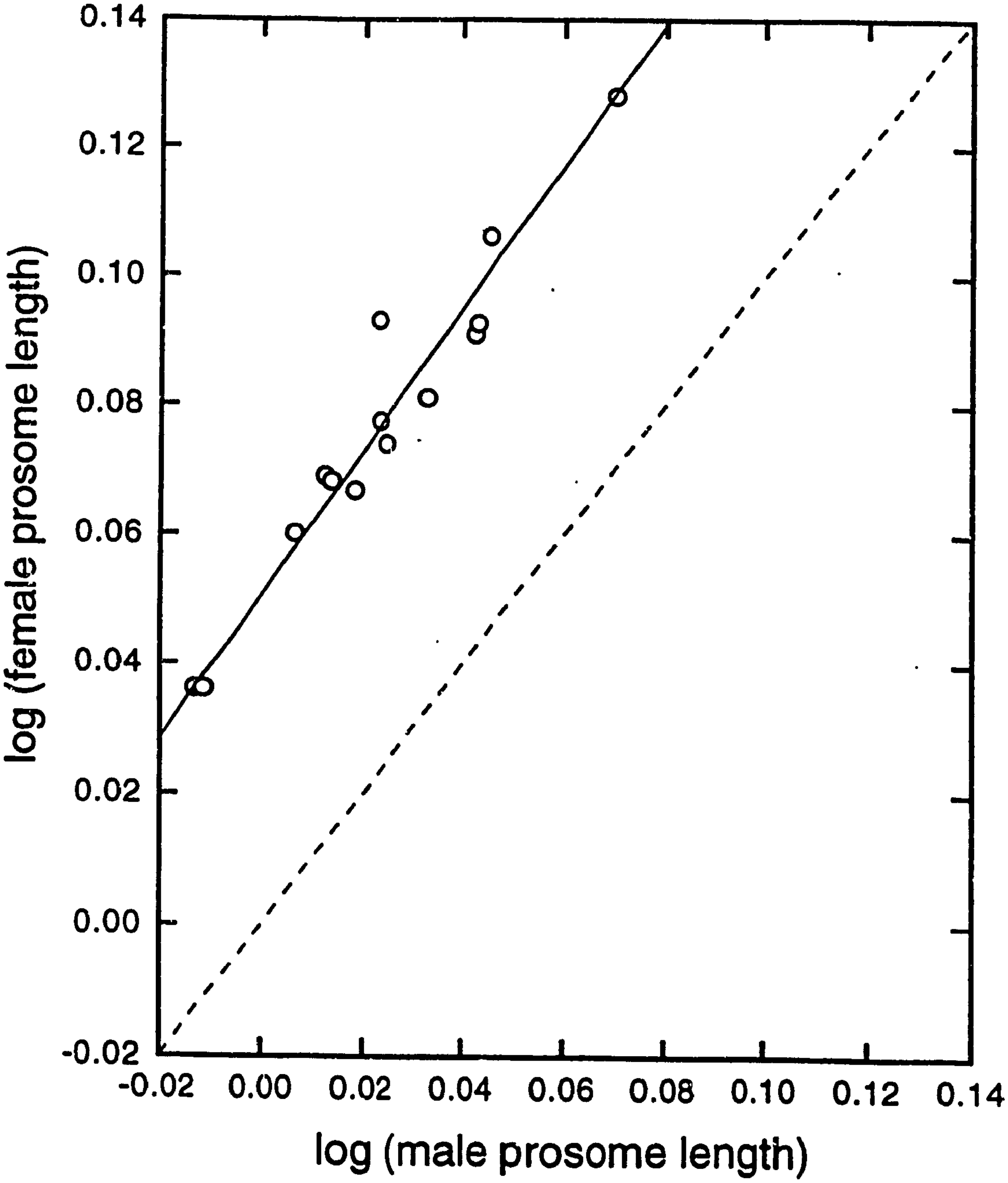
Allometry

Within Hill pond and Barbotte #3, there was no significant allometric effect on sexual size dimorphism (Figures 2 & 3). Across 14 sampling dates of Hill pond, there was significant correlation between log-transformed male and female size, but the model II regression of these two variables (Figure 2) was not significantly different from one. The average female:male size ratio in Hill pond was 1.13. In figure 3, the same pattern was observed across 10 sampling dates of Barbotte #3 pond. The average size ratio in Barbotte #3 pond was 1.08. Thus, within ponds, the size dimorphism does not change relative to absolute size.

There was no significant allometric effect on sexual size dimorphism across the 18 *D. leptopus* populations. Log-transformed female size and log-transformed male size were significantly correlated. However, the slope from the model II regression (Figure 4) was not significantly less than one. Thus, the sexual size dimorphism among populations remains stable over a range of body sizes (male range: 0.96 - 1.62 mm, female range: 1.09 - 1.83 mm).

Furthermore, there was no significant allometric trend among a number of calanoid species from North America (Geddes & Cole 1981) and Australia (Bayly 1978). For three body size measures reported for Australian calanoids (Bayly 1978), and for two body size measures reported for North

Figure 2: Test for allometry in sexual size dimorphism within Hill Pond across 14 sampling dates. The solid line illustrates the model II regression: **log (female size) = 1.10 * log (male size) + 0.05**, ($r = 0.969$, $p < 0.001$). The dashed line represents a 1:1 body size ratio with a slope of one. Confidence limits of the slope: 95% 0.93 - 1.27, 80% 1.00 - 1.21, 60% 1.04 - 1.17.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0.04
0.06
0.08
0.10
0.12
0.14
log (female prosome length)
log (male prosome length)

Figure 3: Test for allometry in sexual size dimorphism within Barbotte #3 Pond across 10 sampling dates. The solid line illustrates the model II regression: **log (female size) = 0.93 * log (male size) + 0.04**, ($r = 0.976$, $p < 0.001$). The dashed line represents a 1:1 body size ratio with a slope of one. Confidence limits of the slope: 95% 0.76 - 1.10, 80% 0.83 - 1.03, 60% 0.87 - 0.99.

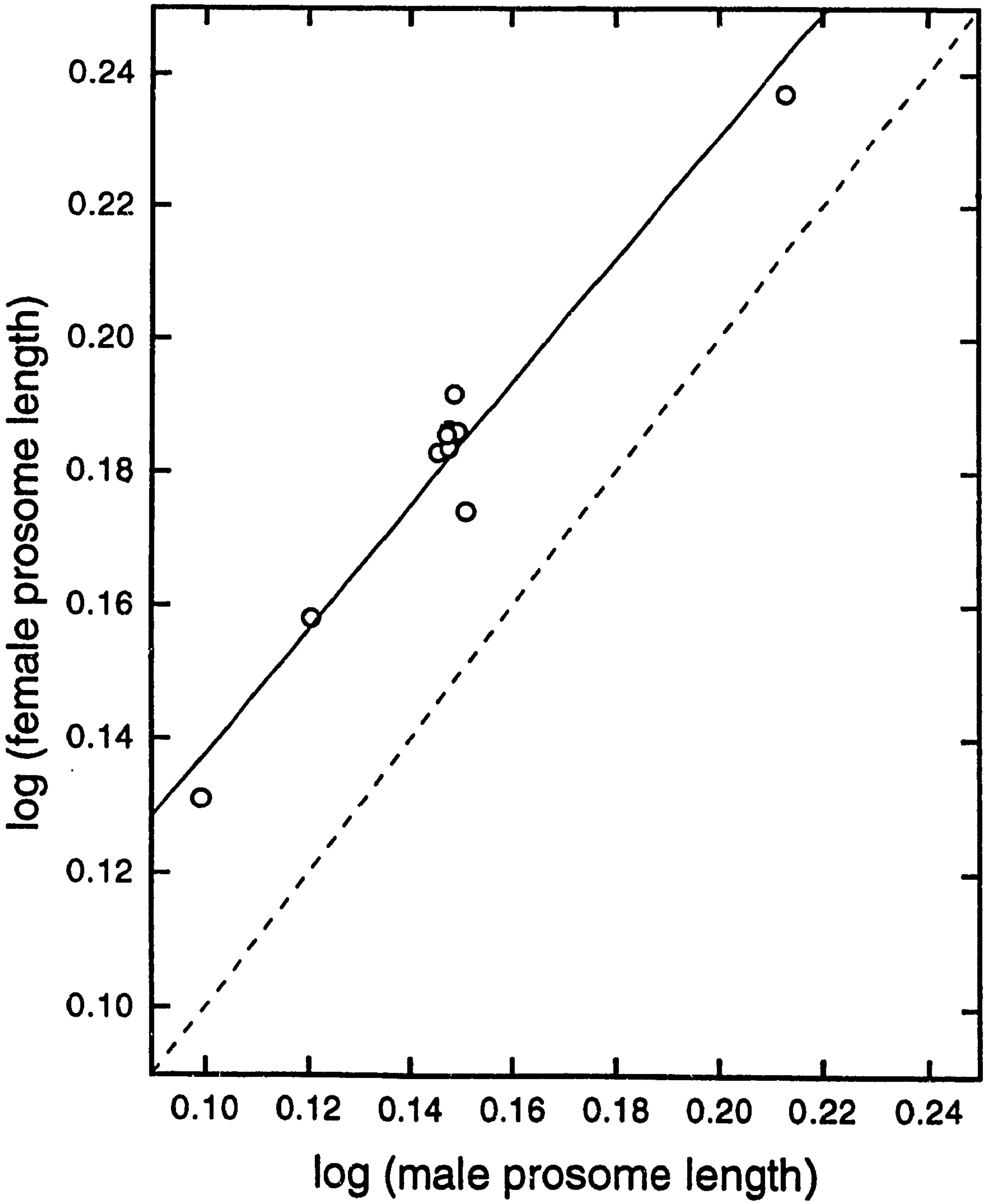
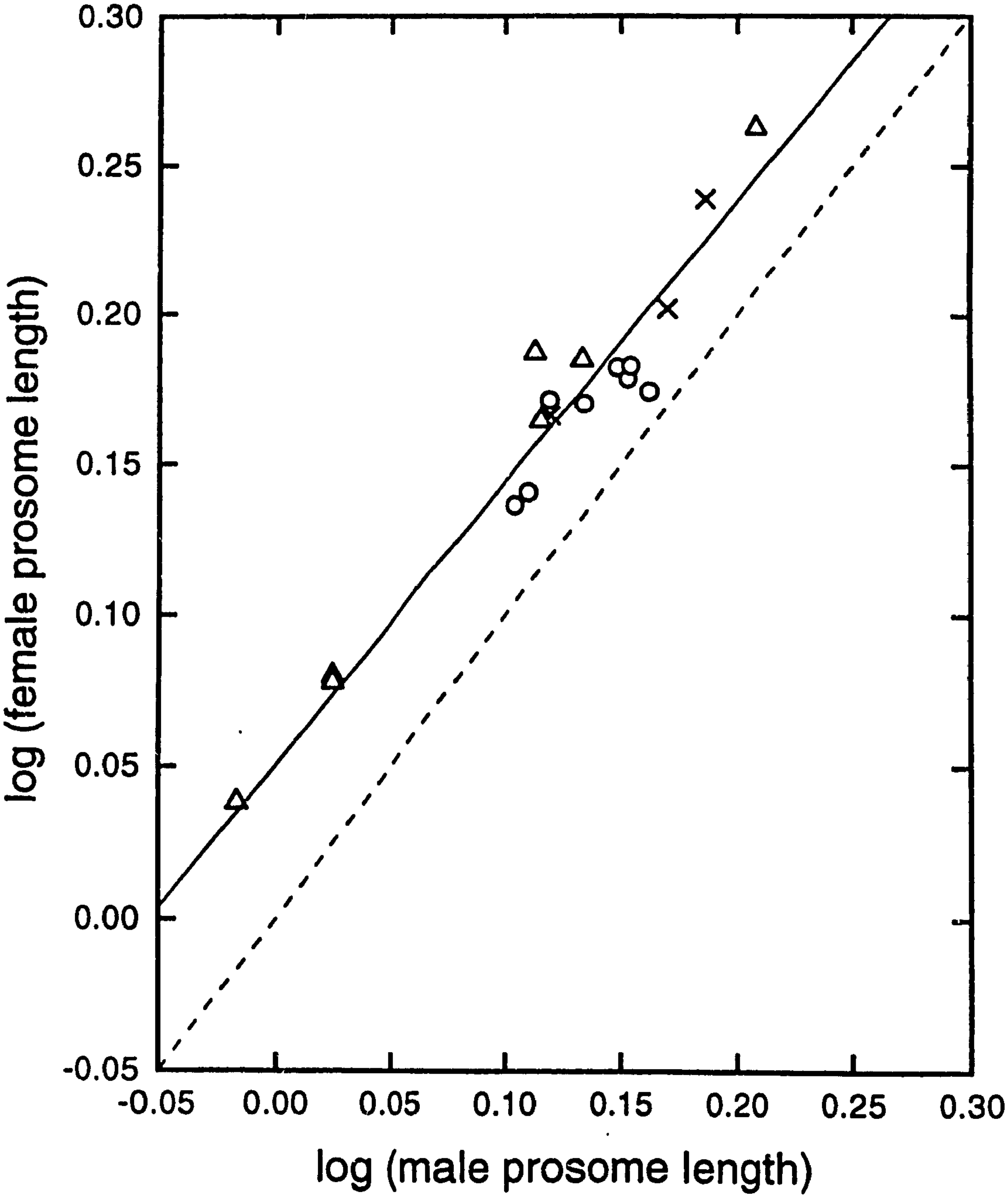

0.24
0.22
0.20
0.18
0.16
0.14
0.12
0.10
log (female prosome length)
0.10
0.12
0.14
0.16
0.18
0.20
0.22
0.24
log (male prosome length)

Figure 4: Test for allometry in sexual size dimorphism across 18 *D. leptopus* populations. The solid line illustrates the model II regression: **log (female size) = 0.94 * log (male size)** + 0.05, ($r = 0.966$, $p < 0.001$). The dashed line represents a 1:1 body size ratio with a slope of one. Confidence limits of the slope: 95% 0.81 - 1.07, 80% 0.86 - 1.02, 60% 0.89 - 0.99.

Δ = population from temporary habitat
O = population from permanent habitat
X = population from unknown habitat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0.25
0.20
0.15
0.10
0.05
0.00
-0.05
log (female prosome length)
-0.05
0.00
0.05
0.10
0.15
0.20
0.25
0.30
log (male prosome length)

American calanoids (Geddes & Cole 1981), there were significant correlations between male and female body size, but the slopes of the regressions between male and female body size were not different from one (Table 2). Thus, among species, the sexual size dimorphism is not affected by the absolute body size.

In addition, within populations, the sexual size dimorphism did not differ with respect to time of year. Across 14 sampling dates at Hill pond, there was no linear relationship between Julian calendar date and sexual differences in prosome length ($F_{(1,12)} = 2.420$, $p = 0.146$). Similarly, across 10 sampling dates at Barbotte #3 pond, the linear regression was not significant ($F_{(1,8)} = 0.512$, $p = 0.495$). Also, there was no quadratic relationship between date and sexual size differences for either Hill or Barbotte #3 pond ($F_{(2,11)} = 1.479$, $p = 0.270$ and $F_{(2,7)} = 0.377$, $p = 0.699$ respectively). Sampling date was organized into four 3-month seasons coinciding with a June-August summer peak and a two-way analysis of variance was performed to examine variance in log-transformed prosome length (Table 3). In both populations, there were significant differences between males and females and between seasons. However, the interaction effects between sex and season were not significant (Table 3) which suggests that in both populations, the sexual size dimorphism did not change relative to season.

Table 2: Test for allometry in sexual size dimorphism in a number of Australian[1] and North American[2] calanoid copepod species. Correlation coefficients and model II confidence limits of the slope were calculated using log-transformed lengths. All correlations of log (female length) on log (male length) were significant ($p < 0.001$).

body size measure	r	no. of spp	slope	confidence limits of the slope %	lower	upper
Australian spp:						
total length	0.946	26	0.993	95%	0.86	1.13
				50%	0.95	1.04
				10%	0.99	1.00
prosome length	0.930	10	0.987	95%	0.69	1.28
				50%	0.87	1.10
				10%	0.97	1.00
end of furcal rami	0.934	16	0.969	95%	0.77	1.17
				50%	0.90	1.03
				10%	0.96	0.98
N.American spp:						
prosome length	0.994	12	0.997	95%	0.92	1.08
				50%	0.97	1.02
				10%	0.99	1.00
base of furcal rami	0.994	32	1.005	95%	0.96	1.05
				50%	0.99	1.02
				10%	1.00	1.00

[1] Bayly 1978

[2] Geddes & Cole 1981

Table 3: Variation in sexual size dimorphism within two *D. leptopus* populations: Hill pond (14 sampling dates) and Barbotte #3 pond (10 sampling dates). Two-way ANOVA of log (prosome length) compares differences between the sexes and between the seasons.

	df	F	p
Hill pond			
Main Effects:			
Sex	1	30.312	0.000
Season	1	4.279	0.050
Interaction Effect:			
Season * Sex	1	0.029	0.865
Barbotte #3 pond			
Main Effects:			
Sex	1	13.514	0.003
Season	3	9.643	0.002
Interaction Effect:			
Season * Sex	3	0.054	0.983

Populations from temporary and permanent habitats

For *D. leptopus*, there was a significant relationship between the permanence of a pond and the sexual size dimorphism of the population. There was a significant negative correlation between the maximum depth of the pond and the difference in length between the sexes in the 18 populations (Figure 5). In addition, the slope of the model II regression was significantly different from zero. Thus, *D. leptopus* populations in temporary ponds tend to be more sexually dimorphic, and those in permanent ponds tend to be less sexually dimorphic.

There was a similar relationship between habitat permanence and sexual size dimorphism for a number of Australian calanoid copepod species whose sizes were reported originally in Bayly (1978). The analysis of covariance compared regressions of log (female size) on log (male size) between temporary and permanent pond species. For two of the reported size measures, total length including longest setae and prosome length, temporary pond species regressions were significantly higher than permanent pond species (Table 4, Figures 6 & 7). For the third size measure, length to the end of furcal rami, a similar but non-significant trend was observed (Table 4, Figure 8). Thus, Australian species in temporary ponds tend to be more dimorphic than Australian species in permanent habitats.

There was, however, no such relationship for 22 North American calanoid species whose sizes were reported

Figure 5: *D. leptopus* Populations from temporary habitats tend to be more sexually dimorphic than those from more permanent habitats. Solid line illustrates the model II regression: sexual size difference = 0.19 - 0.011 * max. depth, ($r = -0.504$, $p = 0.033$). Habitat permanence is estimated by maximum known depth. Confidence limits of the slope: 95% -0.017 - -0.0062, 99.5% -0.020 - -0.0034, 99.9% -0.021 - -0.0015

Δ = population from temporary habitat
O = population from permanent habitat
X = population from unknown habitat

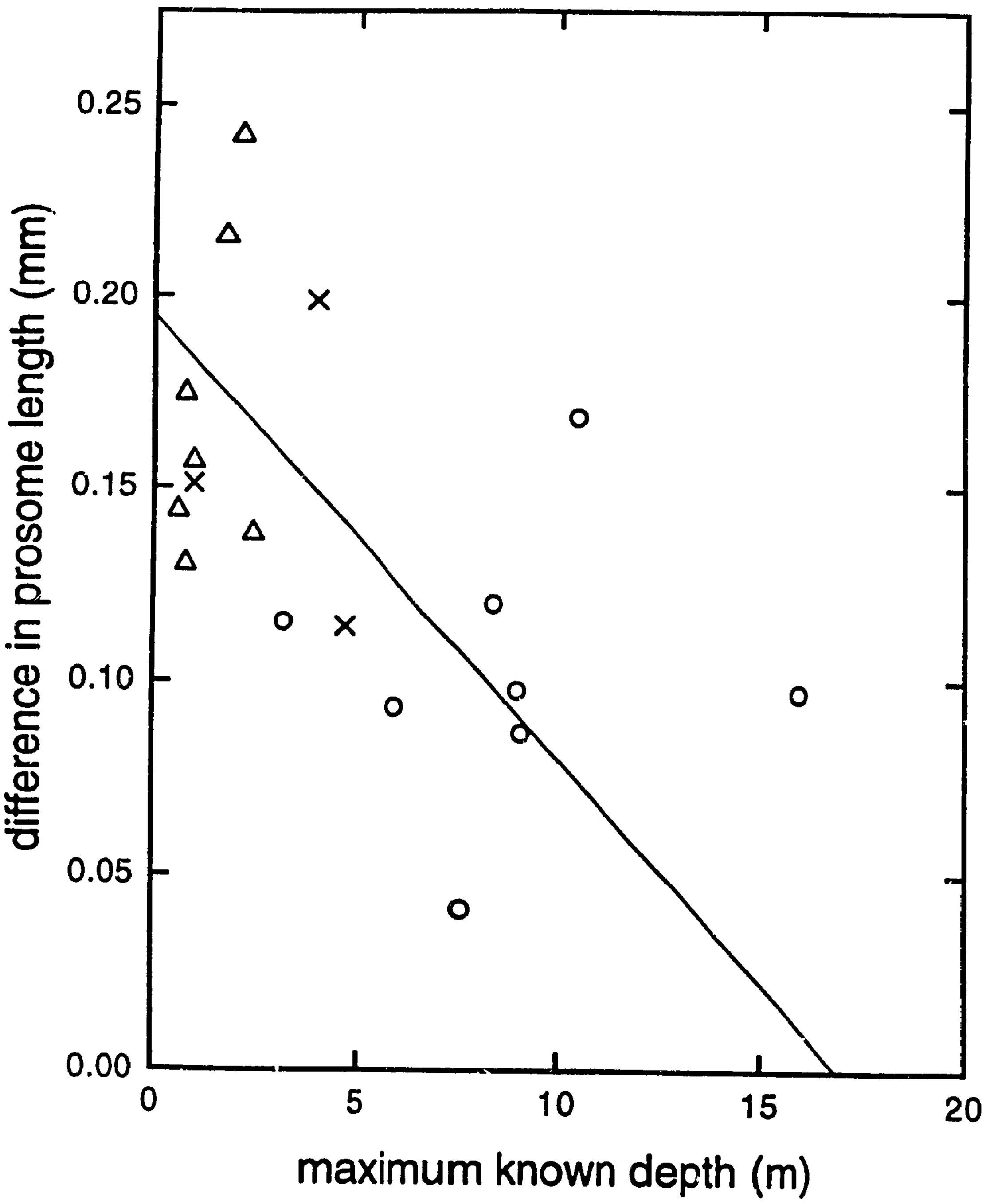

0.25
0.20
0.15
0.10
0.05
0.00
0
5
10
15
20
difference in prosome length (mm)
maximum known depth (m)

Table 4: Summary of Analyses of Covariance of log-transformed female length (FL) with log-transformed male length (ML) among a number of Australian[1] and North American[2] calanoid copepod species for four body length measures. The ANCOVA model is log(FL) = constant + log(ML) + pondtype + pondtype*log(ML). Pondtype refers to whether the species inhabits a temporary or permanent habitat. Analyses are also presented in figures 6, 7, 8 & 9.

body size measure	no. of species	Variable	T (2-tailed)	p
Australian species:				
total length	19	constant	7.249	0.000
		log(ML)	10.369	0.000
		pondtype	-3.035	0.008
		pondtype*log(ML)	0.222	0.828
prosome length	9	constant	8.254	0.000
		log(ML)	10.043	0.000
		pondtype	-4.186	0.009
		pondtype*log(ML)	-1.709	0.148
end of furcal rami	10	constant	5.353	0.002
		log(ML)	4.027	0.007
		pondtype	-1.912	0.104
		pondtype*log(ML)	0.157	0.881
N.American species:				
base of furcal rami	22	constant	5.649	0.000
		log(ML)	36.350	0.000
		pondtype	-0.935	0.362
		pondtype*log(ML)	0.202	0.842

[1] Bayly 1978

[2] Geddes & Cole 1981

Figure 6: Comparison of regressions of log (total female length) on log (total male length) between 8 temporary pond species and 11 permanent pond species from Australia. Regression for temporary pond species is significantly higher than that for permanent pond species. Sizes were originally reported in Bayly (1978).

Δ = population from temporary habitat
O = population from permanent habitat

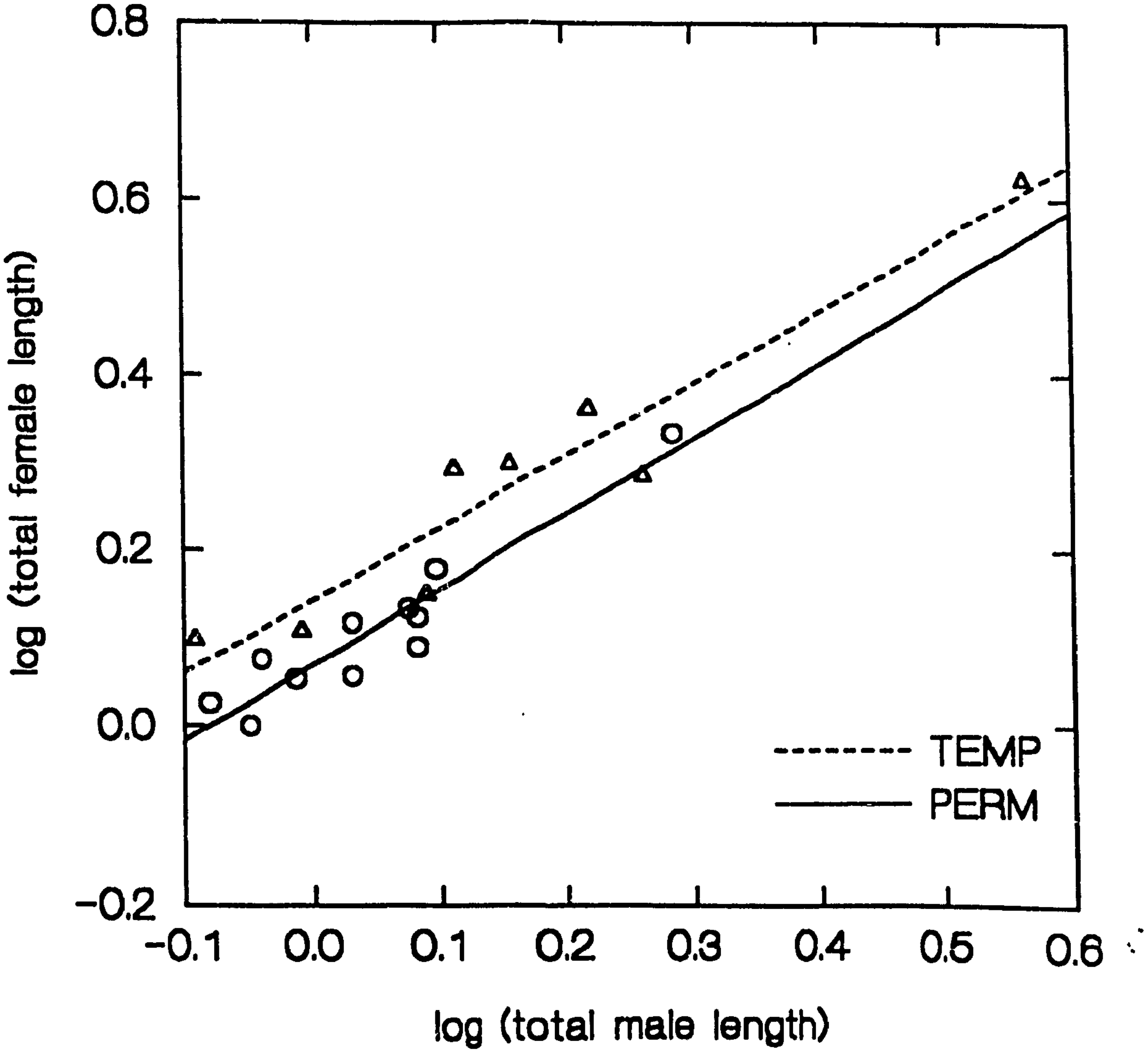

0.8
0.6
0.4
0.2
0.0
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
log (total female length)
log (total male length)
TEMP
PERM

Figure 7: Comparison of regressions of log (female prosome length) on log (male prosome length) between 5 temporary pond species and 4 permanent pond species from Australia. Regression for temporary pond species is significantly higher than that for permanent pond species. Sizes were originally reported in Bayly (1978).

Δ = population from temporary habitat
○ = population from permanent habitat

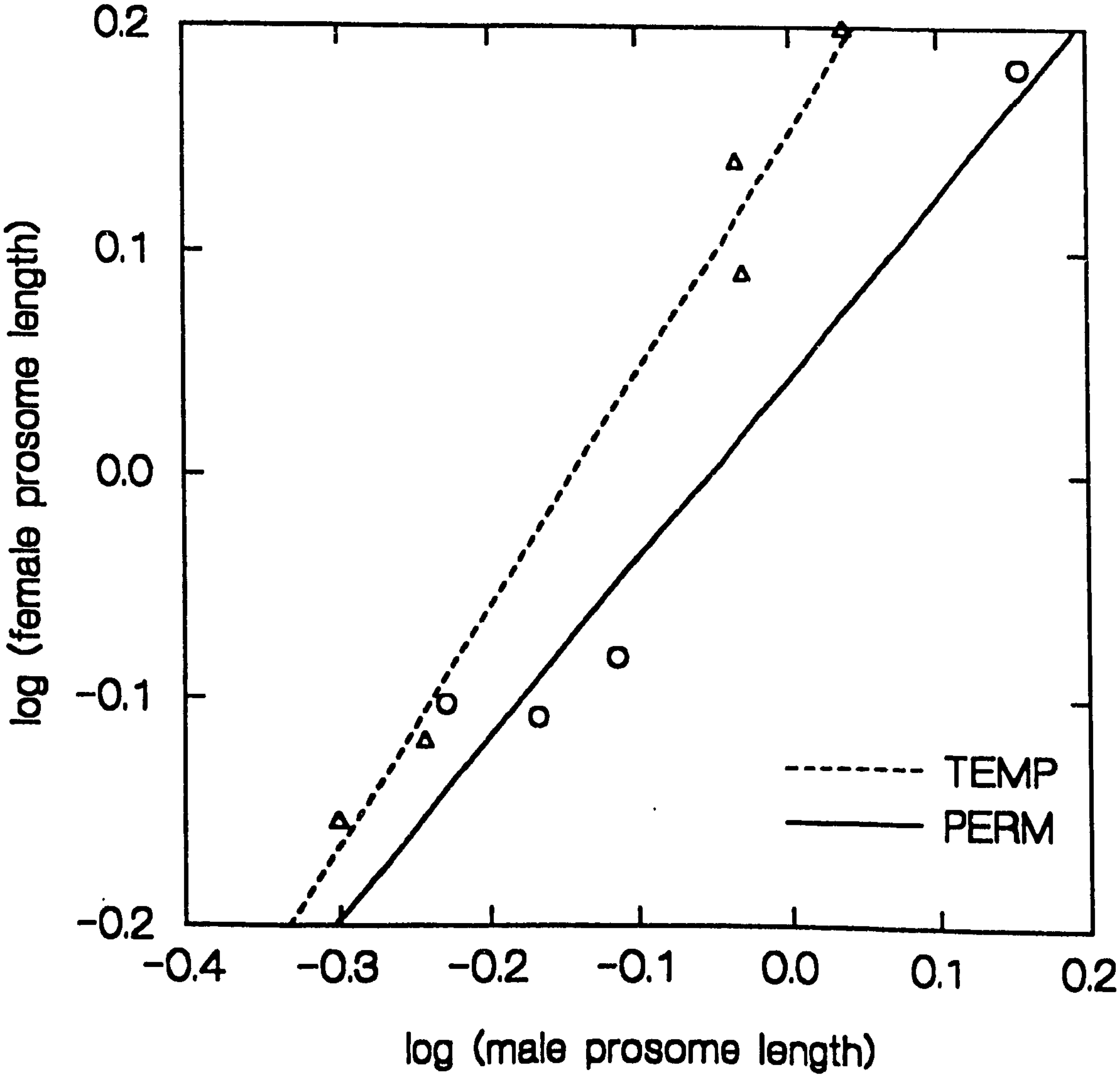
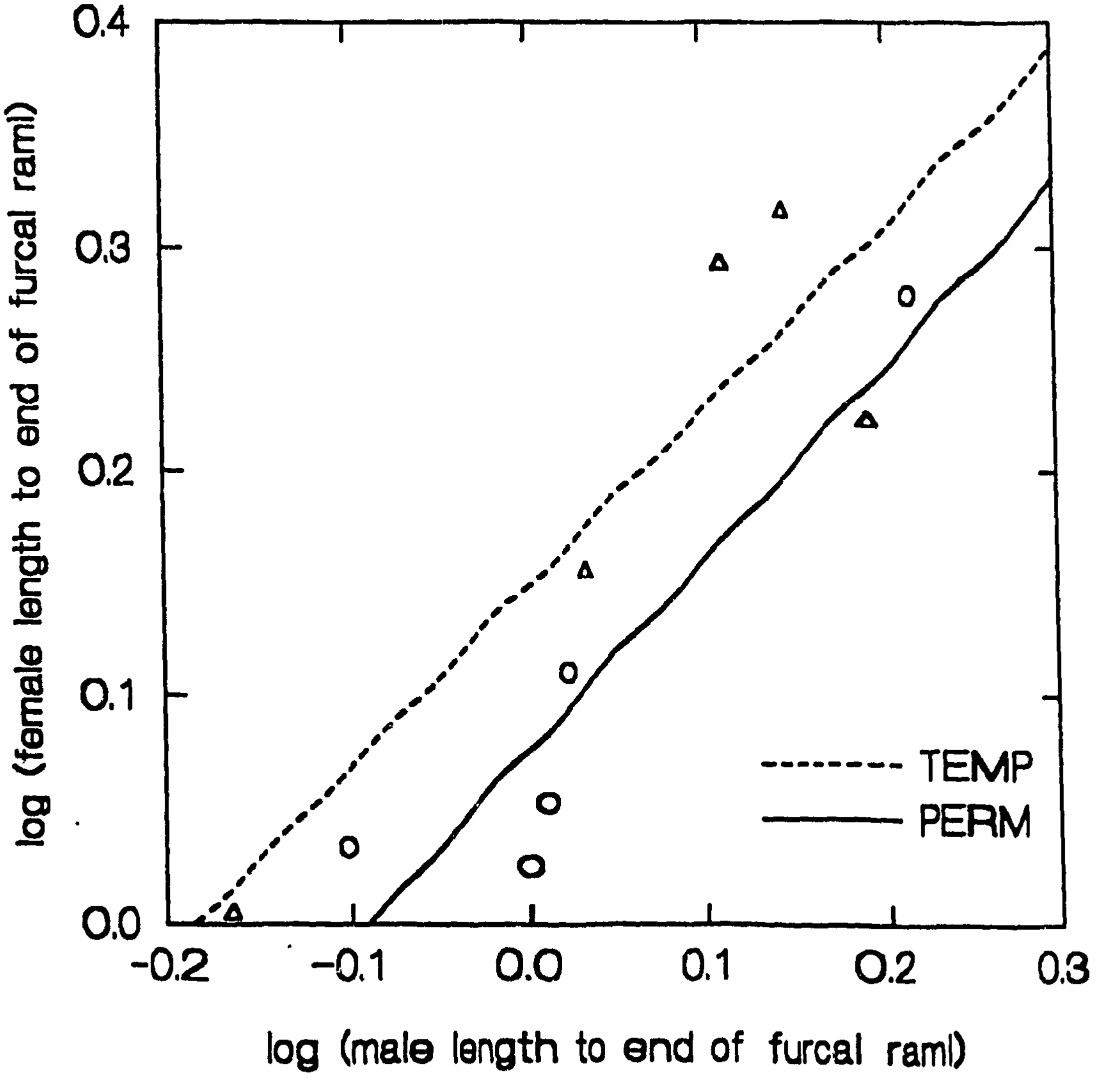

0.2
0.1
0.0
−0.1
−0.2
−0.4
−0.3
−0.2
−0.1
0.0
0.1
0.2
log (female prosome length)
log (male prosome length)
TEMP
PERM

Figure 8: Comparison of regressions of log (female length to end of furcal rami) on log (male length to end of furcal rami) between 5 temporary pond species and 5 permanent pond species from Australia. Regression for temporary pond species is higher than that for permanent pond species. Sizes were originally reported in Bayly (1978).

Δ = population from temporary habitat
O = population from permanent habitat


0.4
0.3
0.2
0.1
0.0
-0.2
-0.1
0.0
0.1
0.2
0.3
log (female length to end of furcal rami)
log (male length to end of furcal rami)
TEMP
PERM

originally in Geddes & Cole (1981). The analysis of covariance found no significant differences between 16 temporary and 6 permanent pond species with respect to their regressions of female size onto male size (Table 4, Figure 9). However, the observed trend was the same as found in Australian copepods since temporary pond species were slightly more dimorphic than permanent pond species.

Developmental constraints

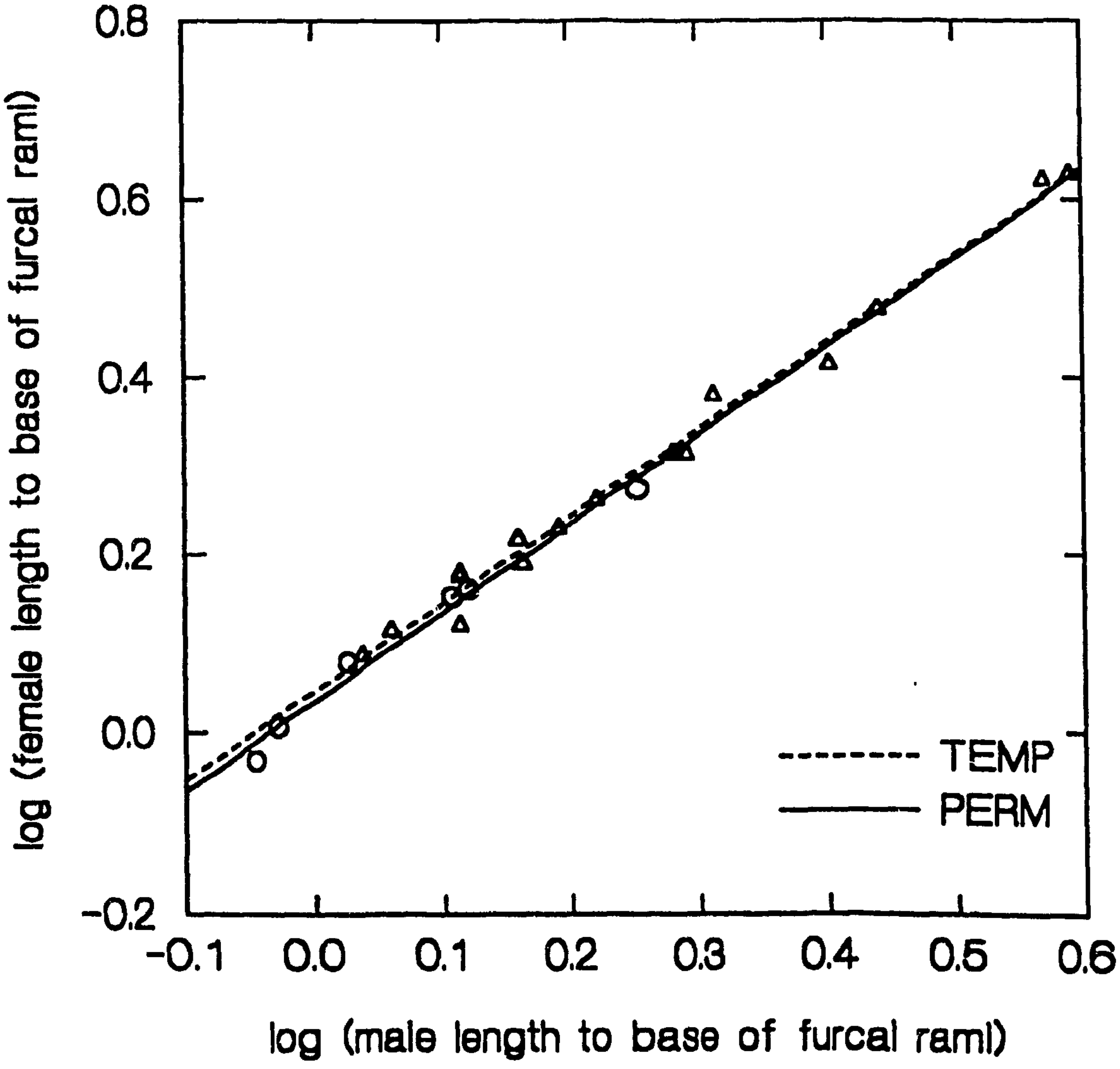
The analysis of variance of post-hatching development time revealed significant differences for both main effects, sex and pond permanence, but the interaction effect was not significant. Females took longer to develop than males, thus, there was significant protandry (Table 5, Figure 10). Populations from temporary habitats took longer to develop than populations from the permanent habitat (Table 5, Figure 10). However, the degree of protandry was not different between temporary and permanent habitats. The nested effect was not significant; hence, differences in development time between individual ponds were not significant (Table 5).

The ANOVA model was highly significant (df = 6, F = 10.31, p = 0.0001) but only accounted for 27% of the variance in post-hatching development time (Table 5). Post-hatching development time was not a normally distributed variable but the variance within groups was homogeneous.

There was no evidence to support the assumption that large body size requires a longer development time. Since

Figure 9: Comparison of regressions of log (female length to base of furcal rami) on log (male length to base of furcal rami) between 16 temporary pond species and 6 permanent pond species from North America. Regression for temporary pond species is slightly higher than that for permanent pond species. Sizes were originally reported in Geddes & Cole (1981).

Δ = population from temporary habitat
O = population from permanent habitat


0.8
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0.2
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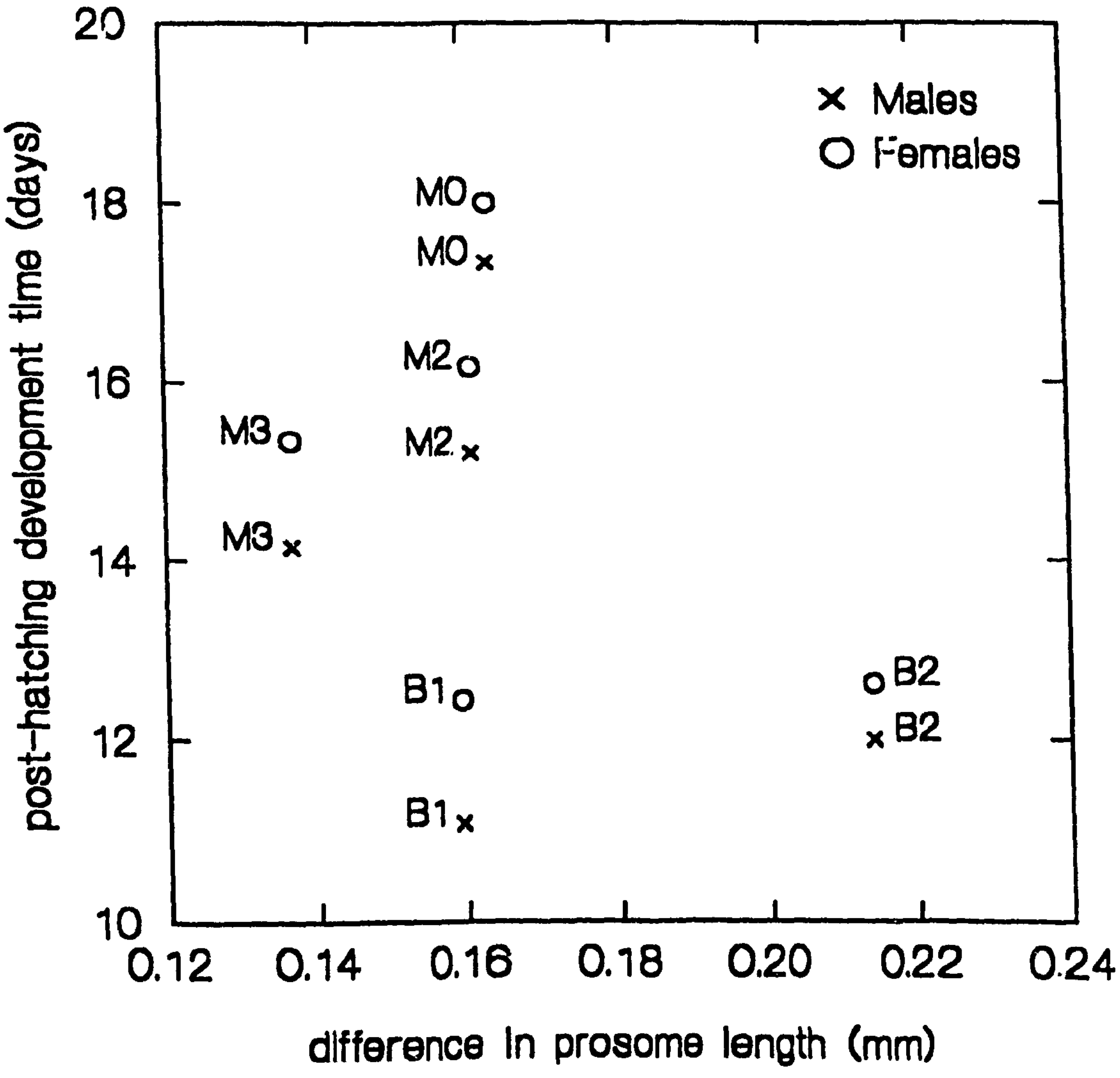
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
log (female length to base of furcal rami)
log (male length to base of furcal rami)
TEMP
PERM

Table 5: Comparison of post-hatching development time between the sexes and between populations from temporary and permanent habitats. The ANOVA model explains 27% of the variance in post-hatching development time ($r^2 = 0.270$).

	df	F	p
Main Effects:			
Sex	1	4.12	0.044
Pondtype	1	16.20	0.028
Interaction Effect:			
Pondtype * Sex	1	0.03	0.854
Nested Effect:			
Pond(Pondtype)	3	2.38	0.072

Figure 10: Comparison of post-hatching development times (days) between males and females and between populations from permanent and temporary habitats.

Temporary ponds: M0 = Malloy 0
M2 = Malloy 2 and
M3 = Malloy 3.
Permanent pond: B1, B2 = replicates from the permanent pond Barbotte #3



20
18
16
14
12
10
post-hatching development time (days)
0.12
0.14
0.16
0.18
0.20
0.22
0.24
difference in prosome length (mm)
× Males
○ Females
M0
M0
M2
M2
M3
M3
B1
B1
B2
B2

significant variance in development time was explained by sex and the two pondtypes (Table 5), I examined correlation coefficients within these groups (Table 6). Spearman rank correlations were calculated since development time is not a normally distributed variable. For the temporary pond populations and the permanent pond population, there was no correlation between log-transformed prosome length and egg-adult development time for either males, females, or the combined male, female data set (Table 6). In addition, for both pondtypes, there was no correlation between log-transformed prosome length and post-hatching development time for either males, females or the combined male, female data set (Table 6). In some cases, the observed trend was opposite to what was predicted. For temporary pond females, there was a significant negative correlation between size and post-hatching development time. Thus, in this lab-rearing experiment, there was no evidence that larger *D. leptopus* individuals within each sex took longer to develop.

There was also no evidence to support the prediction that greater sexual size dimorphism is correlated with greater protandry. There was no significant correlation between sexual size differences and sexual development time differences (Figure 11). In contrast, a negative correlation was observed. In this development time experiment, the replicates that produced populations with a large sexual size dimorphism did not have a large degree of protandry.

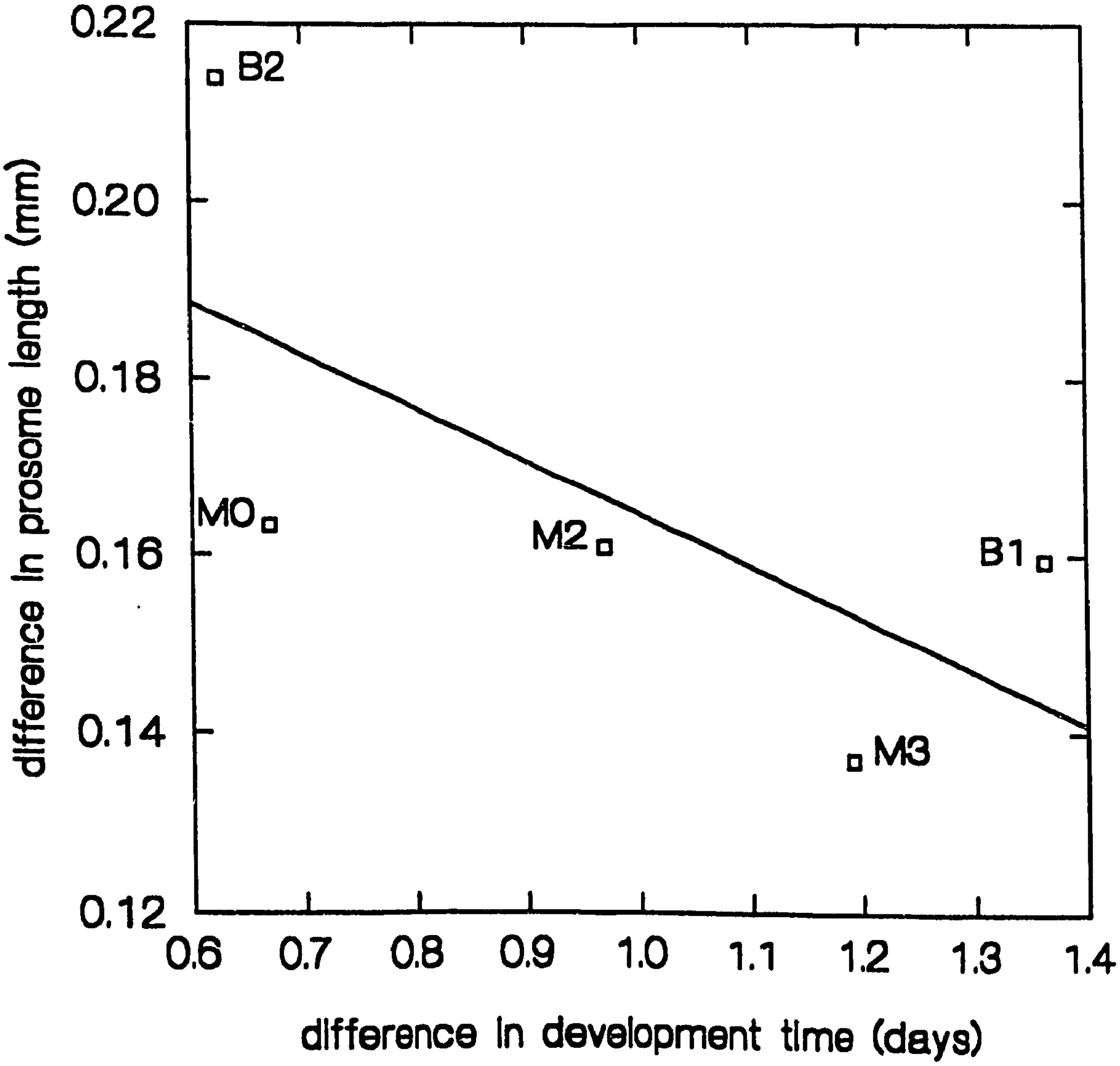
Table 6: Test for a positive Spearman correlation between log-transformed prosome length and two measures of development time (dt): a) egg to adult and b) post-hatching to adult development time.

** p(two-tailed) < 0.001

	n	egg to adult dt vs length		post hatching to adult dt vs length	
Temporary pond populations					
males:	48	-0.033	ns	-0.242	ns
females:	64	-0.071	ns	-0.419	**
males & females:	112	0.036	ns	-0.155	ns
Permanent pond populations					
males:	34	0.079	ns	0.079	ns
females:	26	0.174	ns	0.174	ns
males & females:	60	0.191	ns	0.191	ns

Figure 11: Test of the prediction that more sexually dimorphic populations should have greater protandry. The developmental constraints hypothesis predicts that as development time differences between the sexes increases, size differences between the sexes should increase also. ($r = -0.677$, $p = 0.209$)

Temporary ponds: M0 = Malloy 0
M2 = Malloy 2 and
M3 = Malloy 3.
Permanent pond: B1, B2 = replicates from the permanent pond Barbotte #3


0.22
0.20
0.18
0.16
0.14
0.12
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
difference in prosome length (mm)
difference in development time (days)
B2
M0
M2
B1
M3

DISCUSSION

Allometry

Although hypoallometry is often observed in dimorphic species with females larger than males (Fairbairn & Preziosi 1994), this study found no evidence that body size affects the sexual size dimorphism in copepod populations. There is no allometric effect of size dimorphism within populations nor among populations of *Diaptomus leptopus*. Also, there is no evidence of an allometric effect among a number of calanoid species from Australia or North America. Within copepods, it appears that variance in sexual size dimorphism is not related to variance in absolute body size.

In addition to being consistent over a range of body sizes, the sexual size dimorphism within populations did not differ with respect to time. Within two *D. leptopus* populations, Hill pond and Barbotte #3, the sexual size dimorphism did not vary with julian calendar date nor between seasons. A comparison of the sexual size dimorphisms of the two populations reveals that they are significantly different (Mann-Whitney $U = 140.0$, $p = 0.0$). This consistency of sexual size dimorphism within populations suggests the differences between populations may be adaptive responses to local selection pressures.

Populations from temporary and permanent habitats

My data suggest that the permanence of the habitat is important in determining the degree of dimorphism of the pond. *Diaptomus leptopus* populations in temporary habitats tend to be more dimorphic than those in permanent ones. Australian calanoid species which inhabit temporary populations tend to be more dimorphic than species which inhabit permanent populations. This trend was originally reported by Bayly (1978).

This trend is not significant for North American calanoid species which Geddes & Cole (1981) suggest is due to large intraspecific variation in sexual size dimorphism and the occurrence of many species in both permanent and temporary habitats. My data suggest that the intraspecific variation in sexual size dimorphism follows the same pattern as Bayly (1978) noted. For the three species, *Diaptomus siciloides*, *D. clavipes* and *D. albuquerquensis*, that had large intraspecific variation reported by Geddes & Cole (1981), temporary pond populations were also more dimorphic than permanent pond populations. For *D. albuquerquensis*, the difference in dimorphism between the two types of populations was significant ($t = 4.04$, $0.002 > p > 0.001$).

Developmental constraints

Rodriguez & Jimenez (1990) suggest that the need for rapid development in temporary habitats may select for small size in males. Since larger females are more fecund than smaller ones (Maly 1973, Smyly 1968), it would be expected that temporary populations would be more sexually dimorphic. This logic is similar to the developmental constraints hypothesis proposed by Thornhill & Alcock (1983).

This study was an attempt to confirm that this hypothesis applies to sexual dimorphism in copepods. I did find evidence of protandry in *D. leptopus* as males developed faster than females. However, there was no difference in protandry between populations from temporary and permanent habitats. I expected greater protandry in the more dimorphic populations from temporary habitats.

The hypothesis predicts that larger individuals have a longer development time. In my laboratory rearing experiments, there was no correlation between body size and two measures of development time. Further contradictory evidence includes the observation that laboratory-reared populations with a high sexual size ratio had a low degree of protandry. The theory predicts that populations with high sexual size dimorphism would have greater differences between male and female development time. Also, I observed that populations from temporary ponds took longer to develop than the permanent pond, while the theory predicted the opposite.

Elements of the experimental design may have contributed to my contrary results. In the comparison of laboratory development times, only a small number of replicates were used. Three lab-reared populations, each from a separate temporary pond population, and two lab-reared populations from the same permanent pond were used in total. This lack of replication may have reduced my ability to detect development time differences between individual ponds.

The one permanent habitat I used in the development experiment, Barbotte #3, is not a typical deep permanent lake. It has a maximum depth of only 3.2 metres in the spring and may freeze to the bottom in some winters. The pond tends to be inhabited by invertebrate predators of copepods (e.g. Chaoborus spp.) rather than fish but has been stocked by trout in previous years according to the landowner. The observed result that copepods from temporary ponds take longer to develop than copepods from Barbotte #3 pond may result from the fact that this permanent pond has some temporary pond characteristics.

Also, only one set of environmental conditions were used in the common garden design. This set of conditions may be more similar to natural conditions for some of the populations studied. Thus, the differences observed in the laboratory reared populations may be caused by differential responses to the common garden conditions. For example, based on temperature, the laboratory conditions of 28.5°C were more similar to Barbotte #3 pond summer temperatures than to the group of Malloy ponds summer temperatures (ca. 21°C). Thus, populations from the temporary ponds may have responded to this change in conditions by taking longer to develop. Thus, the result that populations from temporary ponds took longer to develop may be due to the common garden conditions rather than an adaption to temporary ponds.

In spite of the limitations of the experimental design, the development time differences that I found do not explain the variation in sexual size dimorphism between *D. leptopus* populations. Although I found evidence of protandry in this species, the absence of a difference in protandry between temporary and permanent ponds remains a major violation of a prediction of the developmental constraints hypothesis. This suggests that other theories are required to explain the apparent adaptive significance of the variable sexual size dimorphism between *D. leptopus* populations.

My observation of greater female-biased dimorphism in temporary ponds suggests that there is greater selection for large male size in permanent ponds than in temporary ponds or that there is greater selection for large female size in temporary ponds than in permanent ponds. Variation in female size (SD = 0.178) is similar to variation in male size (SD = 0.167) among populations of *D. leptopus*.

Selection for large males in permanent ponds may be important if large males swim faster and therefore increase their encounter rate with females (van Leeuwen & Maly 1991). If low copepod density in a permanent habitat is limiting reproductive success, then increasing the encounter rate with mates becomes important (Byron et al. 1983). Low copepod density may be less of a problem in temporary habitats and small male size may be favoured if there are greater maintenance costs associated with being large (Maly 1983). Grad & Maly (1992) found a negative correlation between male *D. leptopus* body size and the time elapsed before copulation in small laboratory containers suggesting large males encounter females faster than smaller males.

An energetic model developed by Reiss (1989) predicts that smaller males are able to spend more time searching for females since they are able to spend less time feeding than larger males. Thus, this model would predict that smaller males would have an advantage in a large permanent lake since they could spend more time searching for females in a low density population. This model however, assumes that foraging and mate searching are separate events. Calanoid copepods are primarily filter feeders. Their smooth locomotion is partially due to the rotation of mouth appendages (Wetzel 1983) which suggests that foraging time and mate searching time may not be as distinct as the model assumes.

Selection for large males in permanent ponds may also be important because of the presence of visual fish predators. Watras (1983) suggests the importance of mating quickly in a permanent pond to reduce the female gravid phase during which time females are dark and hence, visible against a light background. The reduction of this gravid phase reduces the vulnerability to fish predation.

This selection for large male size through increased encounter rate and faster mating time may be a form of sexual selection. Fairbairn & Preziosi (1994) recognize the importance of male mobility to increase access to females as a mechanism for sexual selection. On the basis of this study, it does not appear that the traditional mechanisms of sexual selection, mate choice and intrasexual competition, are significant. There is no evidence that females can choose males by shaking off a potential mate and there is no evidence of territoriality or intrasexual aggressive interactions.

The differences in sexual dimorphism between populations in temporary and permanent ponds may also be a result of differing degrees of intraspecific competition between ponds. To determine whether this hypothesis applies, it would be necessary to discover whether reduced niche overlap between the sexes occurs in the more dimorphic populations. Gut analysis experiments similar to those performed by Chow-Fraser & Maly (1992) would be required.

Even so, this reduced niche overlap could be a consequence, rather than a cause of the greater dimorphism in the populations living in temporary ponds. To test this theory would require reciprocal transfer experiments to determine if populations with greater dimorphism are more successful than less dimorphic populations under temporary pond conditions and the opposite under permanent pond conditions.

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Appendix: List of stock concentrations to produce Modified MBL Medium (Stemberger 1981). The three vitamin stocks were combined into a one litre container. All stocks were sterilely filtered and then 1 ml of each (including 1 ml of the vitamin stock) was added to one litre of autoclave-sterilized distilled water. Medium was used to produce monoculture of *Cryptomonas erosa* var. *reflexa*.

Macronutrient Stocks	Concentration g/250ml
$NaNO_3$	10.62
$MgSO_4$ $7H_2O$	9 25
$CaCl_2$ $2H_2O$	9.20
Na_2SiO_3 H_2O	7.10
$NaHCO_3$	6.30
K_2HPO_4	1.09
NH_4Cl	1.34

Micronutrient Stocks	
Na_2 EDTA	1.09
$FeCl_3$ $6H_2O$	0.788
$MnCl_2$ $4H_2O$	0.045
H_3BO_3	0.0325
$ZnSO_4$ $7H_2O$	0.0055
$CoCl_2$ $6H_2O$	0.0025
$CuSO_4$ $5H_2O$	0.0025
$NaMoO_4$ $2H_2O$	0.0015

Vitamin Stock	Concentration g/333ml
Thiamine HCl (B_1)	0.10
Biotin (d-Biotin)	0.0005
Cyanocobalamin (B_{12})	0.0005