

Factors Governing Clutch Size in Two Species of *Diaptomus* (Copepoda: Calanoida)

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We conducted a synoptic survey of 11 nonstratifying lakes in eastern Quebec to investigate the relative importance of water temperature, food concentration ([Chl a]), female prosome length, copepod density (population and community densities), and mate availability (sex ratio and density of males) in determining the clutch size of two freshwater copepods, *Diaptomus minutus* and *D. oregonensis*. Multiple regression analyses indicated that 60% of the variation in clutch size of *D. minutus* could be accounted for by temperature and [Chl a] ($n = 33$; $P = 0.0001$), while 80% of the variation in the *D. oregonensis* data ($n = 11$; $P = 0.0017$) was explained by temperature and prosome length. Addition of other variables to either model did not significantly reduce the residual variation. We also investigated the effect of interspecific interaction on the egg-bearing potential of *D. minutus* and found some evidence that animals in sympatry may have lower clutch size than those in allopatry when temperature and food concentration were held constant. By using an independent measure of food and mate availability, we confirmed that clutch size decreased significantly in relation to food limitation for both species, but was unaffected by mate limitation for either.

Nous avons procédé à une étude synoptique de onze lacs de l'est du Québec non marqués par la stratification pour examiner l'importance relative de la température de l'eau, de la concentration d'aliments ([Chl a]), de la longueur du prosoma chez les femelles, de la densité des copépodes (densités des populations et des communautés) et de la disponibilité d'un compagnon ou d'une compagne (ratio de mâles à femelles et densité des mâles), dans la détermination de l'importance des groupes de deux copépodes d'eau douce, *Diaptomus minutus* et *D. oregonensis*. Les analyses de régression multiple ont indiqué que 60 % de la variation dans l'importance des groupes de *D. minutus* pouvaient s'expliquer par la température et la [Chl a] ($n = 33$; $P = 0,0001$), alors que 80 % de la variation observée dans les données relatives aux *D. oregonensis* ($n = 11$; $P = 0,0017$) s'expliquaient par la température et la longueur du prosoma. L'addition d'autres variables à un modèle ou l'autre ne réduisait pas pour la peine la variation résiduelle. Nous avons également examiné l'effet de l'interaction interspécifique sur le potentiel ovigère de *D. minutus* et constaté que les dimensions des groupes d'animaux en sympatrie pouvaient être moins importantes que celles des animaux en allopatrie, lorsque la température et la concentration des aliments étaient maintenues constantes. En recourant à un moyen indépendant de mesurer la disponibilité des aliments et des compagnons ou compagnes, nous avons confirmé le fait que les dimensions des groupes diminuaient considérablement avec la limitation des aliments pour les deux espèces, mais que les dimensions des groupes ne variaient pas avec la limitation des femelles ou des mâles pour aucune des espèces.

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The reproductive capacity of calanoid copepods may depend on several factors that include mating success, length of the oviducal cycle, clutch size, and egg mortality. Of these, more appears to be known about the effect of clutch size than any other variable, perhaps because it is relatively easy to measure on a routine basis. As a result of this level of interest, some generalities are beginning to emerge. For instance, some dramatic seasonal and site-to-site variations in clutch size within both freshwater and marine taxa have been correlated with changes in the body size of females (Smyly 1968; Maly 1973, 1983; Cooney and Gehrs 1980; Elmore 1983), copepod density (Maly 1973), temperature, food availability (Cooney and Gehrs 1980; Checkley 1980a, 1980b), and a combination of the last two (Elmore 1983; Williamson and Butler 1987).

With few exceptions, most investigations have been carried out in the laboratory where usually only one factor at a time was examined or where the species of interest was studied in the absence of potential competitive effects from other diaptomid species. Although there is a large accumulation of data from single-factor, single-species experiments, these results may have limited applicability to natural situations, where populations are exposed to a number of ecological factors, and where ubiquitous species tend to occur with many other species (e.g. *Diaptomus minutus*; Carter et al. 1980). Without some confirmatory field studies where all factors are considered simultaneously, it is difficult to evaluate the relative importance of laboratory-identified factors in determining diaptomid clutch size in lakes.

A method was recently developed by Williamson and Butler (1987) to evaluate the relative effect of food availability and mate density on egg production of *D. pallidus*. They formulated indices, based on quantifiable responses of the oviducal cycle

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to changes in food levels or mate density, to infer food or mate limitation. The food-limitation index (f -index) was calculated as $f = [N/(N+G+O+B)] \times 100$, where N = nongravid females, G = gravid females, with visibly darkened oocytes, O = ovigerous females, bearing external egg sacs, and B = both ovigerous and gravid. An f value of zero indicated that there was no food limitation, since all females were gravid, ovigerous, or both whereas an f value of 100 implied severe food limitation. The mate-limitation index (m -index) was calculated as $m = [G/(G+O+B)] \times 100$. Since diaptomids usually require a successful mating prior to each clutch extrusion. Williamson and Butler interpreted an m value of 100 to indicate extreme mate limitation, but a zero value to indicate no mate limitation, since none of the copepods would be gravid. These indices should be generally applicable to other copepods, provided that life history characteristics of the species examined are similar to those of *D. pallidus*.

In this paper, we investigate the simultaneous effects of surface water temperature, food availability, copepod density, female prosome length, mate availability, and species association on clutch-size variability of *D. minutus* and *D. oregonensis*, copepods commonly found in lakes of eastern North America (Carter et al. 1980). Data from a detailed field survey are used to determine the relative importance of these factors and to construct empirical models to predict diaptomid clutch size through multiple regression analyses. We also use the f - and m -indices as indirect measures of food and mate limitation to provide an independent means of validating the conclusions of the multiple regression analyses. By establishing the relative importance of the different environmental and density-dependent factors, we hope that investigators will concentrate on the more important variables in future studies, and eventually develop a unifying theory to describe the factors that govern reproductive success of *Diaptomus* in nature.

Methods and Materials

The detailed field survey was conducted in 1985 and involved five sampling trips to 11 lakes over a 3-mo period between mid-May and mid-August. On each visit, Secchi depth transparency was determined in duplicate, and water samples were collected for pH measurement. We also recorded the water temperature (T) just below the surface and near the sediment at the deepest station of each water body to determine the stratification characteristics on each sampling date.

Composite water samples were collected in triplicate from representative sites in the lake or pond for [Chl a] (CHL) (Strickland and Parsons 1972). Although CHL is only a crude estimate of food availability, since not all algal particles found in lakes are ingested by *D. minutus* and *D. oregonensis* (P. Chow-Fraser, unpubl.), it is necessarily the variable of choice in synoptic studies because of ease of measurement (e.g. Zimmerman et al. 1983; Pace 1984, 1986). It is also a useful index of trophic status (i.e. Carlson 1977) because of its significant correlation with total phosphorus concentrations (e.g. Dillon and Rigler 1974). In this study, we use CHL as a broad indicator of food availability, although size-fractionated biomass estimates would be more accurate indicators.

On each lake visit, 24–26 samples of zooplankton were collected at randomly determined positions or depths with 2-L Schindler-Patalas traps for estimates of diaptomid density (TD = total adult density of all species in lake, DDM = adult density of *D. minutus*, and DDO = *D. oregonensis*); approxi-

mately half of these were obtained at the top 1 m and half from the bottom 1 m of the lake column. Duplicate qualitative plankton samples were also obtained with a Wisconsin plankton tow-net from a boat or from shore. All zooplankton samples were preserved in 6% formalin in the field for later identification and enumeration in the laboratory. Because we omitted a prefixation step with chloroform-ethanol solution prior to formalin preservation, we may have artificially reduced the number of ovigerous females appearing in all our samples by up to 22% ($n = 7$) and 28% ($n = 5$) for *D. minutus* and *D. oregonensis*, respectively.

The clutch size (CS) and prosome length (L) of 20 females of each species from each of these samples were determined with the aid of a dissecting microscope equipped with stage and eye-piece micrometers; measurements were made to the nearest 0.03 mm. It was sometimes necessary to detach and dissect egg sacs to measure clutch size accurately. We determined mate availability as the male to female ratio (MF) of the first 100 adults encountered in qualitative samples for each species and estimated male densities (MD) using the formula $[(M/(M+F)) \times DD]$ where M and F were the number of males and females, respectively, in the qualitative field subsample and DD was the corresponding copepod density estimated from Schindler-Patalas trap samples.

We extracted relevant information from the qualitative plankton samples to calculate Williamson and Butler's (1987) indices for *D. minutus* and *D. oregonensis* in our lakes. For each species on each lake date, we scored the number of females in the first 100 females encountered that were O , G , B or N , as indicated above, and followed appropriate formulae to calculate these indices (see the introduction). The reduction in the proportion of ovigerous females in our samples, due to omission of a prefixation step prior to formalin preservation, should not interfere with our statistical analyses because the bias occurred consistently in all our samples.

Results and Discussion

Field Survey

Diaptomus minutus occurred allopatrically in five of the 11 lakes sampled in the survey, sympatrically with *D. oregonensis* in four, and sympatrically with *D. birgei* in the remaining two (Table 1). The corresponding CHL and Secchi depth transparency values place all lakes in this study within the mesotrophic-oligotrophic range, except Choiniere, which falls within the eutrophic category (Environment Canada 1981). While in most cases the pH was circumneutral, a few of the lakes located on the Canadian Shield were mildly dystrophic and had slightly lower pH. The lakes were well mixed in most instances, except for Croche Lake which exhibited periodic weak thermal stratification during July. At no time did the temperature differ by more than 6°C between surface and bottom in any lake.

Because of the highly variable patterns of zooplankton population growth rates in these lakes, it was not always possible to obtain relevant information for all species on each lake visit. Therefore, data for only 45 of the 55 lake visits from the survey have been included for further statistical analyses, and these are presented in Tables 2 and 3 for *D. minutus* and *D. oregonensis*, respectively.

We carried out a correlation analysis to explore relationships between CS of *D. minutus* and T , L , CHL, DD, TD, MD, and

TABLE 1. Geographic location, species distribution (DM = *D. minutus*; DO = *D. oregonensis*; DB = *D. birgei*), maximum lake depth (m), mean summer Secchi depth transparency (m), mean summer (Chl *a*) (CHL, $\mu\text{g/L}$), and mean temperature differential between top and bottom waters during the season (*T*-Diff, $^{\circ}\text{C}$) in study lakes. Mean values are based on 5–10 measurements.

Lake	Latitude	Longitude	Depth	Species found	Secchi	CHL	<i>T</i> -Diff
Thibault	45°58'40"	74°01'15"	2.5	DM, DO	1.4	6.9	0.6
Long	45°14'50"	72°19'45"	6.5	DM, DO	3.3	2.7	1.4
Pin Rouge	45°57'40"	74°02'30"	12.5	DM, DO	2.2	6.6	1.0
Cromwell	45°59'21"	73°59'50"	9.0	DM, DO	2.0	5.4	2.8
Roxton	45°28'00"	72°39'20"	6.0	DM, DB	1.8	6.8	1.4
Choiniere	45°25'10"	72°36'22"	14.5	DM, DB	1.0	18.8	1.0
Coeurs	45°58'07"	74°00'35"	7.1	DM	2.1	7.4	0.8
Croche Lake	45°59'21"	73°59'50"	10.5	DM	3.5	2.4	3.7
Croche Pond	45°59'21"	73°59'50"	3.3	DM	2.2	4.5	1.7
Sally	45°10'45"	72°26'20"	2.0	DM	2.2	2.3	1.4
Libby	45°16'35"	72°22'00"	3.5	DM	2.0	5.3	1.6

MF. (The latter was first arcsin transformed but all others were log transformed.) CS was significantly correlated with all variables except MD and MF (Table 4). Although *L* was significantly correlated with CS, we eliminated it from further analysis because of strong covariance between *L* and CHL ($r = 0.67$, $P = 0.001$).

The remaining variables were regressed against CS in two stepwise regression analyses; in one, we excluded TD and in the other we excluded DD. After CHL and *T* were entered into the respective regression models, addition of DD or TD did not explain any significant amount of the remaining residual variation; therefore, both were dropped from subsequent analysis. We then regressed CS against *T* and CHL and obtained the following regression equation:

$$(1) \log CS = -1.18 (\pm 0.347) \log T + 0.22 (\pm 0.071) \log CHL + 2.192 P = 0.0001, r^2 = 0.60, n = 33$$

(numbers in parentheses are the SE). This model explained 60% of the variation in the dependent variable and indicated that clutch size of *D. minutus* was both a positive function of food concentration (Fig. 1a) and a negative function of water temperature (Fig. 1b). The interaction term did not account for any significant amount of the residual variation (slope = -0.01 ; $P = 0.99$) even though there was a significant negative correlation between *T* and CHL ($r = 0.53$; $P < 0.05$).

The strong individual effects of temperature and food concentration have been well documented for several species of *Diaptomus*. Elmore (1983) showed that a temperature decrease from 30 to 20°C produced up to a twofold increase in CS for three subtropical species. Similarly, we found a twofold increase in CS when temperatures decreased from 25 to 20°C when food concentration was held constant (Eq. 1). The strong effect of CHL noted in this study is also consistent with that reported for *D. clavipes* (Cooney and Gehrs 1980), *D. mississippiensis*, *D. floridanus*, *D. dorsalis* (Elmore 1983), and *D. pallidus* (Williamson and Butler 1987). Although each of these two factors had an independent effect on CS, there is a suggestion in our study that both factors act in combination to regulate CS in field populations. This additive effect of temperature and food, however, is unlike the interactive effect noted by Williamson and Butler (1987) who found that starvation effects were more pronounced at high than at low temperatures in their laboratory trials.

To examine the effect of species association (i.e. allopatric versus sympatric occurrences) on clutch size of *D. minutus*, we sorted the entire dataset according to lakes in which *D. minutus*

occurred allopatrically and those in which they occurred sympatrically with *D. oregonensis* or *D. birgei*. We then repeated the regression analysis on the sorted dataset. This procedure increased the r^2 value slightly to 0.64 and 0.69 for allopatric and sympatric lakes, respectively, and yielded the following two equations:

Allopatric:

$$(2) \log CS = -1.11 (\pm 0.429) \log T + 0.26 (\pm 0.087) \log CHL + 2.139 P = 0.0005, r^2 = 0.64, N = 18.$$

Sympatric:

$$(3) \log CS = -1.17 (\pm 0.535) \log T + 0.27 (\pm 0.118) \log CHL + 2.092 P = 0.0009, r^2 = 0.69, n = 15.$$

The slightly improved r^2 value as well as numerically higher regression coefficients for *T* and CHL in Eq. 2 and 3 compared with Eq. 1 suggest that the effect of food concentration on clutch size should be studied separately for allopatric and sympatric populations of *D. minutus*. Although the coefficients in Eq. 2 and 3 were not statistically different (Tukey Kramer test, $P > 0.05$), the intercept associated with allopatric populations was numerically higher. This suggests that when *T* and CHL are held constant, the CS of allopatric copepods are higher compared with sympatric individuals. This is consistent with the observation that on average, CHL associated with allopatric populations are only 56% of the values associated with sympatric populations for essentially the same CS (Table 5).

The lower than expected CS in sympatric populations may mean that interspecific interaction (competition for food) has an adverse effect on the egg-bearing potential of *D. minutus* when it cooccurs with *D. birgei* or *D. oregonensis*, perhaps because both congeners are larger. For instance, the dry weight of *D. oregonensis* is more than twice that of *D. minutus* (3.84–8.66 compared with 1.97–3.55 μg , respectively; Culver et al. 1985) and this disparity in biomass may alone account for the difference in CS per unit CHL between allopatric and sympatric populations of *D. minutus*. Thus, the effect of food on clutch size may operate differently for species in allopatry than those in sympatry when size disparity is involved.

A similar correlation analysis was performed on *D. oregonensis* data (Table 6). In this instance, *T*, *L*, and TD were the only significant correlates of CS. A stepwise regression analysis revealed that after *T* and *L* were entered, addition of TD did not significantly improve the original r^2 value in the model. We then regressed CS against *T* and *L* to obtain the following multiple regression equation:

TABLE 2. Clutch size (CS), female prosome length (L , mm), [Chl a] (CHL, $\mu\text{g/L}$), surface water temperature (T , $^{\circ}\text{C}$), adult diaptomid density (DDM, no./2 L), and male to female ratio (MF) for *D. minutus*.

Lake	Sampling date	CS	L	CHL	T	DDM	MF
Thibault	14 June	6.7	0.76	9.5	15	6.48	1.04
	5 July	5.4	0.80	7.8	24	3.58	1.00
	26 July	5.0	0.77	4.9	22	4.28	0.75
	19 August	5.0	0.80	5.4	20	0.38	0.24
Long	17 May	10.1	0.76	4.3	14	1.44	0.45
	7 June	6.4	0.72	3.4	17	3.56	0.96
	2 July	6.8	0.71	4.1	21	10.41	0.59
	23 July	2.6	0.66	1.2	23	6.41	0.55
	13 August	2.9	0.67	0.7	24	16.12	0.72
Pin Rouge	21 May	15.1	0.82	11.8	14	1.50	0.92
	14 June	4.6	0.80	11.6	16	0.62	0.67
	19 August	—	0.75	1.1	20	0.12	0.20
Coeurs	21 May	—	0.88	7.2	14	0.21	0.31
	14 June	18.6	0.92	12.8	16	0.76	0.79
	5 July	9.0	0.90	9.6	23	5.24	0.43
	26 July	4.9	0.86	2.6	22	1.52	0.39
Croche Lake	16 May	11.2	0.72	2.4	14	3.22	0.85
	11 June	6.4	0.75	5.4	16	0.68	1.22
	4 July	5.1	0.73	2.8	19	0.92	0.22
	25 July	3.7	0.74	0.4	22	0.46	0.18
	14 August	4.6	0.72	1.1	22	0.92	1.63
Sally	17 May	12.8	0.81	3.0	16	1.84	0.84
	7 June	6.1	0.77	3.9	17	3.96	0.59
	2 July	3.6	0.75	2.2	24	15.83	0.96
	23 July	4.7	0.73	1.7	22	17.11	0.49
	13 August	4.7	0.77	0.8	24	11.63	0.50
Libby	17 May	10.0	0.75	6.8	15	0.04	—
	7 June	8.4	0.77	7.7	17	0.46	0.89
	2 July	4.8	0.76	4.0	22	2.48	1.23
	23 July	8.0	0.77	5.9	22	0.52	2.19
	13 August	9.1	0.76	3.7	23	1.81	0.69
Roxton	6 June	8.4	0.80	10.1	15	3.35	—
	19 July	5.4	0.73	2.3	23	1.00	—
Choiniere	6 June	21.2	0.94	29.2	15	0.17	—
	19 July	5.0	0.76	8.2	22	0.68	—
Cromwell	16 May	—	0.79	9.5	18	0.36	0.31
Croche Pond	11 June	—	0.74	8.8	18	1.20	2.03
	4 July	—	0.74	6.3	22	0.10	2.19
	25 July	—	0.74	1.3	23	3.72	1.00
	14 August	—	0.76	4.9	22	1.82	1.19

$$(4) \log CS = -1.681 (\pm 0.406) \log T + 4.177 (\pm 1.183) \\ \log L + 3.175 P = 0.0017, r^2 = 0.80, n = 11.$$

The CS of *D. oregonensis* thus appears to be both a positive function of L (Fig. 2a) and a negative function of T (Fig. 2b); but in contrast with *D. minutus*, does not appear to be related to CHL.

Mate and Food Limitation Indices

The regression of clutch size against the f -index confirmed the significant effect of food availability on clutch size for *D. minutus* (Fig. 3a). Clutch size decreased as a function of the f -index, indicating that clutch size became reduced with decreased food availability. This indirect relationship between

CHL and the f -index suggests that Chl a is an adequate indicator of food availability for this species. Similarly, there was a significant regression between clutch size of *D. oregonensis* and the f -index (Fig. 4a). This, however, deviates from conclusions reached in the earlier section, in which we found no significant correlation between CS and CHL (Table 6). This discrepancy probably stems from the inappropriateness of using CHL as a measure of ambient food availability for *D. oregonensis*, especially because *D. oregonensis* appears to have a more specialized diet than does *D. minutus* (P. Chow-Fraser, unpubl. data). This comparison suggests that food may have emerged as an important determinant of clutch size in the multiple regression analysis (Eq. 4) if measurements of food availability were based on cell counts of edible food items rather than on CHL. The

TABLE 3. Summary data for *D. oregonensis*. Abbreviations and units are the same as in Table 2 except that DDO = adult diaptomid density of *D. oregonensis*.

Lake	Sampling date	CS	L	CHL	T	DDO	MF
Thibault	14 June	—	1.03	9.5	15	—	0.57
	5 July	9.9	1.04	7.8	24	9.90	0.59
	26 July	10.6	1.06	4.9	22	10.60	0.75
	19 August	8.4	1.06	5.4	20	8.35	0.56
Long	17 May	20.3	1.03	4.3	14	0.68	1.08
	7 June	—	1.11	3.4	17	0.12	1.85
	2 July	4.4	0.88	4.1	21	1.48	0.41
	23 July	—	—	1.2	23	1.13	0.67
	13 August	6.0	0.98	0.7	24	0.68	0.50
Cromwell	11 June	—	1.01	9.52	18	0.32	0.67
	4 July	9.4	1.02	6.23	20	1.38	0.72
	25 July	—	1.04	2.83	22	1.22	0.51
	14 August	8.4	1.01	2.7	24	0.64	0.41
Pin Rouge	14 June	14.7	0.97	11.6	16	0.46	0.37
	4 July	10.2	0.97	4.6	22	2.27	0.31
	26 July	—	—	3.7	21	0.38	0.42
	19 August	14.8	1.08	1.1	20	0.37	1.44

TABLE 4. Summary of correlations between clutch size of *D. minutus* and other variables of interest. See Table 2 for explanation of abbreviations.

n	Variable	r	P
33	L	+0.655	0.0001
33	CHL	+0.670	0.0001
33	T	-0.687	0.0001
33	DDM	-0.406	0.0190
33	TD	-0.364	0.0374
29	MF	-0.086	0.6905
29	MD	-0.219	0.2627

lack of a significant relationship between clutch size and the *m*-index also validates the conclusion made earlier that mate availability is not an important predictor of brood size for either species (Fig. 3b and 4b).

General Discussion

We have evaluated the relative importance of temperature, food concentration, prosome length, copepod density, and mate availability on the clutch size of two diaptomid species in 11 shallow, generally well-mixed lakes and ponds. Surface water temperature emerged as a strong negative correlate of clutch size for both *D. minutus* and *D. oregonensis* in our lakes (Eq. 1 and 4; Fig. 1b and 2b). This strong correlation was evident despite our use of surface water temperature, even in lakes that exhibit weak thermal stratification during the open-water season. There was also a very strong positive effect of food concentration for *D. minutus* (Fig. 1a) which was confirmed by the significant regression between CS and the *f*-index (Fig. 3a). Although CS of *D. oregonensis* was not significantly correlated with CHL, there was nevertheless a significant regression between clutch size and the *f*-index (Fig. 4a). Therefore, if more lakes had been sampled or if size-fractionated CHL data had been available, food concentration may also have emerged as a significant predictor of clutch size for this species.

Clutch size of both species was also positively correlated with female prosome length (Fig. 2b) even though the strong

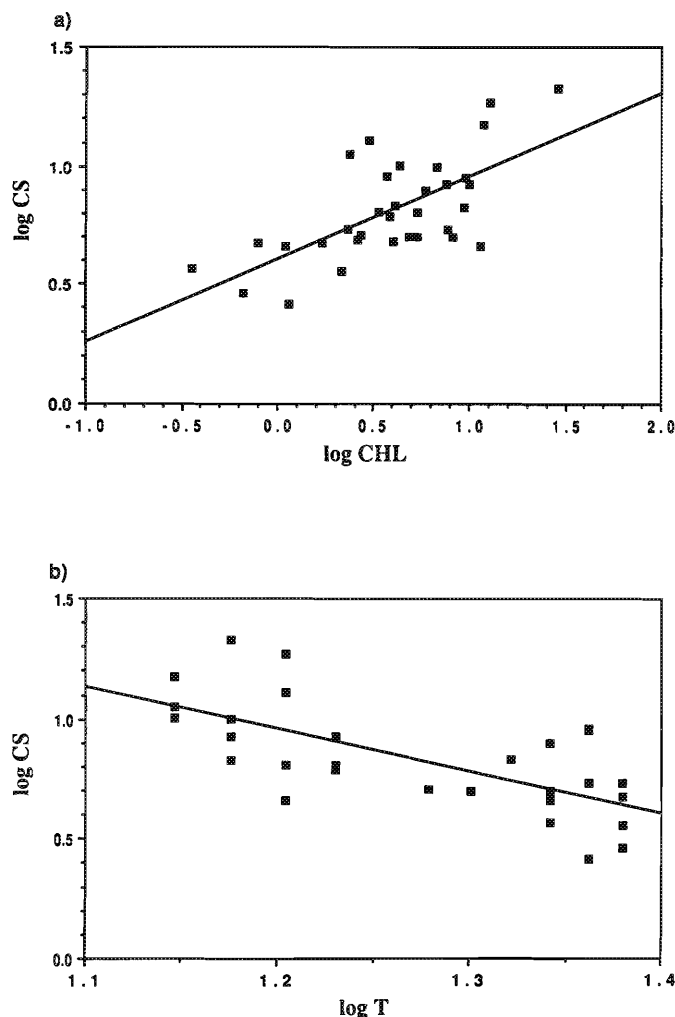


FIG. 1. (a) Log clutch size versus log CHL for *D. minutus*. Equation of the least-squares regression line is $\log CS = 0.3408 \log CHL + 0.6076$; $r = 0.67$, $P = 0.0001$, $n = 33$. (b) Log clutch size versus log temperature for *D. minutus*. Equation of the least-squares regression line is $\log CS = -1.7916 \log T + 3.1102$; $r = 0.69$, $P = 0.0001$, $n = 33$.

TABLE 5. Comparison of mean (SE in parentheses) clutch size (CS) with variables of interest for allopatric and sympatric *D. minutus* populations. See Table 2 for explanation of abbreviations. *Means are significantly different ($P < 0.05$).

Variable	Allopatric	Sympatric
CS	7.536 (0.911)	7.373 (1.265)
L	0.78 (0.014)	0.77 (0.018)
CHL	4.3 (0.77)	7.6 (1.80)*
T	19.8 (0.81)	19.0 (1.01)
DDM	3.86 (1.256)	3.99 (1.140)

covariance between prosome length and food concentration for *D. minutus* eclipses the importance of length as a predictor of clutch size. Of much less importance were copepod density (either population density or total diaptomid density) and mate availability (sex ratio or male density), neither of which had any significant effect on clutch size once the other three variables had been considered. Absence of a significant regression between clutch size and the *m*-index confirms that changes in clutch size for either species are unrelated to mate density.

TABLE 6. Summary of correlations between clutch size of *D. oregonensis* and other variables of interest. See Table 2 for explanation of abbreviations.

n	Variable	r	P
11	L	+0.603	0.0495
11	CHL	+0.215	0.5250
11	T	-0.695	0.0176
11	DDO	-0.337	0.3108
11	TD	-0.643	0.0328
11	MF	-0.107	0.8015
11	MD	-0.207	0.5421

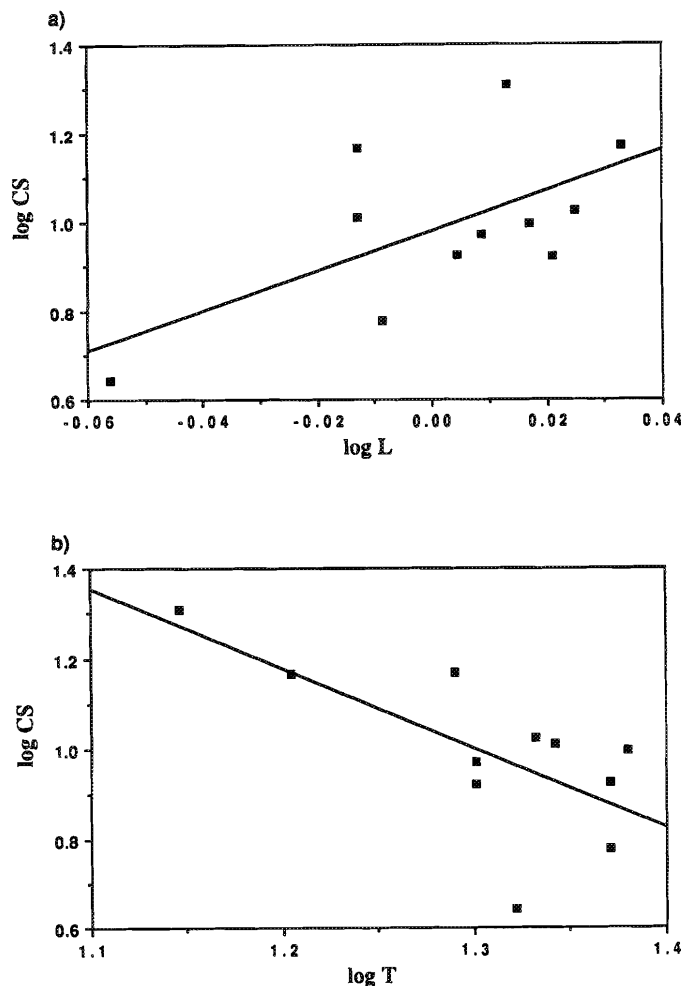


FIG. 2. (a) Log clutch size versus log length for *D. oregonensis*. Equation of the least-squares regression line is $\log CS = 4.5191 \log L + 0.9794$; $r = 0.61$, $P < 0.05$, $n = 11$. (b) Log clutch size versus log temperature for *D. oregonensis*. Equation of the least-squares regression line is $\log CS = -1.7689 \log T + 3.3015$; $r = 0.70$, $P = 0.02$, $n = 11$.

The effects of temperature on egg production have been studied in several freshwater and marine calanoid copepods, with inconsistent findings. Whereas Checkley (1980b) and Elmore (1983) both observed a decrease in clutch size with increased temperature for *Paracalanus parvus* and three subtropical freshwater diaptomids, respectively, Williamson and Butler (1987) found essentially no change in clutch size of *D. pallidus* at 25 compared with 15°C (17.5 and 16.8, respectively). In our study, we also noted an inverse relationship between clutch size

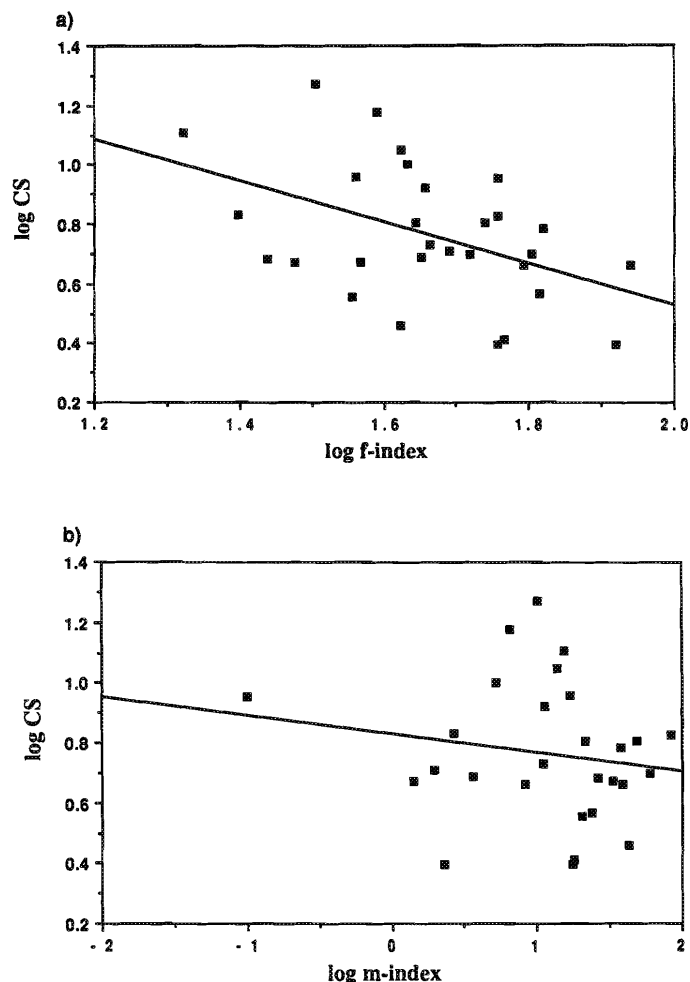


FIG. 3. (a) Log clutch size versus log *f*-index for *D. minutus*. Equation of the least-squares regression line is $\log CS = -0.6955 \log f\text{-index} + 1.9202$; $r = 0.45$, $P = 0.02$, $n = 33$. (b) Log clutch size versus log *m*-index for *D. minutus*. Equation of the least-squares regression line is $\log CS = -0.0607 \log m\text{-index} + 0.8303$; $r = 0.17$, $P = 0.40$, $n = 29$.

and temperature for *D. minutus* and *D. oregonensis*; however, our results differ from earlier studies with respect to the mechanism responsible for lower brood size. Both Checkley and Elmore attributed the reduction in clutch size to the smaller size of females with increased temperature; by comparison, in this study the clutch size of *D. minutus* was clearly more strongly influenced by food level than by body length, indicating that body length is not the primary determinant of clutch size for *D. minutus*. Therefore, the effect of temperature on clutch size in natural populations may vary from species to species, and generalities cannot be made regarding the genus without further research on more species.

Another factor that deserves attention is the effect of temperature on interclutch duration; although Williamson and Butler (1987) did not observe any temperature effects on clutch size of *D. pallidus*, overall egg production was increased because of significantly shorter interclutch duration at the higher temperature. Thus, even if warmer temperatures should bring about reduced clutch size in other species, the associated increase in egg development rate and rate of clutch production may more than compensate for the smaller brood size. This may have important implications to lake ecosystem research, especially in light of the anticipated global changes in weather pat-

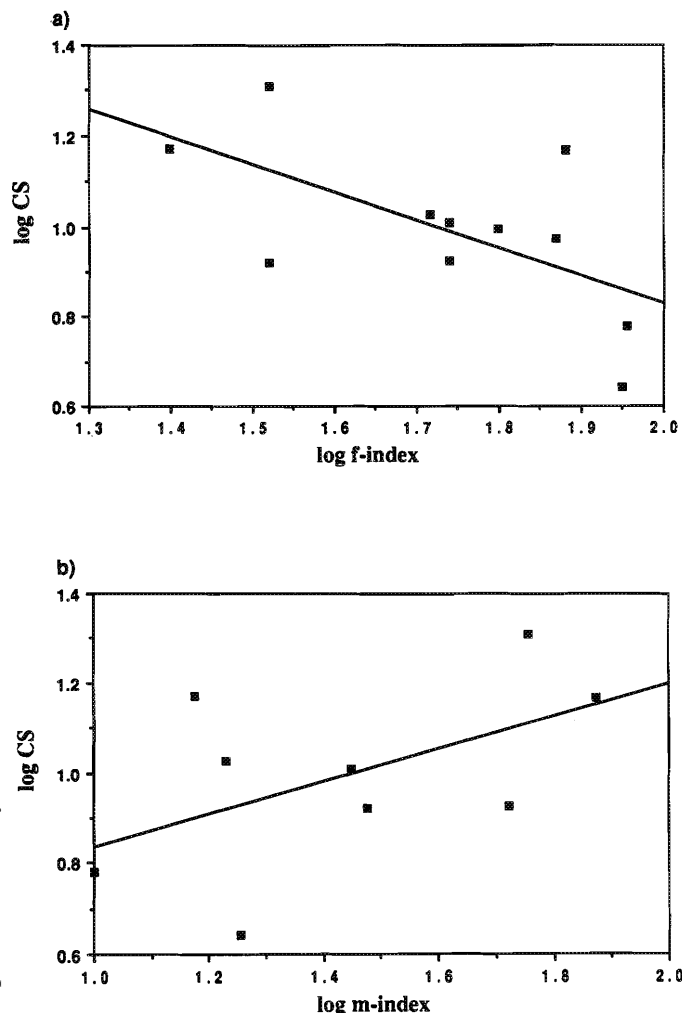


FIG. 4. (a) Log clutch size versus log *f*-index for *D. oregonensis*. Equation of the least-squares regression line is $\log CS = -0.6158 \log f\text{-index} + 2.0605$; $r = 0.62$, $P = 0.04$, $n = 11$. (b) Log clutch size versus log *m*-index for *D. oregonensis*. Equation of the least-squares regression line is $\log CS = 0.363 \log m\text{-index} + 0.472$; $r = 0.53$, $P = 0.15$, $n = 9$.

terms over the next several decades. Future investigations should focus on understanding the mechanism by which temperature influences the various phases of the oviducal cycle and how these interact with food availability to regulate the reproductive capacity of diaptomids in lakes.

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