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Sexual and asexual reproduction in a natural population of Hydra pseudoligactis

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Populations of *Hydra pseudoligactis* were censussed during 1980-1981 in a lake and a small pond in southern Québec. Both natural and artificial substrates (glass slides) were used. Population density rose during the early part of the season to a maximum in June-July, after which a decline in the rate of asexual budding drove density down. The decline in budding rate lagged about 2 weeks behind the increase in density. High local population density on the glass slides reduced rates of budding and caused dispersal from crowded slides. Sexual individuals appeared in the middle of the growing season, near the time of maximal density, when rates of asexual budding had begun to fall. Moreover, sexual individuals were more frequent in the site where and in the year when budding rates were lower; 66% of the variance in the frequency of sexual individuals between dates in the pond was explained by variance in the number of buds borne by asexual individuals. These results are held to be consistent with the interpretation of sexuality as a device to reduce competition between offspring in a spatially heterogeneous environment.

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Les populations d'*Hydra pseudoligactis* d'un lac et d'un petit étang du sud du Québec ont été recencées en 1980-1981. Des substrats naturels et des substrats artificiels (lames de verre) ont été utilisés. La densité de population augmentait au début de la saison pour atteindre un maximum en juin-juillet, après quoi la diminution du taux de bourgeonnement asexuel entraînait une diminution de la densité. Il y avait un délai d'environ 2 semaines entre l'augmentation de la densité et la diminution du taux de bourgeonnement. La densité très élevée de population sur les lames de verre a entraîné une diminution des taux de bourgeonnement et causé la dispersion des hydres sur les lames trop populeuses. Des individus sexués sont apparus au milieu de la saison de croissance, à peu près au moment où les densités étaient maximales et où les taux de bourgeonnement asexuel avaient commencé à diminuer. De plus, les individus sexués étaient plus nombreux aux endroits et aux moments où les taux de bourgeonnement étaient le plus faibles; dans l'étang, 66% de la variance de la fréquence des individus sexués entre certaines dates s'expliquait par la variance dans le nombre de bourgeons portés par des individus asexués. Ces résultats corroborent l'hypothèse qui interprète la sexualité comme moyen de réduire la compétition entre les rejetons dans un environnement hétérogène.

[Traduit par le journal]

Introduction

Coelenterates as a whole, and the hydrozoans in particular, are characterized by a more or less regular succession of sexual and asexual phases in their life history. This heterogonic life cycle has been particularly well studied in the freshwater polyp *Hydra*. The usual mode of asexual reproduction in *Hydra* is by bud production, whereby the genetically identical offspring are dependent on their parent until detachment after about 3-4 days growth. Hydras also reproduce sexually, with some species being hermaphroditic and other gonochoric. Many workers have attempted to identify the factors responsible for the elicitation of sexuality. Loomis (1961) showed that elevated partial pressures of carbon dioxide were effective in stimulating sexuality, as are crowding and starvation (e.g., Kanaev 1952; Burnett and Diehl 1963).

Most studies on *Hydra* sexuality have been performed in the laboratory and little is known about the occurrence and timing of sex in natural populations. Major studies of the dynamics of natural populations of *Hydra* have been performed by Welch and Loomis (1924), Miller (1936), Bryden (1952), and Cuker and Mozley (1981), but only Miller (1936) describes the sexual cycle. In this paper we examine the timing of sexual and asexual reproduction in a natural population of *Hydra pseudoligactis*. Specifically, we address the following questions. (*i*) At what point during the season does sexuality occur?

(*ii*) What is the relationship between population density and sex? (*iii*) How are the rates of sexual and asexual reproduction related?

Materials and methods

This study was conducted at Lac Hertel, a small artificial lake at the McGill University Field Station on Mont St. Hilaire, located about 30 km southeast of Montréal, Qué. Lac Hertel has been described by Kalff (1972). The principal sampling site was a shallow protected area of the lake margin ringed by *Myrica* bushes near the outlet of a small stream. A variety of submerged (*Potamogeton* spp., *Vallisneria americana*) and floating leaved (*Polygonum* spp.) macrophytes grow in the area and most were colonized by *Hydra*. The small ponds scattered on the hillsides were also searched, but *Hydra* was found only in a very small (3×5 m) pond on the forest margin in an abandoned orchard, some 300 m from the lake. These two sampling sites are called North Creek Delta and Orchard Pond, respectively.

Two types of substrate, one natural and one artificial, were used to sample the population of *Hydra* in North Creek Delta. The floating leaves of *Polygonum coccineum* are abundant throughout the season, are rather standard in shape and size, and hydras attached to their underside are easily seen without disturbance. Standard 25×75 mm glass microscope slides were also used and proved to be an excellent artificial substrate readily colonized by hydras. Individually numbered slides were made to float by glueing them to a slip of expanded polystyrene and were retained within 1×1 m floating wooden frames.

In 1980, 40 slides were placed in each of four frames and a total of

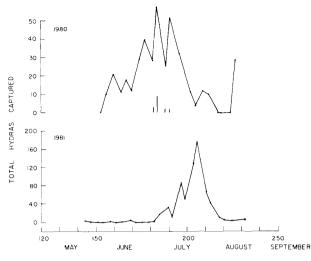


FIG. 1. Samples of *Hydra* from floating *Polygonum* leaves at the North Creek Delta site, 1980 and 1981. The continuous line represents the total number of individuals captured; vertical lines represent the numbers of sexual individuals.

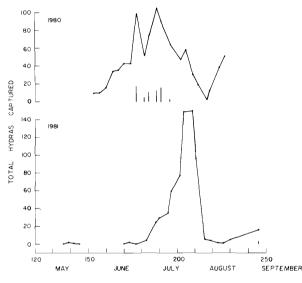


FIG. 2. Samples of *Hydra* from floating microscope slides at the North Creek Delta site, 1980 and 1981 (see Fig. 1 for further explanation).

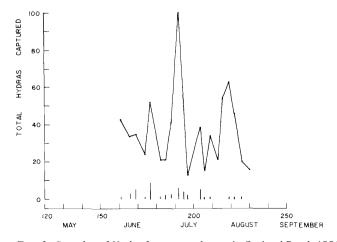


FIG. 3. Samples of *Hydra* from aspen leaves in Orchard Pond, 1981 (see Fig. 1 for further explanation).

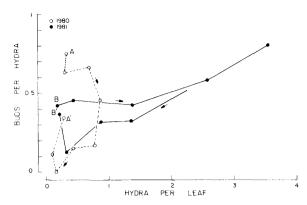


FIG. 4. The relationship between population density and the rate of budding among hydras on *Polygonum* leaves at the North Creek Delta site, 1980 and 1981. A, 9 and 13 June 1980; A', 12 and 15 August 1980; B, 29 June and 2 July 1981; B', 15 August 1981.

40 slides and 40 *Polygonum* leaves were scored on each sampling occasion. In 1981, 25 slides were placed in each of four frames and all were examined at each census, together with 50 *Polygonum* leaves. Both artificial and natural substrates were sampled twice each week from early June to mid-August.

In Orchard Pond there are no macrophytes (most of the hydras appear to be attached to dead leaves) and the heavy public use of the surrounding area prohibited the use of conspicuous artificial substrates. However, we found that if a spray of aspen was put into the pond, the leaves rapidly accumulate a large *Hydra* population. This was adopted as a sampling procedure, with 50 leaves being sampled each week from a spray which had been put into the pond a week previously.

Each *Polygonum* leaf, aspen leaf, or microscope slide was carefully slid into a water-filled sampling tube with as little disturbance as possible. With the tube being stoppered under water, any *Hydra* present were easily visible. The microscope slides were scored on the lake with the aid of a $4 \times$ magnifying glass. The aspen and *Polygonum* leaves were taken to the Mont St. Hilaire laboratory where they were placed on an illuminating slide-viewing screen and examined under a glass. Any individual suspected to be sexual was reexamined under a dissecting microscope.

Results

The total number of individuals captured on Polygonum leaves and microscopy slides in North Creek Delta during 1980 and 1981 is shown in Figs. 1 and 2. The results from natural and artificial substrates correspond quite closely in both years, but there is a substantial difference between the years themselves. In 1980, hydras appeared in early June, rose to a maximum in late June and early July, and then decreased to a very low level by August. The population then seemed to increase again towards the end of August, but by August 20 all available substrates disappeared because the area dried out. In 1981, the hydras did not appear until late June, but then increased very rapidly in numbers to a maximum in late July, when the population density was four or five times greater than in 1980. During August 1981 the population crashed, again recovering slightly later in the month; the area did not dry out in 1981, but samples taken on 3 September, 7 October, and 11 November each yielded fewer than 10 individuals.

The Orchard Pond population behaved quite differently (Fig. 3). Population density was high when the population was discovered in early June 1981 and thereafter fluctuated irregularly until sampling was discontinued in late August.

Figures 4 and 5 are phase diagrams which relate the popu-

TABLE 1. Comparison of mean number of buds borne by solitary and nonsolitary hydras found on floating slides

		Mean no. of buds per hydra						
	Quadrat	l hydra	>1 hydra per slide	Mean	Sample sizes			
Year		per slide			Hydras	Buds	χ^2_1	Р
1980	1	0.538	0.412	0.495	99	49	0.50	0.48
	2	0.561	0.354	0.467	210	98	3.32	0.07
	3	0.466	0.267	0.361	313	113	6.31	0.01
	4	0.347	0.188	0.271	236	64	4.37	0.03
	Pooled	0.468	0.278	0.378	858	324	15.06	0.01
1981	1	0.667	0.699	0.692	182	126	0.03	0.89
	2	0.839	0.818	0.823	130	107	0.01	0.98
	3	0.903	0.688	0.728	169	123	0.86	0.35
	4	0.921	0.896	0.903	134	121	0.01	0.97
	Pooled	0.831	0.760	0.776	615	477	0.38	0.53

NOTE: In most cases solitary individuals bear more buds and in some cases this difference is formally significant. The probabilities cited are two tailed and therefore conservative, since the hypothesis being tested is directional. The combined $\chi^2 = -2 \sum \log_2 P$ for independent samples is 18.1, with P < 0.025. Some data are available for less standard habitat units. On *Polygonum* leaves in 1980, solitary and nonsolitary hydras, on average, bore 0.471 and 0.291 buds, respectively ($\chi^2 = 4.71$, P = 0.03); but in 1981, solitary and nonsolitary hydras bore 0.442 and 0.577 buds, respectively ($\chi^2 = 1.67$, P = 0.20). On aspen leaves in Orchard Pond, solitary and nonsolitary hydras bore 0.269 and 0.238 buds, respectively ($\chi^2 = 0.45$, P = 0.49).

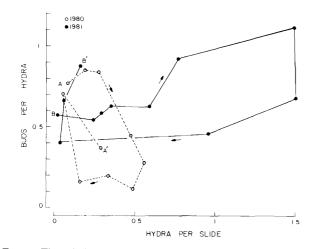


FIG. 5. The relationship between population density and the rate of budding among hydras on floating microscope slides at the North Creek Delta site, 1980 and 1981. A, 5 and 9 June 1980; A', 12 and 15 August 1980; B, 25 June and 2 July 1981; B', 15 August 1981.

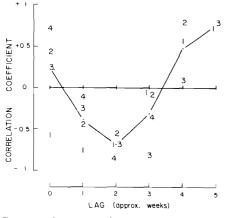


FIG. 6. Crosscorrelegram to demonstrate that mean bud number responds to changes in population density with a lag of about 2 weeks. Sites and years are indicated as follows: 1, floating slides 1980; 2, floating slides 1981; 3, *Polygonum* leaves 1980; 4, *Polygonum* leaves 1981. All samples are from North Creek Delta.

TABLE 2.	Response to local population	den-
	sity on floating slides	

Individuals per slide	Increase or no change	Decrease	Total
1	75	144	219
≥2	17	70	87
Total	92	214	306

NOTE: Entries in the body of table are the number of cases in which the number of hydras increased, remained the same, or decreased in consecutive samples 3-4 days apart. Data are for the individually numbered slides used in 1980 ($\chi_1^2 = 6.41$, P < 0.025).

lation density per sampling unit to the average number of buds borne per individual during 1980 and 1981. In all cases the same pattern emerges. Early in the season the population density is low and the bud number is moderately high. As the buds are released, the population increases while the bud number remains about the same or increases slightly; the population increase was much greater in 1981 than in 1980. Eventually, the population density reaches a point at which bud number begins to decline. At first this deline has little effect on population density, but shortly afterwards density declines in concert with bud number, bringing the population to a point of low density and low bud number. The bud number then again increases and eventually procures a second phase of increase in population density.

This description implies a lagged relationship between population density and bud number, with high population density being associated, after some lapse of time, with a decrease in bud number. We interpret this tentatively as cause and effect, with asexual reproduction being suppressed by high population density. The relationship is quantified in Fig. 6, which is a cross-correlation analysis of the data shown in Figs. 4 and 5. The correlation between population density and bud number is initially zero, but becomes highly negative after a lag of about 2 weeks.

If this relationship is indeed causal, we might expect to find

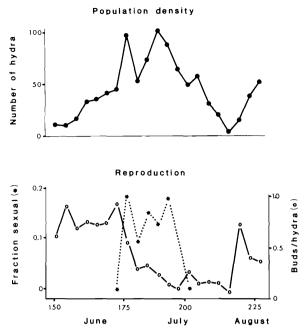


FIG. 7. The patterns of population density, budding rate, and the appearance of sexual individuals. Budding rate (reproduction) remains more or less constant during the initial phase of population increase (population density), but then falls as the maximum population is approached. As it falls, sexual individuals appear (reproduction). When the budding rate recovers, sexual individuals disappear again. Data are from Lac Hertel, 1980.

TABLE 3. Bud protection by sexual and asexual hydras

State	No buds	One bud	Two buds	Three buds	Total	Mean
Asexual Sexual	298	79	19	1	397	0.302
Male	36	6	2	0	44	0.227
Female	19	3	0	0	22	0.136
Total	55	9	2	0	66	0.197

NOTE: Data are from floating slides for the period 26 June to 15 July 1980, when sexual individuals were found. Asexual individuals bore more buds than sexual individuals, and males more than females, but neither difference is significant at P < 0.05 when tested with χ^2 . In Orchard Pond samples, 47 sexual individuals bore an average of 0.319 buds and 695 asexual individuals an average of 0.245 buds each, the difference again being nonsignificant.

a negative correlation between local population density and bud number on any given sampling date. The microscope slides, being as nearly uniform as possible, provide suitable material; we predict that when more hydras are found on a slide, each will bear fewer buds. Table 1 shows that individuals found on floating slides have more buds when solitary than when found in the company of one or more other individuals; the difference is highly significant in 1980 but not in 1981. The number of hydra per slide often changed between sampling dates and Table 2 shows that hydras tended to depart more frequently from slides which bore several hydras than from slides bearing only a single hydra.

The number of sexual individuals captured on the two substrates is indicated in Figs. 1, 2, and 3. It is clear that sexual individuals appear in the North Creek Delta population during the period of maximum population density and that only a small fraction of the population becomes sexual. Sexuality is absent

 TABLE 4. Variation between years at the same site in the frequency of sexual individuals and in the mean buds borne by individuals

	Floating	g slides	Polygonum			
Year	Frequency of sexual individuals	Mean no. of buds per individual	Frequency of sexual individuals	Mean no. of buds per individual		
1980	0.0769	0.3776	0.0464	0.4000		
1981	0.0016	0.7756	0.0061	0.5275		
χ^2	44.7	104.4	18.3	7.6		
P	≪0.01	≪0.01	≪0.01	~0.01		

NOTE: The χ^2 statistic is based on a comparison of the observed and expected number of individuals bearing no buds, one bud, and more than one bud.

TABLE 5. Variation between sites during the same year (1981) in the frequency of sexual individuals and the rate of asexual reproduction (buds)

	Substrate	Total hydras	Sexual		Buds	
Site			N	Frequency	N	Mean
Delta	Polygonum	654	4	0.0061	345	0.5275
	Slides	615	1	0.0016	477	0.7756
	Pooled	1269	5	0.0039	822	0.6478
Orchard	Aspen leaves	697	46	0.0660	182	0.2611

NOTE: All comparisons are highly significant ($P \le 0.01$) when tested by χ^2 , except that the frequency of sexual individuals does not differ between substrates at the North Creek Delta site.

from the minimal populations of late summer and early fall. A later sexual period is normally impossible since the area was dry by 1 September in 1979, 1980, and 1982. In 1981 no sexual individuals were found in September or November and only a single female on 7 October. In contrast, in Orchard Pond both the population density and the frequency of sexual individuals fluctuated irregularly throughout the growing season.

The emergence of sexual Hydra in the Delta population coincided not only with the highest population density, but also with a decrease in the rate of asexual reproduction. Figure 7 shows how between 26 June and 10 July, the period when male and female Hydra were present, the mean number of buds per individual decreased from 0.93 to 0.09.

The sex ratio of *Hydra* is Lac Hertel varied through the season, but overall, males were about twice as common as females. Sexual and asexual individuals bore nearly equal numbers of buds (Table 3).

Discussion

Our major conclusions concern the relationships between local density and levels of sexual and asexual reproduction.

Asexual reproduction by budding tends to create local groups of vegetative offspring; the distribution of hydras per slide is highly aggregated. We have shown that the rate of budding declines as the size of the local group increases (Table 1). To maintain a high rate of reproduction, therefore, the hydras must either disperse or switch to a sexual mode. So long as population density is fairly low, individual hydras disperse away from areas of high local density (Lomnicki and Slobodkin 1966; Table 2). As the overall population density increases, however, the rate of budding is driven down for any local density (Figs. 4 and 5). It is at this point that sexual individuals

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TABLE 6. The relationship between the timing of sex and the rate of asexual reproduction in *Daphnia* spp. (Cladocera), compared with that observed in *Hydra*. The independent variable is the mean number of eggs borne by asexual females; dependent variables are frequency of males, frequency of ephippial (eph) females, or both. Frequencies are transformed to angles for regression analysis; the probability of chance departure from an expected slope of zero (P) is one tailed

Species	Reference	Dependent variable		r	Р
Hydra pseudooligactis	Present study	Frequency of gonadic individuals	-0.708	-0.81	0.002
Daphnia ambigua	Allan 1977, Fig. 2	Frequency of sexual individuals	-0.0042	-0.09	0.32
Daphnia magna	Green 1955, Fig. 3	Frequency of males and	-0.0061	-0.65	0.006
1 0		frequency of eph females	-0.0023	-0.45	0.048
	Hebert 1974, Table 3	Frequency of eph females	-0.0091	-0.41	0.106
	Young 1979, Figs. 1 and 2	Frequency of males and	-0.0024	-0.31	0.089
	e e	frequency of eph females	-0.0039	-0.13	0.284
Daphnia obtusa	Slobodkin 1954, Figs. $15-24$	Frequency of males	<0	$<\!0$	
Daphnia schodleri	Lei and Clifford 1974,	1 5			
1	Tables 2 and 3	Frequency of eph females	-0.0638	-0.59	0.028

NOTE: In general, only results from the middle of the growing season (May through September) are given, but in *D. ambigua* egg numbers were high in early spring and the whole range of the data (January through August) were used. For *D. schodleri*, Lei and Clifford's 1966 observations are used; those for 1967 are sparse but give a result in the same direction. For Hebert's work on *D. magna* the observations for May through September 1971 are used; in a sample taken in the latter part of 1970 he observed sexual females in October–December being most common when brood number, though low, had just increased somewhat. Most of the data used in these analyses were intrapolated from figures; Slobodkin's laboratory data for *D. obtusa* is too poorly reproduced to permit this, but males consistently appeared after a decline in mean brood number.

appear in the population (Figs. 1, 2, and 7). This leads up to suspect that the induction of sexuality is associated with a decline in the success of asexual reproduction. Three independent lines of evidence support this inference.

The first line of argument concerns variation between years at the same site in the frequency of sexual individuals. Our data for floating slides and *Polygonum* leaves are summarized in Table 4; they show that asexual budding was less, and the frequency of sexual individuals was greater, in 1980 than in 1981 on both substrates.

The second line of evidence concerns the variation between sites in the same year in the frequency of sexual individuals. Table 5 shows that the much higher frequency of sexual individuals in Orchard Pond than in Lac Hertel in 1981 is associated with a lower rate of budding.

These patterns are not likely to be attributable to the lower rate of budding of sexual individuals, which will lower the average rate of budding as the frequency of sexual individuals in the sample increases, since sexual individuals are not nearly common enough to cause an effect as large as that observed. Nevertheless, we can easily remove data on sexual individuals from the samples and test the hypothesis that the frequency of sexual individuals increases as the rate of budding among sexually undifferentiated individuals declines. This third line of evidence was evaluated for the Orchard Pond data, where the sample size of sexual individuals was reasonably large and both population density and budding rate fluctuated within short periods of time. Figure 8 shows that the frequency of sexual individuals is strongly correlated ($r^2 = 0.66$) with the budding rate of asexual individuals in the same sample. Moreover, when date, population density, and bud number are all used as independent variables in a multiple regression analysis, only bud number has a significant effect on the frequency of sexual individuals.

The correlation between asexual performance and sexual induction may be rather general, since the appearance of sexual individuals following a decline in the rate of reproduction of asexual females seems commonplace in unrelated heterogonic taxa, such as cladocerans. Studies in which both asexual and sexual reproduction were measured and reported are exceptional, but I have abstracted some data for species of *Daphnia*

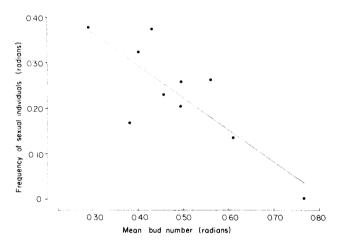


FIG. 8. Relationship between the frequency of asexual individuals and the mean bud number for samples from Orchard Pond, 1981. Both variables are plotted as square-root arc sine transforms. The equation of the regression is y = 0.5797 - 0.708 x, with t = -3.95 and P = 0.002; the coefficient of determination (r^2) is 0.66.

in Table 6. The linear correlation coefficients computed in the table are all negative (though only three of the seven are individually significant at the 5% level), but even so they may tend to underestimate the strength and consistency of the effect; in almost all cases an increase in the population was eventually followed by a decline in the reproduction of asexual females, after which males and ephippial females appeared. A continued very low level of asexual reproduction without sexual individuals may then occur, but since reproduction is shut down almost entirely, the lack of sexuality is trivial. Therefore, the negative correlation of rates of asexual budding with the frequency of sexual individuals in *Hydra* seems to mirror a very general phenomenon.

These observations are of general relevance to theories concerning the maintenance of sex in natural populations. The conventional interpretation of sex is that it preadapts offspring to uncertain future conditions; in heterogonic animals, therefore, it should occur at the end of the growing season (Williams 1975). This view has been challenged by Bell (1982), who collates a mass of comparative evidence to show that asexual rather than sexual reproduction predominates in novel, disturbed, and transient environments. This comparative analysis leads to the conclusion that the primary effect of sexual diversification is to reduce the level of ecological competition between sibs (the "tangled bank" hypothesis). In a heterogeneous environment, the members of an asexual brood will all occupy the same niche or narrow range of niches and will therefore compete strongly with one another if the environment is nearly saturated; the greater diversity of a sexual brood implies a broader ecological tolerance which by reducing competition will elevate the success of the brood as a whole. Heterogonic animals like Hydra should therefore reproduce asexually so long as population density is low enough to permit high rates of budding; when population density increases and budding rate drops, clones should switch to sexual reproduction to produce diverse progeny capable of exploiting new and uncrowded niches. Our results clearly run parallel to the broad comparative patterns described by Bell (1982); sex in our populations of hydras occurred in the middle of the growing season at a period of maximal population density and not in the minimal populations at the end of the growing season; moreover, the frequency of sex is negatively correlated with the rate of reproduction among asexual individuals between dates within a site, between sites, and between years. These results, therefore, give detailed quantitative support to the "tangled bank" interpretation of sex.

Acknowledgements

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