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A Comparative Study of Cannibalism in Six Populations of the Calanoid Copepod, *Diaptomus leptopus* (Forbes)

Gregory D. Shand

A Thesis

in

The Department

of Biology

Presented in Partial Fulfillment of the Requirements
for the Degree of Master of Science at
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ABSTRACT

A Comparative Study of Cannibalism in Six Populations of the Calanoid Copepod, *Diaptomus leptopus* (Forbes)

Gregory D. Shand

Cannibalism is common in species which have overlapping and discrete life stages. Copepods are a typical example of the type of species which exhibit adult cannibalism of juvenile life stages. The scale of observation typically used in cannibalism studies may allow misinterpretation of the results. I used populations of *Diaptomus leptopus* from six independent ponds to determine the effects of body lengths of cannibal and prey, length asymmetry, and scale of observation on cannibalism rate. Five adults and 25 one to three day old nauplii were placed together in 50 ml of water for 12 hours. Separate treatments were run for each sex. Cannibalism rates ranged from 0.000 to 0.053 prey $\cdot$ cannibal^{-1} $\cdot$ hour^{-1} and were significantly different between sexes and ponds. Length asymmetry was the most accurate predictor of cannibalism rate but most of the predictive power came from adult length. Results from large scale observations, while seemingly robust, did not correspond well with results from small scale observations. The implication of scale of observation on interpretation of cannibalism studies is discussed.

Acknowledgements

Many people contributed to this work. As usual it would not have been possible without the assistance and cheerfulness of the **MALY MOB** in general but especially the edition of 1997 - thanks to Karen, Steve, and Maria; special thanks to Margo and Scott. Scott had to leave before he could see this through but I never would have made it through the summer of 1997 without him.

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INTRODUCTION

Cannibalism, the act of killing and eating a member of the same species, has been reported in a diverse spectrum of organisms from protozoans to primates and has been shown to influence life history patterns, competition for resources, and behaviour in many species (Dong & Polis, 1992; Elgar & Crespi, 1992; and see Fox, 1975a, and Polis, 1981, for reviews).

In a cannibal-prey encounter, much as in a predator-prey encounter, it is often an asymmetry between the participants that determines the outcome. Cannibalism tends to increase as asymmetries in size, age, and/or hunger increase (Fox, 1975a; Polis, 1981). In species which have overlapping life stages there is typically an asymmetry in body size (Fagan and Odell, 1996; Polis, 1988). If an asymmetry in body size is a necessary requirement for cannibalism, then those species which have overlapping life stages may be predisposed towards adult cannibalism of juveniles (Polis, 1988). Not surprisingly then, cannibalism has been commonly observed in invertebrate species where overlapping life stages occur (Elgar & Crespi, 1992

Studies of cannibalism within populations where discrete and overlapping age classes occur often use a qualitative estimate of animal size, such as instar or age, rather than an actual measurement (Hopper et al., 1996; Orr et al, 1990). However, many animals which grow through discreet life stages exhibit extremely variable growth in response to both biotic and abiotic factors experienced throughout development. As a consequence of this, both the mean size and distribution of sizes within any one age class can be extremely variable across time. For this reason it can be misleading to infer that instar X will cannibalize instar Y at rate Z at all times. Therefore, it would be preferable to determine the relationship between the actual animal sizes and cannibalism rate.

The assumption that cannibals are larger than their prey appears robust. Few studies have indicated cannibals to be smaller than their prey. The few exceptions involve cases where the prey is a larger/older pupating stage, such as occurs in the caddisfly, *Brachycentrus occidentalis* (Gallep, 1974), or when groups of cannibals mob an individual, such as occurs in the tadpole of the tree frog, *Osteopilus septentrionalis* (Crump, 1986), and in the caddisfly, *Asynarchus nigriculus* (Wissinger et al, 1996). However, few studies have attempted to determine a precise relationship between this size asymmetry and cannibalism rate. These typically indicate the mean size of cannibal and/or prey and often an indicator of the intensity of cannibalism. These mean values often reflect a large number of cases often over a large period of time, sometimes an entire season or more (Anholt, 1994; Van Buskirk, 1992). Typically there are one or two size classes of cannibal, and two or three size classes of prey. This pattern is evident in much of the work on notonectids (Fox, 1975b; Orr et al, 1990), odonates (Hopper et al, 1996; Johansson, 1993; Van Buskirk, 1992), and copepods (Anderson, 1970; Landry, 1978) for example.

The focus of most work in cannibalism, including the above examples, are the demographic and life history consequences of cannibalism (Reaka, 1987; Hunte and Myers, 1984; Anholt, 1994; Fagan and Odell, 1996). In some cases this approach is only a stepping stone to the broader evolutionary question of how a population can support a cannibalistic trait (Stenseth, 1985). While these broader questions are certainly important there remains a gap in the literature concerning the fine grained mechanism and effects of cannibalism.

Demographic Consequences of Cannibalism:

Cannibalism has been shown to affect population demographics in a variety of ways. In the backswimmer, *Notonecta hoffmani*, cannibalism by adults on nymphal stages occurs in response to declining food supply. Cannibalism allows adults to survive periods of low food (Fox, 1975b; Orr et al., 1990), and may limit the population to a single generation per year (Fox, 1975c).

In larvae of the dragonfly, *Tramea carolina*, cannibalism leads to emergence synchrony and reduced variation in the size distribution of the population (Van Buskirk, 1989). The same effect has been found in *Epitheca cynosura*, where emergence synchrony occurs due to cannibalism by older instars exerting size specific mortality on smaller individuals throughout development (Hopper et al, 1996).

In the isopod, *Saduria entomen*, cannibalism by larger individuals increases both the growth rate of cannibals and their size, relative to non-cannibalistic individuals of the same age class. Cannibalism also reduces the variation in the size distribution of younger age classes (Leonardsson 1991).

Changes in population demographics such as recruitment, size distribution, synchronization of life stages, growth rates, and size specific mortality can have a significant impact, not only on the population in which they occur but on the community in which this population exists. Cannibalism studies often conclude that one or more of these demographic variables has been altered.

Size Dependent Cannibalism:

There exists much evidence of the importance of size in relation to cannibalism. Semlitsch and West (1988) found that head capsule width in the noctuid caterpillar, *Litoprosopus futilis*, is an accurate indicator of the outcome of a cannibalistic encounter. When cannibalism occurs it is invariably caterpillars with larger head capsule widths which cannibalize smaller conspecifics. Length asymmetry is also important in mantids There is little cannibalism when the size ratio of cannibal to prey is less than 1.37. Cannibalism occurs almost 100% of the time once this asymmetry value is exceeded (Fagan and Odell, 1996). In odonates larger older animals cannibalize smaller younger animals with varying intensity, but cannibalism is almost non existent among animals of the same instar (Hopper et al, 1996). From the above work, and the majority of other studies on cannibalism, three conclusions can be drawn: 1) larger individuals typically eat smaller conspecifics, 2) there is often a size asymmetry threshold which must be surpassed before cannibalism will occur, and 3) cannibalism is rare between equal sized individuals.

Few studies have explored the size relationship in greater detail. In the reef-dwelling stomatopod, *Gonodactylus oerstedii*, cannibalism is certain to occur when the length asymmetry between adult and conspecific prey exceeds a value of 1.8. The probability of being cannibalized increases as this size threshold is approached (Reaka, 1987). In larvae of the mosquito, *Trichoprosopon digitatum*, cannibalism rates increase as size differences among larvae increase (Sherrat and Church, 1994). Similar relationships have been observed in the desert scorpion, *Paruroctonus mesaensis* (Polis, 1980), in chaetognaths (Pearre Jr., 1982), in three species of gammaridean amphipods (Hunte and Myers, 1984), and in calanoid copepods (Daan et al, 1988). From this body of work it can be seen that the intensity of cannibalism is often related to the relative size differences between individuals and will occur at an increasing rate as any asymmetry threshold which would guarantee cannibalism is approached.

Although these results may seem obvious, they gain importance when demographic consequences are considered in populations where growth rates are temporally variable. In cases where growth varies over time the ìmicro-relationshipî between cannibal and prey can shift, and this shift may have an important impact on the demographic consequences of cannibalism. The standard techniques in practice of relatively long term studies which use instar rather than a real measurement can easily miss any variability in cannibalism rate due to variable growth rates. This is a question of scale; long term studies may underestimate cannibalism rates, while using instar as a size estimate can mask the effects of small changes in length asymmetry on cannibalism rate.

Cannibalism in Copepods:

The ecology and life history patterns of calanoid copepods, as a group, exhibit many of the characteristics associated with cannibalism. Reproduction is sexual and eggs are carried by the female in egg sacs until hatching. The animals hatch into a larvae, called a nauplius. The animal moults through six naupliar stages, gaining rudimentary swimming appendages and the mouthparts required for herbivorous feeding, before it enters the first copepodid stage. Copepodids resemble adults, can be visually sexed in late stages, and develop similar feeding habits as the adult. The animal passes through five or six copepodid stages until the sexually mature adult form is reached (Hutchinson, 1967). Late stage copepodids and adult copepods often supplement their herbivorous diet with a raptorial feeding mode (Dussart & Defaye, 1995).

Developmental duration, larval size and final adult size depend on food and temperature (Dussart & Defaye, 1995). Copepods in a typical habitat will experience variable food and temperature conditions throughout the season, creating temporal differences in size and age-class distributions, which can last from several weeks up to several months. Nauplii and, at times, copepodids, fall into the normal prey size distribution of adult copepods (Wilson, 1973). These ecological and environmental conditions can act in concert to produce situations where cannibalism may occur.

Cannibalism has been indicated in several species of copepod from freshwater to marine habitats. It is invariably late copepodid and adult stages which cannibalize nauplii and early copepodid stages. Onset of cannibalism in these late stages is most likely due to the development of feeding appendages which allow raptorial feeding (Williamson and Vanderploeg, 1988). The intensity of cannibalism in copepods can be very high. Cannibalism in the freshwater cyclopoid *Cyclops abyssorum* accounts for up to 45% of the total dry weight ingested by females during the winter season. The mean probability of being cannibalized in the naupliar stages is 20% with an average cannibalism rate of 0.007 nauplii . adult-1 .

day-1 (Van den Bosch and Santer, 1993). Cannibalism has also been shown to account for over 30% of the mortality in annual standing stock on nauplii in *Cyclops bicuspidatus thonrati*, a freshwater cyclopoid inhabiting Marion Lake, British Columbia (McQueen, 1969). In two Ontario lakes cannibalism by *Mesocyclops edax* accounts for losses of 13.5% and 11.5% of the nauplii per day (Brandl and Fernando, 1979).

Cannibalism is not confined to the generally more raptorial cyclopoid copepods, it is observed in calanoid copepods as well. Cannibalism has been shown to increase the death rate of nauplii in the brackish water calanoid *Sinocalanus tenellus* (Hada and uye, 1991). Studies of *Acartia tonsa*, a marine calanoid copepod, have indicated that cannibalism increases the death rate of nauplii and provides additional food for adults (Landry, 1978; Lonsdale et al. 1979). Clearance rates of between 0.8 and 1.0 liters . adult-1 . day-1 have been measured for the marine calanoid *Labidocera trispinosa* while cannibalizing its own nauplii in lab experiments. It was also shown that *L. trispinosa* remained cannibalistic when offered its own nauplii in concert with nauplii of four other species (Landry, 1978). In a detailed study on the mechanics of cannibalism and prey capture in the calanoid copepod *Diaptomus pallidus* it was determined that the probability of an adult attacking a nauplius upon encounter is 38%. The capture success is 0.06% and the probability of ingestion upon capture is 100% (Williamson and Vanderploeg, 1988).

Studies of copepods have also observed some typical demographic consequences associated with cannibalism in other organisms. In ten experiments, large *Diaptomus arcticus* consumed smaller individuals of the same species from different populations at rates comparable to those for other prey. Most of the natural populations observed in the study exhibited uniformity in body size and copepodid instar. This uniformity was attributed to cannibalism, which eliminated late developing nauplii and early copepodid instars (Anderson, 1970).

Objectives:

The objectives of this work are as follows: 1) quantify rates of cannibalism in six populations of D. leptopus; 2) determine the relationship between cannibalism intensity and the body lengths of cannibal and prey in these six populations of D. leptopus; 3) Determine whether there is significant temporal variation in the rate of cannibalism and whether this variation is related to variation in the body lengths of cannibal and prey; 4) Determine the effects of scale of measurement when generalizing the relationship between the rate of cannibalism and length of cannibal and prey and; 5) determine the effects of cannibalism on the mean size and size distribution of nauplii.

METHODS

COLLECTION SITES

Copepods were collected from six ponds in south-western Quebec (Table 1). Hill Pond and Stoneycroft are located at the west end of the island of Montreal. Stoneycroft is a shallow eutrophic pond surrounded by an open grassy field. Hill pond is a small deep pond formed by rain and possibly ground water filling a man made depression. Malloy 0 and Malloy 1 are located in the Gatineau hills approximately 65 km northwest of Montreal. Truite Rouge and Lac aux Rats are located in Mont-Tremblant Provincial Park approximately 120 km north of Montreal. Truite Rouge was stocked for fishing and may still contain fish. It supports a large frog population. Lac aux Rats supports a large fish population.

Collection and Sorting:

Copepods were collected from field sites by oblique tows with a 80μm mesh Wisconsin tow net. All populations were sampled from the shoreline except Lac aux Rats, which was sampled from the center of the lake due to an almost complete absence of animals in the littoral zone. Samples were placed in 20 l plastic carboys for transport back to the laboratory. Female copepods bearing clutches were removed from the sample by pipette and placed individually in 6 ml wells filled with 100μm-filtered pond water. Males and females without clutches were stored in carboys of unfiltered pond water in a dark cold room (10°C) until used in experiments. Wells containing

Table 1. Location and size of sampled ponds. Sampling dates and the number of trials from each sampling date.

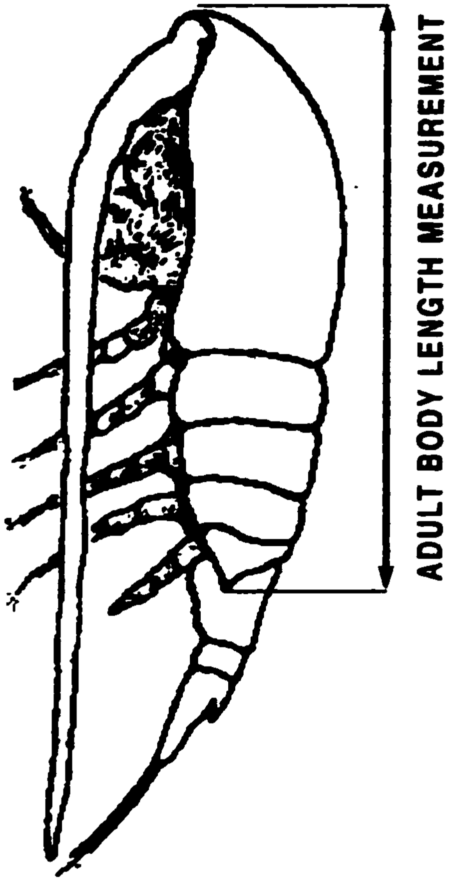
POND	LATITUDE LONGITUDE	MAX. KNOWN DEPTH (m)	WIDTH (m) LENGTH (m)	SAMPLING DATES	TRIALS
Hill Pond	45°25'50" N 73°56'45" W	3	17 35	6/23/97	1 - 2
				7/14/97	3 - 4
				7/21/97	5 - 8
				7/28/97	9 - 12
				8/18/97	13 - 16
Lac aux Rats	46°26'50" N 74°19'38" W	35	400 1150	8/6/97	1 - 4
				8/20/97	5 - 12
Malloy One	45°43'12" N 74°29'02" W	3	35 35	6/23/97	1 - 2
				7/14/97	3 - 4
				7/21/97	5 - 8
				7/28/97	9 - 12
Malloy Zero	45°43'16" N 74°28'55" W	3	75 160	6/23/97	1 - 2
				7/14/97	3 - 6
				7/21/97	7 - 12
Stoneycroft	45°25'44" N 73°56'22" W	1	30 220	6/23/97	1 - 2
				7/14/97	3 - 4
				7/21/97	5 - 8
				7/28/97	9 - 12
				8/18/97	13 - 18
Truite Rouge	46°27'30" N 74°15'30" W	30	240 600	8/20/97	1 - 11

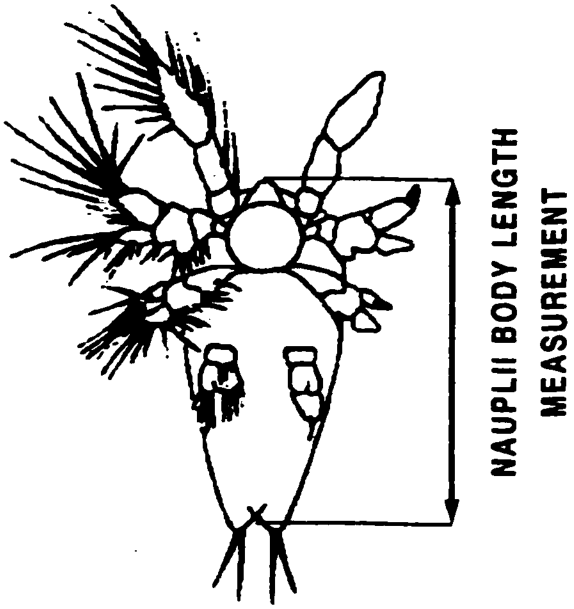
clutched females were checked every 8 - 12 hours and any nauplii that had hatched were removed. Nauplii were stored at room temperature (~21°C), in 100 ml beakers filled with 100μm-filtered pond water and were used in experiments within 3 days of the sampling date. All nauplii were between 1 and 3 days old, corresponding to an approximate instar range of 1 to 3 (Nishikawa, 1995).

Experimental Procedures:

Nauplii were sorted into groups of 25 and placed in 50ml beakers filled with 25ml of 100 μm-filtered pond water. Groups of five adults were removed from the stored pond sample and placed in 50ml beakers filled with 25ml of 100 μm-filtered pond water. At the start of each experiment 25 nauplii and 5 adults were combined in 50 ml of 100 μm-filtered pond water in 250 ml Erlenmeyer flasks. Experiments were performed using males and females separately due to the significant sexual size dimorphism found in this species (Nishikawa and Maly, 1996). Each trial consisted of a male treatment, a female treatment and a control treatment. Control treatments consisted of 25 nauplii in 50 ml of 100 μm-filtered pond water in 250 ml Erlenmeyer flasks. Only non-gravid females were used in experiments. Reproductive status was determined by visual inspection. Females with evidence of a spermatophore or any darkening of the ovaries were excluded. I repeated 3 trials when a female extruded a clutch during the experiment. All flasks were placed on a single shelf in a Conviron™ model 125L

Figure 1. Schematic diagram of body length measurements taken on adult copepods and nauplii.


ADULT BODY LENGTH MEASUREMENT


NAUPLII BODY LENGTH
MEASUREMENT

incubator. Temperature was maintained at 21°C. All experiments ran for 12 hours with constant indirect light provided by one Sylvania™ Cool White 20 watt fluorescent lamp placed 15cm above and facing away from the experimental flasks.

Experiments were terminated by transferring contents of flasks containing male and female treatments into individual vials containing 10 ml of 5% Formalin solution. Controls were immediately scored for mortality by counting live nauplii under a dissecting scope at 2.5x magnification. After scoring, control nauplii were preserved in 5:1 pond water:5% formalin solution.

Experimental trials were scored for the number of nauplii remaining. Adult metasome length and overall naupliar length, excluding caudal spines, were measured using a Wild™ inverted microscope (Figure 1). Adults were measured at 3x magnification (±0.011 mm) and nauplii were measured at 10x magnification (±0.003 mm).

Variables:

Six measured variables were used in the analysis: adult metasome length, control nauplii length, the length of uneaten nauplii remaining in experimental flasks, the number of live nauplii remaining in the experimental flasks, the numbers of live and dead nauplii in the control flasks. Cannibalism rate and length asymmetry (the ratio of adult length to control nauplii length) were derived from these measured variables.

I calculated cannibalism rate to control for naupliar mortality not attributable to cannibalism. Cannibalism rate was determined for each sex in each trial using the following equation:

$$dn/dt = \exp^{-t(ac + m)} \qquad (1)$$

Where:

n = The number of nauplii alive at time t

t = Experimental duration, in hours

a = cannibalism rate

c = The number of cannibals remaining

m = Prey mortality - determined from corresponding control treatment

Cannibalism rate (a) equals the proportion of initial prey which have been eaten per adult per hour.

The prey mortality variable (m in equation 1) was determined from each control treatment using the following equation:

$$dn/dt = \exp^{-t * m} \qquad (2)$$

Where:

n = The number of nauplii alive at time t

t = Experimental duration, in hours

m = Mortality rate

Length asymmetry was derived for each trial by dividing the mean adult length by the mean control nauplii length. As the derived asymmetry value increases, the difference between adult length and nauplii length is increasing. A value of 1 would indicate adult and nauplii of the same length.

ANALYSIS

General:

All analyses were performed on Systat v 7.0 for Windows™. The skew and kurtosis of each variable was tested both within and among ponds using Z-tests. Arcsin square root transformations were performed on all cannibalism rates and log transformations on all adult lengths. No transformations were used on nauplii as they were normally distributed in all cases. Biased influence of outliers was reduced by transformation. Statistical outliers remaining after transformation were removed, although their presence did not alter the significance of any result.

Three-way ANOVA and Tukey post hoc multiple comparison tests were used to assess differences in cannibalism rate, adult body length, and length asymmetry among ponds, between sexes and among dates. Two-way ANOVA and Tukey post hoc multiple comparison tests were used to assess differences in control nauplii length among ponds and dates.

Linear regressions were used to determine the relationship between cannibalism rate and adult body length, control body length, and length asymmetry across all trials and when data were grouped by date and sex, and when data were grouped by pond and sex.

Population Consequences:

Differences between female and male treatments in the length of uneaten nauplii remaining in the experimental flasks were assessed by simple ANOVA within ponds across all trials.

Differences in nauplii length between control and experimental treatments were assessed using Dunnett's test.

RESULTS

Cannibalism Rates:

Cannibalism rate ranged from 0.000 prey . cannibal-1 . hour-1 to 0.053 prey . cannibal-1 . hour-1; the lowest rates were exhibited by males from Stoneycroft and Lac aux Rats and the highest rates by Malloy 1 females (Figure. 2). There was a significant difference in cannibalism rate among ponds (Three-way ANOVA d.f. = 5, 144, F = 265.277, $p < 0.001$) and between sexes (Three-way ANOVA d.f. = 1,144, F = 16.243, $p < 0.001$). There was no interaction on cannibalism rate among ponds and sexes (Three-way ANOVA d.f. = 5,144, F = 0.504, p = 0.773). There was no significant difference in cannibalism rate among dates (Three-way ANOVA d.f. = 1,144, F = 0.167, p = 0.683).

Post Hoc multiple comparisons indicated significant differences in cannibalism rate between sexes and between the six populations (Table 2).

Body length, Temporal Variance and Measurement Scale

Nauplii Length:

Mean length of control nauplii ranged from 0.152mm to 0.303mm where the smallest nauplii were found in Hill Pond and the largest in Truite Rouge (Figure. 3). There was a significant difference in the length of control nauplii among ponds (Two-way ANOVA d.f. = 5, 1609, F = 140.899, $p < 0.001$) (Table 2) and among dates (Two-way ANOVA d.f. = 1, 1609, F = 615.155, $p < 0.001$). There was a significant interaction on control length among ponds and dates (Two-way ANOVA d.f. =

Figure 2. Mean cannibalism rate calculated across all trials grouped alphabetically by pond and grouped by sex. Cannibalism rate equals the proportion of available intraspecific prey eaten per adult per hour. Error bars indicate ±1 S.E.

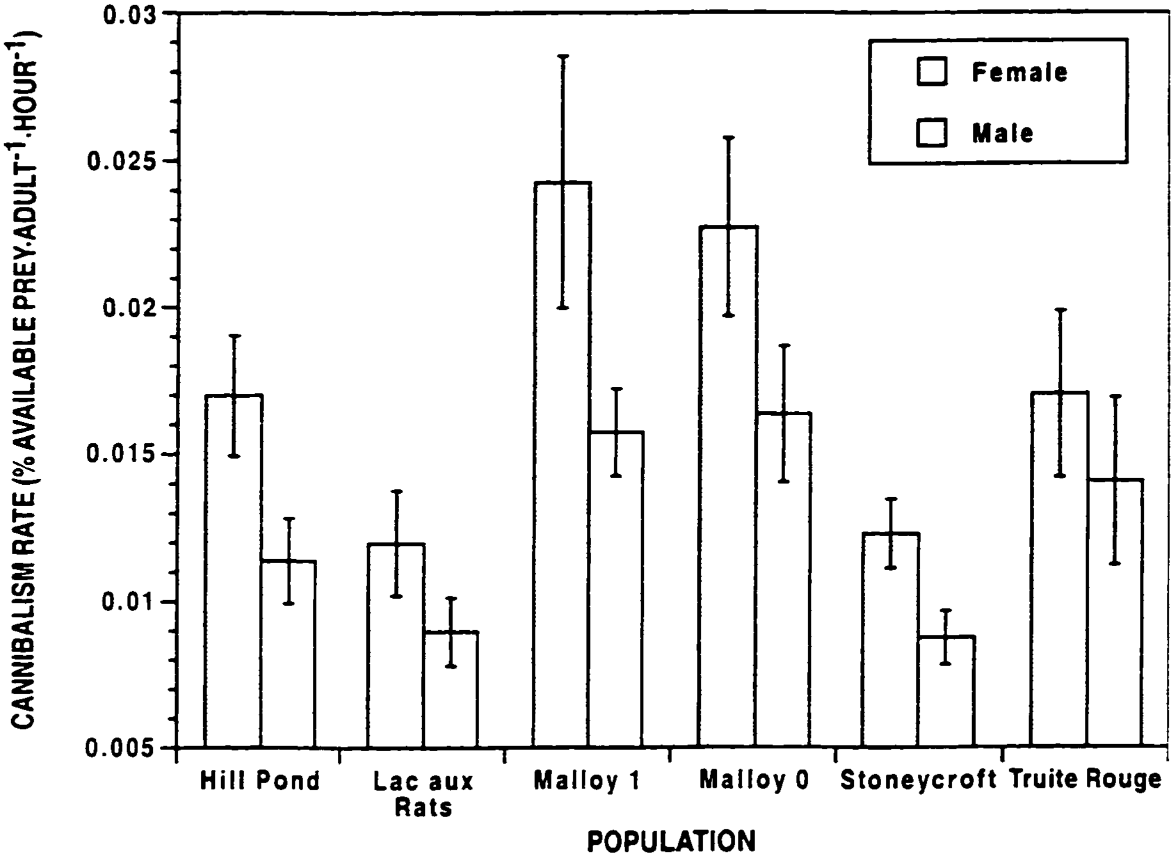

0.03
0.025
0.02
0.015
0.01
0.005
CANNIBALISM RATE (% AVAILABLE PREY·ADULT^{-1}.HOUR^{-1})
☐ Female
☐ Male
Hill Pond
Lac aux Rats
Malloy 1
Malloy 0
Stoneycroft
Truite Rouge
POPULATION

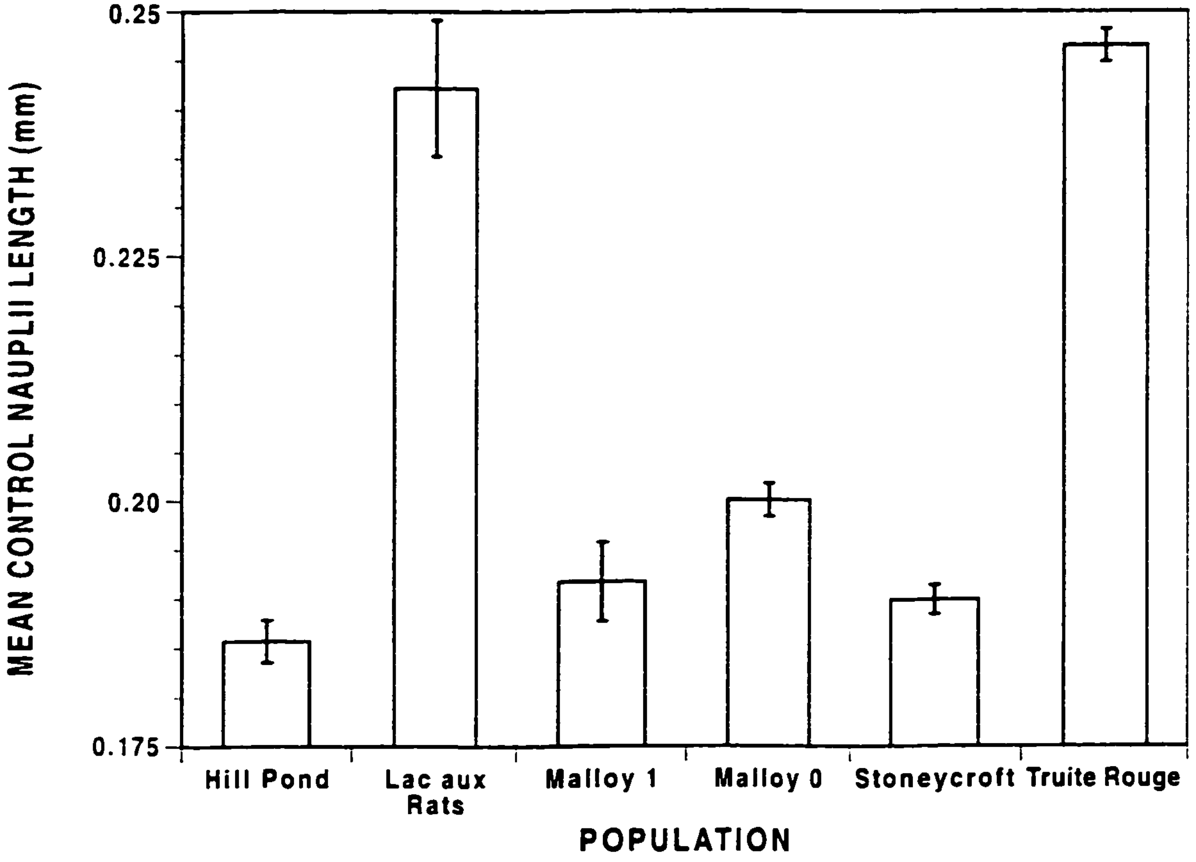
Table 2. Result of Tukey multiple comparisons. The top right portion represents differences in control nauplii length between ponds. The lower left portion represents differences in cannibalism rate between sexes and ponds. An X equals a p value < 0.05.

POND		Hill Pond		Lac aux Rats		Malloy One		Malloy Zero		Stoneycroft		Truite Rouge	
	SEX	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Hill Pond	♀			X		X		X		X		X	
	♂												
Lac aux Rats	♀					X		X		X		X	
	♂												
Malloy One	♀		X	X	X			X				X	
	♂												
Malloy Zero	♀		X	X	X					X		X	
	♂												
Stoneycroft	♀					X		X				X	
	♂	X				X		X					
Truite Rouge	♀												
	♂												

Control Nauplii Length

Cannibalism Rate

Figure 3. Mean control nauplii length ranked alphabetically by pond. Error bars indicate ±1 S.E.


MEAN CONTROL NAUPLII LENGTH (mm)
0.25
0.225
0.20
0.175
Hill Pond
Lac aux Rats
Malloy 1
Malloy 0
Stoneycroft
Truite Rouge
POPULATION

5,1609, F = 163.039, $p < 0.001$). The length of control nauplii was subject to seasonal variation, but this variation was not distributed uniformly across the six ponds.

Overall, there was no significant relationship between control nauplii length and cannibalism rate among ponds either grouped by trial ($r^2 = 0.000$, n = 162, p = 0.892) or grouped by date ($r^2 = 0.001$, n = 40, p = 0.829). The addition of date to the model did not significantly alter the result. When the scale of observation is reduced to within ponds, one pond, Malloy 1, exhibited a significant yet marginal increase in cannibalism rate as length of control nauplii increased. There was no significant relationship between length of control nauplii and cannibalism rate in the other five ponds (Table 3). The addition of date to these regressions did not alter the significance of any result.

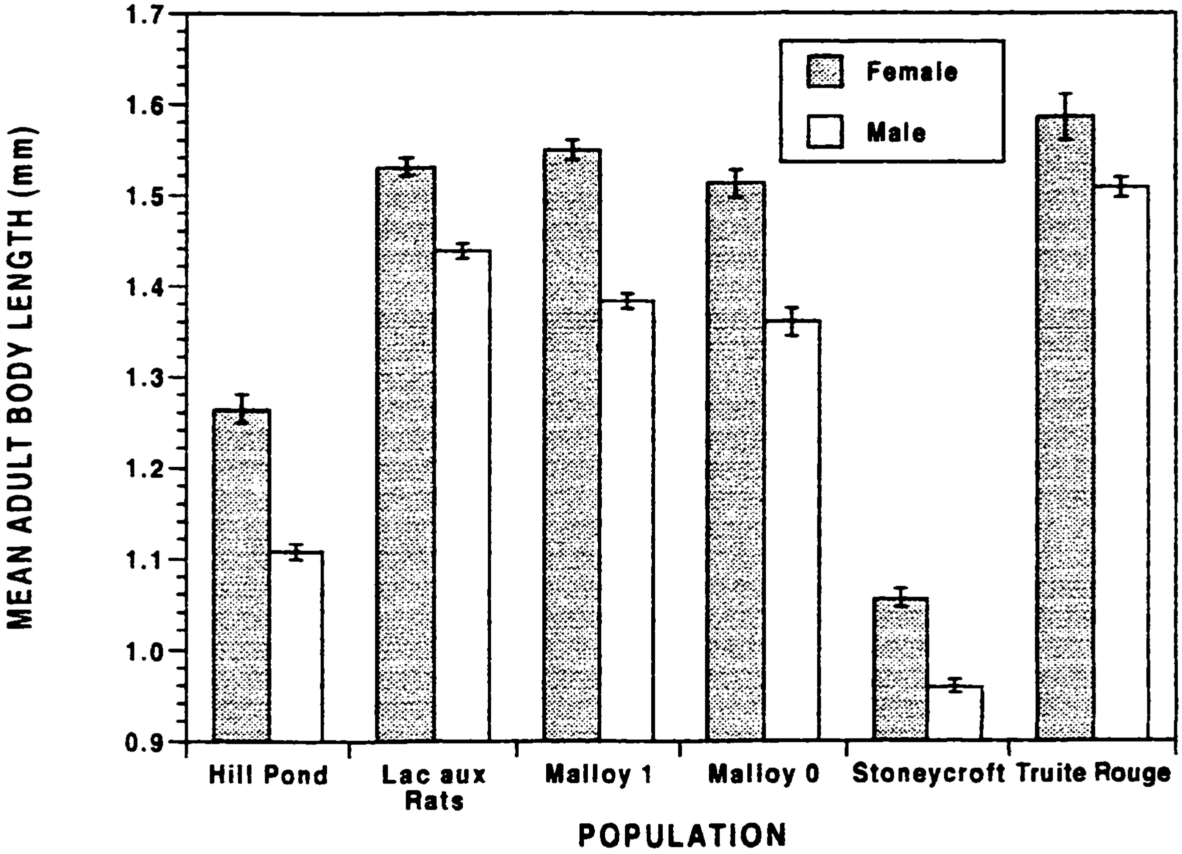
Adult Length:

Adult length ranged from 0.809 mm to 1.811 mm where the smallest adults were males from Stoneycroft and the largest were Truite Rouge females (Figure. 4). There was a significant difference in adult length among ponds (Three-way ANOVA d.f. = 5, 773, F = 271.272, $p < 0.001$), among dates (Three-way ANOVA d.f. = 1, 773, F = 554.006, $p < 0.001$), and between sexes (Two-way ANOVA d.f. = 1,773, F = 13.938, $p < 0.001$). There was a significant interaction on adult length between pond and sex (Two-way ANOVA d.f. = 5,773, F = 6.339, $p < 0.001$) indicating that the sexual dimorphism exhibited by this species is not

Table 3. Comparison of linear regression results of cannibalism rate against control nauplii length. There is a single entry per pond as the same control was used for both sexes. Beta represents the direction of the slope of the regression line. p values for $\alpha = 0.05$.

POND	n	r2	beta	df	F	p
HILL POND	32	.017	-	1, 30	0.509	0.481
LAC AUX RATS	24	.035	+	1, 22	0.809	0.378
MALLOY 1	24	.252	+	1, 22	7.423	**0.012**
MALLOY 0	24	.002	-	1, 22	0.064	0.802
STONEYCROFT	36	.029	+	1, 34	0.034	0.316
TRUITE ROUGE	22	.000	+	1, 20	0.003	0.955

Figure 4. Mean adult body length ranked alphabetically by pond and grouped by sex. Error bars indicate ±1 S.E.


MEAN ADULT BODY LENGTH (mm)
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
Female
Male
Hill Pond
Lac aux Rats
Malloy 1
Malloy 0
Stoneycroft
Truite Rouge
POPULATION

uniform between populations. There was also a significant interaction between pond and date (Two-way ANOVA d.f. = 5,773, F = 322.992, $p < 0.001$) indicating that the seasonal variation in adult length was not distributed uniformly across the six ponds. Post Hoc multiple comparisons indicated significant differences in adult length between sexes and between the six populations (Table 4).

Overall, adult length was significantly related to cannibalism rate across all trials ($r^2 = 0.108$, $n = 162$, $p < 0.001$) (Figure 5a), and when trials were grouped by date, sex, and pond ($r^2 = 0.239$, $n = 40$, $p < 0.01$) (Figure 5b), but was not significantly related to cannibalism when trials were grouped by sex and pond ($r^2 = 0.3$, $n = 12$, $p = 0.059$) (Figure 5c). The addition of date to the model did not significantly alter the result. When the scale of observation is reduced to within ponds, regardless of sex, there was a significant relationship between adult length and cannibalism rate in four of six cases (Table 5). Within ponds, when sexes were assessed individually, there was no significant relationship between cannibalism rate and length of adult females in any of the six ponds. The length of adult males was significantly related to cannibalism rate in three ponds and there was no significant relationship in three ponds. Larger males exhibited a significantly higher cannibalism rate than smaller males in Hill Pond and Malloy 0, while large males in Stoneycroft exhibited a significantly lower cannibalism rate than smaller

Table 4. Result of Tukey multiple comparisons. The top right portion represents differences in length asymmetry values between sexes and ponds. The lower left portion represents differences in adult body length between sexes and ponds. An X equals a p value < 0.05.

POND		Hill Pond		Lac aux Rats		Malloy One		Malloy Zero		Stoneycroft		Truite Rouge	
	SEX	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Hill Pond	♀		X		X	X		X		X	X		X
	♂	X				X	X	X	X		X	X	
Lac aux Rats	♀	X	X			X	X	X		X	X		
	♂	X	X	X		X	X	X	X	X	X		
Malloy One	♀	X	X		X		X		X	X	X	X	X
	♂	X	X	X	X	X		X		X	X	X	X
Malloy Zero	♀	X	X		X	X	X		X	X	X	X	X
	♂	X	X	X	X	X		X		X	X	X	X
Stoneycroft	♀	X	X	X	X	X	X	X	X		X	X	X
	♂	X	X	X	X	X	X	X	X	X		X	X
Truite Rouge	♀	X	X	X	X	X	X	X	X	X	X		
	♂	X	X		X		X	X	X	X	X	X	

LENGTH ASYMMETRY VALUE

ADULT BODY LENGTH

Figure 5. Scatter plots of adult body length against cannibalism rate for all data (A), all data grouped by date, pond, and sex (B), and all data grouped by pond and sex (C). Values on both axes differ between graphs. Line represents least-squares best fit regression equation.

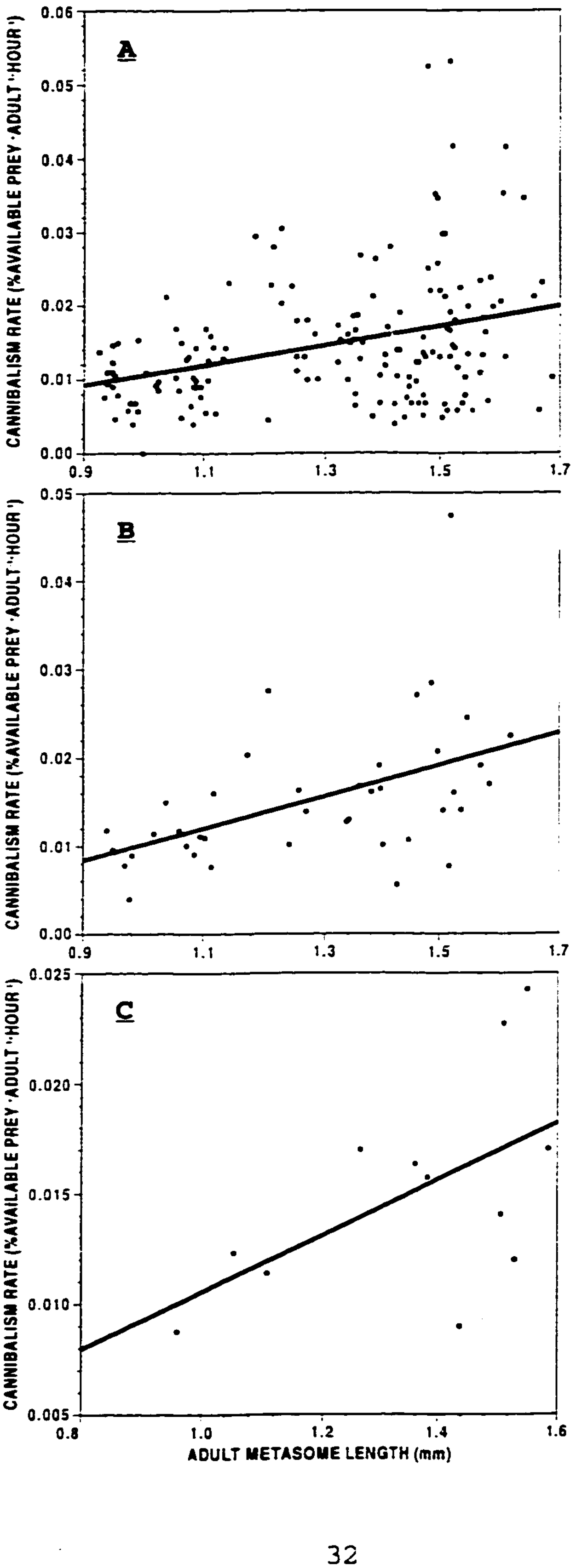

A
B
C
CANNIBALISM RATE (%AVAILABLE PREY·ADULT⁻¹·HOUR⁻¹)
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0.9
1.1
1.3
1.5
1.7
0.05
0.04
0.03
0.02
0.01
0.00
0.025
0.020
0.015
0.010
0.005
0.8
1.0
1.2
1.4
1.6
ADULT METASOME LENGTH (mm)

Table 5. Comparison of linear regression results of cannibalism rate aginst adult body length.

Beta represents the direction of the slope of the regression line. p values for $\alpha = 0.05$.

POND	SEX	n	r2	beta	df	F	P
HILL POND	♀	16	.028	-	1, 14	0.405	0.535
	♂	16	.569	+	1, 14	18.554	**< 0.001**
	ALL	32	.138	+	1, 30	4.82	**0.036**
LAC AUX RATS	♀	12	.176	+	1, 10	2.137	0.174
	♂	12	.030	+	1, 10	0.313	0.588
	ALL	24	.172	+	1, 22	4.564	**0.044**
MALLOY 1	♀	12	.005	+	1, 10	0.060	0.811
	♂	12	.214	-	1, 10	2.716	0.130
	ALL	24	.114	+	1, 22	2.831	0.106
MALLOY 0	♀	12	< .000	-	1, 10	0.006	0.939
	♂	12	.513	+	1, 10	10.573	**0.009**
	ALL	24	.179	+	1, 22	4.798	**0.039**
STONEYCROFT	♀	18	.123	+	1, 16	2.250	0.153
	♂	18	.311	-	1, 16	7.236	**0.016**
	ALL	36	.116	+	1, 34	4.466	**0.041**
TRUITE ROUGE	♀	11	.023	+	1, 9	0.214	0.654
	♂	11	.027	-	1, 9	0.251	0.629
	ALL	22	.018	+	1, 20	0.371	0.549

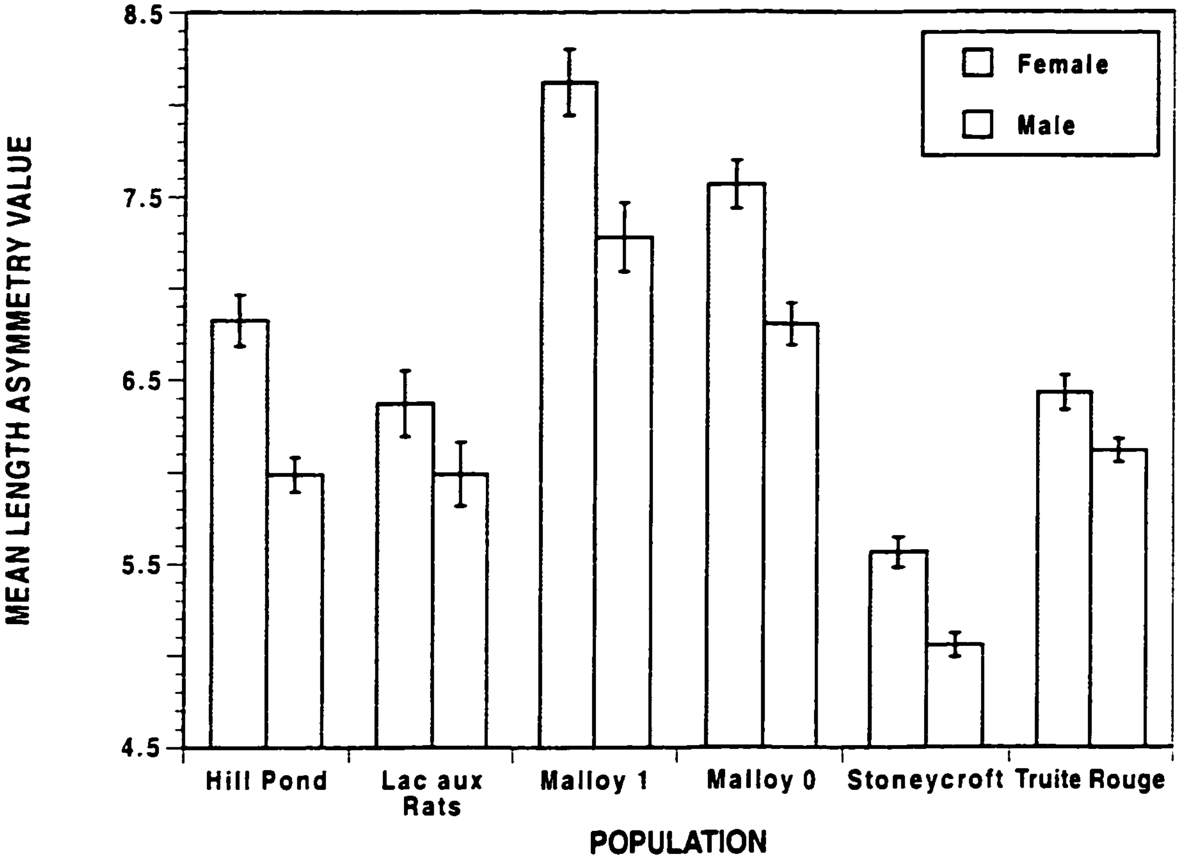
males in the same pond (Table 5).

Length Asymmetry:

Length asymmetry ranged from 3.599 to 10.179 where the smallest asymmetries were found in Stoneycroft and the largest in Malloy 1 (Figure 6). There was a significant difference in length asymmetry among ponds (Three-way ANOVA d.f. = 5, 144, F = 960.325, $p < 0.001$), among dates (Three-way ANOVA d.f. = 1, 144, F = 2557.577, $p < 0.001$), and between sexes (Three-way ANOVA d.f. = 1,144, F = 7.454, $p < 0.001$). There was a significant interaction on length asymmetry between pond and date (Three-way ANOVA d.f. = 5,144, F = 736.088, $p < 0.001$) indicating that the seasonal variation in length asymmetry was not distributed uniformly across the six ponds. Post Hoc multiple comparisons indicated significant differences in length asymmetries between sexes and between the six populations (Table 4).

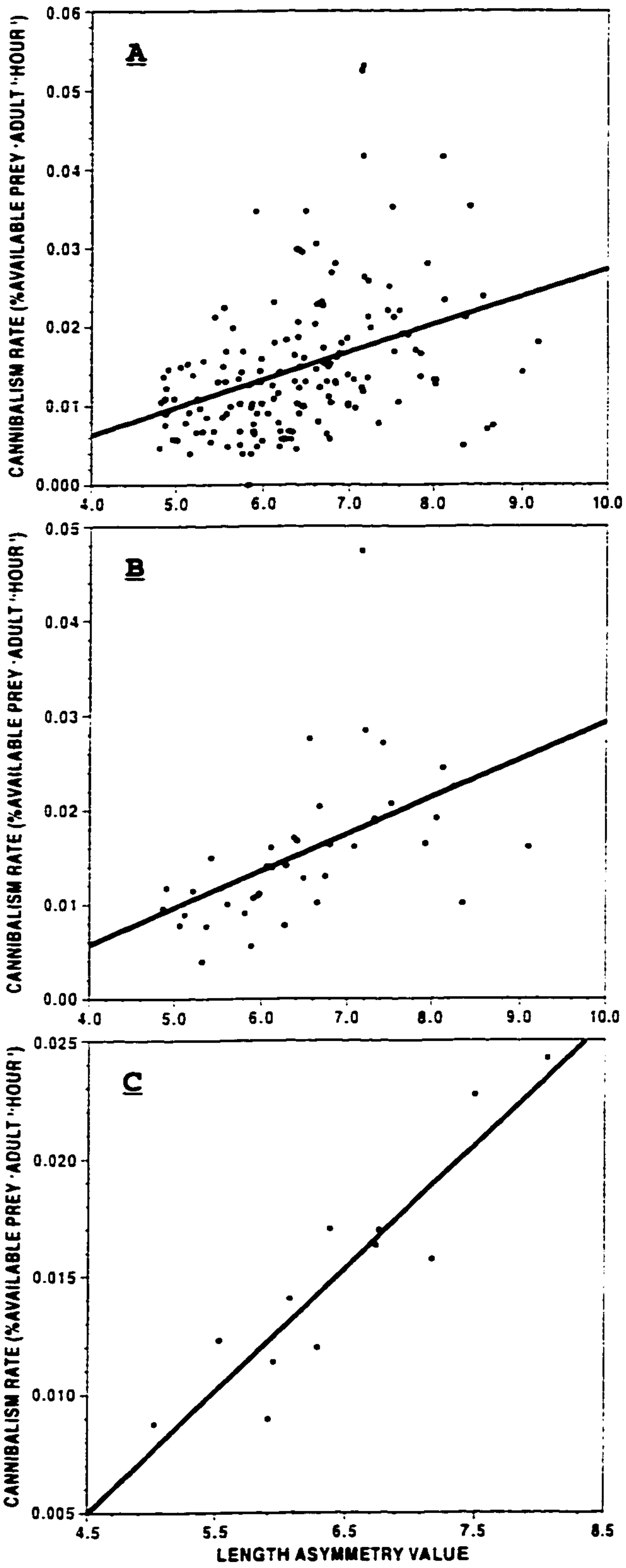
Length asymmetry was generally a significant predictor of cannibalism rate. As length asymmetry increased, cannibalism rate also increased over all trials ($r^2 = 0.145$, $p < 0.001$) (Figure 7a), when trials are grouped by date, sex, and pond ($r^2 = 0.273$, $p < 0.01$) (Figure 7b), and when trials are grouped by sex and pond ($r^2 = 0.833$, $p < 0.001$) (Figure 7c). The addition of date to the model did not significantly alter the result. However, when the scale of observation is reduced to within ponds, cannibalism rate was not significantly related to length asymmetry, regardless of adult sex, in any pond. Within

Figure 6. Mean length asymmetry values ranked alphabetically by pond and grouped by sex. Error bars indicate ±1 S.E.



MEAN LENGTH ASYMMETRY VALUE
8.5
7.5
6.5
5.5
4.5
☐ Female
☐ Male
Hill Pond
Lac aux Rats
Malloy 1
Malloy 0
Stoneycroft
Truite Rouge
POPULATION

Figure 7. Scatter plots of length asymmetry values against cannibalism rate for all data (A), all data grouped by date, pond, and sex (B), and all data grouped by pond and sex (C). Values on both axes differ between graphs. Line represents least-squares best fit regression equation.


A
B
C
CANNIBALISM RATE (%AVAILABLE PREY · ADULT⁻¹ · HOUR⁻¹)
0.000
0.01
0.02
0.03
0.04
0.05
0.06
0.00
0.01
0.02
0.03
0.04
0.05
0.005
0.010
0.015
0.020
0.025
4.0
5.0
6.0
7.0
8.0
9.0
10.0
4.5
5.5
6.5
7.5
8.5
LENGTH ASYMMETRY VALUE

ponds, when sexes are assessed individually, cannibalism rate was only significantly related to length asymmetry in four of twelve cases (Table 6). There was a negative relationship between cannibalism rate and length asymmetry in Malloy 1 females and Stoneycroft males. There was a positive relationship between cannibalism rate and length asymmetry in males from Hill Pond and Malloy 0.

Population consequences:

The mean length of uneaten nauplii differed significantly between treatments and controls (d.f. = 2, 3379, F = 11.349591, $p < 0.001$) across all data. The mean length of nauplii remaining in female treatments was significantly smaller than nauplii remaining in male treatments (Figure 8), and was significantly smaller than the mean length of control nauplii (Figure 8). The mean length of nauplii remaining in male treatments did not differ significantly from the mean length of control nauplii (Figure 8).

Within ponds the mean length of uneaten nauplii was altered by cannibalism in 9 out of 12 cases. In 3 of the 9 cases the mean length of uneaten nauplii was significantly smaller than the mean length of control nauplii. In 6 of the 9 cases the mean length of uneaten nauplii was significantly larger than the mean length of control nauplii. In 3 cases there was no significant difference between mean length of uneaten nauplii and mean control nauplii length (Table 7).

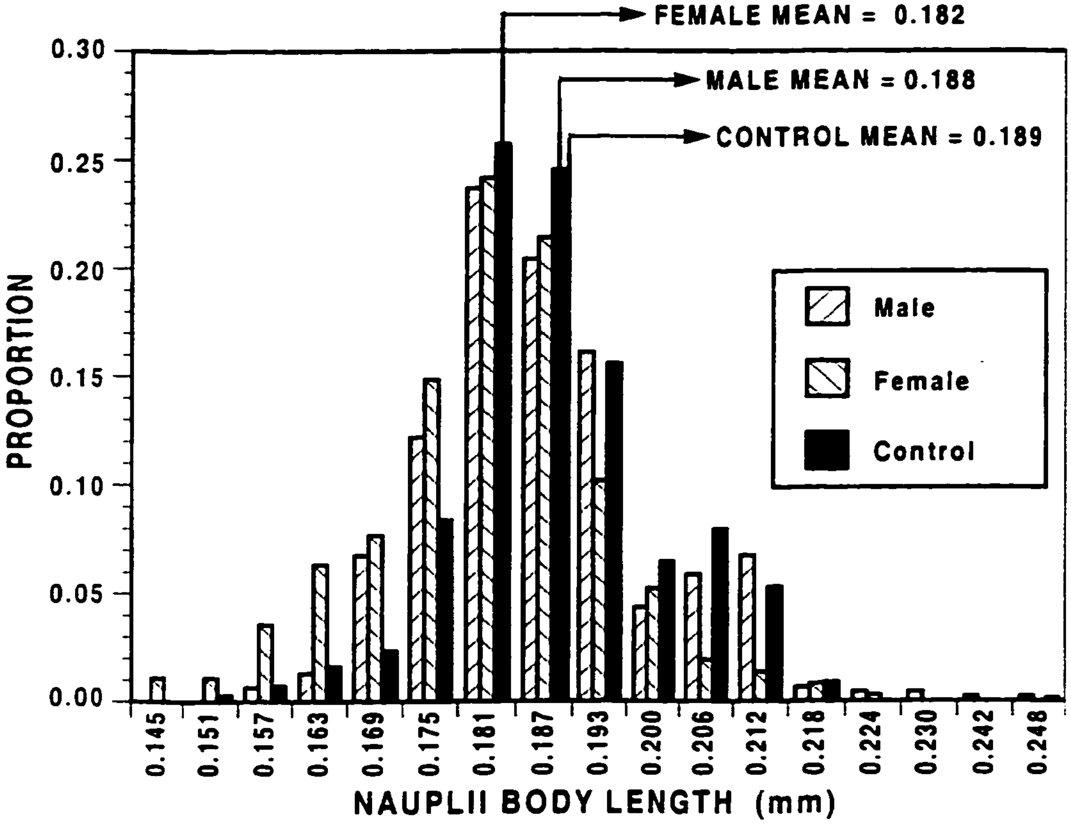
The difference between mean control length and mean

Table 6. Comparison of linear regression results of cannibalism rate against length asymmetry.

Beta represents the direction of the slope of the regression line. p values at $\alpha = 0.05$.

POND	SEX	n	r2	beta	df	F	P
HILL POND	♀	16	.018	-	1, 14	0.255	0.621
	♂	16	.442	+	1, 14	11.091	**0.004**
	ALL	32	.115	+	1, 30	3.891	0.057
LAC AUX RATS	♀	12	.043	-	1, 10	0.444	0.520
	♂	12	.013	+	1, 10	0.137	0.719
	ALL	24	.000	+	1, 22	0.007	0.931
MALLOY 1	♀	12	.335	-	1, 10	5.028	**0.048**
	♂	12	.242	-	1, 10	3.196	0.104
	ALL	24	.027	-	1, 22	0.607	0.444
MALLOY 0	♀	12	.007	-	1, 10	0.069	0.798
	♂	12	.381	+	1, 10	6.161	**0.032**
	ALL	24	.134	+	1, 22	3.392	0.079
STONEYCROFT	♀	18	.047	+	1, 16	0.786	0.388
	♂	18	.356	-	1, 16	8.865	**0.008**
	ALL	36	.031	+	1, 34	1.084	0.305
TRUITE ROUGE	♀	11	.005	+	1, 9	0.048	0.831
	♂	11	.000	+	1, 9	0.003	0.960
	ALL	22	.016	+	1, 20	0.331	0.571

Figure 8. Distribution of control nauplii and uneaten nauplii remaining in female and male treatments. Mean length of nauplii is indicated in all classes. Note that females tend to leave a larger proportion of smaller nauplii while males tend to leave a larger proportion of larger nauplii.


FEMALE MEAN = 0.182
MALE MEAN = 0.188
CONTROL MEAN = 0.189
Male
Female
Control
PROPORTION
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0.145
0.151
0.157
0.163
0.169
0.175
0.181
0.187
0.193
0.200
0.206
0.212
0.218
0.224
0.230
0.242
0.248
NAUPLII BODY LENGTH (mm)

uneaten naupliar length was not related to mean adult length (r2 = 0.001, d.f. = 1, 160, F = 0.1768, p = 0.677), but was related to mean length asymmetry (r2 = 0.177, d.f. = 1, 160, F = 34.3467, p < 0.001) and to mean control nauplii length (r2 = 0.275, d.f. = 1, 160, F = 60.8425, p < 0.001) (Figure 9).

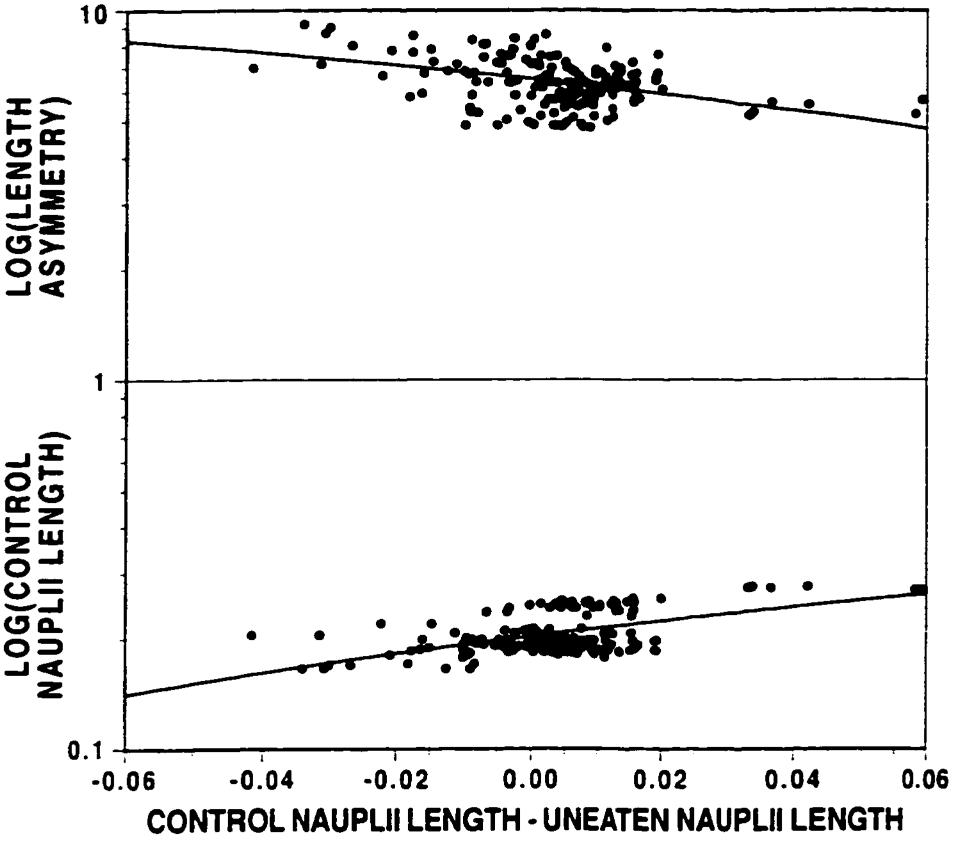
Table 7. Results of Dunnets test comparing mean lengths of control nauplii to uneaten nauplii and results of ANOVA comparing Length of uneaten nauplii between sexes. Column labeled control vs. uneaten indicates significance level of Dunnets test. Column labeled Male vs. Female indicates significance level of ANOVA's. p values at $\alpha = 0.05$.

		NAUPLII LENGTH							FINAL NAUPLII SIZE COMPARISONS	
									CONTROL VS UNEATEN	MALE VS FEMALE
POND	SEX	CONTROL	SE	n	UNEATEN	SE	n	UNEATEN - CONTROL	P	P
Hill Pond	♀	0.18687	0.0006	320	0.17738	0.0011	150	-0.00949	<0.05	<0.01
	♂	0.18687	0.0006	320	0.18445	0.0008	199	-0.00242	<0.05	
Lac aux Rats	♀	0.24375	0.0017	240	0.22943	0.0009	135	-0.01432	<0.05	<0.01
	♂	0.24375	0.0017	240	0.23369	0.0010	158	-0.01006	ns	
Malloy One	♀	0.19249	0.0010	240	0.19813	0.0010	80	0.00564	<0.05	ns
	♂	0.19249	0.0010	240	0.19786	0.0009	112	0.00537	<0.05	
Malloy Zero	♀	0.20167	0.0008	240	0.16890	0.0010	90	-0.00277	ns	<0.01
	♂	0.20167	0.0008	240	0.20459	0.0012	118	0.00292	<0.05	
Stoneycroft	♀	0.19085	0.0006	360	0.18529	0.0007	213	-0.00556	<0.05	<0.01
	♂	0.19085	0.0006	360	0.19112	0.0008	259	0.00027	ns	
Truite Rouge	♀	0.24864	0.0006	220	0.23733	0.0007	107	-0.01131	<0.05	<0.01
	♂	0.24864	0.0006	220	0.24391	0.0007	126	-0.00473	<0.05	

Figure 9. Direction and degree of change in mean nauplii length after treatment vs log(length asymmetry) (A) and log(initial nauplii length) (B). Values are logged strictly for illustration purposes. Least-squares best fit line indicates direction of relationship.

As the length asymmetry decreases, as nauplii approach adult length, larger nauplii tend to be cannibalized more often than smaller nauplii, decreasing the mean nauplii length in the population. As length asymmetry increases, smaller nauplii tend to be cannibalized more often than larger nauplii, increasing the mean nauplii length in the population (A).

As the initial mean naupliar length increases, the difference between initial and final naupliar lengths increase. When the initial mean nauplii length is small, smaller nauplii tend to be cannibalized, increasing the mean nauplii length in the population. When the initial mean nauplii length is large, larger nauplii tend to be cannibalized, decreasing the mean nauplii length in the population (B).


LOG(LENGTH ASYMMETRY)
LOG(CONTROL NAUPLII LENGTH)
10
1
0.1
-0.06
-0.04
-0.02
0.00
0.02
0.04
0.06
CONTROL NAUPLII LENGTH - UNEATEN NAUPLII LENGTH

DISCUSSION

Cannibalism rates:

The cannibalism rates measured in this study were not insignificant. Each adult, on average, cannibalized between 2 and 4 nauplii in 12 hours. It is not known whether cannibalism rates measured over 12 hour periods in this study are representative of daily maximum cannibalism rates. Longer term experiments would have to be used to determine where the increase in rate over time, if any, levels out. However, the observed rates in this study are within the same order of magnitude as previously measured copepod cannibalism rates (Landry, 1978; Van den Bosch and Santer, 1993).

A more important question is whether the rates measured in these experiments can be extrapolated into a field situation. The densities of adults and nauplii used in this study were within the upper end of the range observed in Hill Pond, Stoneycroft, and both Malloy ponds. Density dependent predation rates have been observed in several species of copepods and may be a factor regulating cannibalism rates in *D. leptopus* populations, at least during periods of low nauplii density. Behavioural mechanisms may also reduce the losses to cannibalism in the field if spatial separation exists between nauplii and adults. In handling nauplii during this study I observed that they tended to remain near the surface layer of the water while adults were normally located deeper in the water column. Whether nauplii are distributed in this way in the field is not known.

Cannibalism rates measured in this work are certainly high enough to affect recruitment significantly. Mating intensity in *D. leptopus* ranges from 1 to 57 % of females bearing clutches (DeFrenza et al, 1986). If an average clutch size is 15 eggs then a conservative estimate of recruitment reduction due to cannibalism could be as high as 50% at the peak reproductive periods, and perhaps higher at other times of the season. Larger mean clutch size would reduce the effect of cannibalism on recruitment but may increase nauplii mortality in other ways. If cannibalism is a major factor affecting nauplii mortality, as has been suggested for other species of copepod (McQueen, 1969; Brandl and Fernando, 1979; Landry, 1978; Lonsdale et al. 1979; Daan et al., 1988), then a trade off may be occurring between selection for larger clutches, to proportionally reduce losses to cannibalism, and increased mortality due to other factors related to larger clutch size, such as smaller nauplii and increased predation risk to the clutched adult female. This is a twist on the lifeboat theory (Van den Bosch et al, 1988) which proposed that adults could survive periods of low alternate food if they resorted to cannibalism of nauplii until alternate food levels returned to normal.

Nauplii and Adult Length:

Nauplii length alone did not have a significant impact on the rates of cannibalism.

Larger adults tended to eat more nauplii. There are exceptions, however: females from Lac aux Rats, the third largest adults, have the largest nauplii and fall into the middle of the asymmetry value scale, yet their cannibalism rate is the third lowest, much lower than expected. Males from this population also exhibit lower cannibalism rates than expected. Lac aux Rats is the only population with vertebrate predators. It is possible that high rates of cannibalism are selected against in populations which are vulnerable to the high predation rates from vertebrate predators. There is circumstantial evidence that the presence of a large vertebrate predator may affect the distribution of copepods in Lac aux Rats. This is the largest lake I sampled and it was necessary to collect samples from the centre of the lake. There were no copepods in the littoral zone but there were high densities of juvenile fish, presumably a dangerous predator to both adult and juvenile stages of copepods.

The trend of larger animals cannibalizing more prey could be a function of reduced handling time, or it could be due to satiation levels varying with adult body length, or both. Neither handling time nor satiation were measured in this study. It is likely that handling time does decrease as the length asymmetry increases. Further study will be required to determine how handling time contributes to cannibalism rate in these animals.

If larger adults do consume more nauplii, are they affecting the rate of increase of the populations with large adults more than the populations with small adults? The number of eggs per clutch increases with body length (McLaren, 1965, Landry, 1978). Therefore, larger cannibals, while eating more nauplii, may not be having a greater impact on the population than smaller cannibals which eat fewer nauplii. Both large and small adults may be eating the same proportion of their individual reproductive capacity.

The situation changes in ponds where there is a broad size distribution of adults. The fitness of the small adults is reduced by a greater amount than that of large adults suffering equal numbers of nauplii lost to cannibalism. This may create an asymmetry in the fitness impact of cannibalism between small and large adults in populations where there is a large size distribution of adults. This could act to reduce adult size variation within populations by favouring larger adults. In populations where the growth rate is temporally variable there may be a selective advantage to develop when growth rates are high, bear diapausing eggs which will hatch after growth rates slow, thereby exposing nauplii to smaller adults and reducing the possible impact of losses to cannibalism.

length asymmetry:

In this study the asymmetry between adult length and nauplius length proved to be more important than either individual component. However, it is not clear how the two components of this asymmetry each contribute to the outcome of any encounter. The ideal way to separate the two components would be to use nauplii of the same length when testing the effect of adult size, and adults of the same length when testing the effect of nauplii size. The realities of the work make this impossible. I used early naupliar stages to reduce the effect of variable growth rates and hence, larger variances in the size distributions of nauplii. There was a range of nauplii sizes within trials sometimes greater than 0.05 mm. This translates into a substantial distribution of length asymmetries within trials. Therefore neither adult length or nauplii length results are independent of asymmetry effects. When assessed separately, Cannibalism rate was not significantly related to the length of nauplii, but there was a significant relationship between cannibalism rate and the length of adults. This indicates that even with the variance in the size distribution of nauplii, all nauplii used have a roughly equal probability of being cannibalized by any single length class of adult. From this it can also be seen that, in this study, adult length contributes more to the effect of the length asymmetry than nauplii length.

Temporal Effects:

There was a seasonal effect on cannibalism rate, control length, adult length, and length asymmetry. However, date did not significantly contribute to the ability of any of the regression models to predict cannibalism rate. This result indicates that date is related to the length of the adults and it is adult length which is most closely related to cannibalism rate. Nauplii length is expected to covary with adult length, and length asymmetry is derived from adult length. Therefore date did not provide any additional information which is relevant to the prediction of cannibalism rate.

Measurement Scale:

There was a strong relationship between cannibalism rate and both adult length and length asymmetry. When looking at adult length, the relationship was strongest when using the means by date and sex. The relationship was significantly positive, as larger adults cannibalized more nauplii than smaller adults. However, the same strength of relationship did not exist within the individual ponds.

When looking at length asymmetry the relationship was strongest when using the means by pond and sex. The relationship was significantly positive, as cannibalism rate increased as length asymmetry increased. However, as in adult length, the same strength of relationship did not exist within the individual ponds.

When the data are grouped by pond, or by subgroupings within ponds such as date, the effects of large differences in adult length and length asymmetry may overemphasize the strength of the relationship of each variable to cannibalism rate. Within ponds we have a finer grained picture which often indicates that the ìmicro-relationshipî can be very different than that predicted by the larger scale investigations. In this study the grouping means used in the regressions are analogous to the mean sizes of instars typically used in cannibalism studies. Within populations, the finer grain, we see that the relationships do not always correspond to the conclusions of a larger grained study. Hence, the actual day to day relationships between body lengths and cannibalism rate within populations may differ significantly from that predicted by the larger scale study.

Population Consequences:

As well as altering the rate of increase of a population, cannibalism changes the size distribution of nauplii. In most cases the mean size of nauplii remaining uneaten in the cannibalism experiments was significantly smaller than that of the control nauplii. This is a common result of cannibalism. In larvae of the dragonfly, *Tramea carolina*, cannibalism leads to emergence synchrony and reduced variation in the size distribution of the population (Van Buskirk, 1989). The same effect has been found in larvae of the dragonfly, *Epitheca cynosura*, where emergence synchrony occurs due to cannibalism by older instars exerting size specific mortality on smaller individuals throughout development (Hopper et al., 1996). In the isopod, *Saduria entomon*, cannibalism reduces the variation in the size distribution of younger age classes (Leonardsson, 1991). Most of the natural populations observed in a study using the copepod, *Diaptomus arcticus*, exhibited uniformity in body size and copepodid instar. This uniformity was attributed to cannibalism, which eliminated late developing nauplius and early copepodid instars (Anderson, 1970).

The trend of the mean size of nauplii remaining uneaten in the cannibalism experiments being significantly smaller than that of the control nauplii also may indicate that there are some sizes of nauplii, usually the larger ones, which suffer greater losses from cannibalism. I hesitate to call it size selective cannibalism in this study as alternate explanations have not been researched. Larger nauplii may have an increased encounter rate with adults due to activity level or size, or large nauplii may not evade capture as well as small nauplii once encountered.

Conclusion:

I have found that mean length asymmetry is a strong predictor of cannibalism rate. Adult length contributed significantly more to the asymmetry than nauplii length. Larger adults tend to eat more prey than smaller animals. There was significant temporal variation in cannibalism rate most probably caused by temporal variations in adult length. Date did not contribute anything significant to the prediction of cannibalism rate. There was a significant difference in the results depending upon the scale of observation used. Relationships observed using large scale observations, using mean values when comparing ponds and sexes, rarely agreed with small scale observations within ponds. This is significant as much of the present literature on cannibalism uses a large scale observation perspective. This is not to say that cannibalism is not occuring, it is, but the relationship between cannibalism rate and the independent variables used may be masked by the scale of observation used. The mean size and size distribution of the nauplii is altered, in most cases, by cannibalism. This indicates that there are some sizes of nauplii which are more vulnerable to cannibalism than others.

Future work should focus in two directions: on the different interpretations of results due to scale of observation, and on behavioural mechanisms related to cannibalism and avoidance of cannibalism exhibited by both cannibal and prey.

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