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EFFECT OF TEMPERATURE AND SALINITY ON THE LIFE HISTORY OF CAPITELLA CAPITATA (TYPE I)

City University of New York PH.D. 1985

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EFFECT OF TEMPERATURE AND SALINITY ON THE LIFE HISTORY OF *CAPITELLA CAPITATA* (TYPE I)

BY

CHRISTINE M. REDMAN

A dissertation submitted to the Graduate Faculty
in Biology in partial fulfillment of the requirements
for the degree of Doctor of Philosophy, The City
University of New York.

1984

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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ABSTRACT

EFFECT OF TEMPERATURE AND SALINITY ON THE LIFE HISTORY OF *CAPITELLA CAPITATA* (TYPE I)

BY

CHRISTINE M. REDMAN

JOHN H. TIETJEN - ADVISOR

The principal life cycle characteristics of *Capitella capitata* Type I (Annelida: Polychaeta) were measured under five experimental regimes: high temperature, high salinity (18 degrees C., 30 ppt); high temperature, low salinity (18 degrees C., 20 ppt); control or mid-range (15 degrees C., 25 ppt); low temperature, high salinity (12 degrees C., 30 ppt); low temperature, low salinity (12 degrees C., 20 ppt). The square root of the total number of offspring per female, mean number of offspring per brood, interval between broods and mean brooding time all showed significant treatment effects at a probability level of .05 or less (ANOVA). Experimental regime had no significant effect on the number of broods per female. Survivorship curves and life tables were prepared for all conditions except low temperature,low salinity in which very few individuals survived. Length of life in decreasing order was as follows: control(59 weeks); high temperature, high salinity (43 weeks); low temperature, high salinity(33 weeks); high temperature,low salinity (17 weeks). Net reproduction (*Ro*) and intrinsic natural increase (*r*) were calculated from the life tables; the latter using Euler's equation. There is no presumption that these experimental conditions resulted in maximum values of these parameters; the internal evidence, including brood size and number of offspring, suggests food was not limiting. Net reproduction in the several conditions was 36.69 (HTHS); 2.19 (HTLS); 41.75 (C); 2.16 (LTHS). Intrinsic rate of natural increase was 0.261 (HTHS); 0.070 (HTLS); 0.194 (C); and 0.039 (LTHS).

Hermaphroditic individuals were included among the parental animals and functioned as females; occasional hermaphrodites appeared among the progeny.

Of the life history traits that have been suggested to be important from an evolutionary point of view, mean offspring per brood, brood interval, incubation time, square root of total number of offspring, *r*, *Ro*, mortality and relation of reproductive effort to adult mortality have been shown in this study to be significantly influenced by environmental change.

Key Words: Polychaeta Annelida life tables hermaphroditism life history strategy

ACKNOWLEDGMENTS

This dissertation marks the conclusion of my doctoral studies. There was much enjoyment, and there were many challenges, in the course of its completion. To all who shared them, I thank you. I offer a very special thanks to my family: to my mother, who encouraged her children to travel as far as they could on paths of their own choosing; to my father, for his quiet, but fierce pride in my accomplishments; and to my brothers, for laughter and encouragement and patience, along the way. I wish to thank as well the members of my dissertation committee, especially Professor John H. Tietjen, for suggestions and criticisms during the course of my research. I am very grateful to Dr. Judith P. Grassle for her generous contribution of experimental material and advice and to Professor Jane C. Gallagher, for reading two drafts, a task above and beyond the call of duty. Finally, this thesis is dedicated to Professor Martin Sacks, whose confidence in my ability to succeed contributed, in large measure, to my success.

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INTRODUCTION

Pianka (1970) introduced the idea of considering species as _r_ or _K_ strategists. _K_ strategists are more likely to be found in fairly constant or predictable environments, while _r_ strategists are usually found in variable or unpredictable ones. Mortality among _K_ strategists tends to be directed and density dependent while among _r_ strategists it is frequently catastrophic and density independent. Survivorship curves among _K_ strategists are usually Type I (low mortality to some age, followed by steep mortality) or Type II (a constant risk of death per unit time or a constant number of deaths per unit time); often they are Type III among _r_ strategists (steep juvenile mortality, followed by high survivorship) (Pianka, 1978). _K_ strategists will maintain a fairly constant equilibrium population over time; population size of _r_ strategists tends toward disequilibrium and is variable over time. Short life spans predominate among _r_ strategists, longer ones among _K_ strategists. The introduction of this perspective initiated a considerable body of empirical and theoretical study which examined and elaborated upon this original approach.

Some of this discussion was approached from the perspective of resource allocation. The problem of life history strategy is then the optimal allocation of resources to maintenance, growth and reproductive activities (Gadgil and Bossert, 1970; Gadgil and Solbrig, 1972; Pianka, 1976) in order to maximize Malthusian fitness. Malthusian fitness, $\underline{m}$, is frequently considered equivalent to the intrinsic rate of natural increase, $\underline{r}$. Gadgil and Bossert (1970) describe a profit for cost analysis of reproductive effort. Successful reproduction figures as profit and reduction in survival and growth and diminution of future reproduction figure as loss. The long term cost of any episode of reproduction is considered in relation to a semelparous (single reproduction) or iteroparous (repeated reproduction) habit. Predictions from models like these will vary depending upon the starting assumptions and not all authors are in agreement on these. Reproduction may be assumed to be "cost-free", that is, have no effect on future survival or fecundity. Bell (1980) points out that such an assumption is inadequate to explain the evolution of long-lived semelparous organisms. One can consider that reproductive effort varies with age. Gadgil and Sobrig (1972) take population density into account. Under high density independent mortality, an organism is under positive pressure to allocate a greater proportion of its resources to reproductive activities than one in a similar environment under density dependent regulation.

A number of authors have viewed life history strategies within the framework of temporal and spatial fluctuation. Green (1969) and Grassle (1972) point out the importance of genetic variability in populations exposed to fluctuating environments. Genetic diversity in a population adapts the population to unpredictable events beyond the physiological tolerance of any individual in the species. Murdoch (1966), Cohen (1968) and Nichols _et al._ (1976) discuss adaptation to changing conditions through shifts in life table parameters. Murdoch gives the example of old adult survival increasing after a poor breeding season. This group of individuals persisted into the following season and contributed to that season's breeding effort. This sequence of events, then, involved an alteration in fecundity and longevity. Cohen presents a model with two contrasting modes: in the first, all individuals reproduce; in the alternate mode, only a fraction of the population reproduces. Nichols _et al._ discuss opportunistic life strategies as those in which an individual can shift a longer distance along the continuum of _r_ to _K_ characteristics, including reproductive parameters such as _r_ and iteroparity. All of these studies are attempts to predict constellations of population characteristics that will result from various selection pressures.

Stearns (1976) provides a comprehensive review of the studies on life history tactics. He identifies the key life history traits as brood size, size of young, age distribution of reproductive effort, the relationship of reproductive effort to adult mortality and the variation of these traits in progeny. Wilbur *et al.* (1974) include, in addition, age at first reproduction, fecundity-age regression, degree of parental care, and juvenile, as well as adult, mortality. Istock (1982) adds degree of sexuality. The general theoretical problem, which all these models attempt to answer, is whether it is possible to predict a combination of traits that will occur in a species as a result of natural selection in specific circumstances. Hairston *et al.* (1970) suggest that natural selection will always select for optimal Malthusian fitness. They do not consider *r* equivalent to *m*. Therefore, a strategy for maximizing *m* could involve decreasing *r*. They further point out that *r*, as an integrating parameter, cannot be selected for; only contributing parameters are subject to selection pressure. These authors define *m* as a measure of genotypic rate of increase and *r* as a measure of the ability of a population to grow under a given set of conditions. Various authors have examined the effects of selection pressure on life table parameters. Lewontin (1965) points out that small absolute changes in development rates (on the order of 10%) will result in major changes in fertility (on the order of 100%). A number of authors have discussed the importance of litter size and number of litters (Cole, 1954; Murphy, 1968; Schaeffer, 1974a). Charlesworth (1973) points out the necessity of identifying relative effects on the intrinsic rate of increase of changes at different ages, in the age specific mortality and fecundity rates. Schaeffer (1947b) concludes that the optimal life history maximizes, for each age class, the expected fecundity for that age, plus the sum of all future expected fecundities, each discounted by an appropriate power of *e* to the minus *m*. Anderson and King (1970)suggest that population size, age structure and gene frequency are mutually interactive and together determine the behavior of a population under selection. They also suggest (1971) that each genotype in a population is subject to *r* or *K* selection or a mixture of the two, depending on population size.

From the perspective of evolutionary theory, the polychaetes present a rich field for study (Bellan, 1977). *Capitella capitata* in particular, because of the existence of a sibling species complex, may prove to be a useful tool in the further elaboration of life cycle strategies.

Capitella capitata Fabricius is a capitellid polychaete of cosmopolitan distribution and reported broad tolerance (Smidt, 1951; Rasmussen, 1956; Hartman, 1961; Tulkki, 1963; Anger, 1977; Warren, 1977). It has been reported to withstand low oxygen levels as well as sediment contaminated with oil (Reish and Barnard,1960; Grassle and Grassle, 1974). Unfortunately, several sibling species (Grassle and Grassle, 1976; J.P. Grassle, 1980) have been subsumed under this name, making it difficult to judge which ecological or physiological characteristics can be expected to be pertinent in any current field study. Adult size can vary from 1 to 30 mm or more and has been reported to be influenced by salinity (Muus, 1967). The sexes are separate and one or more broods can be produced in a year. Two different courses of larval development have been reported: the typical pelagic one aqnd a more unusual benthic (direct) one (Rasmussen, 1956; 1973). The life cycle can be completed in 30 to 60 days (Reish and Barnard, 1960; Rasmussen, 1956). This species is frequently present in normal estuarine areas in low numbers (Grassle and Grassle, 1974), but can reach very high population levels when conditions are favorable. *C. capitata* is occasionally and irregularly reported to occur in large numbers in deeper waters (Hartman, 1961). It is considered by some authors to be an indicator of pollution (Reish and Barnard, 1960). *Capitella capitata* occurs locally, both in Long Island Sound (personal observation) and the New York Bight (Reid, NMFS,Sandy Hook,N.J., personal communication).

C. capitata has been characterized as an opportunistic species. Such species usually exhibit one or more of the following characteristics: lack of equilibrium population size, density independent mortality, high *r* (ability to increase rapidly), high birth rate, poor competitive ability, good dispersal ability and use of a high proportion of resources to reproduction. They are, therefore, usually considered to be *r* strategists. It has been suggested that mortality can be used as a measure of the degree of opportunism (Grassle and Grassle, 1974).

Grassle and Grassle (1976) reported that *C. capitata* is a complex of up to six sibling species. These have not been formally described at this time and are referred to as Types. Based on electrophoretic studies, it was determined that any pair of these species have, at most, two alleles in common of eight to ten that have been studied. Morphological differences are not conspicuous, but reproductive modes and life histories are considerably more distinct. As many as five species can be recovered in a single sample and the percent occurrence of species in a given sample varies widely over time.

In this study, data were collected so that a life table could be constructed based on a culture of laboratory reared animals of known type. This information provides a quantitative description of several of the "opportunistic" life history characteristics of *C.capitata*:

fecundity, mortality, age at first reproduction and degree of iteroparity. *C. capitata* Type I was chosen for this study because of its short generation time, reported to be 30 to 40 days at 20 degrees C. (Grassle and Grassle, 1976).

Temperature and salinity are the two most significant factors affecting the distribution of marine benthic invertebrates. They are,in addition,relatively easy to control in a laboratory situation. Five regimes of temperature and salinity were used in this study. The ranges were chosen in consultation with other *Capitella* workers (personal communication, J.P. Grassle; K. Tenore, U.Maryland). A control condition was established with temperature and salinity at the midpoint of each range. Under each experimental condition the following population characteristics were determined: *r*, *Ro*, longevity, mortality, number of broods, size of broods and interval between broods, in order to assess the effects of salinity and temperature on these life history parameters as well as to examine the models of life history strategies in the light of these particular life histories.

MATERIALS AND METHODS

Experimental Procedures

The life history of Capitella capitata (Type I) was monitored under five experimental regimes: low temperature, high salinity (LTHS = 12 degrees C., 30 parts per thousand [= p.p.t.]), low temperature, low salinity (LTLS = 12 degrees C., 20 p.p.t.), intermediate temperature and salinity (C = 15 degrees C., 25 p.p.t.), high temperature, high salinity (HTHS = 18 degrees C., 30 p.p.t.) and high temperature, low salinity (HTLS = 18 degrees C.,20 p.p.t.).

Animals were cultured in 10 cm diameter glass finger bowls. At the start of each experiment, an average of 1.0 grams (wet weight) of azoic mud (frozen and thawed) and 25 ml of filtered natural sea water adjusted to the appropriate temperature and salinity were added to a culture dish. The dish was labelled with respect to experimental regime and water level. In each dish was placed a young female from a culture dish maintained at control temperature and salinity. A female was selected for the experiment as soon as the pale white bands on the ventral surface, which represent the beginning of the development of the ovaries, were evident. As soon as possible, two males identified by the appearance of testes and genital setae, were added to the dish. Each dish was covered by a second glass dish and each dish and cover were sealed with a two inch rubber band. These were termed mx dishes and were maintained in incubators of appropriate temperature under a 12 hour light-dark regime. The five experimental conditions were set up in random order.

At weekly intervals the water in each was changed, 0.5 grams of azoic mud was added and the salinity adjusted by the addition of ten drops of distilled water. Salinity was checked at frequent intervals,every second or third day for the first week and always after a dish had been uncovered for an extended period (i.e. while counting). An American Optical 10419 Refractometer was used to measure salinity and distilled water was added to the dish when necessary. At six week intervals the animals were removed from the dish and the dish swirled and emptied. Without washing the dish, 1.0 grams of azoic mud and 20 drops of distilled water were added. Water of appropriate temperature and salinity was added to the pre-marked line. The worms were then returned to the dish. This procedure prevented excessive accumulation of fecal pellets and uningested particles. Dishes were examined every 48 hours and the condition of ovaries as well as the presence and condition of genital setae noted. When a male was seen to have protruding genital setae or to have shed them, an additional male was added to the dish as soon as possible.

When a brood tube was produced, one day was allowed to elapse and then the tube was examined daily until hatching. In general, the brood tube was left in the mx dish until the developing trochophores showed green guts and the presence of eyespots. At this time, the brood tube (containing the female and the trochophores) and the male were moved to an lx dish. The brood tube was dissected away from the surrounding sediment before it was moved. An lx dish was prepared in the same manner as an mx dish except that only 0.07 grams of azoic mud were added. The tube was examined daily until the emergence of the trochophores. Upon emergence, trochophores were counted by removing them to a separate dish with a finely drawn pasteur pipette. Adults were removed and returned to the mx dish. Settled juveniles were counted by sorting through the sediment with a "nematode picker" (an unbarbed root canal file mounted in a piece of plastic tubing). Trochophores were then returned to the lx dish. Progeny were counted on day 0 (day of emergence) and on days 1, 3, 7, 9, 11, 14, 17, 20 and at weekly intervals thereafter until the death of the last individual. lx dishes were fed 0.14 grams of azoic mud on days 1, 5, 8, 15, 19 and 22. The cohort was fed 0.14 grams per week after that until the termination of the experiment. The water in lx dishes was changed weekly. lx dishes were maintained under the same conditions described for mx dishes.

Each brood produced after the first was treated in the same manner except that it was discarded after the day 3 count since survivorship was determined on the first cohort. When a first brood female survived to reproduce, the brooding female was removed during the weekly count, the tube dissected open, eggs or larvae counted, and the female returned to the culture dish.

Over the course of the experiment, males were replaced as soon as possible after the genital setae began to protrude or were shed. Replacement males were chosen from the following sources in this order of preference: 1) from the series of stock dishes that provided the experimental animals (i.e. carry-over or C-0 dishes), but never from the dish of origin of the female, 2) from a separate stock dish 3) from a C-0 series prior or subsequent to the one in question.

All the animals used in this experiment were *Capitella capitata* Type I provided through the courtesy of Dr. Judith Grassle (Marine Biological Laboratory, Woods Hole). Stock animals were maintained at intermediate (control) conditions (15 degrees C., 25 p.p.t. salinity) in the same incubator as the control dishes. Stock dishes were fed and changed weekly and were periodically cleaned of fecal pellets and refractory particles. Sieved,frozen azoic mud was also kindly provided by Dr. J. Grassle. Aliquots were thawed as needed and kept in the 15 degree C. incubator.

To provide experimental animals for the first replicate a brood tube was isolated from a stock dish. All initial experimental pairs were drawn from the progeny of this tube and were thus siblings. Dishes in this replicate were begun with one male and one female. In addition to preparing the first replicate experimental dishes(5/7-8/3/80),five carry-over dishes were prepared (6/23-7/1/80). These dishes were started either with a pair of adults or with a brood tube. The animals for the second replicate were selected from these dishes (carry-over 2 or C-O 2). Individuals from the same dish were never mated and thus the second replicate consisted of cousin crosses. Second replicate experimental dishes were set up from 9/10 through 10/7 and were begun with one female and two males. Third replicate carry-over dishes were set up from 8/21 through 9/24 with one female and two males (cousin crosses). Third replicate experimental dishes were set up from 12/15/80 through 2/5/81. New stock animals were obtained in January 1981 and from these C-O 4 dishes were prepared (2/12-5/9/81). The fourth replicate experimental dishes were prepared from these (6/4/81-6/22/81); in most cases a female (hermaphrodite) was added with one male and an additional male was added later. No individuals from the same C-O dish were mated.

In the first replicate,each experimental dish was aged for a minimum of two days, in the following manner: one gram of sediment from the culture of origin was placed in the experimental dish, the dish was filled with water appropriate to the experimental condition, the dish was covered, sealed with a rubber band and placed in the appropriate incubator. At the time of use, the dish was swirled and emptied, examined under 20x magnification and any capitellids removed. The dish was then prepared as previously described. Both lx and mx dishes were "preincubated". No dishes were "preincubated" in succeeding replicates.

In the first replicate, no dishes needed to be replaced (i.e. on account of injury, dedifferentiation, etc.) so the randomly chosen order of preparation was the one actually followed. In the second and third replicates, when a dish had to be replaced, it was moved to the last position in order of preparation. Thus, the actual order in which the dishes were prepared, while still random, was somewhat different from the initially planned order. The fourth replicate dishes were set up in decreasing order of longevity of the progeny as indicated by the preceding replicates.

Hermaphroditic individuals were present in all the C-O stocks. (A hermaphroditic individual has testes, genital setae and developing ovaries.) None were used in the first or second replicate, one in the third and all of the fourth replicate consisted of hermaphrodite/male matings.

On a few occasions, individuals appeared carrying particles that appeared to be gregarines in the gut. Heavily "infested" individuals were avoided. The gregarines were assumed to occur randomly throughout the experiment. Wagenbach, et al. (1983) reported the gregarines had no effect on Capitella capitata Type I fecundity.

The second and third broods of HTHS and the second brood of HTLS were counted according to the schedule described above for first broods until day 20. The second brood of the C condition was counted to day 25 and the third brood to day 20. These additional counts were made in order to determine the day of post emergence on which a count would reveal the maximum number of organisms.

Statistical Procedures

The number of broods per female, the total number of offspring produced per female, female age at first reproduction, interval between broods, brooding time (incubation time or time from egg deposition to appearance of swimming trochophores) and mx female longevity were analyzed using analysis of variance (ANOVA). The technique employed was space/time analysis of variance (random blocks). This method requires that the last treatment of the first replicate be initiated before any treatment of the second replicate. The specifics of culture initiation are described in a preceding paragraph.

Those data sets with complete matrices(a data item for every replicate of every treatment) were analyzed using VS BASIC AVA (factorial design,analysis of variance program). These included number of broods per female and average number of offspring per brood. Those data sets with incomplete matrices were analyzed using the SPSS program ANOVA. These data sets included female age at first reproduction, interval between broods and brooding time.

The number of broods per female, total number of offspring and mean offspring per brood were analyzed after transformation to their square roots. All data sets with an F value significant at the .05 level or less were subsequently examined for differences among means using the T method (Sokol and Rohlf, 1982).

Life Table Preparation

Preparation of life tables followed Birch (1948), Hummon (1974) and Vandermeer (1981). The number surviving at the beginning of an age interval out of 100 born is $\underline{lx}$; the number dying in the age interval is $\underline{dx}$ ($\underline{lx}$ - $\underline{lx}$+1); the mortality rate per 100 alive at the beginning of the age interval is $\underline{qx}$ ($\underline{dx}$/$\underline{lx}$);the number alive at the midpoint of the age interval is $\underline{Lx}$ ([$\underline{lx}$ + $\underline{lx}$+1]/2); total lifetime remaining for all individuals attaining the age $\underline{x}$ is termed $\underline{Tx}$; the expectancy of life or mean lifetime remaining to those attaining the age interval is $\underline{ex}$;and the age specific natality (number of offspring per female at the age interval) is $\underline{mx}$.

When a life table is prepared for an organism that is strictly dioecious and in which the sexes are clearly distinguishable at birth,the survivorship column ($\underline{lx}$) includes only females and the natality column ($\underline{mx}$) only female offspring. Preparation of the tables in this way would have required assumption of a 1:1 sex ratio and equivalent survivorship for both sexes. These conditions are not met for *Capitella capitata* (Type I): hermaphrodites occur occasionally, sex of the offspring is not apparent until well into the organism's life span, no evidence was collected either for or against a 1:1 sex ratio and insufficient data were collected to determine if there is a survivorship differential by sex. In the preparation of the present tables the *lx* column includes all survivors and the *mx* column all offspring.

A life table was prepared for each experimental condition. In some cases this involved combining two or more tables (replicates of an experimental condition). To start the table, the successive counts of swimming individuals were corrected: if 12 individuals were counted on day 1 and 14 individuals counted on day 2, the day 1 count was changed to 14 because the culture vessels were closed systems and there could be no egress or ingress of organisms. The initial survivorship (*lx* at time 0) was calculated by summing the number of individuals in each replicate at time 0 and setting the sum equal to 100. One or any convenient multiple of ten can be used. The number alive at each interval was summed and calculated as a proportion of 100 to generate *lx*+1, etc. Where reproduction occurred in the same time interval in more than one replicate, the number of progeny was summed and entered as *mx* for that time interval.

Net reproduction was calculated as Σ *lxmx*/*lo*. This parameter can be calculated as Σ *Lxm*x/*lo* which assumes all births to have occurred at the midpoint in each age interval. In the absence of any evidence to support this assumption, the former method was used.

Intrinsic rate of natural increase was calculated using Euler's equation according to the method of Birch (1948). Σ *lxmx*/100 was used to correct for an *lo* other than one.

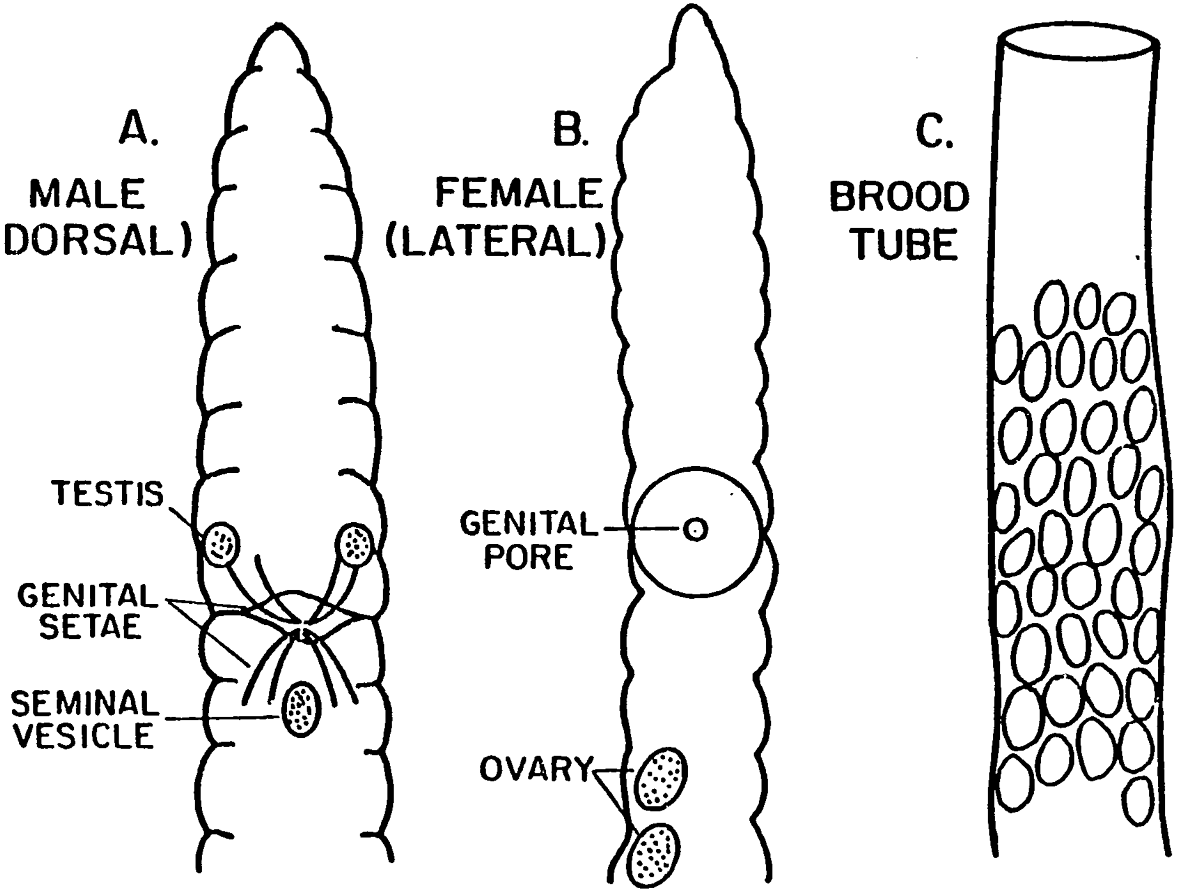
RESULTS

Appearance and development of brood tube

The first recognizable sign of male sexual maturity is the appearance of paired testes laterally between the seventh and eighth segments. These are white in color. Next very small, highly refractory paired double genital setae are seen dorsally in the eighth and ninth segments. These are arranged so that,when extruded from the body wall,they curve toward each other like the prongs of calipers. Finally a single median whitish body (seminal vesicle?),similar in appearance to the testes, can be seen between the posterior pair of genital setae (Figure 1A). The first sign of a sexually differentiating female is the appearance of a pair of white bands extending ventrolaterally. These gradually resolve into pale white dots which then develop a dark concavity. These become yellowish in color, increase in size and eventually appear as clumps of small, round, yellow eggs. A female with clumps of yellow eggs is ready to produce a brood tube. At this time, lateral pores between the seventh and eighth segments become conspicuous, owing to the appearance of a border of smooth tissue surrounding them. These frequently become more pronounced as the female ages (Figure 1B).

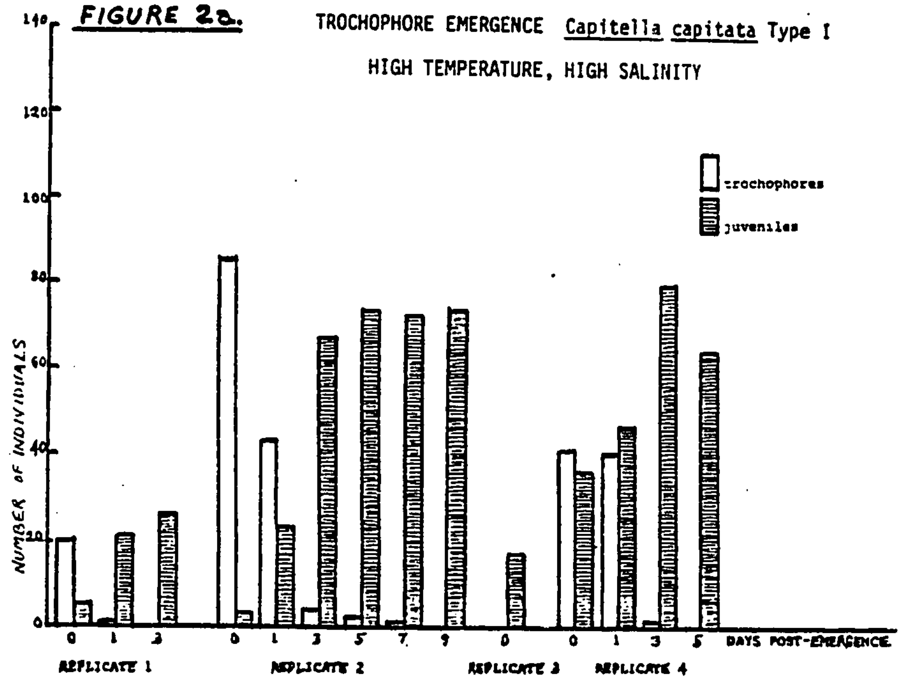
The fertilized eggs are deposited in a mucus tube of her production (Figure 1C). She cohabits this tube with

FIGURE I. DIAGRAMS OF REPRODUCTIVE STRUCTURES- _Capitella_ _capitata_ Type I



the developing trochophores until they emerge as swimming larvae. Upon deposition in the tube the eggs are round, white and opaque and usually close packed. The first sign of embryonation is a dark concavity, centrally located. As development proceeds the eggs become yellowish and translucent and begin to assume a cylindrical shape. As gastrulation and the ensuing morphogenesis proceed, allowing the observer to see a coelomic space, black pigment spots appear at the poles of the embryo. Two of the anterior pigment spots become distinguished by their larger size and regular borders; these will become the eyespots. As the trochophores approach the time of emergence, the entire animal achieves a pale green cast. With further development, the green color darkens and becomes localized in the digestive tract. At about the same time the eyespots will have assumed their red color. Before emergence, the trochophores can be seen to be moving independently. This movement by individuals consists of characteristic antero-posterior contractions and is distinguishable from the movement of the mass of trochophores which results from the mother's movement in the tube. Development of individuals in a tube is not synchronous. This asynchrony was observed in all experimental regimes, but was most pronounced in low temperature, low salinity. The periods of emergence for each experimental regime are shown in Figure 2. Occasionally under control conditions (second replicate,

FIGURE 2a.


TROCHOPHORE EMERGENCE *Capitella capitata* Type I

HIGH TEMPERATURE, HIGH SALINITY

FIGURE 2b.

TROCHOPHORE EMERGENCE

Capitella capitata Type I

HIGH TEMPERATURE,LOW SALINITY

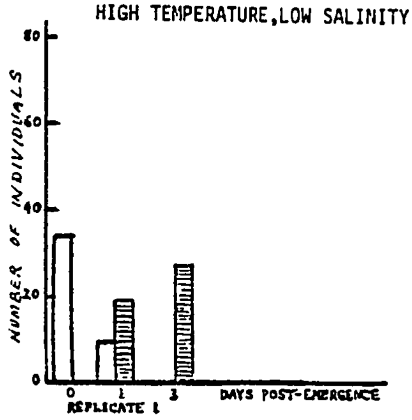
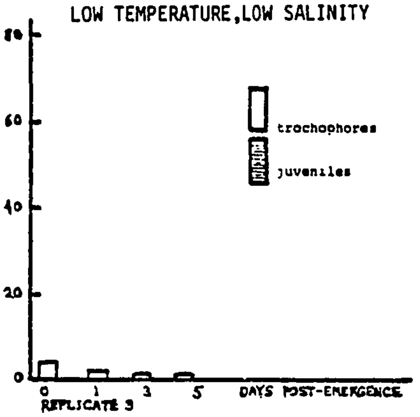


FIGURE 2c.

TROCHOPHORE EMERGENCE

Capitella capitata Type I

LOW TEMPERATURE,LOW SALINITY



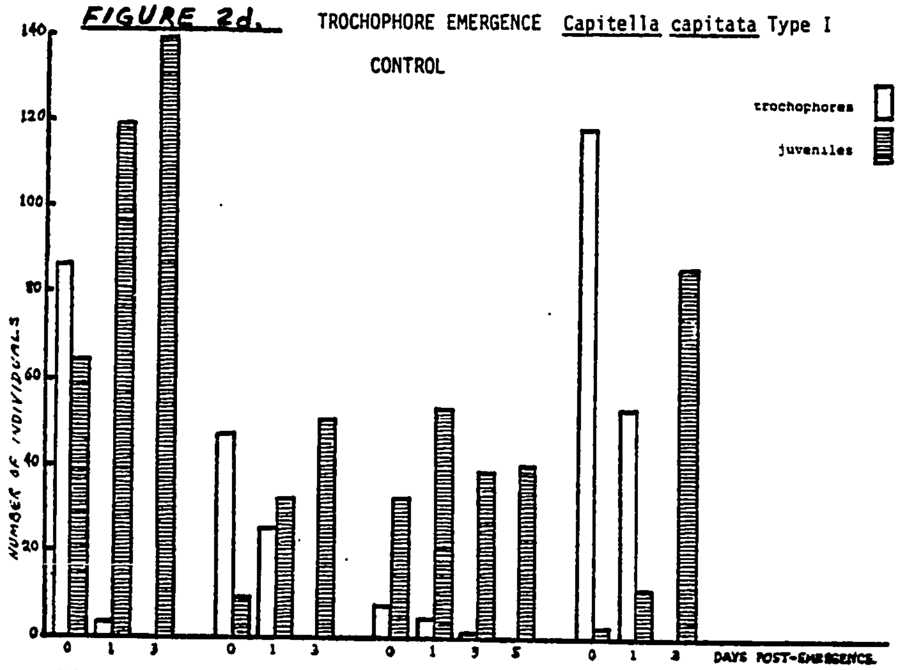


FIGURE 2d. TROCHOPHORE EMERGENCE *Capitella capitata* Type I

CONTROL

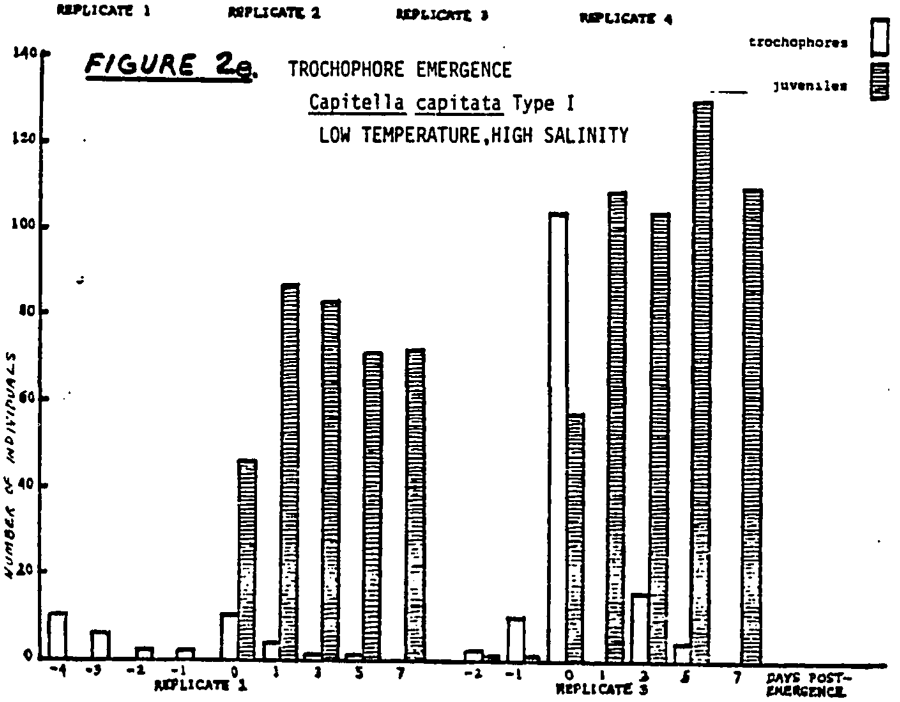


FIGURE 2e. TROCHOPHORE EMERGENCE

Capitella capitata Type I

LOW TEMPERATURE, HIGH SALINITY

first and third broods) emergence continues for two or three days; however, this pattern is always evident under low temperature, high salinity conditions. It is not clear whether the early emergents survive since the settled individuals counted the previous day cannot be distinguished from newly settled individuals. Immediately after emergence trochophores are photopositive. After a brief period of swimming the trochophores metamorphose into the benthic form and settle (Figure 2a-e). Immediately presettlement individuals can be recognized by the fact that when found on the bottom of the dish they can still be induced to swim by gentle prodding but will settle very rapidly to the bottom again.

On six occasions, it was observed under low temperature conditions (both low and high salinity) that the female retained mature eggs in the coelom either while she differentianted the next egg set or was brooding an egg mass.

Older individuals show an increasing opacity of the body wall and, occasionally, deposition of black material laterally. In six instances the female was observed to have mature eggs at the time of death (first and second control females; first and fourth replicate low temperature, low salinity females; third and fourth replicate low temperature, high salinity females). The third replicate low temperature, high salinity female produced a brood on day 300 which failed to develop. On day 332 the anterior half of the worm was found. By day 345, that portion of the worm had produced a brood tube. The female was dead on the 350th day; the eggs failed to develop.

Worms of both sexes appeared to be able to lose several posterior segments without apparent diminution of vigor. Hill, Grassle and Mills (1982) reported that regeneration does not appreciably affect maturation or oogenesis in this organism.

Reproduction

Analysis of variance (ANOVA) of the number of broods and on the square root transformation of that data set showed no significant treatment effects. This was true whether all successful broods (those producing viable trochophores) or all broods set were considered.

The square root of the total number of offspring per female show significant treatment effects at the .05 confidence level (Table 1). The means of high temperature, low salinity and low temperature, low salinity are significantly lower than the remaining conditions (Table 2). Mean number of offspring per brood was significantly affected by treatment ($p < .005$, Table 3). The T method for a posteriori comparison of means yields a minimum significant difference (MSD) of 49.369. Thus the following pairs of means are significantly different from each

Source	df	SS	MS	F	p
Treatment	4	1157.03400	289.25830	3.15701	.05
Error	15	1374.3640	91.62422		
Total	19	2531.39700			

Table 1. ANOVA: Square root of total number of offspring per female in *Capitella capitata* Type I.

	HH	HL	C	LH	LL
Mean	18.577	1.541	16.751	12.618	0.5

Table 2. Mean values (square root) of total number of offspring per female in *Capitella capitata* Type I.

HH= high temperature, high salinity
HL= high temperature, low salinity
C = control
LH= low temperature, high salinity
LL= low temperature, low salinity

Source	df	SS	MS	F	p
Treatment	4	14327.5200	3581.880	7.00614	.005
Error	15	7668.7270	511.24830		
Total	19	21996.2500			

Table 3. ANOVA: Mean number of offspring per brood in *Capitella capitata* Type I.

other: high temperature, high salinity > high temperature, low salinity;high temperature, high salinity > low temperature,low salinity; high temperature,low salinity < control; and low temperature, low salinity < control. These relationships are illustrated in Figure 3, which shows Gabriel ranges (Sokol and Rohlf, 1982).

No indication of a correlation between brood size and female age or brood size and interval between broods was found.

Age of the female at first reproduction was not found to be significantly affected by treatment. The range of ages from the time of emergence of the mother to first reproduction was 58-203 days. The minimum occurred under conditions of high temperature, high salinity and the maximum under conditions of low temperature, high salinity (Table 4).

Interval between broods showed a significant treatment effect at a probability level of .025 (Table 5). The T method (adjusted degrees of freedom) for a posteriori comparison of means yields an MSD of 24.907. The following pairs of means are significantly different from each other: low temperature,high salinity > high temperature,high salinity; low temperature,high salinity > high temperature,low salinity; low temperature,low salinity > high temperature, high salinity; low tempera-

	HH	HL	C	LH	LL
Mean	85	104	120	147	94
Range (days)	(58-117)	(81-130)	(78-145)	(69-203)	(91-97)
n	4	3	4	3	2

Table 4. Mean and range of female age at first oviposition in *Capitella capitata* Type I.

Source	df	SS	MS	F	p
Main Effects	7	2178.261	311.180	2.836	.054
R	3	370.262	123.421	1.125	.378
T	4	1808.000	452.000	4.120	.025
Residual	12	1316.471	109.706		
Total	19	3494.733	183.933		

Table 5. ANOVA: Interval between broods in *Capitella capitata* Type I.
R= replicate T=Treatment

ture, low salinity > high temperature, low salinity; and low temperature, low salinity > control. These relationships are illustrated in Figure 4.

Mean brooding time (incubation time or time from egg deposition to trochophore emergence) showed a significant treatment effect at a probability level of .049 (Table 6). The T method (adjusted degrees of freedom) yielded an MSD of 22.870 indicating low temperature, high salinity > high temperature, high salinity; low temperature, high salinity > high temperature, low salinity; low temperature, low salinity > high temperature, high salinity; and low temperature, low salinity > high temperature, low salinity (Figure 5).

Tables 7 through 10 are life tables for the four experimental conditions which yielded sufficient data to generate them. In only one brood, in one replicate (replicate 3, second brood) did any viable trochophores emerge under low temperature, low salinity conditions (4 individuals). The high temperature, high salinity table was generated from data from four replicates, the low temperature, high salinity table from data from three replicates (no reproduction in the second replicate), the control table from data from four replicates and the high temperature, low salinity table from only one replicate (only the first replicate produced viable offspring).

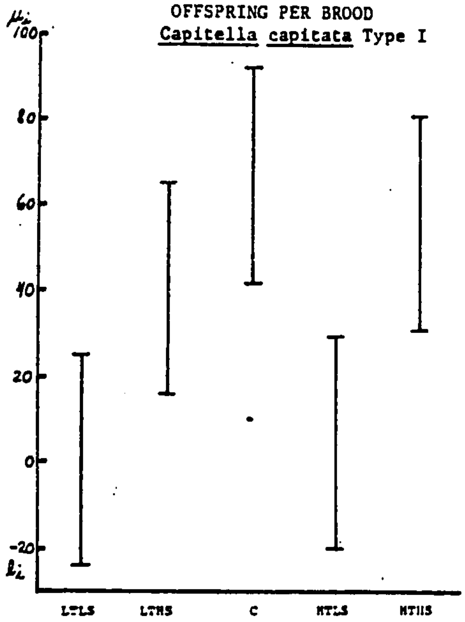


FIGURE 3. GABRIEL RANGES: MEAN OFFSPRING PER BROOD
Capitella capitata Type I

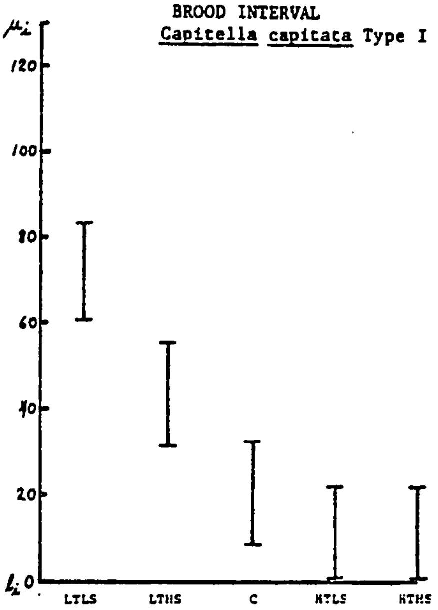


FIGURE 4. GABRIEL RANGES: mean BROOD INTERVAL
Capitella capitata Type I

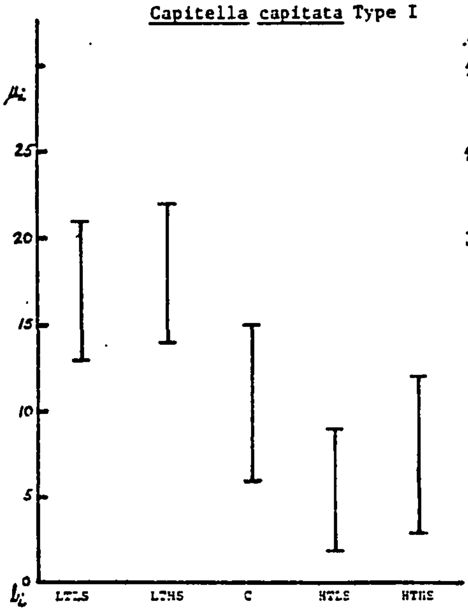


FIGURE 5. GABRIEL RANGES: MEAN BROODING TIME
Capitella capitata Type I

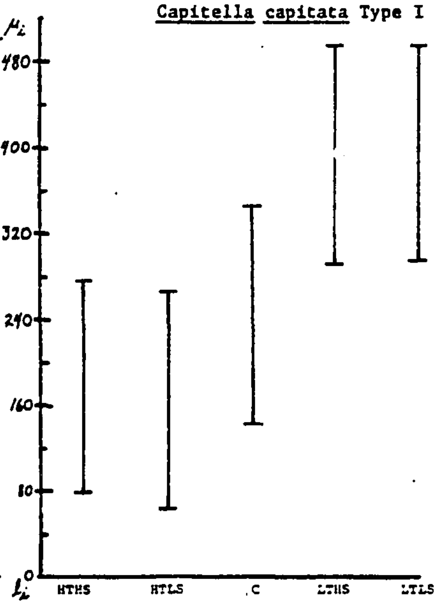


FIGURE 7. GABRIEL RANGES: LONGEVITY mx FEMALE
Capitella capitata Type I

Source	df	SS	MS	F	p
Main Effects	7	224.244	32.035	2.225	.107
R	3	35.130	11.710	0.813	.511
T	4	189.114	47.278	3.283	.049
Residual	12	172.809	14.401		
Total	19	397.052	20.897		

Table 6. ANOVA: Mean brooding time in *Capitella capitata*
Type I.
R=replicate T=treatment

Table 7. Life Table of *Capitella capitata* Type I: high temperature, high salinity (combined replicates).

Week	lx	dx	qx	Lx	Tx	ex	mx	lxmx
	100	27.85	.28	86.08	321.28	3.21		
1	72.15	12.79	.18	65.76	235.20	3.26		
2	59.36	22.83	.38	47.95	169.44	2.85		
3	36.53	18.72	.51	27.17	121.49	3.33		
4	17.81	5.94	.33	14.84	94.32	5.30		
5	11.87	4.56	.38	9.59	79.48	6.70		
6	7.31	0.46	.06	7.08	69.89	9.56		
7	6.85	2.74	.40	5.48	62.81	9.17		
8	4.11	0	0	4.11	57.33	13.95	26	106.86
9	4.11	0.46	.11	3.88	53.22	12.95	134	550.74
10	3.65	.91	.25	3.20	49.34	13.52	54	197.10
11	2.74	0	0	2.74	46.14	16.84	17	46.58
12	2.74	.46	.17	2.51	43.40	15.84		
13	2.28	0	0	2.28	40.89	17.93		
14	2.28	.45	.20	2.06	38.61	16.93	122	278.16
15	1.83	0	0	1.83	36.55	19.97	61	111.63
16	1.83	0	0	1.83	34.72	18.97	54	98.82
17	1.83	0	0	1.83	32.89	17.97	5	9.15
18	1.83	0	0	1.83	31.06	16.97	131	239.73
19	1.83	0	0	1.83	29.23	15.97	101	184.83
20	1.83	0	0	1.83	27.40	14.97	104	190.32
21	1.83	0	0	1.83	25.57	13.97	137	250.71
22	1.83	.46	.25	1.6	23.74	12.97		
23	1.37	0	0	1.37	22.14	16.16		
24	1.37	0	0	1.37	20.77	15.16	134	183.58
25	1.37	0	0	1.37	19.40	14.16	130	178.10
26	1.37	0	0	1.37	18.03	13.16		
27	1.37	0	0	1.37	16.66	12.16	72	98.64
28	1.37	0	0	1.37	15.29	11.16	21	28.77
29	1.37	0	0	1.37	13.92	10.16	105	143.85
30	1.37	0	0	1.37	12.55	9.16		
31	1.37	0	0	1.37	11.18	8.16	128	175.36
32	1.37	0	0	1.37	9.81	7.16	58	79.46
33	1.37	.46	.34	1.14	8.44	6.16		
34	.91	0	0	.91	7.30	8.02	134	121.94
35	.91	0	0	.91	6.39	7.02	150	136.50
36	.91	0	0	.91	5.48	6.02		
37	.91	0	0	.91	4.57	5.02	149	135.59
38	.91	0	0	.91	3.66	4.02	62	56.42
39	.91	0	0	.91	2.75	3.02		
40	.91	.45	.49	.69	1.84	2.02		
41	.46	0	0	.46	1.15	2.50	20	9.2
42	.46	0	0	.46	.69	1.50		
43	.46	.46	1.00	.23	.23	.50	123	56.58
44	0			0		0		
45								
46							29	
47								
48							73	
49							68	

Table 8. Life Table of *Capitella capitata* Type I: high temperature, low salinity (first replicate).

Week	lx	dx	qx	Lx	Tx	ex	mx	lxmx
	100	31.25	.31	84.38	340.85	3.41		
1	68.75	6.1	.09	65.70	256.47	3.73		
2	62.65	37.65	.60	43.83	190.77	3.05		
3	25.00	0	0	25.00	146.94	5.88		
4	25.00	3.12	.12	23.44	121.94	4.88		
5	21.88	0	0	21.88	98.50	4.50		
6	21.88	6.25	.29	18.76	76.62	3.50		
7	15.63	6.25	.40	12.51	57.86	3.70		
8	9.38	3.13	.33	7.82	45.35	4.83		
9	6.25	0	0	6.25	37.53	6.00		
10	6.25	0	0	6.25	31.28	5.00		
11	6.25	0	0	6.25	25.03	4.00	32	200
12	6.25	3.12	.50	4.69	18.78	3.00		
13	3.13	0	0	3.13	14.09	4.50	6	18.78
14	3.13	0	0	3.13	10.96	3.50		
15	3.13	0	0	3.13	7.83	2.50		
16	3.13	0	0	3.13	4.70	1.50		
17	3.13	3.13	1.00	1.57	1.57	.50		
18	0	0	0	0				

Table 9. Life Table of *Capitella capitata* Type I: Control (combined replicates).

Week	lx	dx	qx	Lx	Tx	ex	mx	lxmx
	100	27.56	.28	86.22	387.83	3.88		
1	72.44	18.11	.25	63.39	301.61	4.16		
2	54.33	20.73	.38	43.97	238.22	4.38		
3	33.60	13.65	.41	26.78	194.25	5.78		
4	19.95	8.66	.43	15.62	167.47	8.39		
5	11.29	3.42	.30	9.58	151.85	13.45		
6	7.87	2.36	.30	6.69	142.27	18.08		
7	5.51	0	0	5.51	135.58	24.61		
8	5.51	.79	.14	5.12	130.07	23.61		
9	4.72	0	0	4.72	124.95	26.47		
10	4.72	.78	.17	4.33	120.23	25.47		
11	3.94	0	0	3.94	115.90	29.42	57	224.58
12	3.94	0	0	3.94	111.96	28.42		
13	3.94	0	0	3.94	108.02	27.42	17	66.98
14	3.94	0	0	3.94	104.08	26.42		
15	3.94	0	0	3.94	100.14	25.42		
16	3.94	0	0	3.94	96.20	24.42	119	468.86
17	3.94	0	0	3.94	92.26	23.42		
18	3.94	0	0	3.94	88.32	22.42	57	224.58
19	3.94	0	0	3.94	84.38	21.42		
20	3.94	0	0	3.94	80.44	20.42	216	851.04
21	3.94	0	0	3.94	76.50	19.42	110	433.40
22	3.94	0	0	3.94	72.56	18.42	161	634.34
23	3.94	0	0	3.94	68.62	17.42	69	271.86
24	3.94	0	0	3.94	64.68	16.42	26	102.44
25	3.94	.79	.20	3.55	60.74	15.42		
26	3.15	.26	.08	3.02	57.19	18.16	26	81.90
27	2.89	0	0	2.89	54.17	18.74		
28	2.89	0	0	2.89	51.28	17.74	44	127.16
29	2.89	0	0	2.89	48.39	16.74		
30	2.89	0	0	2.89	45.50	15.74		
31	2.89	0	0	2.89	42.61	14.74	58	167.62
32	2.89	.27	.09	2.76	39.72	13.74	99	286.11
33	2.62	0	0	2.62	36.96	14.11		
34	2.62	0	0	2.62	34.34	13.11	61	159.82
35	2.62	0	0	2.62	31.72	12.11		
36	2.62	0	0	2.62	29.10	11.11	28	73.36
37	2.62	0	0	2.62	26.48	10.11		
38	2.62	0	0	2.62	23.86	9.11		
39	2.62	0	0	2.62	21.24	8.11		
40	2.62	0	0	2.62	18.62	7.11		
41	2.62	0	0	2.62	16.00	6.11		
42	2.62	1.57	.60	1.84	13.38	5.11		
43	1.05	0	0	1.05	11.54	10.99		
44	1.05	0	0	1.05	10.49	9.99		
45	1.05	0	0	1.05	9.44	8.99		
46	1.05	0	0	1.05	8.39	7.99		
47	1.05	0	0	1.05	7.34	6.99		
48	1.05	0	0	1.05	6.29	5.99		
49	1.05	0	0	1.05	5.24	4.99		
50	1.05	.26	.25	1.05	4.19	3.99		
51	.79	0	0	.92	3.14	3.97		
52	.79	.27	.34	.66	2.22	2.81		
53	.52	.26	.50	.39	1.56	3.00		
54	.26	0	0	.26	1.17	4.50	2	.52
55	.26	0	0	.26	.91	3.50		
56	.26	0	0	.26	.65	2.50		
57	.26	0	0	.26	.39	1.50		
58	.26	.26	1	.13	.13	.50		
59	0			0		0		

Table 10. Life Table of *Capitella capitata* Type I: low temperature, high salinity (combined replicates).

Week	lx	dx	qx	Lx	Tx	ex	mx	lxmx
	100	24.78	.25	87.61	262.17	2.62		
1	75.22	15.57	.21	67.44	174.56	2.32		
2	59.65	33.14	.56	43.08	107.12	1.80		
3	26.51	4.03	.15	24.50	64.04	2.42		
4	22.48	11.82	.53	16.57	39.54	1.76		
5	10.66	4.90	.46	8.21	22.97	2.15		
6	5.76	3.17	.55	4.18	14.76	2.56		
7	2.59	1.44	.56	1.87	10.58	4.08		
8	1.15	.57	.50	.87	8.71	7.57		
9	.58	0	0	.58	7.84	13.52	95	55.1
10	.58	0	0	.58	7.26	12.52		
11	.58	.29	.50	.44	6.68	11.52		
12	.29	0	0	.29	6.24	21.52	75	21.75
13	.29	0	0	.29	5.95	20.52		
14	.29	0	0	.29	5.66	19.52		
15	.29	0	0	.29	5.37	18.52		
16	.29	0	0	.29	5.08	17.52		
17	.29	0	0	.29	4.79	16.52		
18	.29	0	0	.29	4.50	15.52		
19	.29	0	0	.29	4.21	14.52		
20	.29	0	0	.29	3.92	13.52	54	15.66
21	.29	0	0	.29	3.63	12.52		
22	.29	0	0	.29	3.34	11.52		
23	.29	0	0	.29	3.05	10.52	61	17.69
24	.29	0	0	.29	2.76	9.52	18	5.22
25	.29	0	0	.29	2.47	8.52	13	3.77
26	.29	0	0	.29	2.18	7.52		
27	.29	0	0	.29	1.89	6.52		
28	.29	0	0	.29	1.60	5.52		
29	.29	0	0	.29	1.31	4.52	161	46.69
30	.29	0	0	.29	1.02	3.52		
31	.29	0	0	.29	.73	2.52		
32	.29	0	0	.29	.44	1.52	16	4.64
33	.29	.29	1	.15	.15	.52	158	45.82
34	0					0		
35								
36								
37							57	
38								
39							138	
40								
41								
42							15	
43								
44							16	
45								
46								
47								
48								
49								
50								
51								
52								
53							18	
54								
55								

_Ro_ and _r_ calculated from these life tables appear in Table 11.

Data on the age at sexual differentiation was too sparse to allow any generalizations (Table 12), owing to the early, heavy mortality in all cases. When only one sex is indicated, that individual was the sole survivor. An individual was identified as male as soon as the testes were observable. The appearance of the genital setae followed.

The survivorship curves from the combined life tables are plotted in Figure 6.

Table 13 shows the maximum longevity of individuals in each condition and the sex of the last survivor. Again, the data are insufficient to draw any generalizations.

The longevity of the _mx_ female showed significant treatment effects at the .005 probability level (Table 14). The T method showed high temperature, high salinity significantly lower than low temperature, high salinity; high temperature, high salinity < low temperature, low salinity; high temperature, low salinity < low temperature, high salinity; and high temperature, low salinity < low temperature, low salinity (Figure 7).

Dedifferentiation

On several occasions, adults showing mature sexual

	HTHS	HTLS	C	LTHS
r	.261	.070	.194	.039
Ro	36.69	2.19	41.75	2.16

Table 11. _r_ and _Ro_ for _Capitella capitata_ Type I under various regimes.

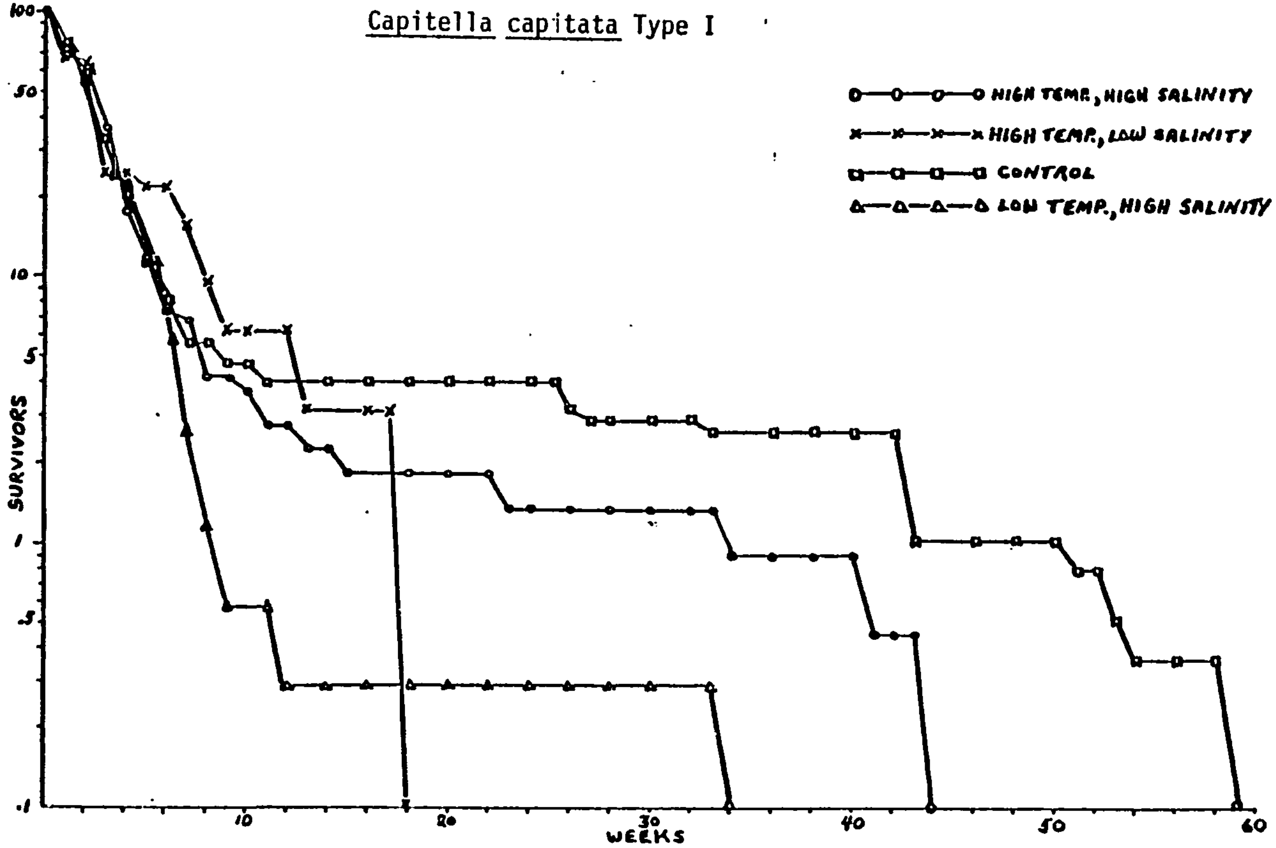
	Regime									
	HH		HL		C		LH		LL	
Replicate	sex	days P.E.	sex	days P.E.	sex	days P.E.	sex	days P.E.	sex	days P.E.
1	f	33	f	91	f	97	u	(33)	*	*
	m	33			m	83				
2	u	(41)	*	*	u	(34)	*	*	*	*
3	u	(5)	*	*	u	(35)	m	132	*	*
4	m	88	*	*	u	(38)	u	(46)	*	*

Table 12. Age at Sexual Differentiation in *Capitella capitata* Type I.

P.E.= post emergence
m= male
f= female
u= undifferentiated (life span in days)
*= no viable offspring

FIGURE 6: SURVIVORSHIP CURVES

Capitella capitata Type I



	Regime									
	HH		HL		C		LH		LL	
	long.	sex	long.	sex	long.	sex	long.	sex	long.	sex
Replicate										
1	301	f	125	f	372	m	32	u	*	*
2	40	u	*	*	39	u	*	*	*	*
3	4	u	*	*	34	u	237	m	*	*
4	285	f/h	8	8	37	u	46	u	*	*

Table 13. Maximum Longevity in Survivorship Cohorts in *Capitella capitata* Type I.

long.= longevity in days
m= male
f= female
f/h= female or hermaphrodite
u= undifferentiated
*= no viable offspring

Source	df	SS	MS	F	p
Treatment	4	208464.600000	52116.16000	6.19416	.005
Error	15	126206.300000	8413.75400		
Total	19	334670.900000			

Table 14. ANOVA: *Capitella capitata* Type I *mx* female longevity.

characteristics dedifferentiated. In the first low temperature, low salinity replicate the female dedifferentiated (no ovarian tissue at any stage of development) 25 days after the start of the experiment. New eggs differentiated and on day 100 the individual was mature. This female never produced a successful brood. The same pattern occurred in the second low temperature, low salinity replicate: dedifferentiation by day 61, followed by differentiation to mature conditions by day 154. No brood was produced. In the third low temperature, high salinity replicate, the female dedifferentiated by day 11. On day 30 she was observed to have a large number of mature eggs. This female produced a brood tube on day 89.

A number of males also dedifferentiated (i.e. no testes or genital setae could be seen): one in the third high temperature, low salinity replicate (day 53) and two in the third low temperature, low salinity replicate (days 243 and 249). During the course of the first low temperature, low salinity replicate males were observed regenerating genital setae. On day 112, one individual was observed losing one pair and growing a new pair. A male was observed on day 187 with one regular size pair and one diminutive pair of genital setae.

Atypical Brooding Behavior

On four occasions a brood tube was abandoned. Shortly before her death the first replicate high temperature, high salinity female abandoned a tube (her 26th brood). The fourth replicate low temperature, high salinity female abandoned her second tube. When the tube was dissected a day later, trochophores emerged. The fourth replicate low temperature, low salinity female abandoned her first and second tubes. The first replicate high temperature, high salinity female was observed to have left a brood tube (her 20th) one day and to have returned to it 24 hours later. Viable progeny resulted from this tube. On one occasion, two females were found occupying a brood tube (the first brood of the first replicate control female). On three occasions a male was observed occupying a brood tube. One such occured during the emergence of the second brood of the fourth replicate high temperature, high salinity female. A tube (the first) abandoned by the fourth replicate low temperature, low salinity female was observed occupied by a male during a subsequent observation. A male was observed in the third brood tube of the third replicate control female. Many atypical larvae were subsequently reported.

On three occasions, a male and female were observed occupying the same tube (not a brood tube). In none of the cases was a brood tube produced shortly thereafter. These occurred in the second replicate of high temperature, high salinity; the second replicate of low temperature, high salinity; and the first replicate of low temperature, low salinity. The last case is one in which the female dedifferentiated and subsequently redifferentiated.

Atypical Eggs and Larvae

During the course of the experiment various atypical eggs and larvae were observed. Both in situations where the brood tube was dissected and when it was left intact, eggs were observed that gave no evidence of having initiated development. Five individuals were observed that had the usual trochophore shape, but exhibited what appeared to be an undifferentiated mass of cells internally (two under high temperature, low salinity; one under high temperature, high salinity; one under low temperature, high salinity; and one under control conditions). The high temperature, high salinity individual did have eyespots and cilia. Trochophores that lacked the typical green gut were occasionally observed under all conditions except high temperature, low salinity. Usually a very small proportion of a brood would exhibit this condition. On five occasions (three under low temperature, high salinity; one under control and one under high temperature, high salinity conditions) both trochophores and juveniles were observed with bifurcate tails. The individual in control conditions survived at least 14 days and exhibited a bifurcate gut. Occasional curved or crooked posterior ends were observed.

Four individuals (first replicate high temperature, high salinity; second replicate high temperature, low salinity; first low temperature, high salinity) had atypical shapes: three had anterior ends reminiscent of planaria, one looked rather like a miniature tadpole.

Atypical Development Including Benthic Larvae

On two occasions, a brood was observed to complete development without the presence of the female. During the first high temperature, high salinity replicate, an abandoned brood tube was observed on day 84 of the experiment. On day 90, when trochophores were seen swimming, the tube was opened. The brood included 104 individuals (65 trochophores, 35 juveniles, 4 incompletely developed individuals). On the 106th day of the third replicate control condition, the female's sixth brood tube was observed. The next day she abandoned it. She was never observed to return to it. On the 117th day the tube was opened; it produced 99 individuals (61 trochophores, 38 juveniles).

On two occasions trochophores metamorphosed in the brood tube. The fifth brood tube of the third control replicate was dissected open when the female left it. Fifty-two of the 54 progeny had metamorphosed. Similarly, the first brood of the fourth low temperature,high salinity replicate was opened after the female left; the majority of the 95 individuals were juveniles.

Hermaphroditism

A. As initial condition:

Those instances where an hermaphroditic individual was used as the starting female are described in Materials and Methods. All behaved as functional females and all data concerning them were reported in the appropriate sections.

B. Protandrous hermaphrodites:

On several occasions males became hermaphrodites in the presence of females carrying eggs (Table 15). Holbrook and Grassle (1984) suggested females may exert an inhibitory effect on the expression of hermaphroditism in this species. The observations in this study do not provide evidence that is consistently supportive of that mechanism.

In the first replicate control dish the female died on day 118. No additional observations were made until day 154 when an individual with genital setae and differentiating eggs, but no obvious testes, was seen brooding a tube with numerous progeny. In the third low temperature, low salinity mx dish, one male showed developing ovaries two days after the female died.

C. Protogynous hermaphrodites

The first replicate female under low temperature, high salinity conditions was reported on day 547 (after

replicate	condition	days post start*
2	LTHS	276
2	LTHS	389
3	LTHS	244
3	LTHS	246
3	C	205
3	C	295

Table 15. Occurrence of Protandrous Hermaphrodites in *Capitella capitata* Type I.

* days post start does not reflect the age of the males, since new males were added as needed, as described in Materials and Methods.

five broods) to have numerous tightly packed eggs and one or one pair of genital setae. The setae were noted again on day 566. Egg development continued without reproduction or further report of male characteristics until the female's death on day 663. The second replicate female under control conditions produced two broods. On day 41 she was observed to be dark in color and containing 4 or 5 mature eggs. She dedifferentiated and remained so until day 70, when testes developed. On day 72, testes and developing eggs could be seen. Mechanical malfunction had resulted in a temperature increase in the holding chamber just prior to the day 80 observation. This female produced a third brood on day 84.

D. Hermaphrodites in Survivorship Cohorts

Hermaphroditism in survivorship cohorts occurred in two experimental conditions: high temperature, high salinity and control. In the first replicate high temperature, high salinity cohort, with five individuals surviving (day 82), one individual showed both testes and eggs. That individual did not survive to the next observation. On day 188 (two individuals surviving) an individual, formerly a female, exhibited eggs and genital setae. In the fourth replicate high temperature, high salinity cohort, on day 102 (one individual surviving) a former male showed eggs and testes. In the first replicate control cohort, on day 133 (15 individuals surviving) two individuals, one formerly female and one formerly undifferentiated, showed eggs and testes. On day 154 (11 individuals surviving), a third individual (former state not known) had eggs and testes. This pattern of occurrence is consistent with the observation (Holbrook and Grassle, 1984) that hermaphroditism increases as density decreases.

DISCUSSION

Life History Strategy

With reference to some characteristics , *Capitella capitata* is the traditional '*r* strategist' described by Pianka in 1970. Survivorship curves generated under four different experimental conditions (low temperature, low salinity - no data) are Type III (Figure 6). The length of life of the last survivor varied by nearly thirty five percent (18 weeks under high temperature,low salinity; 59 weeks under control). This result is consistent with the suggestion (Green, 1969; J.F. Grassle, 1972) that an effective way to cope with a variable environment is to provide extensive genetic diversity in each generation. Population size is variable in time and the species exhibits high density independent mortality (Grassle and Grassle, 1974).

Stearns (1976) listed key life history traits - those characteristics upon which natural selection could be expected to impact. Among these is brood size. This study shows clearly the susceptibility of this trait to environmental influence. The square root of the total number of offspring was significantly lower in the two low salinity conditions than in the others. A second characteristic of interest in this regard is the relation of reproductive effort to adult mortality (Stearns, 1976; Charlesworth, 1973). In both of the high temperature regimes(Tables 7,8), reproductive effort continues virtually throughout the life span,while under control conditions (Table 9), it tapers off during the last third of the life span. Stearns (1976) further suggests examination of these traits in the progeny. In the one instance where female and progeny data are compared, longevity, the females are strikingly longer lived than their offspring. Under control conditions,the female lived twice as long as her longest lived offspring and under LTHS, three times as long. Longevity, in this instance, is apparently not hereditary; selection by a specific environment does not result in a narrowly adapted next generation with respect to this characteristic.

Wilbur *et al*. (1974) suggested that age at first reproduction and fecundity age regression were important traits in the evolution of a life history strategy. In the present study, environmental conditions had no significant effect on age at first reproduction and there was no correlation between female age and brood size. Murdoch (1966), Cohen (1968) and Nichols *et al*. (1976) considered adaptation to changing conditions through shifts in life table characteristics. The extent of this phenomenon is well documented by this study. Mean number of offspring per brood, interval between broods, incubation time and the square root of the total number of offspring were all significantly affected by environmental conditions. Nichols _et al_. (1976) described opportunists as species which can shift a relatively longer distance along the continuum of a characteristic that extends from a strict _r_ mode to a strict _K_ mode. This is a useful way to describe such species. It was demonstrated by the variations in _r_, _Ro_ and mortality in this study. Intrinsic rate of natural increase shifted from 0.039 (low temperature, high salinity) to 0.261 (control); _Ro_ from 2.16 (low temperature, high salinity) to 41.75 (control)(Table 11) and the shift in mortality is most conspicuous in a comparison of high temperature, low salinity (Table 8) and control (Table 9).

Of the life history traits that have been suggested to be important from an evolutionary point of view, mean offspring per brood, brood interval, incubation time, square root of total number of offspring, _r_, _Ro_, mortality and relation of reproductive effort to adult mortality have been shown in this study to be significantly influenced by environmental change. There is no evidence for an effect on survivorship curve, age at first reproduction, number of broods or correlation between female age and fecundity. This does not invalidate the use of the latter set in life history strategy models, for they may be valid for other organisms. The study does, however, provide an extensive body of empirical observation in support of the theoretical constructs cited above.

Of particular interest in this study were the large variances associated with almost all the characteristics studied. The range in female age at first reproduction (69-203 days), in the number and size of broods within a condition (28 broods - 1 brood; 5-150 individuals), in days required to reach sexual maturity within a single experimental condition (33-88 days) and between the longevity of mothers and offspring, all very strongly support the idea that variation is very important to the survival strategy of this species (Green,1969;J.F. Grassle, 1972). The distance along any environmental continuum that is spanned by the members of a cohort greatly exceeds the physiological tolerance of any single individual. Such a multiplicity of genetic combinations increases the chance that some will survive a changed environment. Rather than employing the usual interpretation of the action of natural selection, preserving those individuals with a similar, adaptive genotype, it may be more appropriate to consider an additional, or alternative, evolutionary strategy, whereby a constellation of genes in a population is selected through the survival of a diverse group of individuals.

Life Tables

Mortality is significant in the early portion of the life span, regardless of experimental condition, and then decreases considerably at about the tenth week. Dorsett (1961) indicated a post-larval mortality of 37% in *Polydora ciliata* (Johnst.). George (1966) reported a growth pause and increased mortality in 10 day old (10 degrees C., 30 p.p.t.), 3 setiger larvae of *Scolecolepides viridis* (Verrill). He suggested the pause might result from the final disappearance of yolk granules and the transition to an outside food source. Since the appearance of the gut changed in post settlement individuals in this study, some of the early juvenile mortality may be associated with adjustment to a deposit feeding mode of existence. Expectation of further life increases in the mid-portion of each table. The low temperature, high salinity table is conspicuously different from the other two in its brevity. Considered with the fact that low temperature, low salinity conditions produced insufficient data to generate a table, it appears that low temperature (in the range of this study) is decidedly suboptimal for population growth, in spite of the fact that it was not excessively detrimental to most aspects of reproduction. Reproductive activity persists for the duration of the animal's life under high temperature, high salinity and low temperature, high salinity conditions, but diminishes near the end of the table under control conditions. Only under control conditions (Table 9) is there a fairly clear peak in age specific birth rate (mx). This occurs from week 16 to week 22. In contrast, the peak in age specific birth rate in *Ophryotrocha diadema* (Åkesson, 1982) is quite conspicuous in the three genetic strains that were studied and occurs before week 10.

Net reproduction and intrinisic rate of natural increase

According to the calculations of *Ro* for each regime, all the populations were increasing except low temperature, low salinity. Ranked in order of magnitude of increase, from largest to smallest, the populations appear thus: control; high temperature, high salinity; high temperature, low salinity; and low temperature, high salinity. Low temperature, low salinity has no *Ro* becasue there were insufficient data to generate a table and can be considered to be decreasing. *Ro* under control conditions (41.75) was only slightly larger than the value for high temperature, high salinity. So, when viewed from the perspective of the life table, which integrates mortality and fecundity, the effects of salinity are seen to reduce the chances of a population persisting in a low salinity environment by an order of magnitude. Values for *Ro* calculated in this study are smaller than those determined by Åkesson (1982) for three genetic strains of *O. diadema*. Since culture conditions in the two experiments were quite different (i.e. food source, density, salinity), it cannot be determined whether this represents a real difference between the two species or is associated with the culture conditions.

The value *r* was calculated using Euler's equation according to the method described by Birch (1948). Values for *r* ranked in decreasing order of magnitude appear as follows: high temperature, high salinity; control; high temperature, low salinity; low temperature, high salinity; and (by implication) low temperature, low salinity. The value *r* is one of the most useful concepts in population biology and, perhaps not surprisingly, one of the most difficult to define with precision. Broadly defined it is the instantaneous coefficient of population growth. If the true *r* could be measured, it would constitute a baseline against which population characteristics in other conditions could be measured. A real *r* must be measured under optimal conditions. This is much easier to approximate for bacteria or for unicellular animals than for any other organisms on account of the brevity of generation time of the former. The optimum habitat for *Capitella capitata* may include some optimum density. While it could be argued that a few young organisms in an uninhabited environment (even if it is a culture dish) with optimum temperature and salinity and unlimited food, constitutes an optimum situation, it is really not clear, without prior experimentation, that the organism's optimum density is low (Allee effect), (Birch, 1948). There are a considerable number of values of r that can be measured under varying conditions of temperature, salinity, density. etc. There will also be different values of r associated with different population age structures. Preferably r is measured when the population has reached a stable age distribution (Birch, 1948; Vandermeer, 1981). At this point it is useful to consider Caughley and Birch's (1971) classification of rates of increase. The authors suggest that a particular observed rate of increase be termed r; a rate implied by the prevailing schedules of survival and fecundity be termed r_s and a maximum rate in a population with a stable age distribution in a specified environment, be termed r_m. They specify that r_m (the intrinsic rate of natural increase) must be determined as the rate at which a newly established population increases or by fitting a curve to the growth of a population after its density has been artificially reduced. The rate r_m is a special case of r_s, starting at very low densities. The authors indicate that r can be calculated by regressing the natural log of the population size on time; r_s can be calculated from a life table and a fecundity table, using Euler's equation. This assumes that maximum physiological reproduction will occur at low densities. It is not clear that this is the case for every organism, as suggested above. It is also not clear that the physiological maximum in reproduction is expressed under a stable age distribution. This may differ for different organisms. The r that was calculated in this study does not meet the requirements for either r_s or r_m, but partially meets criteria for both. It was calculated on a prevailing age distribution, which was not necessarily stable (r_s) and it used population information collected at relatively low densities, in in a highly specified environment (r_m).

Although the data for these life tables was collected under the relatively straightforward circumstances of following a cohort until death, two of the tables are limited by the skew between the *mx* and *lx* columns. In both high temperature, high salinity and low temperature, high salinity there were progeny that could not be included in the r and *Ro* determinations because none of the cohort attained the age of the mother at the time that reproduction occurred. For those two conditions, r and *Ro* may be underestimated. Only a considerably greater number of replicates might possibly obviate this difficulty.

A number of values of r were presented in Banse's (1982) discussion of mass scaled respiration and intrinsic growth rate in meiofauna. Only values calculated, rather than estimated, were considered for comparison. (All values have been converted to daily rates.) Of twenty values representing hydroids, rotifers, nematodes and copepods, only three were within the same order of magnitude as those calculated in this study. These were *Protohydra leukarti* (hydroid): 0.078; *Oncholaimus oxyuris* (nematode): 0.022; and *Tisbe persimilis* (benthic harpacticoid copepod): 0.098. *C. capitata* values (this study) were: high temperature, high salinity: 0.037; high temperature, low salinity: 0.010; control: 0.023; low temperature, high salinity: 0.006. These values are not strictly comparable because of the method of calculating *r*. All the cited values were calculated using a variation of the generation time formula (r = ln Ro/ T). The values for *Tisbe* (Volkmann-Rocco and Fava, 1969) calculated *Ro* on a female only life table, in contrast to the present study where sexes could not be distinguished. The values for *O. oxyuris* and *P. leukarti* were calculated on females only and did not take juvenile mortality into account (Heip,1977;Heip *et al.*,1978). While the *Capitella* values are lower than the others reported by Banse, they compare favorably with Birch's (1948) insect data. Values for *Calandra* (rice weevil) are 0.017, 0.061, 0.109, depending on temperature. There is a wide range in the reported values. Banse's values may represent over-estimates (1984) and the *Capitella* values under-estimates due to the skew of *lx* and *mx* values. Even within groups of very similar mass, wide variations exist. Values of *r* calculated for *O. diadema* (Åkesson, 1982) are larger than those for *Capitella*. Methods of calculation of *r* were the same, but *O. diadema* is consistently hermaphroditic. As with *Ro*, it is not clear whether this represents a difference between the species or between culture conditions. Comparison of values among many studies is made more difficult, since *r* can be calculated by more than one method and under various conditions (see discussion of *r* above). No easy generalization is apparent, either with respect to body size, life cycle complexity (number of metamorphoses or molts) or habitat (planktonic, benthic or terrestrial). A most instructive comparison would be among values of *r* calculated for more of the other *Capitella* sibling species under uniform conditions.

In spite of the difficulties associated with definition and comparability of *r* values, there are compelling reasons to collect data in a way that allows this value to be calculated. Hummon and Hummon (1975) discuss the advantages of life table use in assessing tolerance limits of a population (in this case, *Lepidodermella squamata*) to suboptimal environmental conditions or pollutants. They suggest that inasmuch as demographic life history data tend to integrate the n-dimensions of the niche hypervolume into single parameter units (*ex* , *Ro* , *r*), effects of gradient alterations on a single parameter can be analyzed with a great deal more sensitivity than using traditional measures of somatic lethal limits. Their work demonstrated that statistically significant alterations of longevity and reproductive rate occur with concentrations of DDT at 5 ppm and above. Allen and Daniels (1982) used a life table approach to evaluate chronic exposure of Eurytemora affinis to Kepone. It was pointed out in this study that survivorship and reproductive characteristics may indicate different critical levels for chronic effects,demonstrating again the usefulness of r, which integrates survivorship and fecundity information and assesses the capacity of the population for increase under given conditions.

Longevity of mx Female

There is a distinct difference in longevity means between the mx female and the last survivor in the cohort, especially in the last three conditions:

	HH	HL	C	LH	LL
female	179	167	247	397	399
cohort	157.5	125	120	105	---

Densities in the mx dishes and lx dishes were different but it is difficult to attribute decreased longevity to crowding in an animal that usually congregates in clumps. The longevity of the female is very clearly temperature related, but the longevity of the cohorts shows an inverse pattern. The early histories of mothers and offspring were different. Mothers were raised in higher density situations prior to sexual maturity and very low densities thereafter. Offspring were left with each other for their whole lifespan. One could also argue that the available food was different, but in no case did food appear to be limiting, i.e. all particlate matter compacted into pellets. It seems possible that a genotype like that of the mother does not appear in the brood. This supports the hypothesis that adaptation occurs through wide variation in genotypes, rather than selection of one particular genotype (J.F. Grassle, 1972).

Reproduction

Since there was no treatment effect on the number of broods produced, the ability to succeed in a given environment must be determined by other factors. Salinity is clearly an important limiting factor. The square root of the total number of offspring showed high temperature, low salinity and low temperature, low salinity to be conspicuously smaller than the remaining conditions. With mean offspring per brood as a measure, high temperature, high salinity was significantly higher than high temperature, low salinity and low temperature, low salinity, but overlapped low temperature, high salinity and the control condition. Ranked in order,from high to low (mean offspring) the conditions are: control; high temperature,high salinity; low temperature, high salinity; high temperature, low salinity; and low temperature, low salinity (Figure 3). Thus, salinities below 25 p.p.t. would clearly limit population growth. Temperature does not have an effect on the overall number of individuals produced in a female's life. However, it does affect the interval between broods. Low temperature, low salinity and low temperature, high salinity intervals are longer than the other experimental conditions (Figure 4) which form a cluster. Thus, low salinity will have a less adverse affect on the reproductive interval at higher temperatures. The female's age at first reproduction was not significantly affected by any of the experimental conditions. It appears that initiation of reproduction is not altered by environmental changes, at least within the range used in this study, since animals under control conditions (the conditions under which all animals were raised) had no advantage over the others in this regard.

Age at Sexual Differentiation

While the data in Table 12 do not provide any information regarding which sex differentiates first within a cohort, it should be noted that the first individuals to achieve recognizable sexual maturity in the stock dishes were almost always male. In a natural population, with individuals from several broods present, this would favor non-sib matings. As Olive and Garwood (1981) point out, in their study of *Nereis* species,if the age of sexual maturity were strictly determined, and all animals were breeding at the same age, successive year groups would become genetically isolated.

Brood production and development

Franzen (1956) relates Eisig's suggestion that while the genital setae of capitellids function as organs of copulation and ejaculation, in *Capitella* they are specialized to function as organs of spermatophore production. Nothing that I observed during the period of this study allows me to confirm either a copulatory function or a function in spermatophore production. Histological studies would perhaps provide additional information about the role of these structures.

Production of a brood tube for developing larvae occurs elsewhere among the polychaetes, including among the sabellids, serpulids and spionids, and brood protection is not unusual among opportunistic polychaetes (Franzen, 1956; Grassle and Grassle, 1974). The presence of the mother is considered to be necessary for successful brooding (Franzen, 1956; Bellan *et al*., 1972). This is usually the case, but there are exceptions which are discussed below. The absence of synchrony in trochophore development, which can be observed in the tube, may simply be a function of time elapsed from fertilization. Since emergence usually occurs in a single, fairly brief episode (within 24 hours, except for low temperature, high salinity), it does not seem that any significant advantage accrues to earlier or later emergence. Failure to spawn completely has been observed both in *Capitella capitata* Type I (J.P. Grassle, pers. comm.)and in *Nereis diversicolor*. In *N. diversicolor*, the oocytes can persist for two months, but eventually disintegrate (Dales, 1950). This was observed only under low temperature conditions, regardless of salinity, in the present study. It is difficult to say whether it was caused by gamete inviability, embryo inviability or sperm shortage. The fact that the trochophores show a strong photopositive response shortly after emergence would suggest adaptation to algal feeding; no experiments were done to confirm this.

Dedifferentiation

Egg resorption was an infrequent phenomenon and always occurred under low temperature conditions. Hutchings (1973) reported that in a Northumberland population of *Melinna cristata* (Ampharetidae), not all potential breeders spawned; some resorbed mature gametes and released a second batch. He noted that his study population is near the southernmost limit of the species distribution and environmental conditions are sub-optimal. Olive, et al. (1981) reported periodic breeding failure in two species of Nephthys. Oosorption occurs. The authors suggest this is a means of maintaining a sympatric distribution. Two species in close proximity will remain separate if their gametes ripen at different times. This study's result seems to be closer to the situation described by Hutchings. The low temperature, low salinity experimental condition may be so close to the reproductive limits of tolerance that the ordinary metabolic pathways cannot produce viable eggs. Perhaps viable eggs can be produced under these stressful conditions only after an alternate enzyme pathway is induced or some genomic alteration occurs.

Atypical Eggs and Larvae

The occurrence of undeveloped eggs was noted in all experimental conditions. Therefore, if it is a function of environmental conditions the cause lies either in the water (natural sea water, Long Island shore, adjusted with "instant ocean" sea salt) or with the food (azoic mud, Woods Hole). This has been observed by other workers (J.P. Grassle, Woods Hole, personal communication). Failure of egg development may be due to insufficient sperm or may simply represent the baseline egg mortality under a given set of conditions.

The colorless trochophores are not easily explainable, since it isn't known whether they actively feed while swimming or subsist on stored yolk. If they actively feed, then the colorless gut may result from a shortage of algal food.

The appearance of unusual trochophores occurs in all experimental regimes and, like the undeveloped eggs, it is either a result of some aspect of the culture conditions or represents a baseline level of one aspect of larval mortality. Increased mortality during metamorphosis is not an unusual occurrence. It actually represents the cost to the individual and the species of having two radically different lifestyles, as in insects, molluscs, and many amphibians.

Hermaphroditism

Hermaphroditic individuals occurred in a variety of circumstances. Protandrous hermaphrodites were observed in low temperature, high salinity and control conditions, in the presence of females with eggs. Thus, reduced female fertility is not the explanation. It has been observed by Holbrook and Grassle (1984) that hermaphroditism occurs as a result of excessive inbreeding. Since the same culture was maintained through the third replicate, and hermaphroditic individuals occurred most frequently in the third replicate, this is certainly possible. However, hermaphroditic individuals appear among the progeny in the first and fourth replicates, those least likely to show effects of inbreeding. In addition, the occurence of these individuals in only some of the experimental conditions suggests a more detailed explanation is necessary. Warren (1976), in her review of the genus *Capitella*, indicates that *C. capitata capitata* has multiple male genital spines (from one to five or more pairs) and sometimes includes hermaphroditic individuals. She also observed male characteristics in gravid females of the species. Reish (1977) also reported females with genital hooks producing viable eggs in one population of *C. capitata* and similar females producing inviable eggs in a different population. However, the relationship between the types described by Grassle and Grassle (1976) and the species used by Warren or Reish is not clear.

Hermaphroditism is quite common among invertebrates, and in some groups is virtually the only means of reproduction (Hirudinea, Platyhelminthes, Gastrotricha). While the polychaetes are generally considered to be dioecious, hermaphroditism is not that rare an occurrence (Ghiselin, 1969). Studies on *Ophryotrocha* show that in this genus sexuality is a very complicated affair. Bacci (1951) reported that *O. puerilis* showed transitory male phases, especially while young. He suggested that the sexual condition showed the characteristic signs of continuing variation. Parenti (1960) reported self fertilization in *O. labronica*. Although Grassle and Grassle (1976) reported that self-fertilization occurs in *C. capitata* (Type I), no evidence of it was observed in this study. Åkesson (1970) described the Leghorn strain of *O. labronica* as hermaphroditic, while a strain from Naples was gonochristic (dioecious). None of the experimental conditions employed on the Naples strain changed the sex ratio. In a later work (1972), Åkesson studied three strains with different but constant sex ratios which could be changed by selective breeding. In 1978, Åkesson identified a new species of the *labronica* group in cross-breeding experiments. Holbrook and Grassle (1984) tested three strains of *Capitella capitata* Type I: one with a higher proportion of males, one with a higher proportion of females and one composed of progeny of males that became hermaphroditic after a short period of isolation. During the course of the entire experiment there was little difference in the rapidity of the sex change between the high and low male groups. There were too few animals in this study to draw any conclusions about the genetics of this trait, and the precise genetic basis of sexuality in Capitella is not yet clear.

Ghiselin (1969) proposed three general groups of theories to explain the occurrence of hermaphroditism. His Gene Dispersal model points out the advantage of hermaphroditism in a small founder population. Six hermaphroditic individuals, that will outcross, can constitute an effective breeding (more importantly recombinational) population of six. This will be true even if the hermaphroditism is sequential and not simultaneous. A group of six dioecious individuals could, by chance, be a single sex and therefore, be a non-breeding population. Hermaphroditism would, then, be of obvious value to a weedy or colonizing species. Ghiselin's models have been criticized on the grounds that they are based on comparisons among phyla, a level at which it is not possible to test them by empirical methods (Williams,1975). The body of data on Ophryotrocha (cited above) and data gathered on the Capitella species group, will provide an excellent basis for the evaluation of these models.

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