An Abstract of the Dissertation of

Barry Adolph Vittor for the degree of Doctor of Philosophy
in the Department of Biology to be taken September 1971

Title: Effects of the Environment on Fitness-Related Life History Characters in *Tigriopus californicus*

Approved: Peter W. Frank
Peter W. Frank

The effects of several environmental factors on fitness-related life history characters of *Tigriopus californicus* were investigated in field and laboratory studies. Animals were collected from splash pools at Charleston, Oregon, La Jolla and Pacific Grove, California. All areas are characterized by extreme fluctuations in both salinity and temperature.

Population density and clutch size of field populations were highly variable throughout the year, but were not correlated. Neither parameter, moreover, was correlated with temperature, oxygen, or salinity. Mean clutch size for all Charleston samples were 46.1 ± 20.0 eggs. Sex ratio was not correlated with either salinity or temperature. The three regions differed with respect to mean clutch size, and female body size: the ranking of locations was La Jolla, Pacific Grove, Charleston, for both characters. Body size was positively correlated with clutch size.

No stages of *T. californicus* revived and developed after experimental desiccation over periods from one to three months. Colonization of pools during spring storms is prob-

ably accomplished via inshore current transport of animals swept from pools which are essentially permanently populated.

At 20°C in 100% seawater, fecundity was sensitive to food levels below 0.022 mg per female per 2 days. Clutch size, but not number, was limited by food availability. Clutch size was also reduced by increased density of animals in vials, in laboratory studies.

Photoperiod had no effect on egg production. Fecundity, via both clutch size and number, was affected by temperature-salinity interactions. Over the ranges tested, from 15° to 25°C and 50% to 150% seawater, maximum egg production occurred at 15°C, 150% seawater; minimum fecundity was observed at 25°C, 150% seawater. Developmental time and mean longevity decreased with temperature. The former character varied from 18 days at 25°C to 32 days at 15°C, the latter from 75 days at 25°C to 130 days at 15°C. Male sex ratio increased from 54% at 15°C to 70% at 25°C; salinity had some effect on sex ratio, but affected neither developmental time nor longevity. Intrinsic rate of increase ranged from 0.105 per day at 15°C to 0.155 per day at 25°C; salinity did not affect $\underline{r}$. Increased environmental stability of laboratory cultures had no influence on fitness-related characters.

There appeared to be regional differences in growth rates of Tigriopus populations raised in the laboratory. Those from La Jolla and Pacific Grove increased fastest at 25°C, and slowest at 15°C; the opposite was true for

Charleston populations. When individual females selected at random from these cultures were tested for life history characters, no populational differences were found to explain the observed patterns in actual population growth rates.

Selection for opportunism seemed to have reduced variability in developmental time (coefficient of variation = 7.0%), egg size (8.2%), and survivorship (11.3%). Variability was greatest with respect to the number of clutches produced (46.5%), probably because *r* is insensitive to late-produced broods.

Phenotypic plasticity was observed in the responses of *T. californicus* to varied temperature and salinity, with respect to sex ratio, clutch size and number, and perhaps developmental time. Egg size was sensitive to no environmental changes.

A more empirical approach to the investigation and designation of life history strategies is proposed. This model suggests alternatives to the current usage of an *r*- to *K*-selected continuum; species may be described as dispersal-selected, low resource-selected, maternity function-selected, etc.

EFFECTS OF THE ENVIRONMENT ON FITNESS-RELATED LIFE HISTORY CHARACTERS IN *TIGRIOPUS CALIFORNICUS*

by

BARRY A. VITTOR

A DISSERTATION

Presented to the Department of Biology
and the Graduate School of the University of Oregon
in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

September 1971

EFFECTS OF THE ENVIRONMENT ON FITNESS-RELATED LIFE HISTORY CHARACTERS IN *TIGRIOPUS CALIFORNICUS*

INTRODUCTION

The population dynamics of numerous species have been examined, including those of the vole, *Microtus agrestis* (Leslie and Ranson, 1940); flour beetles, including *Tribolium* (Park, et al., 1941); the rotifer, *Floscularia conifera* (Edmondson, 1945); the barnacle, *Balanus balanoides* (Hatton, *In* Deevey, 1947); the rice weevil, *Calandra oryzae* (Birch, 1948); *Lucilia cuprina* (Nicholson, 1950); *Daphnia obtusa* (Slobodkin, 1954); passerine birds (Lack, 1956); *Drosophila serrata* (Birch, et al., 1963); *Parus major* (Perrins, 1965); *Drosophila pseudoobscura* (Dobzhansky, et al., 1964); the copepod, *Tigriopus californicus*; and many others. All of these investigations have served to illustrate the processes of population growth, fluctuations, and occasionally decline, but few (Lack; Birch, et al.; Dobzhansky, et al.; and some others) have offered conclusions regarding the evolutionary processes operating on the components of these dynamics.

In order to describe the autecology of any species, one must know how environmental variability influences the fitness-related characters of the species. Fitness of an individual is measured as the number of offspring it produces which contribute to future generations. Fitness is also, then, defined in terms of how well an individual genotype is adapted to its environment. Natural selection will favor those genotypes which are most fit in a given environment. Therefore, those components of a species' life history which contribute to its fitness will be responsive to natural selection. Intrinsic rate of increase, r, may be used as an estimate of maximum contribution to future generations (assuming stable age structure, no emigration or immigration, and no intraspecific competition). This parameter can be used to compare population growth rates under different conditions. Complementary data on actual population growth rates are helpful, although it is usually impossible to distinguish the contributions to growth of individual characters under these conditions. In addition to measuring the components of r, one must estimate the energetic demands of and degree of selection for, characters such as body size, protective coloration, maintenance, dispersibility, predator avoidance, territoriality, etc. Any of these may have measurable effects on reproductive and mortality functions.

The marine copepod, Tigriopus californicus, is of peculiar interest from the standpoint of the problems cited above. Splash zone pools along the Pacific coast contain few animals in the winter, but support tremendous population blooms during the late spring and early summer. For example, densities may be lower than 10 females per liter one week, but over 5000 adults per liter only 4 weeks later. Such pools may evaporate and be refilled as many as three times during the summer and fall.

One would wonder, then, what kinds of selective pressures are exerted on a species encountering such highly variable conditions, and what kinds of evolutionary responses this species has developed in adapting to its fluctuating environment.

Selection for Reproductive Strategy

The intrinsic rate of increase of a population is determined by the age at first reproduction (developmental time), survivorship and birth schedules, and sex ratio. Several workers have shown that r is often more sensitive to changes in developmental time than fecundity or survivorship (Cole, 1954; Dobzhansky, et al., 1964; Lewontin, 1965; MacArthur and Wilson, 1967; Murphy, 1968; Gadgil and Bossert, 1970). Lewontin, for example, showed that a doubling of fecundity from 5000 to 10,000 offspring can increase r from 0.510 to 0.565; an equal increase in r would result from reducing developmental time from 8.6 days to 7.2 days (a one-sixth reduction).

In fluctuating habitats, resources vary greatly with respect to availability. Selection will favor those genotypes which have the highest r, as long as the population increases in an "ecological vacuum"(Pianka, 1971). Developmental rate should be maximized, and as a result, its variance should be low (Fisher, 1929). Ultimately, developmental time would become canalized, via "developmental canalization" (Waddington, 1957). Higher fecundity will also be favored, of course, especially during the initial exploitation of a newly-colonized habitat (Lewontin, 1965; Bagenal, 1966; Johnson and Cook, 1968; Murphy, 1968; Poulson and White, 1969; Hairston, et al., 1970; Pianka, 1971). According to MacArthur and Wilson (1967), it is the ratio of births to deaths that will be maximized under these circumstances; this will be accomplished through decreased deaths rather than increased births. They have termed this life history strategy as "r-selected."

Hairston, et al. (1970) have shown, however, that the r-selected strategy of MacArthur and Wilson (1967) must actually be considered as maternity function selection ("b-selection"). The intrinsic rate of increase *per se*, according to its derivation from the logistic equation (Lotka, 1924), cannot be selected for, since it is a constant based on constant age-specific survivorship and birth functions, as well as stable age distributions. Therefore, one should speak only of selection for the individual components of r.

Stable and species-saturated environments are characterized by predictably low resource availability, due to low productivity or high population density; inter- and intraspecific competition may be severe in these environments, with the result that density-dependent selection acts on reproductive functions. The concept of K as a maximum population, given a logistic growth model, was first mentioned by Pearl and Reed (1920) and Gause (1934); interpretations of the evolutionary significance of a more general carrying capacity, K, have appeared more recently.

Selection under stable conditions will favor delayed reproduction, increased longevity, and decreased reproductive effort. Advantage may be placed with individuals which produce a few very large offspring, if, for example, food resource availability or predation pressure are a function of body size. "K-selected" populations should exhibit only minor fluctuations in numbers, high standing crop of biomass, and slow turnover.

Since the definitive paper of MacArthur (1962) on selection for r and K, ecologists have become increasingly aware of the significance of determining how selective pressures affect components of a species' life history. Of course, several years earlier, Cole (1954) had developed the groundwork for this area of ecology in his insightful paper on the population consequences of life history phenomena. He stated that life history characters are adaptive; that is, they are subject to selection, and will be changed as a species adapts to its environment. Thereafter, and especially after MacArthur (1962) emphasized the dichotomy between *r* and *K* as the dimensions of life history strategies, nearly all statements on the subject have either assumed that selection *does* act on a one-dimensional continuum of fitness-related characters, or made this assumption to facilitate discussion of the problem. That is, once it was accepted that there were two extremes of reproductive strategy--*r*-selected and *K*-selected--all components of a species' life history, including reproduction, were collectively defined in terms of where these characters placed the species along the presumed *r* to *K* continuum.

Included in all discussions of *r*- and *K*-selection has been the assumption that it is the stability of the environment which ultimately determines life history strategies. And, since environmental stability can be described as a one-dimensional regime, varying from completely unstable to completely stable, the one-dimensional view of life histories has been reinforced. In the case of cave species, however, where food is scarce and densities are very low, it is conceivable that intense intraspecific interactions do not occur. If, then, density-dependent pressures are not present, the populational criteria upon which *K*-selection is based will not apply; under these circumstances, observed life history strategies are probably better described as "resource-selected," and another dimension must be added to our concept of stable environments. This kind of selection appears to have resulted in decreased metabolic rate and increased efficiency in the cave fish, *Ambyopsis spelaea* (Poulson and White, 1969). They associate life history characters which result in slower rates of increase in *Ambyopsis* (large eggs, long developmental time) with increased metabolic efficiency in this species. Completely canalized metabolic efficiency seems to be assumed by Ricklefs (1968), who states that the "food-limited hypothesis" is a suitable explanation for the evolution of clutch size in passerine birds. This hypothesis holds that feeding capabilities of the parents limit, and have evolved with, brood size in these birds. Thus, the environmental constraints on tropical passerines may be analogous to those on cave-dwelling fish.

A good example of the one-dimensional continuum approach is given by Cody (1966), who oriented his discussion of the evolution of low clutch size along those lines. He stated that "maximum contribution to future generations will be achieved by those individuals which utilize, to increase K, some of the energy conserved by reducing r." Cody also stated that in more stable environments selection is for K, not r, and the increased inter- and intraspecific competition due to higher densities causes decreased clutch size, as less energy is devoted to reproduction. Similar statements have been made by Scott (1962) for trout; Lewontin (1965) for Drosophila melanogaster; Bagenal (1966) for plaice; Murdoch (1966); MacArthur and Wilson (1967); Murphy (1968); Ricklefs (1968) for passerine birds; Poulson and White (1969) for cave species; Tinkle (1969) for tropical lizards; Gadgil and Bossert (1970); and, most recently, Pianka (1971). Pianka summarized the controversy over r- and K-selection by stating (p. 592) that "certainly no organism is completely 'r-selected' or 'K-selected,' but all must reach some compromise between the two extremes."

Although, as shown above, Cody (1966) did ascribe to the concept of the r to K continuum, he also suggested that the "Principle of Allocation" could be useful in describing the evolution of fitness-related characters. Hairston, et al. (1970) have also made the assumption that the functional relationships between birth and death functions are such that "optimization of one necessitates a cost to the other." For example, the amount of energy required to avoid predation must detract from energy available for reproduction. Or, the maintenance costs of a marine invertebrate may increase with salinity and temperature; again, this would make less energy available for reproduction. Dispersibility may be the most important limiting factor to certain species; energy must be devoted to the production of wings, or spines, or digestion-resistant seed coats. In cases of dispersibility and maintenance, as with some cave species perhaps, density-dependent selective pressures do not exert the greatest influence on life history characters; since the assumptions behind the concept of *r*- and *K*-selection are not met, these terms should not be applied. Hairston, et al. [redacted] pointed out, for example, that natural selection for life history characters will occur in three types of ecological conditions: "(1) in a population growing exponentially for a long period in a favorable environment; (2) in a population saturating its environment under conditions of complete density dependence; (3) in a fluctuating population affected principally by density-independent factors."

The over-emphasis on selection for *r per se* has precluded the observation that high reproductive output may be the result of selection for another life history character. For example, small seeds and spores may be more easily dispersed than large, heavy ones; because little energy is put into each propagule, many offspring can be produced. Mortality of young will be high (as shown by Williams, 1966), but the probability of reaching new resources increases with number of offspring, and is the character selected for. At present, opportunistic species are by definition *r*-selected. They exhibit high fecundity, short developmental time, and reduced longevity. As I have pointed out, however, one must distinguish the actual selective forces which produce these traits. It would be misleading to imply that all species which have these characteristics represent examples of r-selection.

A more empirical and realistic approach toward the evolution of life history phenomena has been developed by Strong (1971), who studied the amphipod, Hyalella azteca. He too has suggested that life history selection may operate along any of several gradients. I feel that earlier and existing approaches, which attempt to explain all life history strategies in terms of an r- to K-selection continuum, are too synthetic, and result in the loss of too much information to be useful.

Genotype and Population Homeostasis

Variation in life history characters can be both environmental and genetic in origin. Selection may result in the presence of genotypes which give rise to specific phenotypes, or genotypes which are plastic in their expression (Lewontin, 1958; Allard and Bradshaw, 1964; Bradshaw, 1965). For example, Johnson and Cook (1968) have provided data showing that different buttercup populations have their own characteristic ranges of fecundity. These ranges are produced by genotypes which vary in appearance over different sets of environmental conditions. Each range is adapted to the particular selective regime encountered, including high elevation-short growing season, and low elevation-long growing season conditions.

Many authors, including Lewontin (1956), Waddington (1957), Birch (1960), and Levins (1968) have discussed genotype and population homeostasis.

According to Lewontin (1956), "a genotype is homeostatic if individuals of this genotype can so adjust their physiology and morphogenesis as to survive and leave offspring in a wide variety of environments." On the other hand, "a population or species is homeostatic if its genotypic or phenotypic composition can be so adjusted as to assure its survival in a variety of environments." Bradshaw (1965) has stated that plasticity is shown by a genotype "when its expression is able to be altered by environmental influences," and "plasticity is applicable to all intragenotypic variability." He further stated that random variability (developmental noise) can be considered to represent plasticity, since plasticity "does not...have any implications concerning the adaptive value of the changes occurring, although many types of plasticity may have important adaptive effects." According to this definition, plasticity is not the same as Thoday's (1953) "phenotypic flexibility," since the latter does imply adaptive value. However, Bradshaw has not been convincing in his attempts to show that the terms are not synonymous: all of his examples of plasticity can be considered to have real adaptive value, and thus, are subject to selection. To avoid semantic problems and still compare the three terms, I will consider genotype homeostasis, or phenotypic flexibility, to be based on *adaptive* plasticity in response to environmental change. On the other hand, population homeostasis involves the capacity for rapid genetic change via polymorphisms or changes in gene frequencies in the population.

In variable environments, even plastic genotypes may not be able to respond adequately to very sudden or severe changes. The survival of the population will depend on population homeostatic mechanisms, as suggested above. Generally, when environmental changes occur *more* frequently than once a generation, plasticity will be favored. The former situation seems to apply to populations of Drosophila pseudeobscura; genetic changes do occur in response to extreme seasonal fluctuations (Wright and Dobzhansky, 1946). Both Levine (1952) and Epling, et al. (1953) pointed out that the frequencies of the three inversion types considered by Wright and Dobzhansky could not be explained on the basis of heterosis. Rather, the coadaptiveness of pairs of these types was determined by particular selective regimes; changes in the environment resulted in changes in the relationships between types, and consequently, in their relative frequencies in the population. Similar observations on color changes in the isopod, Sphaeroma, have been reported by Bishop (1969). Levins (1968) and Ehrlich and Raven (1969) [redacted] have stated that in variable habitats "co-adapted" genetic combinations which have high average fitness in a variety of environments will be favored; changes in the genetic composition of the population will be resisted. According to this point of view, which is equivalent to Bradshaw's phenotypic plasticity, opportunistic species like Tigriopus californicus would be expected to exhibit genotype homeostasis with respect to fitness-related life history characters.

Phenotypic Plasticity and Evolution of Life History Phenomena

Bradshaw (1965) has stated that all phenotypic responses to the environment are physiological in origin. Physiological changes may be manifested through morphological changes. For example, leaf size may decrease in response to temperature changes, or egg number may decrease under food-poor conditions. If only fitness-related characters are considered, we can show how the concepts of phenotypic plasticity and evolution of life history phenomena are related.

Let us assume that members of two genotypes of the same animal species are raised under identical conditions. Genotypes a and b assimilate equal amounts of energy during their lifespans, but a individuals exhibit a large coefficient of variation in the cost of maintenance. Type a animals which have used little energy for maintenance produce more offspring than type b individuals, which are not plastic and have a low coefficient of variation in both maintenance costs and egg production. Type a animals allocating much energy for maintenance produce few eggs. Under these conditions, the average fitness for genotypes a and b can be the same.

If environmental conditions are changed so that b individuals require a great deal of energy to maintain themselves, their fitness will be uniformly low compared to the average fitness of type a animals. In this case, the more fit a genotype will increase in the population. As shown earlier, selection will favor phenotypic plasticity in fluctuating environments, when changes occur more often than once a generation. In such a population, moreover, one would expect to find large intragenotypic variation in some life history characters; there would be a reduction in the degree of variability in characters which had increasingly high fitness values (Fisher, 1929).

In stable habitats the maintenance of either a plastic or a polymorphic population may not be favored by natural selection; a population of individuals with similar fitness would develop. Indeed, Poulson and White (1969) have reported that cave environments select for reduced genetic variability as well as reduced rate of increase. Here too, however, one would expect a gradient in variability between extremes in characters related to fitness. For example, if offspring size was most subject to selection, variability and heritability in this character would be low.

The description of a species or race in terms of selection for life history phenomena must take into account the genetic mechanisms on which selection operates. Because the selective regimes of stable and fluctuating environments are by definition very different, it is not unreasonable to expect that different genetic systems have evolved in them.

In summary, then, the problem to be investigated in this study is two-fold: first, I will describe the effects of the important environmental factors on the fitness-related characters and population growth of Tigriopus californicus. Second, I will show how these relationships illustrate selection for life history phenomena of species living in fluctuating environments, and will give evidence for the significance of the principles of phenotypic plasticity and allocation of energy to this process.

DESCRIPTION OF THE SPECIES AND ITS TREATMENT

Tigriopus californicus is a harpacticoid copepod found in high tidepools in the marine intertidal from Vancouver Island to Baja California. Two species of Tigriopus occur in the British Isles--T. fulvus (Fraser, 1936) and T. brevicornis (comita and Comita, 1966). T. japonicus has been described from Japan by several writers, including Igarashi (1963). Egloff (1967) examined the effects of changes in sex ratio on population growth in T. californicus from the Monterrey area on the west coast.

The morphology of T. californicus has been described at length by Monk (1941), and will only be summarized here. There is great sexual dimorphism in adults; males have geniculate first antennae, by which they can easily be identified after the copepodid V stage. These antennae are used to grasp the female during copulation. Females have narrower antennae; the presence of ovaries and developing eggs creates a dark body coloration which distinguishes the female from the male. Growth is determinate; full body size (about 1.20 mm in length) is reached upon the molt into the copepodid VI, or adult, stage. In the field, animals may appear bright orange, apparently due to their incorporation of carotenoid pigments from ingested plant material.

The life cycle of T. californicus females raised at 20°C in the laboratory is summarized in Table 1. Eggs are held in the brood sac for about 4 days. After hatching, Tigriopus goes through six naupliar and six copepodid stages. Within 20 days, females reach the copepodid IV stage and are seized by mature males. Copulation lasts an average of 5 days. The first egg sac is produced about 3 days later; from 15 to

Table 1. Life cycle of female *Tigriopus californicus*, raised at 20°C in 100% seawater.

Age (days)	Event in Cycle	Female Size ($mm^3 \times 10^{-5}$)	Growth Rate ($mm^3 \times 10^{-5}$/day)
4	Nauplii hatch from brood sac	25	12
20	Female seized by male	270	290
25	Female released by male	1720	340
28	First brood produced	2750	
	(Female produces up to 20 broods after the single copulation)		20
40 to 85	Female releases last brood		
50 to 95	Female dies	3150	

20 consecutive broods may be produced by this single copulation. There is a great deal of variability in both the age of last egg production and in age at death; the former ranges from 40 to 85 days, the latter from 50 to 95 days.

Tigriopus is a detrital feeder. Egloff (1967) has shown that it is not equipped with filter feeding apparatus, even though Gibor (1956), working with an unspecified form of Tigriopus, suggested that selective feeding on living Dunaliella viridis does occur. Generally food does not seem limiting in high tidepools. During the winter, organic debris accumulates from runoff and spray; productivity appears to be high in the late spring and summer, especially among the benthonic diatoms and macro-algae such as Enteromorpha.

There are no known predators on Tigriopus. Splash pools support no fish, and virtually no other crustaceans. Shore birds have not been reported to feed on Tigriopus. Egloff (1967) found that appreciable cannibalism on nauplii occurs, especially under crowded conditions.

Fitness-Related Characters

Life history characters which are related to fitness in T. californicus include developmental time, egg size, sex ratio, number of eggs per clutch, number of clutches, survivorship, and body size (since clutch size may be a function of body size). Measurement of these characters under varied environmental conditions were thought to reflect individual and genotype fitness measures under those circumstances.

The potentially important environmental stresses which may operate on T. californicus are food availability, temperature, salinity, photoperiod, and degree of stability. The methods by which these factors were tested are described in a following section.

Field Studies

Most field observations were made in tidepools at Cape Arago and Shore Acres state parks, near Charleston, Oregon (latitude 43° 20'). A total of 17 pools were examined at these locations, in monthly samples during the period from Junem 1968 to October, 1970. The number of pools sampled on each date varied depending upon whether evaporation had occurred, or on the presence of animals. Table 2 summarizes the locations and sizes of these pools.

Regional populations were sampled at La Jolla, California (latitude about 33° 40') and Pacific Grove, California (latitude about 39° 40'), on March 16 and March 14, 1970, respectively. Additional areas examined for *Tigriopus* populations were Santa Barbara and Eureka; California, and Seaside, Oregon. Only scattered, sparsely-populated pools were found in the first two locations; samples taken at Seaside were not used because of the constraints of laboratory space. Populations there appeared to be similar to those studied at Charleston. Only one set of field data was collected at La Jolla and Pacific Grove. In August of 1970 I was unable to obtain samples fo *Tigriopus* populations at these sites, because the water in every pool had evaporated.

The following data were obtained by examining animals in two replicate 50 ml samples: population density (number per liter); sex ratio (%males); clutch size; egg size (mm^3); and female body size (mm^3). Egg size was estimated as $\pi d^3/6$; female size was estimated as $\pi d^2 h/12$. In addition, temperature, salinity, pH and oxygen concentration were measured. The homogeneity of *Tigriopus* samples was difficult to ensure, because this animal tends to seek the bottom of the pool when the water is disturbed. The average coefficient of variation (SD x 100%/Mean) for all pairs of

Table 2. Locations and sizes of pools sampled for *Tigriopus* at Shore Acres and Cape Arago state parks.

Pool	Average Depth (cm)	Approximate Area (m^2)	Height Above MLLW (m)
Shore Acres (SA)			
1	16	105.0	6.0
2	20	30.0	6.0
3	15	75.0	4.0
4	10	50.0	4.0
5	10	1.0	3.0
Cape Arago (CA)			
1	5	0.05	2.5
2	18	0.15	2.5
3	5	0.2	3.5
4	3	0.1	3.5
5	3	0.1	3.5
6	14	0.2	3.0
7	8	1.0	2.5 [a]
8	5	0.02	2.5
9	6	0.02	2.5
10	8	0.25	2.0 [a]
11	5	0.2	2.0 [a]
12	8	0.2	2.5 [a]

[a] pools located on the leeward side of a large rock

density estimates in the field was 26%.

Egg size and number, and female body size, were determined for 10 females selected at random from each population. Eggs are carried in a single brood sac, encased in a tight membrane. This sac can be teased from the female with a fine glass needle without damaging her. A 30% solution of Chlorox (dilute NaOCl) was used to dssolve the sac membrane (after Egloff, 1967), so that the eggs could be counted and measured under a dissecting microscope.

Sex ratios were based on observation of all adults in each 50 ml sample. The sexual dimorphisms noted earlier made it possible to sex adults without a microscope.

Pool temperature was measured with a laboratory thermometer, which was accurate to 0.1°C. Seasonal temperature ranges for the La Jolla and Pacific Grove areas were obtained from the United States Weather Bureau (1970). Egloff (1967) has shown that pool and air temperatures differ only slightly, due to the shallowness and exposure of splash zone pools. Therefore, the air temperatures obtained from the Weather Bureau were thought to reflect actual pool water temperatures.

Salinity was measured with a hand refractometer, which was accurate to 1.0 o/oo. This device made it possible to determine salinity in the field, and thus avoid the potential effects of evaporation.

Estimates of pH were made using narrow-range Hydrion paper. This technique was compared with a laboratory model pH meter, and found to be accurate to within 0.2 pH units.

Oxygen concentration was measured to within 0.1 ml/liter with a YSI portable polarographic oxygen electrode. Generally, pools were shallow (less than 10 cm deep), and exposed to steady winds. As a result, dissolved oxygen levels were nearly always at saturated levels for a given temperature and salinity.

Laboratory Studies

Population culture series. Laboratory colonies of Tigriopus were established from eight populations: four from Charleston, and two each from La Jolla and Pacific Grove.(see Table 3 for population and region designations). These colonies were started with 10 females on May 1, 1970. Two replicate colonies for each of the eight sources were maintained at 15°, 20° and 25°C (temperatures were held within 1.0°C throughout). Each culture was grown in 500 ml of 100% seawater; this volume was maintained by adding small amounts of deionized distilled water daily. Tetramin brand dried algae and animal matter fishfood was added at least once a week so that detritus was abundant while the populations were increasing. About two weeks after the populations reached what appeared to be peak densities, food was no longer added.

A second series of cultures was set up on July 1, 1970, using females from the populations described above. Two replicates of each of the eight source populations were again established in 500 ml of 100% seawater, but were grown at room temperature, which varied from 15° to 28°C during the study. At irregular intervals, distilled water was added to return each beaker to about 100% seawater. Salinities were allowed to range from 38 o/oo to 85 o/oo during the study. Food was added at irregular intervals throughout, in large quantities.

Every colony was sampled at two-week intervals, for several months. Each census was based on two replicate 50 ml samples, which were treated as described above for field collections. Population data described above were obtained from each pair of samples. Salinity and pH were monitored as in field populations.

Table 3. Designations of populations used in laboratory studies of *Tigriopus*.

Regional Location	Designation	Representative Populations
La Jolla	LJ	I-A, I-H
Pacific Grove	PG	III-C, III-E
Charleston	C	IV-A, IV-E, IV-G, IV-I

These two series were designed to provide information on actual population growth rates, sex ratio, egg number and size, and female size, for Tigriopus from different local and regional populations. This data is useful in identifying ecotypic variation in these variables, and thus, in life history strategies. Females from these cultures enabled me to make comparisons between stable and fluctuating environment effects on this variation.

Food effects. To test the influence of food availability on reproductive functions, a series of seven food concentrations (again, using Tetramin fishfood) was prepared in filtered seawater. This series ranged from 0.013 to 0.220 mg per female per 2 days. One drop (0.02 ml) of each suspension was fed to the appropriate group of replicate females on alternate days.

All of the females used in this experiment came from a laboratory colony set up with animals from Cape Arago. Ten replicate females were isolated during copulation, at each food level. They were raised in separate 30 ml glass vials of 100% filtered seawater at 20°C. The water in each vial was changed once a week to prevent the accumulation of metabolic wastes. Each female was observed daily. When a brood sac developed, the female was removed to moist filter paper. The sac was teased away from the femlae with a glass needle, and she was returned to her vial. This technique proved to be quite satisfcatory; less than 4% mortality occurred from handling, and brood production did not seem to be impaired. Each egg sac was treated as described earlier. All females were observed in this fashion, until death. Total number of clutches and age at death were recorded for each animal.

Photoperiod, temperature, and salinity effects on rate of egg production. Females were tested to determine the possible effects of light, temperature and salinity interactions on reporductive activity. The sudden onset of population increase in the spring suggested that these factors may trigger reproductive and developmental processes. Females were raised under combinations of the following conditions:

Photoperiod: 0, 8 and 14 hours per day
Temperature: 10°, 15°, 20° and 25°C
Salinity: 25%, 50%, 100% and 150% seawater.

Six replicate females were raised under each of the 44 test conditions (at 10°C, only the 0 and 8 hour photoperiods were used). Each animal was monitored daily, until up to eight broods had been produced (most individuals raised at 10°C never produced more than two broods).

Temperature and salinity interactions. A subsequent series of animals was conducted using females from each of the 24 stable cultures (eight source populations, three temperatures). Ten replicate females were raised in each of three salinities (50%, 100% and 150% seawater), at the temperature in which they were cultured (15°, 20° and 25°C). Excess food was present at all times. Egg size and number, number of clutches, and longevity were recorded for each female.

Developmental time, brood sex ratio, and survivorship were estimated for broods from two females selected at random from each of the 24 stable cultures. The females were allowed to acclimate to the test conditions (temperature-salinity combinations mentioned above) for one week. Broods produced after this period of acclimation were allowed to hatch; 25 nauplii were raised from each brood, in 60 ml specimen jars, under constant conditions. Developmental time was measured as the time from the first appearance of a brood sac to the first production of broods by the female offspring. Brood sex ratios were estimated after the offspring had reached maturity (as a result, possible bias in the survival to sexual maturity of males and females may have influenced observed sex ratios). Survivorship was determined on the basis of bi-monthly censuses of each group of offspring.

Effects of density on clutch size. Pearl (1932) and Walker(1967), among others, have shown that interference can reduce reproduction in dense populations. Such interactions may be a function of access to available food, as well as oviposition sites, as in *Nasonia vitripennis*. The production of metabolic wastes has been shown to inhibit egg production in other species.

Two replicates of each of five densities--2, 10, 20, 40, and 80 animals per 25 ml--were raised in 100% seawater at 20°C. Excess food was present in all vials; the water was changed every fourth day. Each vial contained equal numbers of males and females. Mean clutch size and egg volume was measured at four-day intervals, using techniques described earlier. This procedure was followed through four consecutive broods.

Stability effects on life history characters. To investigate possible life history responses to a change from fluctuating to stable environmental conditions, four groups of *Tigriopus* were tested in the laboratory. Table 4 gives the design for this series of tests. Females in the "Before" group were obtained from the 16 laboratory cultures grown at 20° and 25°C, on May 20, 1970 (less than one month after these cultures were established). "After" females were obtained from all 24 stable cultures on October 20, 1970, about six months after those cultures

Table 4. Experimental design for testing for the effects of stability on life history characters in *Tigriopus*.

Background of Test Females			
Before Culture	After Culture	Unstable Culture	Field Populations
	15°C	15°C	15°C
20°C	20°C	20°C	20°C
25°C	25°C	25°C	25°C

were established. Considering overlapping generations, effectively less than 10 generations were raised in the 25°C colonies before the "After" series was conducted. "Unstable" females represented the colonies grown in fluctuating room conditions (that is, fluctuating salinity and temperature conditions). The "Field" group was composed of females collected at Charleston on October 31, 1970; these animals were allowed to acclimate to test temperatures for about two weeks, before they were isolated.

All of these females were raised in 30 ml vials of 100% seawater, with abundant food, until death. Individual fitness-related characters were measured as before. Estimates of developmental time, brood sex ratio, and survivorship were obtained as in a previous section.

Dispersal and desiccation resistance. Egloff (1967) suggested that *Tigriopus* is carried for short distances by the shore crab, *Pachygrapsus crassipes*, as well as by wave action. Inshore currents were thought to transport animals for longer distances. These possibilities were investigated briefly in this study.

Plankton tows were made in the surf zone below *Tigriopus* pools on several occasions in the spring of 1969, with a No. 20 mesh net. No *Tigriopus* were ever observed in these samples, even though the net was dragged across rocky surfaces where animals might be found. In the spring of 1970, 12 large plastic containers were placed in the high intertidal at Cape Arago and Shore Acres. Seven of these were lost to unusually high swells; the other five contained some seawater, but no *Tigriopus* (some other unidentified crustaceans were found). Several *Pachygrapsus* were collected at Cape Arago, near pools containing adult *Tigriopus*. No copepods were found when these crabs were rinsed in seawater and 70% methanol (Egloff, 1967, reported that dilute formalin was effective in removing Tigriopus from the appendages of shore crabs). The magnitude of these efforts was insufficient, of course, to resolve any of these three problems. Further work on dispersibility is needed.

In order to test for desiccation resistance and temperature interactions, animals collected at Cape Arago were raised for one month at room temperature in fingerbowls containing 1 cm of sand and 100 ml of 100% seawater. After a period of population increase, the water in each bowl was allowed to evaporate. Subsequent treatment of these samples is summarized in Table 5.

At no point during this test were larval or adult Tigriopus observed to have survived desiccation for periods of up to three months. Microscopic examination of the residues in each bowl revealed the presence of no identifiable bodies or egg sacs. It may be, of course, that the conditions necessary to successful resistance to, or recovery from, desiccation were not provided. It would appear nonetheless that the preceding observations on dispersal are not valid in fact; dispersal from populations not affected by complete evaporation may be necessary to ensure the survival of the species.

Table 5. Experimental design of test for desiccation resistance in *Tigriopus*.

Colony	Salinity Conditions After Evaporation	Temperature Treatment After Evaporation
1 a, b	All samples rinsed with deionized distilled water; water maintained at 50% normal seawater	10°C throughout
2 a, b		10°/4 weeks; 15°/4 weeks
3 a, b		15°C throughout
4 a, b		15°/4 weeks; Rm. Temp./4 weeks
5 a, b		Rm. Temp. throughout
6 a, b through 10 a, b	Distilled water added to all residues; water maintained at 100% normal seawater	Same series as above
11 a, b through 15 a, b	50% seawater added to all residues; water maintained at 150% normal seawater	Same series as above

RESULTS

Field Observations

Charleston, Oregon. The results of monthly field observations at Charleston are provided in Table 13, in the Appendix. Pool temperatures ranged from a midday high of 27.7°C (82.4°F) in June of 1969, to a midday low of 6.2°C (43.2°F) in November of 1969. A low of about 4°C was observed in January of that year, before regular sampling was begun. Salinity fluctuated greatly throughout the study period; rainfall resulted in salinities as low as zero o/oo, in pools exposed to drainage. High salinities, over 80 o/oo, were observed in April, 1970, in pools least affected by both spray and freshwater runoff. All pools examined were subjected to ranges of from 10 to 45 o/oo; generally, low salinities occurred in winter and spring, high salinities in the summer and fall.

Unusually low pH's were observed at both Cape Arago and Shore Acres (Table 13). Values ranged from 5.0 to 8.6 during the study period. High pH is expected during the day, due to a decrease in carbonic acid levels from photosynthesis. Low pH is usually attributed to the production of carbonic acid by respiration. Doty (1957) states that tidepools may have pH's of 7.5 during the night, while photosynthesis raises pH to 9.0 to 10.0. Emery and Stevenson (1957) pointed out, however, that bacterial formation of organic acids may lower pH to less than 5.7 in estuarine sediments. In pools inhabited by Tigriopus, detrital decomposition may account for low pH values. In addition, CO2 may accumulate from respiration.

Both population density and mean clutch size were highly variable, both between pools and between sampling dates. Densities were low during the period from November through January; by early April, when pool temperatures had reached 18°C, densities of about 2500 adults per liter were observed. After a period of decline (until late July), densities increased further, to over 4500 adults per liter.

Even when developmental time lag was taken into account, there were no significant correlations between population density and either salinity or temperature. Nor was density correlated with clutch size. In fact, in the pool which had the highest density observed in the field (over 15,000 adults per liter), high mean clutch size was also noted (71.3 eggs per clutch). Mean clutch size for all population samples at Charleston was 46.1 ± 20.0. This mean was the same as that reported by Egloff (1967) for <u>Tigriopus</u> populations in the Pacific Grove area. At Charleston, population means ranged from 12.0 to 109.8 eggs per clutch; Egloff found a somewhat higher range of 15 to 140 eggs per clutch at Pacific Grove.

Brood sizes were not correlated with temperature, salinity, or oxygen concentration. Correlations were found between brood size and female body size; larger females produced larger broods ($r = 0.45$; $p < 0.001$). Body size itself was not correlated with any measures of the pool environment, including population density. It is possible that more frequent sampling would have provided a more accurate tracking of possible influences on all three of these biological variables.

No correlation was found between sex ratio and pool temperature. Egloff (1967) had reported that higher temperatures seemed to induce increased male sex ratio. Mean sex ratio for all pools was 45.0 ±14.5%. This is somewhat different than Egloff's observation of 52 ±15% males at Pacific Grove.

Regional populations. Monthly air temperature and rainfall data for La Jolla (San Diego), Pacific Grove (Monterrey), and Charleston (Bandon) during 1970 are summarized in Fig. 1. Air temperatures have been shown by Egloff (1967) to correspond closely to pool temperatures, due to the general shallowness of splash pools, as well as their exposure. Both La Jolla and Pacific Grove received little rain during about half of the year, while Charleston was subjected to only a 2-month period of drought during the summer. However, Charleston did experience temperature ranges at least as wide as those of the more southern locations. La Jolla, although it received the least rain, may have had the most equitable temperature regime: fluctuations were more gradual and less pronounced. In all three areas, it appeared that periodic evaporation of splash pools could be attributed to high temperatures and low rainfall. At Charleston, however, some pools did persist despite these conditions. Nonetheless, it seems unlikely that such pools as CA 6 (Table 13) can be considered stable with respect to environmental conditions.

Data collected at these three locations are summarized in Table 6. Of the physical and chemical data, temperatures differed the most between sites: La Jolla pools showed high temperatures even in March, 1970. Salinity was most variable at Charleston, due to differences in the susceptibility of pools to runoff water. Population density and sex ratio were highest at Pacific Grove, while La Jolla females were largest and carried the largest broods.

No attempt was made to correlate population density with other variables on the basis of this single survey of the three regions. However, I did find that areas differed with respect to both clutch size and body size, as noted above. These two characters were correlated among La Jolla females ($r = 0.72$; $p < 0.02$), and Charleston females

REGIONAL CLIMATOLOGICAL DATA

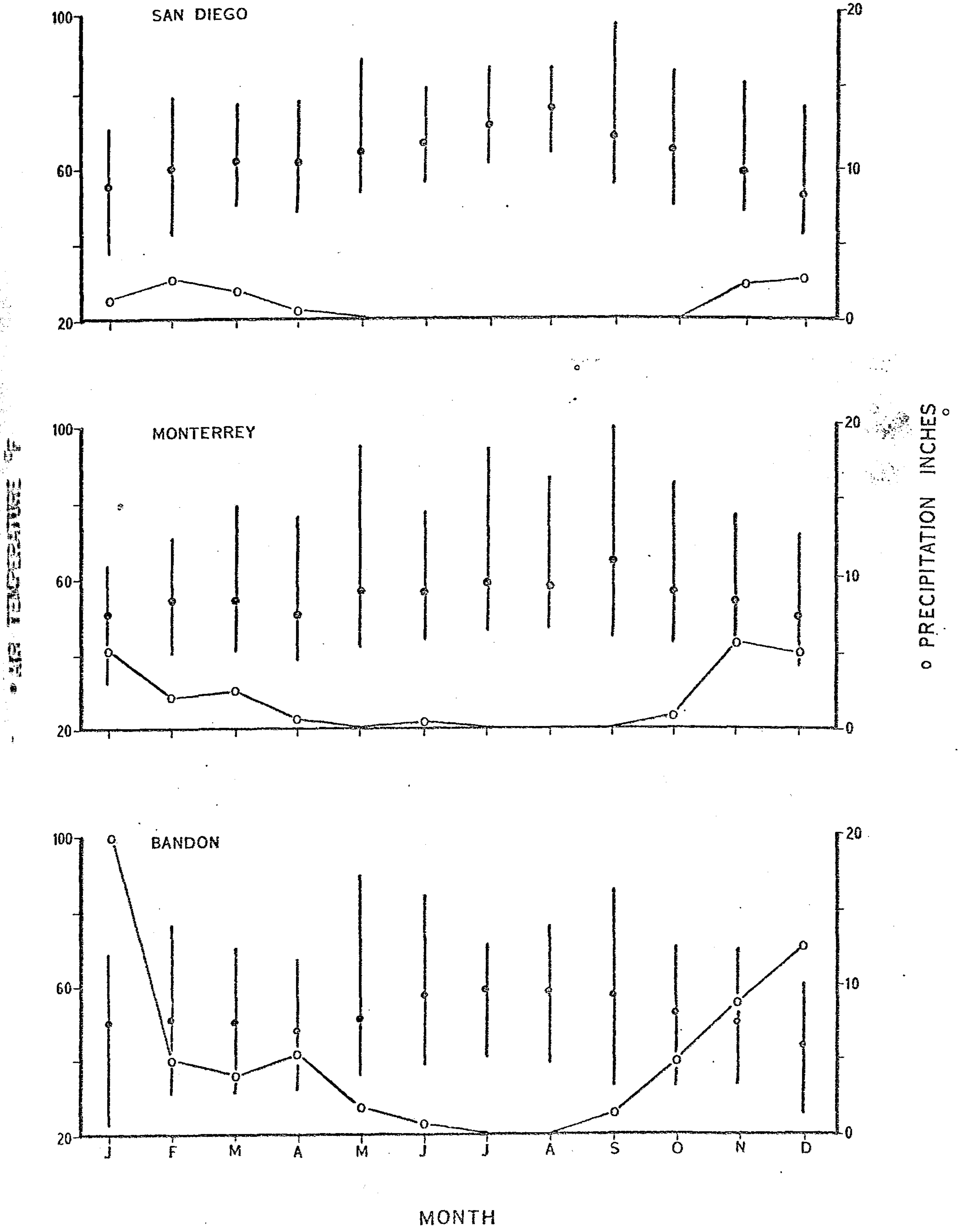


Table 6. Means and standard deviations for data collected at three regional locations during the spring of 1970. Each observation is the average of 10 samples.

Measurement	Regional Population		
	La Jolla	Pacific Grove	Charleston
Temperature °C	25.9±0.8	19.8±2.5	17.5±1.0
Oxygen ml/liter	4.1±0.1	4.7±0.4	5.3±0.8
Salinity o/oo	42.4±2.3	41.7±2.3	39.7±20.4
pH	6.0±0.4	6.1±0.8	6.0±0.4
Population Density No/liter	521±474	1742±1928	366±639
Sex Ratio % male	44.5±5.5	49.9±10.1	40.6±13.6
Female Size mm3	0.0387± 0.0014	0.0356± 0.0010	0.0328± 0.0009
Clutch Size	84.3±5.0	38.7±3.2	61.1±7.9

($r = 0.80$; $p < 0.01$), and perhaps among Pacific Grove females ($r = 0.50$; $0.10 > p > 0.05$). The hierarchial ANOVA for brood size is summarized in Appendix Table 14. The greatest source of variance was attributed to between-region differences. Analysis of body sizes showed that the three regions differed in this respect also ($F_{2,26\ df} = 12.43$; $p < 0.01$).

Laboratory Studies

Food effects on reproduction. Food abundance affects egg production, as shown in Fig. 2. When less than 0.022 mg dry weight of Tetramin was provided per female every other day, total egg volume fell off sharply (Fig. 2-A). This was reflected by the absence of linearity in these points ($F_{5,50\ df} = 3.26$; $p < 0.01$). Egg production did not increase with increased food, above the observed critical level. These food effects were not attributable to changes in egg size, but were due to clutch size as seen in Fig. 2-B. Again, these points did not fit a linear regression ($F_{5,50\ df} = 2.96$; $p < 0.01$); however, there were significant differences between clutch sizes at the seven food levels ($F_{6,50\ df} = 8.03$; $p < 0.001$). The number of clutches produced was not affected by food concentration (Fig. 2-B). That is, food paucity reduced the number of eggs per clutch, rather than clutch number or egg size. This would allow flexibility in reproductive effort, without limiting either the ability to produce subsequent clutches, or the ability to provide eggs with adequate nutrition for development. In subsequent tests, at least 0.033 mg Tetramin were provided per adult *Tigriopus*, every other day.

Photoperiod, temperature, and salinity effects on rate of egg production. The results of a three-way ANOVA for the test for the

EFFECTS OF FOOD ON EGG PRODUCTION

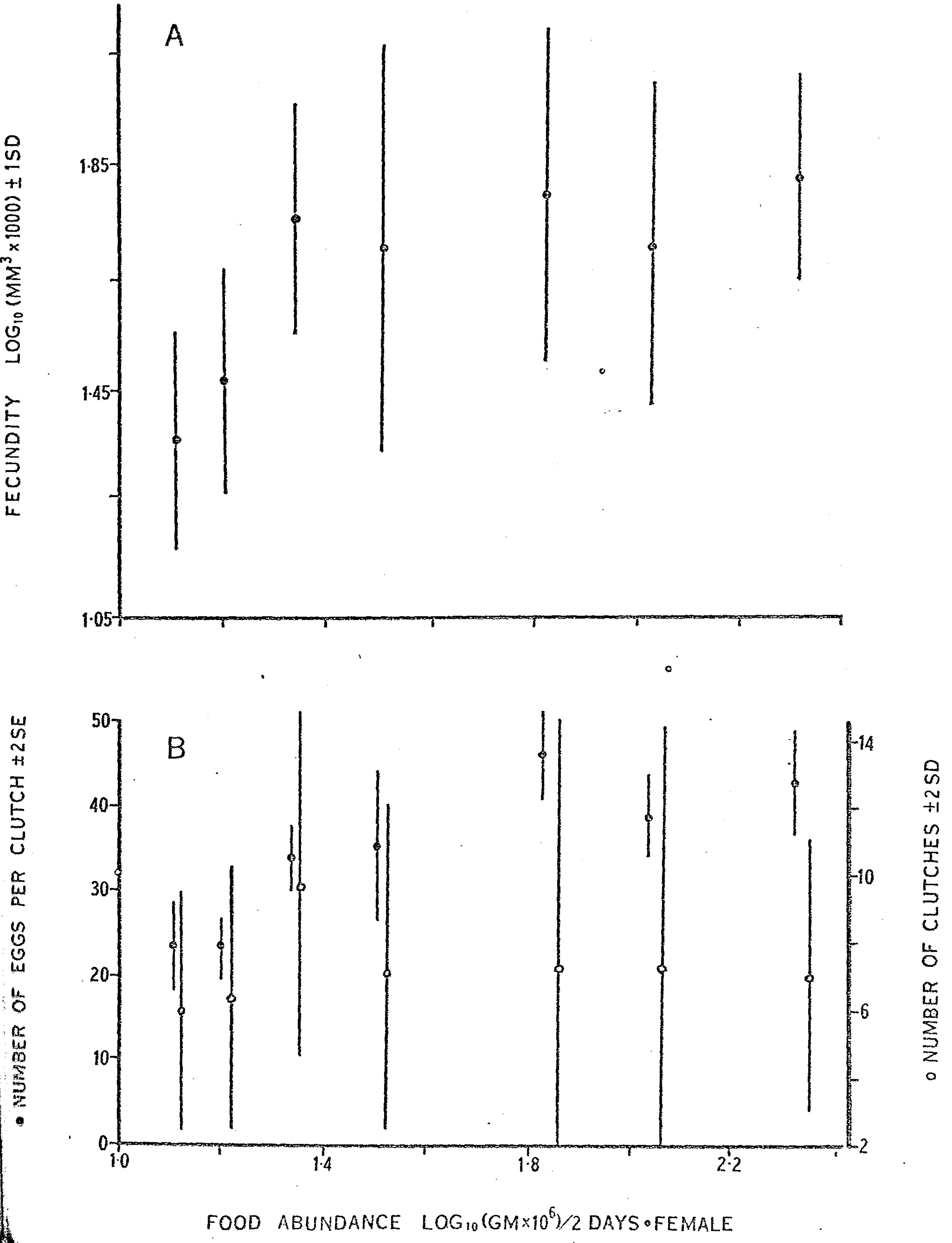


Fig. 2

interaction effects of these three variables are summarized in Appendix Table 15; the actual data are presented in Table 7. Light had no effect on rate of egg production, by itself or in combination with either salinity or temperature. The temperature-salinity interaction, however, was highly significant. Maximum rate of egg production occurred at 25°C, in 100% seawater. In 150% seawater, egg production was fastest at 20°C, suggesting that increased salinity stressed the metabolism of females at 25°C. Similarly, in 25% seawater, brood production was limited. Low temperatures inhibited egg production also; few broods were formed at 10°C, under all other conditions. Optimal conditions for egg production appeared to be 20°C, 100% seawater.

Temperature-salinity interactions. Both temperature and salinity had significant effects on total egg volume, as shown in Fig. 3. In order to establish a frame of reference to compare temperature effects at different salinities, the origin of each line in Fig. 3 was set at 50% seawater. Subsequent points represent the percent deviation from the 50% observations. The relative positions of lines in Fig. 3-A are consistent with the ranking of actual fecundity values. Table 8 summarizes a three-way ANOVA for fecundity.

The gross effects of salinity were not significant; the temperature-salinity and population-salinity interactions were significant. Total egg volume was highest in 150% seawater, 15°C conditions, and lowest in 150% seawater, 25°C conditions. This may suggest that metabolic stresses are lower under the former conditions, as has been reported for some shrimps by Kinne (1964). Population differences with respect to fecundity were significant, over all combinations of temperature and salinity. La Jolla females produced a greater volume of eggs than did

Table 7. Effects of Photoperiod, Temperature, and Salinity on the Rate of Egg Production. Rate is expressed as the average number of eggs produced per day per female ± its standard deviation.

Temperature °C	Salinity 25%			50%			100%			150%		
	0 hrs	8 hrs	14 hrs	0 hrs	8 hrs	14 hrs	0 hrs	8 hrs	14 hrs	0 hrs	8 hrs	14 hrs
10°C	a	a	b	0.96 ±0.14	3.23 ±1.11	b	4.77 ±1.07	3.85 ±1.73	b	0.64 ±0.19	2.36 ±1.61	b
15°C	1.62 ±0.69	1.20 ±0.87	1.34 ±0.55	4.97 ±1.96	10.47 ±3.25	8.94 ±3.11	12.35 ±1.49	15.53 ±3.28	15.47 ±4.35	18.57 ±3.44	8.46 ±3.03	10.87 ±4.86
20°C	0.63 ±0.20	2.72 ±1.11	1.71 ±0.41	16.76 ±3.30	17.02 ±8.27	16.35 ±5.71	18.50 ±5.55	20.09 ±6.13	22.08 ±4.31	22.80 ±4.91	20.14 ±6.54	17.82 ±5.35
25°C	1.35 ±1.16	4.07 ±0.61	1.27 ±0.19	14.48 ±3.29	12.16 ±4.80	14.62 ±5.99	26.70 ±3.45	25.63 ±3.08	21.94 ±6.77	16.31 ±6.70	14.35 ±7.04	13.67 ±4.23

a No egg production observed during the test period

b No females tested under these conditions

SALINITY-TEMPERATURE EFFECTS ON EGG PRODUCTION

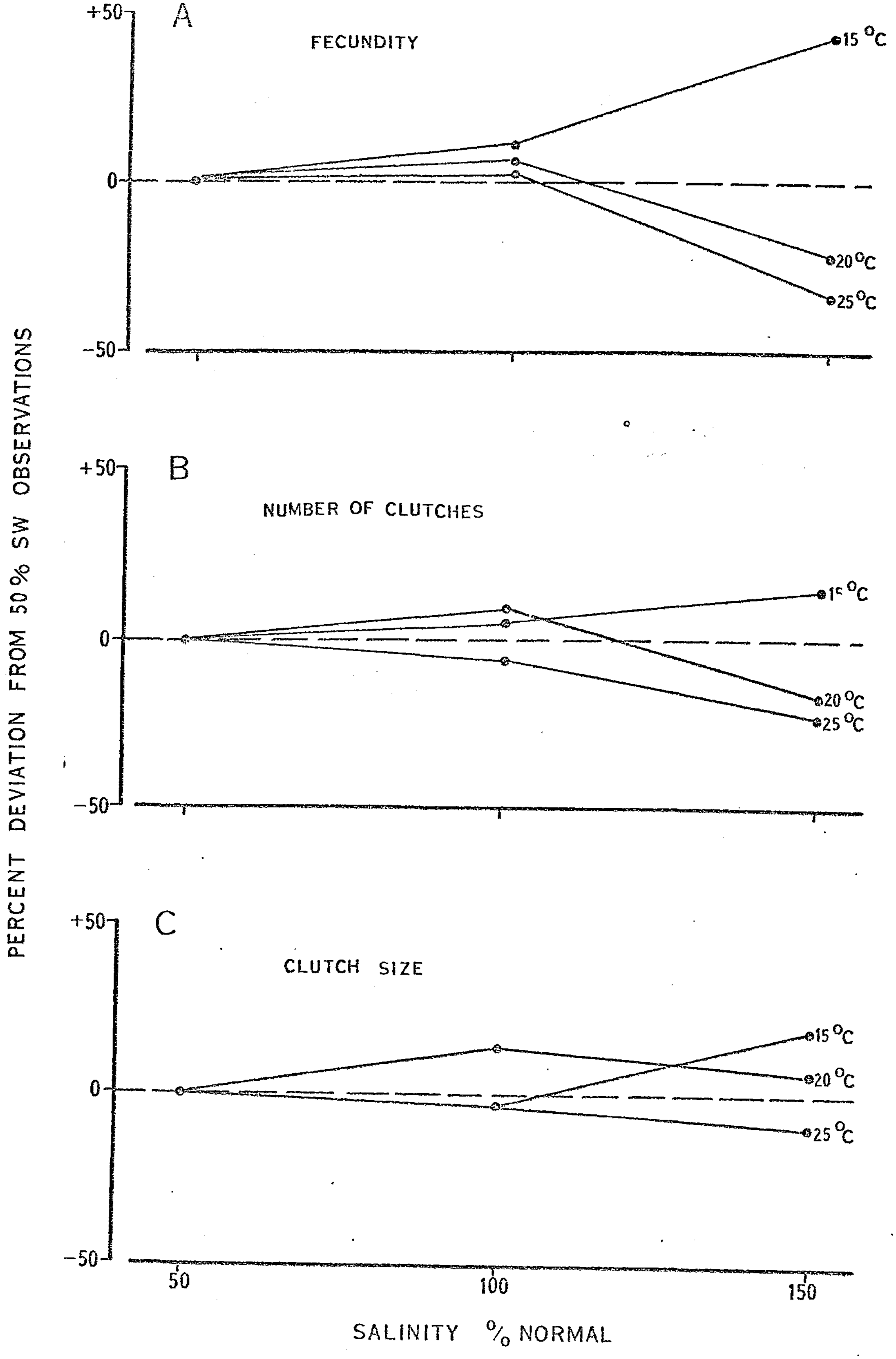


Fig. 3

Table 8. Components of three-way ANOVA of temperature, salinity and population effects on fecundity.

Source of Variance	df	SS	MS	F
Main Effects:				
Temperature	2	1.143	0.572	47.67 [a]
Salinity	2	0.059	0.030	NS
Population	7	0.754	0.108	9.00 [a]
First Order Effects:				
Temperature-Salinity	4	0.401	0.100	8.33 [a]
Temperature-Population	14	0.686	0.049	4.08 [a]
Salinity-Population	14	0.547	0.039	3.25 [b]
Second Order Effects:				
Temperature-Salinity-Population	28	0.323	0.012	

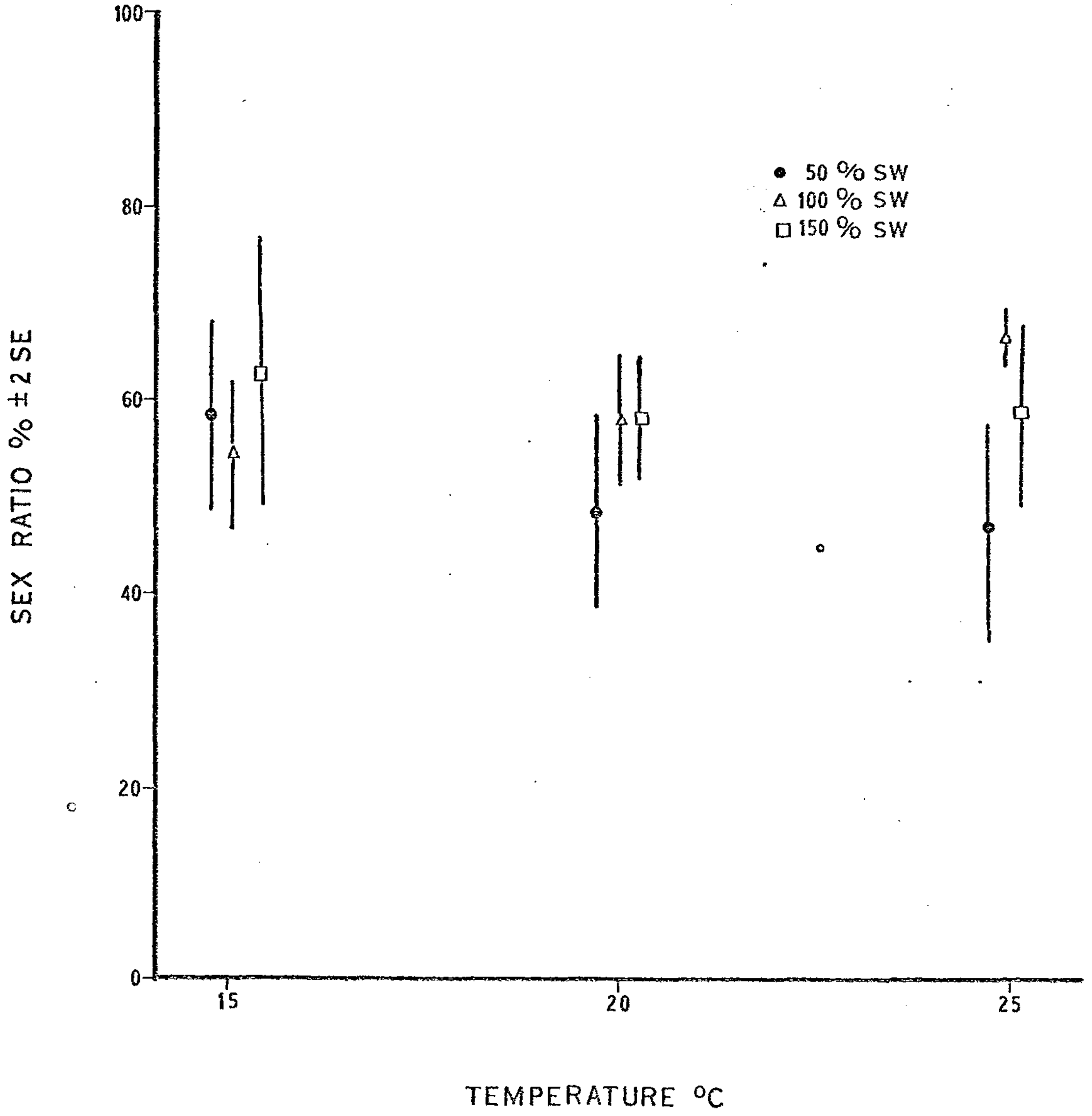
a $p < 0.001$

b $p < 0.005$

other females.

Increased fecundity resulted from increased number of clutches and increased clutch size (Fig. 3-B, 3-C). Egg size did not vary under any conditions. Analyses of these data are loctaed in Tables 16, 17, and 18, respectively, in the Appendix. The gross effects of salinity on clutch size were not significant. However, significant interactions with both temperature and population indicated that salinity did affect clutch size, depending upon water temperature and location. Clutch size was highest among La Jolla females; this was consistent with earlier observations of field collections. The number of clutches produced was affected by all salinity, temperature, and population interactions. Generally, as salinity increased, clutch number decreased; the same was true for temperature effects. While La Jolla females produced more clutches than either Pacific Grove or Charleston females, they too were adversely affected by the 25°C, 150% seawater combination.

Observations of the effects of temperature and salinity on sex ratio were not completely consistent with those of Egloff (1967). Male sex ratio decreased with temperature in 50% seawater, and increased with temperature in 100% seawater (Fig. 4); none of the temperature, salinity or population interactions were significant, however (analysis of these data is summarized in Appendix Table 19). Moreover, in this test series, male sex ratios were not generally higher at 25°C, as reported by Egloff. In an earlier test, however, in which animals were raised only in 100% seawater, male sex ratios were 0.54 at 15°C, 0.59 at 20°C, and 0.66 at 25°C; these means differed significantly despite large variances ($F_{2,70\ df} = 5.22$; $p < 0.001$). This inconsistency in experimental results may have been created by differential male and female survivorship in



TEMPERATURE-SALINITY EFFECTS ON MALE SEX RATIO

Fig. 4

response to extreme temperature-salinity conditions.

Developmental time was affected by temperature (Fig. 5), but not by salinity (analysis provided in Appendix Table 20). Although developmental time decreased as temperature increased, the relationship was not linear: the decrease in time from 15° to 20°C was not as great as the decrease from 20° to 25°C. The average developmental time was about 18 days at 25°C, 27 days at 20°C, and 32 days at 15°C. Individual populations differed with respect to developmental time, but there was no geographic effect on this variable in Tigriopus.

Longevity to 10% survivorship was also affected by temperature, and not by salinity, as shown in Fig. 6. Populations did not differ with respect to longevity. Longevity was 129.4 ± 16.9 days at 15°C, 116.8 ± 10.2 days at 20°C, and 85.7 ± 13.7 days at 25°C; it appeared that the 20°C, 100% seawater condition was most equitable, as reflected by the low coefficient of variation of longevity under that set of conditions (about 9%). Survivorship of adult males was the same as that of adult females.

The intrinsic rate of increase, r, increased linearly with temperature (Fig. 7). Sex ratio effects on r have been described elsewhere (Egloff, 1967); Fig. 7 shows how observed sex ratios, as contrasted with 50% sex ratios, affected the calculations of r values. The sex ratios used here were obtained from broods raised in 100% seawater only (temperature effects for these animals were described above). Actual females sex ratios were less than 50%, and resulted in lower r values. Despite decreased numerical fecundity and survivorship at 25°C, r increased, due to shorter developmental time. Developmental time had a major effect on maternity functions, and thus, on rates of increase.

Intrinsic rate of increase was not affected by salinity (Fig. 8).

DEVELOPMENTAL TIME VS TEMPERATURE

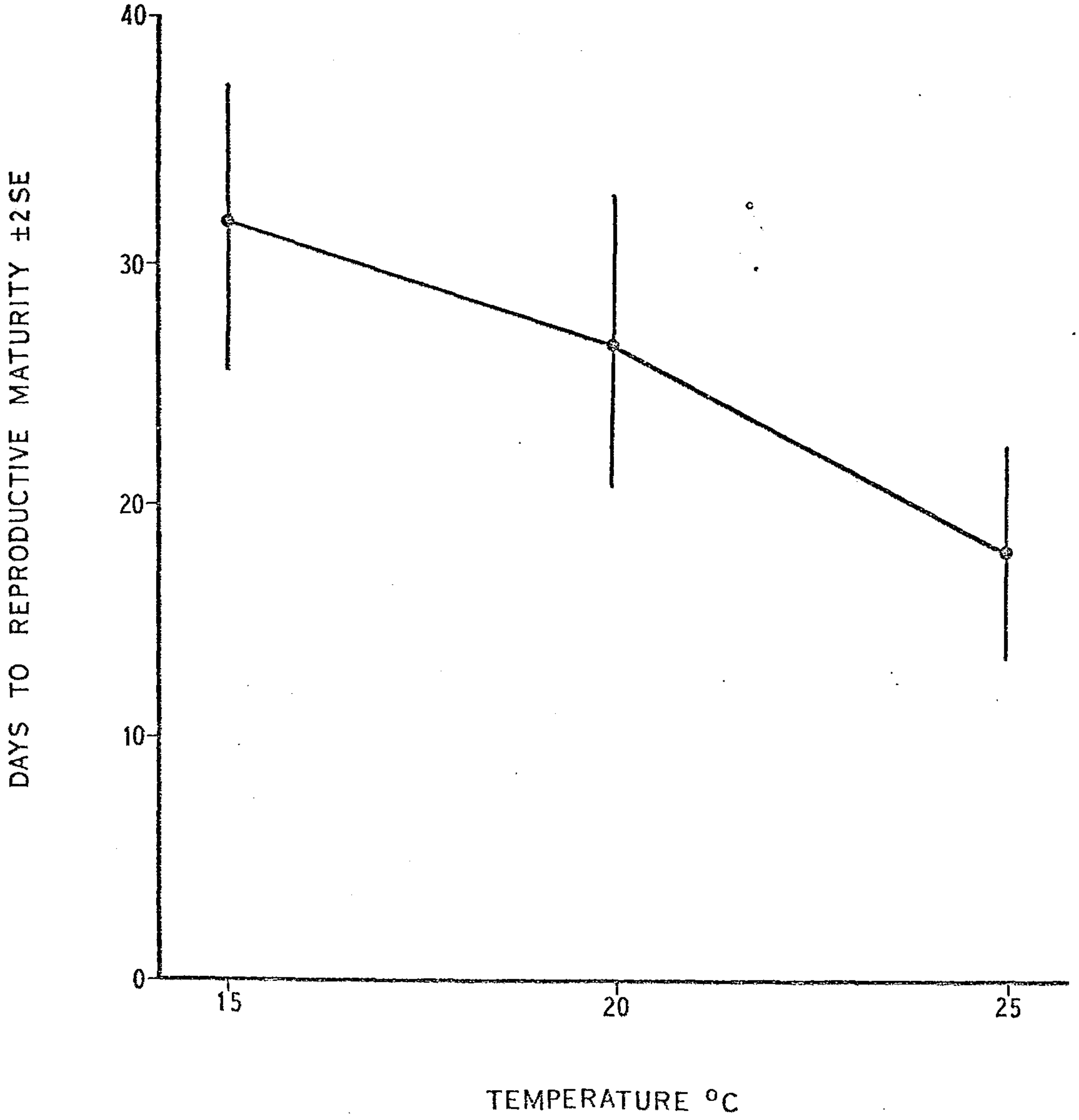
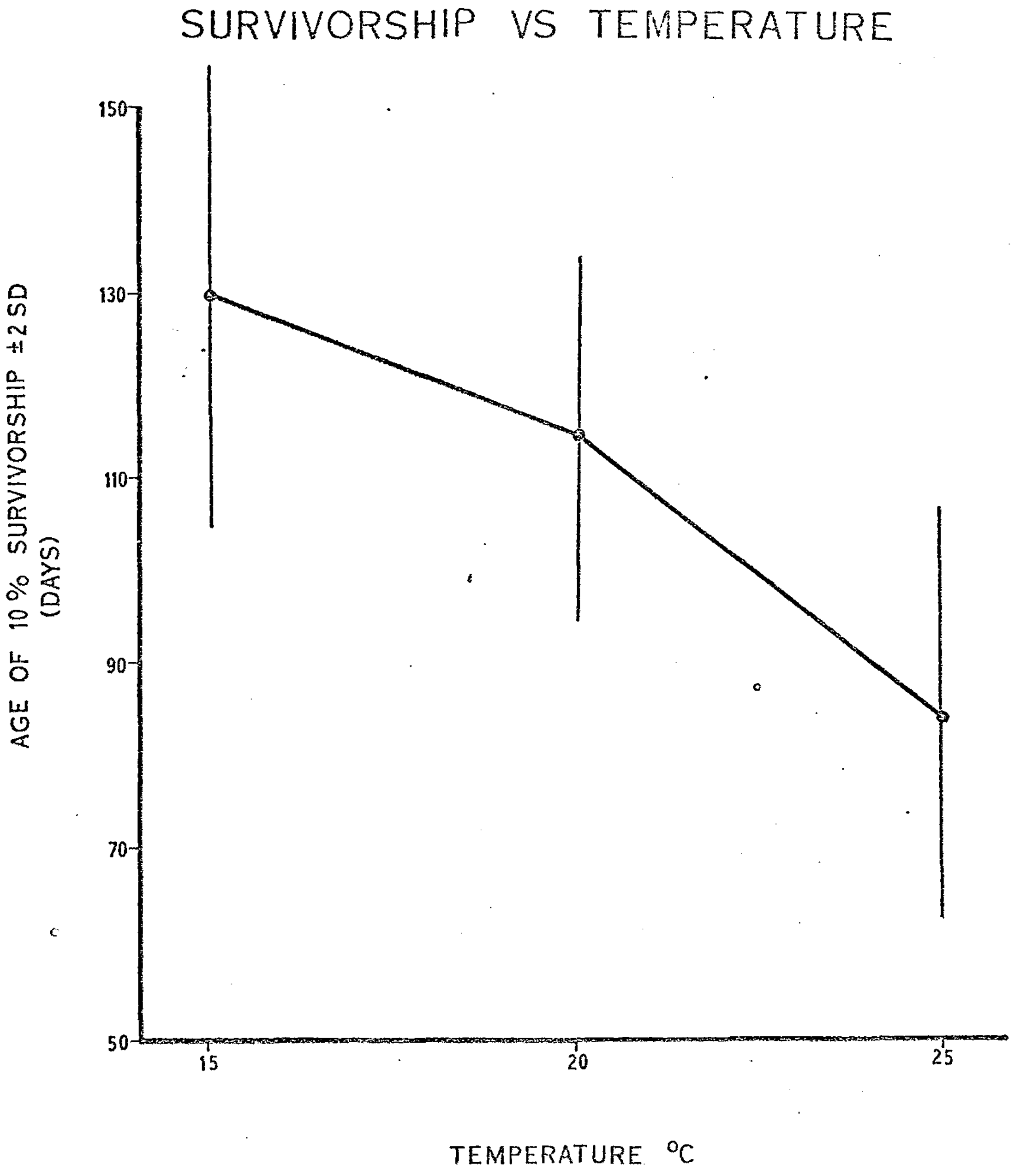
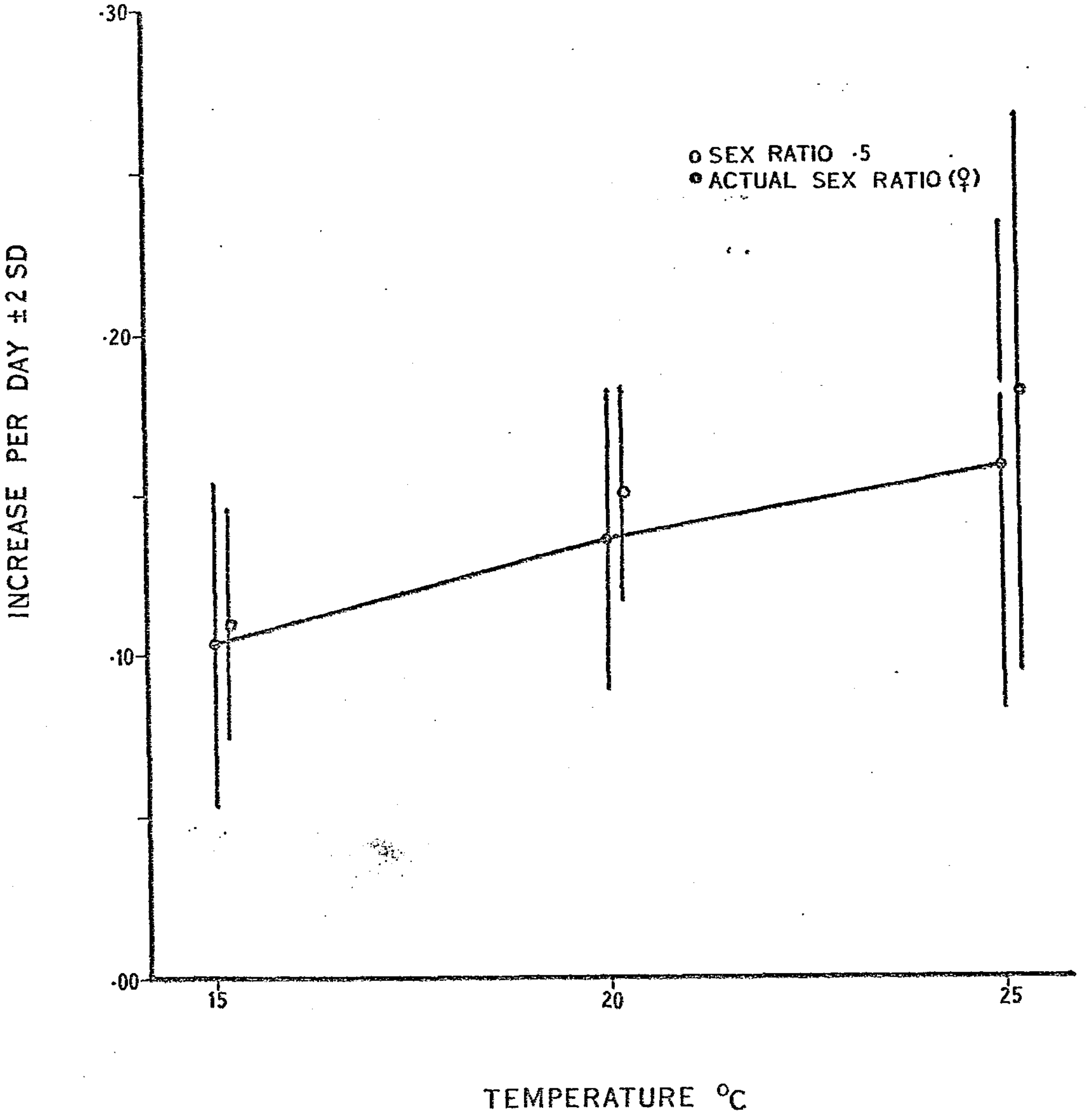


Fig. 2


SURVIVORSHIP VS TEMPERATURE
AGE OF 10 % SURVIVORSHIP ±2 SD (DAYS)
150
130
110
90
70
50
15
20
25
TEMPERATURE °C



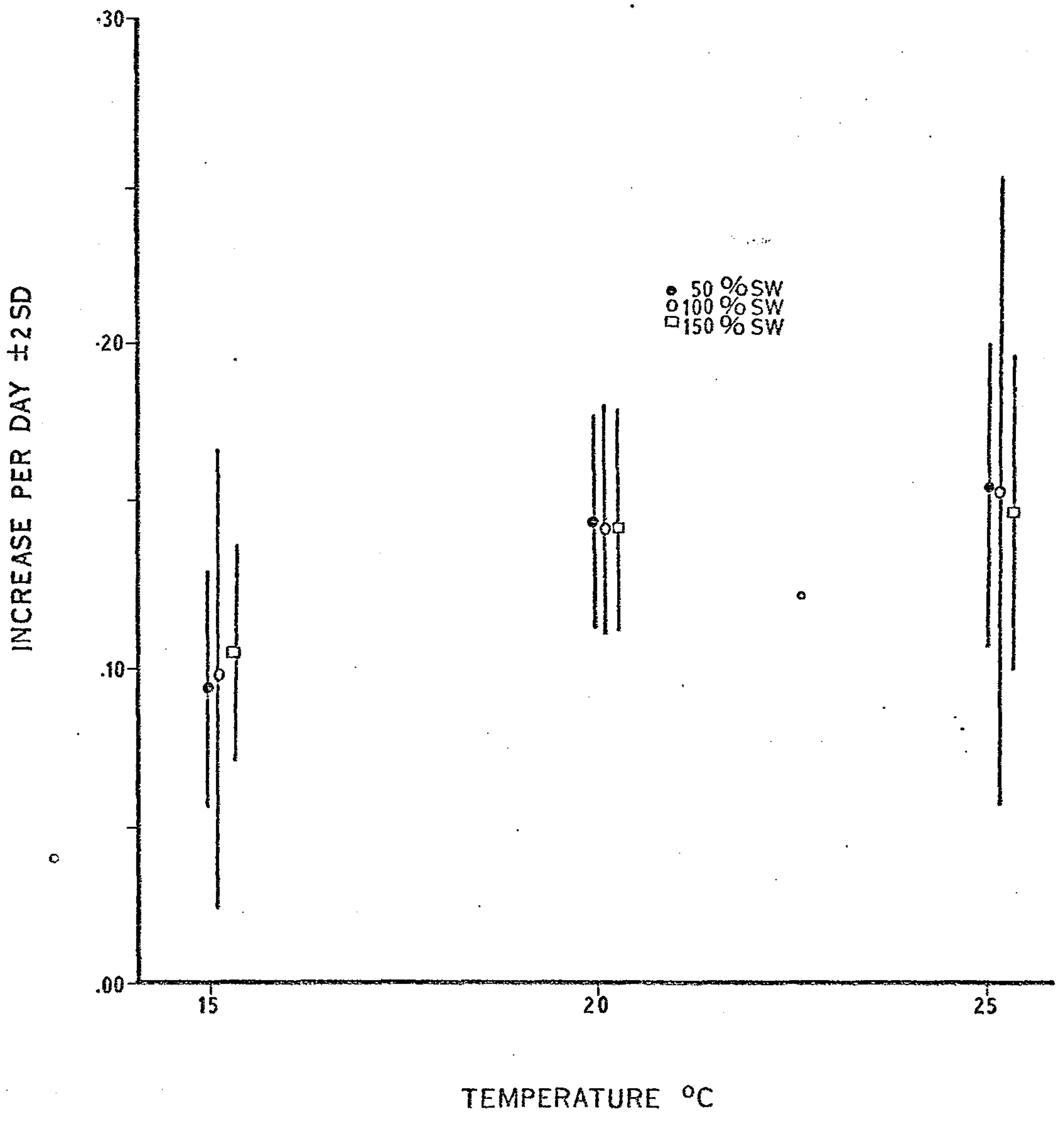
INTRINSIC RATE OF INCREASE VS TEMPERATURE

Fig. 7

Analysis of this series of r determinations is summarized in Appendix Table 21. Neither the gross nor the interaction effects of salinity on r were significant, despite increased fecundity in 150% seawater, at 15°C.

Populations differed with respect to r in the latter series, but not in the former. In both cases, it appeared that individual populations differed more from each other than did regions.

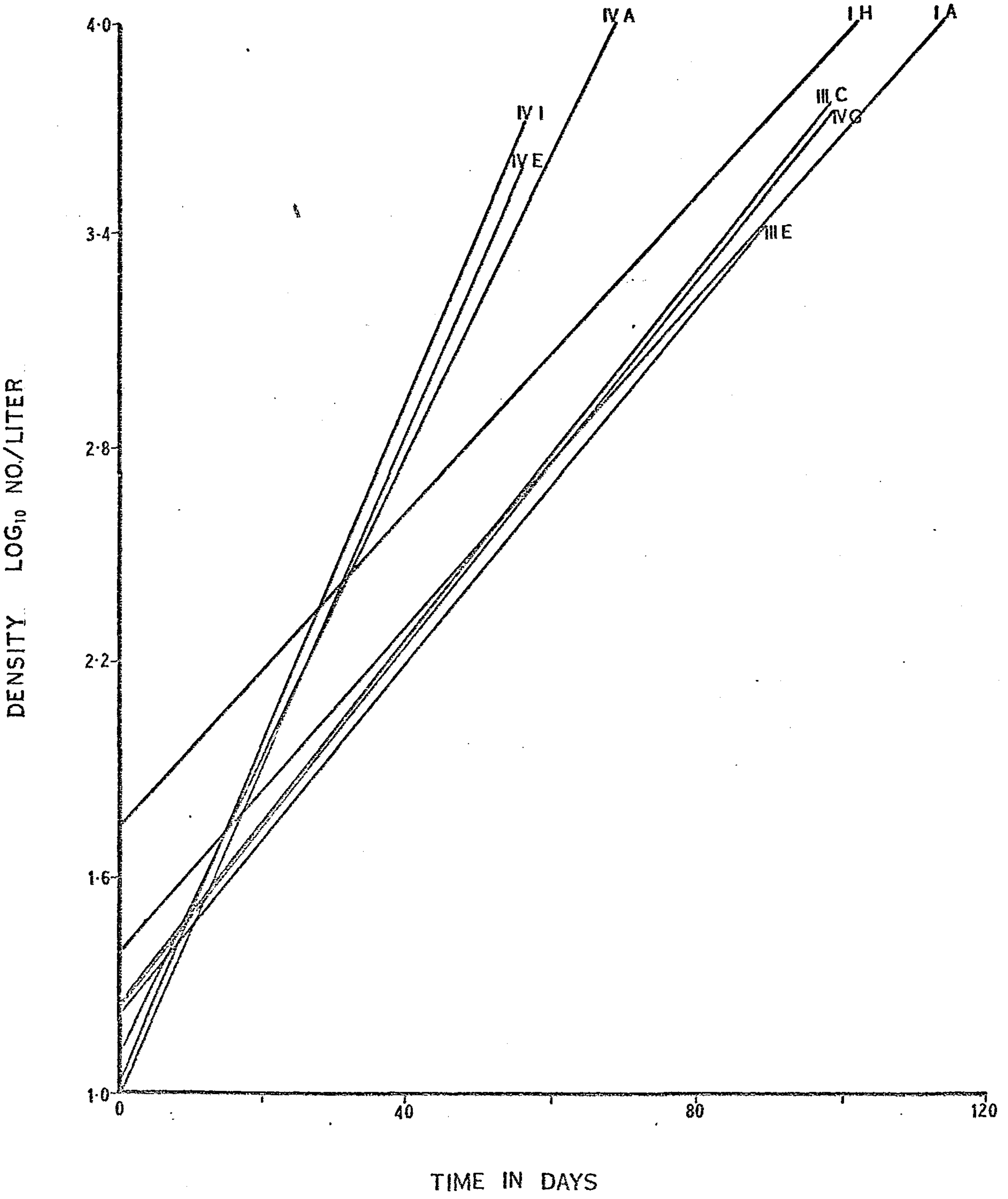
Temperature effects on colony population increase. Regional differences may have existed in estimates of population growth rates based on bi-monthly censuses of laboratory cultures. Results of these censuses are summarized in Figs. 9, 10, and 11. Each of these lines represents the mean rate of actual population growth during the initial period of exponential increase. These regressions (density vs. time) are not different from one another at any temperature. It did appear, however, that La Jolla populations did poorly at 15°C, while Charleston populations generally increased rapidly at this temperature. Pacific Grove populations were intermediate between the other locations. The populations were very similar at 20°C. Differences were again found at 25°C: two of the Charleston populations increased more slowly at this temperature than at 15°C. The two other Charleston colonies grew more rapidly than either than either La Jolla or Pacific Grove populations at 25°C. One of these (IV-G), however, did not persist at 25°C; both replicates decreased after the 40th day, and never recovered. In addition, the other colony (IV-I) was generally more similar to La Jolla and Pacific Grove populations than to other Charleston populations. The southern populations increased most rapidly at 25°C, as was expected on the basis of earlier estimates of temperature effects on r.



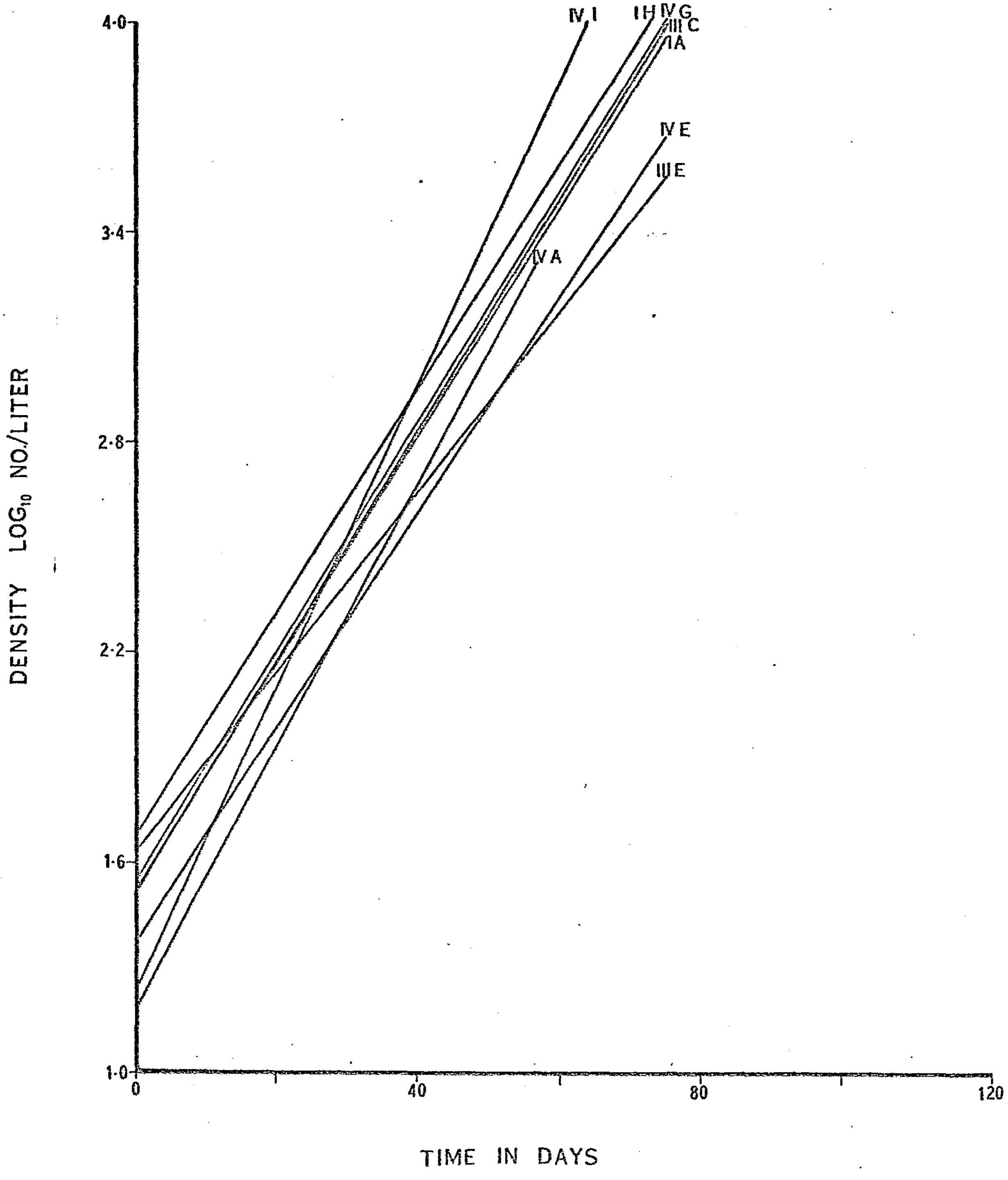
INTRINSIC RATE OF INCREASE

Fig. 2

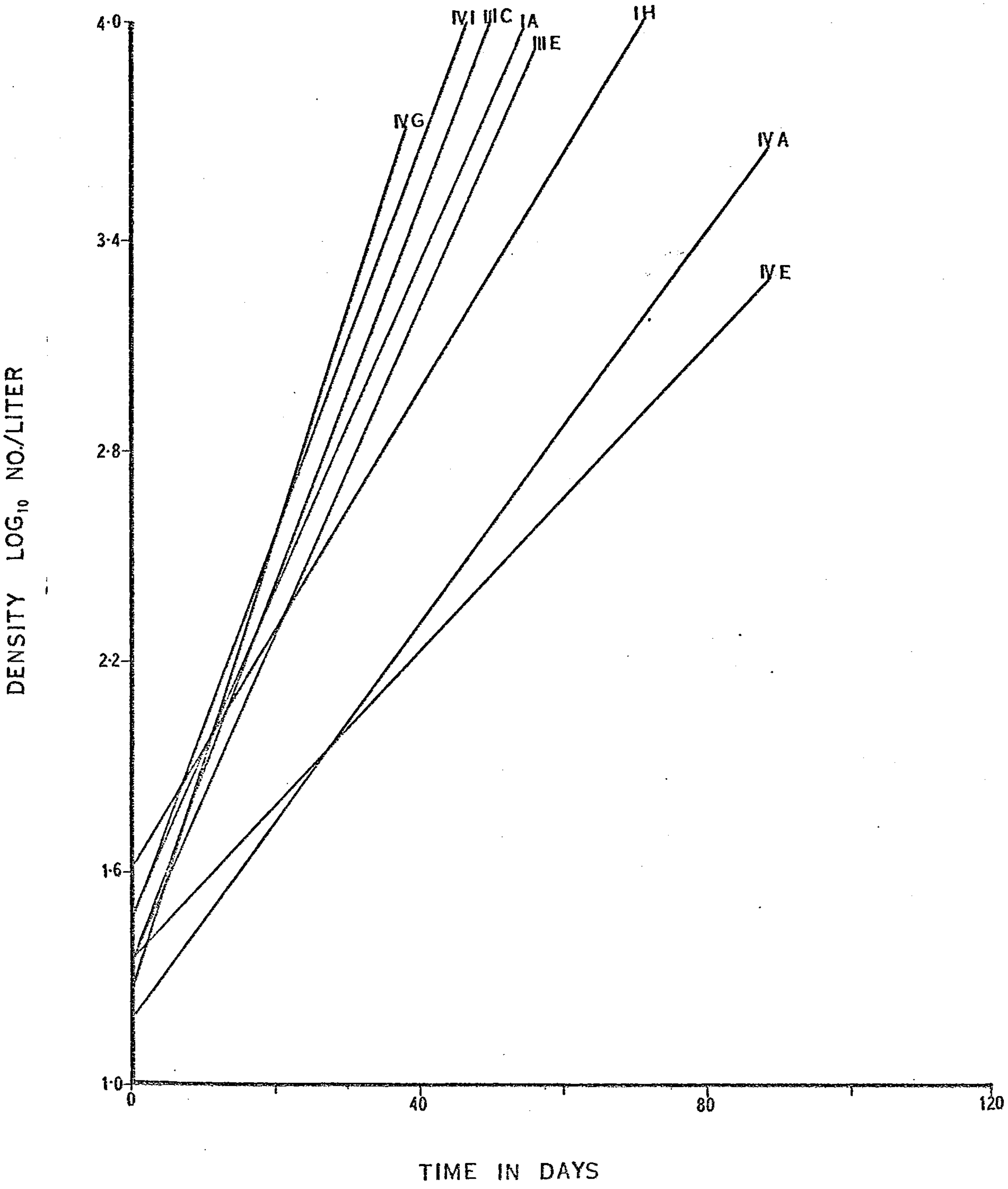
INITIAL POPULATION GROWTH RATES—15 C



INITIAL POPULATION GROWTH RATES–20C



INITIAL POPULATION GROWTH RATES–25C



The lack of correspondence between calculated r values and estimated rates of increase in *Tigriopus* colonies is unaccounted for. Temperature-density effects on survivorship may operate differently on animals from different locations. As a result, errors in the assumptions underlying the estimates of actual rates of increase are possible sources for discrepancies.

Density effects on clutch size. Clutch size is a linearly decreasing function of population density (Fig. 12). At the same time, variability increases with density. That is, the ability of individuals to accommodate increased interference and other density effects was not uniform in the populations tested. At the highest test density (which was similar to densities observed in field and laboratory samples) the coefficient of variation was about 41%. Analysis of these data is summarized in Table 22 in the Appendix.

Stability effects on life history characters. Generally, culturing colonies of *Tigriopus* under stable laboratory conditions had no effect on fitness-related characters (Table 9). No differences were observed between treatments (Before, After, Unstable, Field females), with respect to developmental time, fecundity, sex ratio, and survivorship. Slight differences in fecundity did occur between Before and After females, however. Volumetric fecundity was higher among Before females from both Pacific Grove and Charleston ($t_{62\ df} = 2.56$; $p < 0.01$ for Pacific Grove; $t_{122\ df} = 3.51$; $p < 0.001$ for Charleston). Before and After fecundities were similar among La Jolla females ($t_{68\ df} = 1.67$; $p < 0.05$).

Female body size differed with respect to treatment ($F_{3,40\ df} = 6.8$; $p < 0.001$). However, most of this difference was apparently due to original field measurements. Animals collected in field populations

EFFECTS OF DENSITY ON CLUTCH SIZE

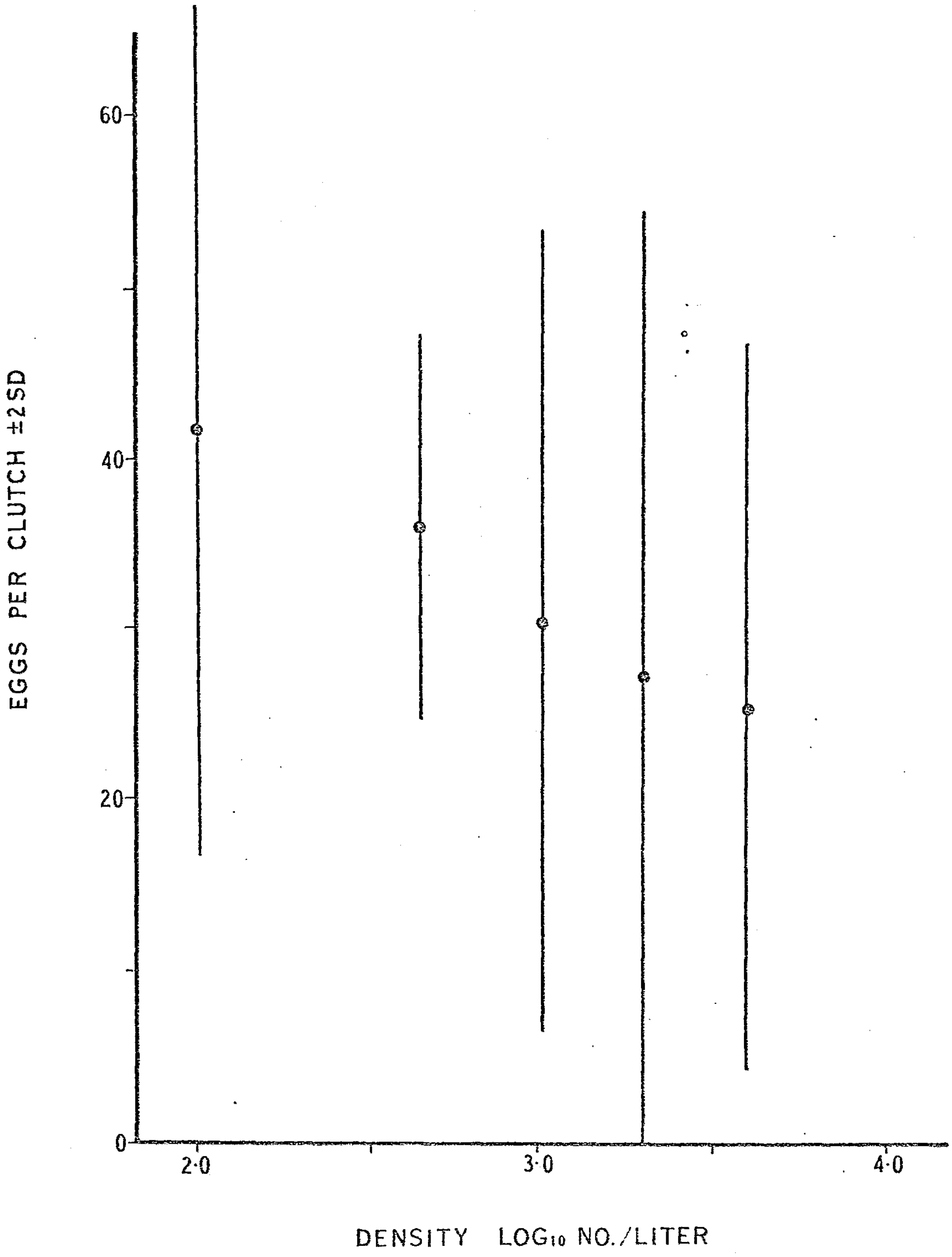


Table 9. Summary of means, standard deviations, and significance of sources of variation in fitness-related characters in _Tigriopus_ _californicus_.

Test Conditions		Developmental Time (days)	Longevity (days)	Body Size [a] (mm^3)	Male Sex Ratio (%)	Fecundity (mm^3)
		Life History Character				
Before:						
	20°C	28.8 ± 3.2	108.9 ± 6.1	0.0359 ± 0.0065	0.53 ± 0.06	0.070 ± 0.024
	25°C	18.6 ± 2.0	78.9 ± 15.0		0.59 ± 0.09	0.064 ± 0.016
After:	15°C	32.4 ± 3.2	130.7 ± 17.9	0.0291 ± 0.0048	0.64 ± 0.21	0.068 ± 0.042
	20°C	27.6 ± 1.1	107.3 ± 14.7		0.71 ± 0.23	0.061 ± 0.031
	25°C	17.6 ± 1.1	84.2 ± 9.6		0.74 ± 0.12	0.044 ± 0.025
Unstable:	15°C	32.0 ± 2.1	128.6 ± 17.1	0.0250 ± 0.0016	0.48 ± 0.13	0.044 ± 0.017
	20°C	25.2 ± 1.7	125.6 ± 4.9		0.61 ± 0.11	0.030 ± 0.014
	25°C	18.4 ± 1.2	94.1 ± 12.8		0.69 ± 0.07	0.037 ± 0.010
Field:	15°C	32.4 ± 0.9	125.0 ± 20.5	0.0283 ± 0.0059	0.44 ± 0.16	0.082 ± 0.017
	20°C	25.1 ± 0.8	119.0 ± 2.5		0.70 ± 0.18	0.042 ± 0.009
	25°C	19.9 ± 1.9	75.0 ± 6.3		0.57 ± 0.08	0.035 ± 0.008

Table 9. (continued)

	Developmental Time	Longevity	Body Size	Male Sex Ratio	Fecundity
Source of Variation:					
Between Populations	NS	NS	NS	NS	NS
Between Treatments	NS	NS	$p \leq 0.001$	NS	NS

[a] Body size estimates obtained from combined temperature data.

seemed to be more robust than laboratory animals, although females cultured at 15°C were larger also. Significant temperature effects on body size were not found overall, however.

These results are difficult to evaluate for two reasons: (1) the number of generations may have been insufficient for observable effects of directional selection to have occurred; (2) density fluctuations in stable cultures may have been great enough to simulate unstable environmental conditions, so that selection would not have operated differently enough on the four treatments. Further experimentation, under more rigidly controlled conditions, may reveal whether the presence of stable conditions can cause shifts in fitness-related characters in this species.

Variability in life history characters. According to Fisher (1929), strong natural selection for a character will result in decreased variability in that character. A good measure of variability is the coefficient of variation, or the percent of the mean represented by the standard deviation. Coefficients for fitness-related characters in Tigriopus over all sets of laboratory conditions are summarized in Table 10. Developmental time was least variable, as would be predicted for opportunistic species like Tigriopus. Egg size was also highly canalized, but fecundity was variable, due to high variability in both clutch size and number of clutches produced. Clutch number exhibited the greatest variability (over 46%). To determine whether this variability was actually a characteristic of Tigriopus females, and not of handling during laboratory tests, a hierarchial ANOVA was performed on these data; the analysis is summarized in Appendix Table 23. In fact, the variance due to series effects (time of handling) was not as great

Table 10. Coefficients of Variation for Fitness-related Life History Characters in *Tigriopus californicus*, Averaged Over All Sets of Laboratory Conditions.

Life History Character	Coefficient of Variation (%)
Developmental time	7.0
Egg size	8.2
Longevity	11.3
Body size	15.6
Sex ratio	22.7
Clutch size	33.2
Number of clutches	46.5
(Volumetric fecundity)	(37.2)

as that due to populational differences in the number of clutches produced. It appeared that experimental technique contributed the least to total variance in this character, while individual differences contributed the most.

Prolonged brood production thus was not highly selected for in this species; this is consistent with the observation that r was least sensitive to late-produced broods, regardless of their size.

Phenotypic plasticity. The ability of genotype expression to be altered by environmental changes was estimated on the basis of temperature-salinity interaction effects on females cultured under stable laboratory conditions. These estimates were based on the assumption that genetic variability decreases in response to environmental stability and extensive inbreeding due to founder effects. No real evidence that inbreeding was sufficient to generate population differences was obtained, however. Table 11 contains the results of these estimates. Tigriopus females were highly plastic over the range of temperature conditions, but exhibited responses to varied salinity only in the number of clutches produced, and perhaps, in sex ratio. Plasticity was demonstrated in clutch size, number of clutches, and perhaps developmental time, when temperature-salinity interactions were considered. Egg size was not affected by any set of environmental conditions.

It is possible that these observations were the result of polymorphisms in the populations studied, rather than phenotypic plasticity, since sophisticated culture methods designed to increase homogeneity were not feasible in this study. Breeding tests and possibly the use of electrophoresis (in spite of small animal size) would be valuable in in identifying the degree of genetic variability in this species.

Table 11. Phenotypic Plasticity in Tigriopus, Estimated as the Ability of Fitness-related Characters to be Altered by Different Environmental Conditions.

Life History Character	Source of Differences		
	Temperature	Salinity	Temperature-Salinity
Developmental time	$p < 0.001$	NS	$0.05 < p < 0.10$
Egg size	NS	NS	NS
Longevity	$p < 0.001$	NS	NS
Body size	NS	a	a
Sex ratio	$p < 0.001$[b]	$0.05 < p < 0.10$	NS
Clutch size	$p < 0.001$	NS	$p < 0.005$
Number of clutches	$p < 0.001$	$p < 0.001$	$p < 0.001$

[a] No estimate obtained

[b] This observation was made in 100% seawater only; in a subsequent test, temperature effects were not found.

DISCUSSION

Fluctuating marine environmenta are characterized by temporally variable producctivity, exposure to wave action and desiccation, temperature, salinity, oxygen, and biotic interactions. Species which inhabit such areas must not only be capable of withstanding wide extremes in these elements, but must also be able to exploit favorable conditions when they occur. There is strong selection for high rates of increase in such species. A good example of the opportunistic life history strategy among marine invertebrates is Tigriopus californicus. Short generation time (about 18 days at 25°C), together with generally high fecundity, allows this species to multiply rapidly in splash pools newly formed by spring tides and rainfall. Longevity is short, ranging from 75 days at 25°C to 130 days at 15°C. However, pools inhabited by Tigriopus often persist less than 50 or 60 days during the summer and fall. Consequently, extant populations are not characterized by high turnover of biomass through a progression of generations.

Environmental Effects on Life History Characters

The emphasis in this study has been focused on the description of the life history responses of T. californicus to varied environmental conditions, in both the field and the laboratory. The effects of food, temperature, salinity, and stability in these three variables, are of major importance in the ecology of populations of Tigriopus, and are discussed below.

There has been much discussion about variability in productivity, and speciation (MacArthur, 1965; Paine, 1966; Margalef, 1969). MacArthur, for example, stated that extreme temporal variability in resources will select against specialist species, and favor generalists (like *Tigriopus*, which is a detrital feeder). It has been postulated that constancy in the rate of production results in intense interspecific competition, and eventually, in speciation, via partitioning of resources. In environments characterized by variable productivity, selection favors species which are most capable of utilizing food resources for reproduction. When productivity is low, most of these species escape the environment via diapause or emigration. Fewer species are supported under such conditions. The variability in both food and water quality in splash pools in the marine intertidal can be assumed to be responsible for the paucity of species there. *T. californicus*, and probably the other animal species present in these pools, is sensitive to changes in both conditions, as reflected by changes in life history characters such as developmental time, sex ratio, longevity, clutch size and number, and body size.

Low food levels result in smaller clutch size, but affect neither egg size nor the number of clutches produced. This agrees with the findings of Comita and Comita (1966), who observed that *T. brevicornis* is sensitive to algal cell concentrations below 50 cells per ml. They did not state whether clutch number is affected, but did show that net egg production is low when food is short. They also found that survivorship was influenced by food availability; corresponding data were not obtained in this study, for *T. californicus*.

Food quality and abundance are perhaps the most universal limiting factors to natural populations of animals. The literature on this subject is extensive; some copepods and other invertebrates are discussed below. Individual species differ greatly in their life history responses to food-limited conditions. For example, fecundity is limited by food-poor conditions in the rotifer, Proales sordida (Lynch and Smith, 1931); Lucilia cuprina (Nicholson, 1950); Calanus finmarchicus (Marshall and Orr; 1952, 1961); Lymnaea elodes (Eisenberg, 1966); Diaptomus gracilis (Chapman, 1969); and Calanus helgolandicus (Mullin and Brooks, 1970). Lynch and Smith also found that longevity in Proales sordida is decreased by low food levels.

Decreased fecundity in species of Daphnia is accompanied by increased longevity in D. longispina (Dunham, 1938), and decreased number of females producing eggs in D. obtusa (Slobodkin, 1954); in D. retrocurva and D. galeata, smaller females are less affected by a paucity of food than large individuals (Brooks, 1946). Unlike Tigriopus, Pseudocalanus minutus females do not produce smaller clutches in response to low food levels; rather, the rate at which broods are produced is reduced (Corkett and MacLaren, 1969).

In all of these species, population growth will be affected by food. Density-dependent regulation can also operate via interference or accumulation of metabolic wastes. Either of these mechanisms could obtain with T. californicus: clutch size decreases with population density, even though food levels are maintained above the limiting concentration per female. Since r is affected by a reduction in clutch size, some degree of density-dependent regulation of population growth may exist. However, extreme oscillations in population size suggest that the responsiveness of females to density is inadequate to prevent periodic population crashes, even if population age structure were taken into account (see St. Amant, 1970, for discussion of detection of population regulation).

Egg-production is density-dependent in Drosophila melanogaster; according to Pearl (1932), crowding effects operate primarily through collision or interference action of flies upon one another. Tribolium confusum, on the other hand, is sensitive to accumulation of metabolic wastes. Females raised in heavily conditioned media produce fewer eggs; sperm production by males is also affected (Park and Woollcott, 1937). Frank (1952) has shown that natality decreases as density increases in the cladocerans, Daphnia pulicaria and Simocephalus vetulus. Density may operate through reduction of oxygen and/or crowding effects on feeding activity. Walker (1967) found that interference among female parasitic wasps (Nasonia vitripennis) results in the production of fewer fertilized eggs. In dense populations, intraspecific competition for oviposition sites is severe, resulting in decreased fecundity. Egg resorption may occur in response to host-limiting conditions. High larval densities, moreover, result in high male sex ratios, and reduced adult longevity.

Fecundity in T. californicus may also be indirectly affected by food availability. In many species of invertebrates, body size is determined in part by nutrition; clutch size, or reproductive effort, is correlated with body size. These variables are correlated in Tigriopus. Observed regional differences in body size and clutch size may be attributable to the abundance or quality of food during growth and development.

Many species avoid deteriorating environmental conditions by means of facultative or obligatory diapause. Diaptomus stagnalis, for example, produces eggs resistant to both high temperature and desiccation (Brewer, 1964). Hatching occurs in the spring, in response to reduced oxygen. No such processes seem to occur in Tigriopus. Females are not sensitive to changes in photoperiod, nor are they able to resist desiccation. Eggs which can survive desiccation for up to three months have not been found, but the development of stages which can survive different sets of adverse conditions (for example, six months of desiccation, etc.) has not been ruled out by this study. It appears that overwintering is accomplished by the survival of a few females which continue to feed and reproduce despite low water temperatures ranging from 4° to 6°C. The ability of of *Tigriopus* to cling to the substrate and avoid being swept out of pools during winter storms seems to be essential to the survival of these populations. Animals which do overwinter successfully reproduce rapidly when temperatures increase in the spring. More importantly, developmental time decreases, and population growth is stimulated. Despite my observations to the contrary, it would seem that spring storms carry propagules to neighboring pools via inshore currents, and new populations are established. In addition, Egloff (1967) reports that *Tigriopus* can be carried from pool to pool on shore crabs, and thereby increase the dispersion of propagules from what are essentially permanent source populations.

Both temperature and salinity are important in these overwintering and exploitative processes. Maturation is delayed by reduced temperature; body size, however, may be increased, and thus improve the egg-carrying capacity of females. In fact, clutch size does appear to increase somewhat among females raised at 15°C, as compared with those raised at 20° and 25°C. Field collections did not reflect this pattern, however. In *T. brevicornis*, the opposite is true: clutch size decreases with temperature (Comita and Comita, 1966). Female *Pseudocalanus minutus* increase in size with temperature; clutch size is correlated with body size (MacLaren, 1965). Although development is speeded by higher temperatures, longevity is decreased in *Tigriopus*. Survivorship is negatively correlated with temperature in *Diaptomus gracilis* also (Chapman, 1969). Survivorship is generally inversely proportional to previous reproductive effort (Murdoch, 1966); therefore, increased rate of egg production at higher temperatures will detract from female longevity.

Egg size appears to be highly canalized in *T. californicus*, and is not affected by changes in either temperature, food, or salinity. Similarly, egg size of *Pseudocalanus minutus* is correlated with neither temperature nor body size (MacLaren, 1965). Barnacle egg size does not appear to be related to environmental conditions either (Barnes and Barnes, 1968), although selection may favor larger eggs among cold-water species (Barnes and Barnes, 1965). Canalization of egg size occurs among plant species as well as animals. Puckeridge (1967), for example, has shown that seed weight is the least sensitive reproductive character of wheat, *Triticum aestivum*, to varied plant density. Harper, et al. (1970) stated that most variation in seed size occurs between locations, between seasons, or in response to interspecific competition; little variability is attributable to intraspecific interactions.

Fitness-related characters of *Tigriopus* are less sensitive to salinity than to temperature. High and low salinities generally reduce egg production, but have little effect on developmental time, longevity, or sex ratio. The interaction effects of temperature and salinity on fecundity are, however, highly significant. It is interesting to note that *T. californicus* females are most fecund in 150% seawater at 15°C; egg production decreases at all other extremes (over an experimental range of 15° to 25°C, and 50% to 150% seawater). From the studies of Pannikar (1940) with the shrimps *Leander serratus* and *Palaemonetes varians*, and Kinne (1964) with these species and *Penaeus duorarum* and *Penaeus aztecus*, different marine crustaceans are stressed differently by combinations of salinity and temperature. These shrimps, for example, showed improved survivorship in low salinity-high temperature, and high salinity-low temperature situations. According to Pannikar, when these species are subjected to diluted media, "the minimum osmotic pressure of blood compatible with life is lower, the higher the temperature, and hence the osmotic work required in maintaining hypertonicity is less at higher temperatures." In other words, even in homoiosmotic species (those that regulate to within a narrow range of internal concentration), metabolic stress is reduced because less regulation occurs in high temperature-low salinity conditions. The physiological basis for this relationship has been reviewed by Kinne, who stated that the rate of passive Na^+ uptake increases with temperature, but the rate of loss does not. Therefore, more energy is needed for active secretion of excess Na in warm, hypersaline situations. At low temperatures, the rate of uptake decreases by itself, but the rate of loss is about the same. As a result, less energy must be used to remove or retain Na^+ in cold, hypersaline waters. In Hemigrapsus, for example, low salinity-low temperature conditions elicit the greatest oxygen consumption; according to Kinne, increased osmoregulation heightens the metabolic stress on Hemigrapsus under these conditions.

Many marine crucstaceans are poikilosmotic; that is, they conform to external seawater concentrations to a large extent. Included among such species are the spider crab, Maja, Pagurus, and the parasitic copepod, Lernaeocera branchialis (Krogh, 1939). Presumably, osmoconformers have reduced maintenance costs over a much wider range of temperature-salinity conditions than do osmoregulators. From the data collected in this study, Tigriopus appears to be most similar to the latter group; that is, its energy expenditure for regulation (as manifested by changes in reproductive output) is sensitive to changes in temperature-salinity conditions.

The question of why Tigriopus has evolved this pattern of metabolic response, considering the natural history of the species, is an interesting one. Both temperature and salinity are highly variable throughout the year in the field. Reproductive activity, in terms of brood size, is variable also, although no correlations between these factors were found in field populations. In high temperature-high salinity conditions in the laboratory, energy seems to be diverted away from reproduction, and presumably, to osmoregulation. Successful regulation of internal concentrations under these conditions is reflected in the general insensitivity of the most highly fitness-related characters of Tigriopus (developmental time, egg size, longevity, sex ratio) to these conditions. Therefore, under conditions of metabolic stress, those characters with low fitness value will be most affected by changes in energy distribution in the individual. The apparent existence of an optimum temperature-salinity regime for the fecundity of Tigriopus probably reflects a more important, but not visible, optimum for developmental time, egg size, etc. Longevity, and thus, overwintering, is hot limited by salinity, but is enhanced by low temperatures. The sensitivity of developmental time to temperature, but not salinity, is of selective value in the high intertidal: salinities may increase or decrease with temperature, due to variability in rainfall; opportunists like Tigriopus must be able to track temperature and corresponding changes in productivity, independently of salinity (which does not necessarily correspond to seasonal fluctuations in food availability).

Tigriopus females raised under stable as opposed to fluctuating culture conditions did not in general differ with respect to fitness-related characters. It is possible that selection for life history characters which confer advantage to individuals under some conditions of high density and environmental stability (larger body size, larger larval size, fewer offspring, increased longevity, increased developmental time) could have occurred in Tigriopus colonies had they been cultured for more than 10 generations. On the other hand, the apparent absence of genetic change in any of these characters should not be completely unexpected. There is no reason to believe that adaptations provided by metabolic and morphological flexibility (individual buffering) should be any less fixed than those which adapt a species to narrow ranges of environmental conditions. According to Allard and Bradshaw (1964), "in inbreeding species there is evidence that buffering can be a property of specific genotypes not associated with heterozygosity." Therefore, selection will tend to canalize those genetic combinations which best buffer an individual against its environment, in the cases of species which inhabit fluctuating environments (Waddington, 1957).

Tigriopus' opportunistic life history strategy, then, is well-adapted to the high intertidal habitat. Both overwintering and dispersal seem to be fortuitous events, perhaps because selection has favored life history characters which permit the most rapid population growth in colonized pools, rather than escape from deteriorating conditions.

Egloff (1967) has reported that temperature affects r less than fecundity, but more than sex ratio, in T. californicus. In view of the observations made in the present study of this species, this conclusion appears unwarranted. I have shown that temperature exerts a major influence on developmental time; the sensitivity of r to developmental time should suggest that any factor, such as temperature, which affects maturation will by definition affect r. Fecundity, which is not positively correlated with temperature, does not affect r to the same extent, or in the same direction, as developmental time. Male sex ratio may increase with temperature, over a range of 15° to $25^{\circ}C$; Egloff has postulated that high temperatures have an inductive effect on egg sex determination, so that brood sex ratios are increased. This suggests that sex ratio is plastic in its response to environmental changes. I have observed, with Egloff, that sex ratio changes do affect r. Egloff proposed that, since male sex ratio increases seasonally (as temperatures increase during the summer), variable sex ratio must provide this species with an intrinsic density-dependent population regulation mechanism (population density usually increases seasonally also). His explanation of the adaptive value of sex ratio implies group selection: density and male sex ratio are correlated with temperature, and as pools become more crowded in the summer, increased sex ratio eases the pressure of population growth. Presumably, this enhances the probability of survival and success of existing members of the population. At the same time, however, Egloff gives evidence for the independence of sex ratio and population density under laboratory conditions; similar observations were made in the present study. Moreover, sex ratio is of only secondary importance to population increase. The effects of developmental time far outweigh those of sex ratio changes with temperature. It appears that Williams (1966; p. 151) is justified in stating that "there is no convincing evidence that sex ratios ever behave as a biotic adaptation."

Many of the points of disagreement in observations in this study and that of Egloff (1967) may be attributable to a number of differences in laboratory and field techniques, as well as differences in emphasis. Egloff fed his animals on the green alga, Platymonas; Tetramin dried fishfood was used in the present study. How various food types might influence life history characters was tested in neither investigation. In addition, this study considered all of these characters equally, while Egloff focused his efforts on the problem of sex ratio.

Life History Characters in Fluctuating Environments

The evolutionary responses of Tigriopus to the environmental and life history relationships discussed above are of great interest, and serve to illustrate selection for opportunism in species inhabiting fluctuating environments. The life history strategy of T. californicus illustrates Levins' (1968, p. 19) model for species in fine-grained environments, with convex fitness sets. That is, the range of changing environmental conditions experienced is generally smaller than the individual's tolerance. The strategy of Tigriopus does seem to be the expression of a single phenotype, which is plastic with respect to many characters, is adapted to an intermediate set of conditions, and yet is able to function moderately well even in environmental extremes. Lewontin (1965) has stated that selection for intermediate phenotypes will not be accompanied by variability in colonizing species, because a sudden change in environment could result in the loss of those individuals that varied in the wrong direction. Similarly, close tracking of the environment would not occur. In fact, Tigriopus does exhibit great variability in many life history characters (especially fecundity, via both clutch size and number), in response to laboratory conditions. Little variability exists in those characters with the highest fitness values--developmental time (coefficient of variation = 7.0%), egg size (8.2%), and longevity (11.3%). At the same time, this latter group is least responsive to changes in environmental conditions. Williams (1966) has shown that egg size, fecundity and mortality are closely related. Species which produce many offspring provide little resources per egg, and mortality is high as a result. The converse is true for species which produce few offspring. Among opportunistic species generally, egg size will be selected for on the basis of a minimum size balanced against mortality before maturity. In the case of Tigriopus, selection has canalized egg size.

It is interesting to note that the greatest variability is found in the number of clutches produced. According to MacArthur and Wilson (1967), rapid development and increasing the span over which reproduction occurs are usually more effective than increasing fecundity when selecting for increased r in colonizing species. Therefore, number of clutches should be maximized more than clutch size, and according to Fisher (1929), be less variable. Gadgil and Bossert (1970), however, have shown that maternity function selection can involve a semelparous reproductive strategy; they have termed such species "big bang" reproducers. In Tigriopus, up to 20 broods are produced by a single female; the value of this iteroparous strategy may lie in adaptation to periodic deterioration of splash pool conditions, as well as random dispersal of females to other pools. Thus, the colonizing ability of Tigriopus will be enhanced by the ability of females to produce several broods, in addition to high intrinsic rate of increase, which is relatively insensitive to late-produced broods. Nonetheless, it would appear that selection for multiple clutches has not been strong enough to reduce variability.

Life history strategies characterized by the traits described above for Tigriopus (early maturation, decreased longevity, high fecundity) have been termed maternity function selected by Hairston, et al. (1970). In fact, selection actually operates on the components of the individual's maternity function. Some other organisms that fit into this category include bacteria, semelparous fishes, and perhaps *Drosophila* (Lewontin, 1965). Other opportunists may, however, exhibit high *r* values which are the result of dispersal selection (see Table 12 for the classification of life history strategies), rather than maternity function selection *per se*. For example, Cole (1954) pointed out that the production of 2×10^{13} spores per generation by the giant puffball, and 10^5 eggs per day by the parasitic tapeworm *Taenia*, suggests selection for dispersibility rather than population growth. The low probability of success in reaching favorable habitats has greater significance in selection for these reproductive rates than does the need to fill those habitats. Janzen (1969) has suggested, too, that smaller seed size in legumes vulnerable to attack from bruchid beetles is a dispersal mechanism designed to increase the probability of escape from predation. The distinction between these two strategies may become trivial when one considers species such as marine invertebrates with external fertilization and pelagic larvae. In this case, dispersal and population increase or recruitment pobably exert equally strong selective pressures on life history characters.

The Study of Life History Phenomena

This study of the life history responses of *T. californicus* to a fluctuating environment has suggested a new approach to the investigation and designation of life history strategies. The definition and evolution of fitness-related characters has been dealt with by Williams (1966), who stated (p. 26) that "the theoretically important kind of fitness is that which promotes ultimate reproductive survival." *How* "reproductive survival" is accomplished is "the central biological problem"(p. 159).

In Table 12 I have suggested that selection has favored and resulted in different designs for survival, or life history strategies. Those designated "maternity function" and "dispersal" selected have evolved in adaptation to fluctuating environments, as discussed above. These two strategies represent the extreme cases of selection for natality: in the former, developmental time is maximized; in the latter, selection favors maximization of fecundity, as well as developmental time. Both strategies are opportunistic. In stable environments, energy is devoted to somatic survival; longevity and developmental time are increased, and body size is generally increased. Metabolic efficiency may be greatly increased, as among some cave species (Poulson and White, 1969). The strategy "low resource:density-dependent" corresponds to the "K-selected" strategy of MacArthur and Wilson (1967); species use their assimilated energy for improved competitive ability rather than population increase. Intermediate strategies include "parental care," which involves selection for brooding behavior (which itself may limit female fecundity, as in the starfish *Leptasterias hexactus*). Protection of young may, of course involve increased investment in reproduction, where energy is allocated for structures which are lost during parturition (for example, fleshy fruits, placentae, protective foam of some amphibians, etc.). The strategy of "predator avoidance" has been alluded to earlier; a good example of the contrast between energy allocation for predator avoidance and dispersal has been described by Janzen (1969) for tropical legumes. Many species of legumes produce toxins which discourage predation by bruchid beetles; these species produce few seeds on the average, although each seed may be larger. Those species which do not produce toxins are found to produce many small seeds, which are more easily dispersed. "Food size" selected species include animals which are limited in the

Table 12. Alternative life history strategies, based on the distribution of energy to adaptation to different selective regimes.

	Life History Strategy		
	Maximization of Natality	Intermediate	Maximization of Longevity
Type of Selective Pressure	Maternity Function	Parental Care	Low Resource: Density-dependent
	Dispersal	Predator Avoidance	Low Resource: Density-independent
		Food Size	
Ratio of Reproductive to Somatic Investment	High		Low

food available to them by their food capturing and/or eating apparatus. Barnes and Barnes (1965), for example, have suggested that cold-water barnacle species may have evolved larger size in order to filter larger food particles. Each of these strategies is comprised of a spectrum of fitness-related characters; there may well be more than the five alternative strategies suggested here.

Williams (1966, p. 159) has also pointed out that one can categorize biotic adaptations as either favoring somatic survival or promoting reproductive effort. Sacher (1966) developed the concept of the "caloric lifespan" to explain patterns of senescence. This idea can be extended to form the basis for the investigation and description of life history phenomena generally, as I have done in Table 12. Cody (1966) took preliminary steps in this direction with his discussion of the "principle of allocation," and Levins (1968) has shown how allocation of energy affects fitness in fluctuating environments. Gadgil and Bossert (1970) provided additional evidence for the significance and validity of this approach to life history strategies with their description of cost and profit functions in reproductive effort. Harper, et al. (1970) have suggested that seed size and seed number in plants represent alternative strategies in the disposition of energy resources devoted to reproduction.

As indicated in Table 12, the ratio of reproductive investment (RI) to somatic investment (SI) will be related to the selective regime encountered. In <u>T. californicus</u>, somatic investment can be estimated as

$$SI = (Vf)(t_f)/t_m \tag{1}$$

or, as

$$SI = V_f/t_m + \frac{(t_m)(C_y) + (t_a)(C_a)}{t_f} \tag{2}$$

where

V_f = Female biomass in mm^3

t_m = Developmental time in days

t_f = Female longevity in days, including developmental time

t_a = Length of adulthood in days

C_y = Maintenance costs to young

C_a = Maintenance costs to adults.

Growth is determinate in Tigriopus; females attain maximum size upon reaching reproductive maturity. Therefore, the first quotient in equation (2) is equivalent to the amount of energy devoted to growth. A more general statement of SI would be

$$SI = \frac{\text{Maximum Biomass}}{\text{Time to Maximum Size}} + \text{Maintenance Costs} .$$

Maintenance costs are an expression of the caloric requirements of osmo- or thermoregulation, predator avoidance, nest building, food capturing, poison synthesis, etc.

The amount of energy allocated to reproductive functions in female Tigriopus may be defined as

$$RI = V_e/t_e \qquad (3) \quad \text{where}$$

V_e = Total egg volume in mm^3

t_e = Duration of egg production in days .

The ratio RI:SI has little value in comparing individuals in a population, unless there is evidence that genetic and phenotypic changes are taking place. Ecotypic variation in fitness-related characters, in terms of energy allocation to the components of RI and SI, can be identified within a species. In addition, differences between species, and thus, differences in the evolution of life history strategies within and between environments, can be described on this basis. For example, species which are "parental care" selected--such as Leptasterias hexactus, which is limited in the number of offspring produced by its ability to cover and brood its eggs (T. Niesen, personal communication)--should exhibit a lower RI:SI ratio than the tapeworm, Taenia, but a higher ratio than Ambystoma, which must utilize more energy to find food, and produces few offspring. Species which allocate a great deal of energy to predator avoidance can devote less to reproduction, yet reproductive survival (as described by Williams, 1966) is best served by this expenditure. In fact, Janzen (1969) has shown that legumes which have toxic seed constituents produce an average of 13.9 seeds per m^3 of canopy, while those which do not produce toxins carry 1020 seeds per m^3.

The extent to which species can adjust their RI:SI ratio to changing environmental conditions will depend upon their degree of phenotypic plasticity. That is, species which have canalized population-stabilizing life history characters will be less flexible in their distribution of energy resources. (This argument is circular at this level, but can be demonstrated by the collection of the appropriate energy utilization data.) In relatively stable habitats, where selective pressures are constant, flexibility will not be favored; shifts in energy allocation will not occur. In variable environments, such as the splash pools inhabited by Tigriopus, species may evolve physiological plasticity to allow the exploitation of available resources. Any plastic response must be assumed to be achived through the redistribution of energy during development. For example, the energy used to increase inflorescence number may have been diverted from some other character, such as longevity. In Tigriopus, the need for increased osmoregulation in warm, hypersaline waters will be met by diverting energy from egg production. In other marine invertebrates, the ratio of RI:SI may vary, depending upon the availability of food and the costs of maintenance in different environments.

It is important to remember that in every environment, selection will favor adaptation. Each alternative life history strategy proposed in Table 12, then, describes the major selective pressure operating on fitness-related characters over a continuum of environmental variability. How each strategy illustrates adaptation to its selective regime can be determined on the basis of how a species allocates its energy resources to be most fit in that environment.

SUMMARY

The effects of several environmental factors on fitness-related life history characters of Tigriopus californicus were investigated in field and laboratory studies. Animals were collected from splash pools at Charleston, Oregon, La Jolla and Pacific Grove, California. All areas are characterized by extreme fluctuations in both salinity and temperature.

Population density and clutch size of field populations were highly variable throughout the year, but were not correlated. Neither parameter, moreover, was correlated with temperature, oxygen, or salinity. Mean clutch size for all Charleston samples was 46.1 ± 20.0 eggs. Sex ratio was not correlated with either salinity or temperature. The three regions differed with respect to mean clutch size, and female body size: the ranking of locations was La Jolla, Pacific Grove, Charleston, for both characters. Body size was positively correlated with clutch size.

No stages of T. californicus revived and devloped after experimental desiccation over periods of from one to three months. Colonization of pools is probably accomplished via inshore current transport of animals swept from pools which are essentially permanently populated.

At 20°C in 100% seawater, fecundity was sensitive to food levels 0.022 mg per female per 2 days. Clutch size, but not number, was limited by food availability. Clutch size was also reduced by increased density of animals in vials, in laboratory studies.

Photoperiod had no effect on egg production. Fecundity, via both clutch size and number, was affected by temperature-salinity interactions. Over the ranges tested, from 15° to 25°C and 50% to 150% seawater, maximum egg production occurred at 15°C in 150% seawater; minimum fecundity was observed at 25°C in 150% seawater. Developmental time and mean longevity

decreased with temperature. The former character varied from 18 days at 25°C to 32 days at 15°C, the latter from 85 days at 25°C to 130 days at 15°C. Male sex ratio increased from 54% at 15°C to 66% at 25°C; salinity had some effect on sex ratio, but affected neither developmental time nor longevity. Intrinsic rate of increase, r, ranged from 0.105 per day at 15°C to 0.155 per day at 25°C; salinity did not affect r. Increased environmental stability of laboratory cultures had no effect on fitness-related characters.

There appeared to be regional differences in growth rates of *Tigriopus* populations raised in the laboratory. Those from La Jolla and Pacific Grove increased fastest at 25°C, and slowest at 15°C; the opposite was true for Charleston populations. When individual females selected at random from those cultures were tested for life history characters, no populational differences were found to explain the observed patterns in actual population growth rates.

Selection for opportunism seemed to have reduced variability in developmental time (coefficient of variation = 7.0%), egg size (8.2%), and survivorship (11.3%). Variability was greatest with respect to the number of clutches produced (46.5%), probably because r is insensitive to late-produced broods.

Phenotypic plasticity was observed in the responses of *T. californicus* to varied temperature and salinity, with respect to sex ratio, clutch size and number, and perhaps developmental time. Egg size was insensitive to environmental changes.

A more empirical approach to the investigation and designation of life history strategies is proposed. This model suggests alternatives to the current usage of an r- to K-selected continuum; species may be described as dispersal selected, low resource selected, maternity function selected, etc.

APPENDIX

Table 13 Physical, chemical, and biological data collected in monthly samples of splash zone pools at Charleston, Oregon.

Date Population[a]	Temperature (°C)	Oxygen (ml/liter)	Salinity (o/oo)	pH	Population Density (no./liter)	Male Sex Ratio (%)	Female Body Size (mm^3)	Clutch Size (no. eggs)
June 28, 1969[b]								
SA 1	25.3	5.9	3.0	6.4		No Tigriopus observed		
SA 2	26.2	5.7	5.0	6.5		No Tigriopus observed		
SA 3	27.8	5.6	3.0	6.4			17.8	4.3
SA 5	27.0	5.6	4.0	6.5			71.3	30.8
July 6, 1969								
SA 2	24.1	6.0	10.0	6.8		No Tigriopus observed		
SA 3	26.0	5.8	10.0	7.0			30.3	10.9
SA 5	26.2	4.6	38.0	8.2			60.8	12.7
August 2, 1969								
SA 1, 2, 5		Evaporated				Evaporated		
SA 3	25.2	4.6	33.0	7.3			17.8	4.2
SA 4	24.0	3.9	58.0	8.0			12.0	3.2
CA 1	21.0	4.9	40.0	8.0			46.4	9.2
CA 2	20.0	4.8	43.0	8.0			32.6	8.3
August 24, 1969								
SA 1, 2, 3, 4, 5		Evaporated				Evaporated		
CA 1	22.0	4.9	36.0	7.9			30.2	5.8

Table 13. (continued)

Sample	Temperature	Oxygen	Salinity	pH	Density	Sex Ratio	Body Size	Clutch Size
CA 2	18.5	5.4	34.0	8.2				51.4 ± 13.5
Sept. 27, 1969								
CA 1	18.3	5.4	35.0	8.2		No Tigriopus observed		
CA 2	18.3	5.4	35.0	8.2		No Tigriopus observed		
CA 3	21.2	5.1	39.0	8.5				65.3 ± 14.0
CA 4	20.9	5.0	42.0	8.3				72.8 ± 11.5
CA 5	20.9	5.1	37.0	8.3				38.2 ± 7.9
Oct. 25, 1969								
CA 1	12.6	6.4	32.0	8.0	780	68	0.0161 ± 0.0049	28.3 ± 9.4
CA 2	12.4	6.4	32.0	8.1	480	50	0.0302 ± 0.0045	43.0 ± 8.0
CA 3	11.8	7.0	20.0	8.4		No Tigriopus observed		
CA 4	11.8	6.7	26.0	8.5	780	41	0.0277 ± 0.0035	24.8 ± 3.4
CA 5	12.0	7.0	18.0	8.1	40	10	0.0186 ± 0.0049	49.7 ± 12.3
CA 6	12.1	6.8	30.0	8.5	400	31	0.0274 ± 0.0061	23.8 ± 5.5
Nov. 29, 1969								
SA 1	7.5	8.1	7.0	7.6		No Tigriopus observed		
SA 3	7.5	7.2	25.0	8.0		No Tigriopus observed		
SA 4	7.6	7.0	26.0	8.0		No Tigriopus observed		
CA 1	7.8	6.6	33.0	8.2	620	60	0.0278 ± 0.0047	49.4 ± 6.3
CA 2	7.3	6.6	33.0	8.2	200	50	0.0295 ± 0.0037	47.4 ± 12.9

Table 13. (continued)

Sample	Temperature	Oxygen	Salinity	pH	Density	Sex Ratio	Body Size	Clutch Size
CA 4	6.2	8.5	5.0	8.2		Few animals present		
CA 6	7.2	6.6	33.0	8.4	40	50	0.0314 ± 0.0061	28.7 ± 8.9
Dec. 20, 1969								
CA 1	12.0	6.0	58.0	8.0	60	36	0.0272 ± 0.0028	41.4 ± 4.3
CA 2	12.3	7.6	3.0	8.2	20	31	0.0297 ± 0.0049	42.9 ± 7.8
CA 4	12.8	7.4	2.5	8.0	120	34	0.0320 ± 0.0052	51.6 ± 15.6
CA 6	11.5	7.7	2.0	8.6	200	16	0.0265 ± 0.0031	28.2 ± 8.6
Jan. 17, 1970								
CA 1	12.5	6.8	20.0	6.3	20		0.0316 ± 0.0049	41.7 ± 10.8
CA 2	12.0	7.0	15.0	6.5	80	50	0.0308 ± 0.0028	47.1 ± 15.5
CA 4	13.1	7.5	1.0	5.3	20		0.0387 ± 0.0069	52.3 ± 10.6
CA 6	12.5	7.5	6.5	5.3	180	44	0.0310 ± 0.0043	31.0 ± 6.9
CA 7	12.9	7.4	3.0	7.1	300	13	0.0301 ± 0.0051	46.4 ± 12.2
March 7, 1970								
CA 1	12.1	6.0	28.0	6.2		No Tigriopus observed		
CA 2	12.0	6.0	28.0	6.4		Few animals present		
CA 4	12.3	5.9	30.0	6.3	40	50	0.0325 ± 0.0056	44.3 ± 15.3
CA 6	12.0	7.1	11.0	5.4	760	37	0.0333 ± 0.0043	31.8 ± 7.4
CA 7	11.8	6.0	31.0	6.2	2180	67	0.0340 ± 0.0056	46.1 ± 6.2
April 5, 1970								
SA 1	16.3	5.6	33.0	6.4	50	52	0.0357 ± 0.0056	75.2 ± 16.0
SA 3	18.0	5.2	44.0	5.8	10		0.0338 ± 0.0027	104.1 ± 15.4

Table 13. (continued)

Sample	Temperature	Oxygen	Salinity	pH	Density	Sex Ratio	Body Size	Clutch Size
SA[redacted]4	18.0	4.8	40.0	6.5	30	40	0.0365 ± 0.0048	94.4 ± 18.1
CA[redacted]1	16.3	5.5	38.0	6.0		No Tigriopus observed		
CA[redacted]2	16.2	5.5	41.0	5.7	160	63	0.0330 ± 0.0059	65.0 ±17.5
CA[redacted]4	17.3	6.9	0.0	5.3	30	40	0.0334 ± 0.0050	62.6 ± 11.6
CA[redacted]6	17.0	5.3	44.0	6.0	1870	43	0.0330 ± 0.0058	24.0 ± 5.2
CA[redacted]7	17.8	5.5	39.0	6.6	50	30	0.0269 ± 0.0049	36.2 ± 3.3
CA[redacted]8	18.8	3.8	82.0	6.0	220	45	0.0312 ± 0.0070	51.2 ± 15.6
CA[redacted]9	19.4	4.4	57.0	5.8	1200	51	0.0305 ± 0.0025	49.7 ± 8.6
CA[redacted]10	17.5	6.2	19.0	5.8	40	25	0.0345 ± 0.0069	48.5 ± 7.4
April 28, 1970								
SA[redacted]1	17.0	6.2	21.0	6.0	100	10	0.0337 ± 0.0099	54.5 ± 16.3
SA[redacted]3	20.0	5.8	20.0	5.4	80	50	0.0330 ± 0.0034	71.6 ± 26.7
CA[redacted]1	23.5	4.9	30.0	5.8		Few animals present		
CA[redacted]2	16.0	5.6	30.0	5.9	90	55	0.0377 ± 0.0066	88.0 ± 30.3
CA[redacted]4	18.0	6.4	11.0	5.7		Few animals present		
CA[redacted]6	19.0	6.7	2.0	5.0	1700	30	0.0311 ± 0.0041	26.2 ± 7.1
CA[redacted]7	19.4	5.2	27.0	6.0	130	31	0.0302 ± 0.0044	59.9 ± 20.7
CA[redacted]8	20.6	5.1	38.0	5.8	900	47	0.0353 ± 0.0021	57.6 ± 11.1
CA[redacted]9	20.0	5.2	37.0	6.0	900	49	0.0345 ± 0.0019	57.6 ± 5.4
CA[redacted]10	18.0	6.1	20.0	5.9	70	14	0.0331 ± 0.0076	52.5 ± 13.9

Table 13. (continued)

Sample	Temperature	Oxygen	Salinity	pH	Density	Sex Ratio	Body Size	Clutch Size
May 30, 1970								
SA 1	22.0	6.3	1.0	6.5	230	52	0.0200 ± 0.0028	39.9 ± 11.3
SA 3	22.0	6.2	5.0	6.3	150	27	0.0345 ± 0.0072	30.1 ± 10.5
CA 1	23.2	4.1	52.0	6.0	180	33	0.0372 ± 0.0092	108.6 ± 29.7
CA 2	18.5	4.4	41.0	5.9	900	44	0.0302 ± 0.0071	77.9 ± 14.6
CA 4	20.0	6.6	0.0	5.7		No Tigriopus observed		
CA 6	18.0	6.3	13.0	6.9	1140	61	0.0360 ± 0.0056	25.7 ± 4.8
CA 7	20.5	5.8	17.0	6.9	1090	48	0.0346 ± 0.0056	30.4 ± 12.1
CA 8	19.0	4.5	54.0	6.6	2590	63	0.0301 ± 0.0037	40.2 ± 6.7
CA 9	22.4	4.7	47.0	6.2	730	47	0.0330 ± 0.0049	26.6 ± 7.7
July 10, 1970								
SA 1	23.3	5.5	17.0	6.1	810	46	0.0186 ± 0.0034	15.7 ± 6.6
SA 3	26.0	4.6	29.0	6.1	260	46	0.0231 ± 0.0047	35.0 ± 9.0
SA 5	18.5	6.0	18.0	6.2	1420	62	0.0373 ± 0.0077	56.2 ± 18.8
CA 1	21.0	4.4	64.0	6.0	2060	43	0.0350 ± 0.0044	27.3 ± 6.0
CA 2	16.2	5.4	43.0	6.1	3120	41	0.0250 ± 0.0041	21.2 ± 2.2
CA 6	17.0	5.1	14.0	6.2	530	55	0.0216 ± 0.0038	24.5 ± 8.7
CA 8	16.8	4.3	70.0	6.1	2560	56	0.0306 ± 0.0053	30.6 ± 8.0
CA 9	20.2	4.4	63.0	6.5	1690	49	0.0316 ± 0.0063	24.7 ± 5.5
CA 11	20.5	4.5	50.0	5.9	2020	49	0.0396 ± 0.0070	53.1 ± 13.3

Table 13. (continued)

Sample	Temperature	Oxygen	Salinity	pH	Density	Sex Ratio	Body Size	Clutch Size
August 9, 1970								
SA[redacted] 1	22.1	5.8	14.0	6.6		Few animals present		
CA[redacted] 1	20.3	4.5	62.0	6.5	2010	54	0.0285 ± 0.0026	24.2 ± 5.2
CA[redacted] 2	16.0	5.0	53.0	6.3	3700	49	0.0319 ± 0.0062	41.4 ± 4.0
CA[redacted] 6	15.0	5.6	42.0	6.6	3850	47	0.0289 ± 0.0059	34.9 ± 16.3
CA[redacted] 8	15.4	4.6	64.0	6.3	4080	58	0.0274 ± 0.0059	27.9 ± 4.4
CA[redacted] 9	19.8	4.4	54.0	6.3	4590	74	0.0309 ± 0.0047	26.2 ± 4.1
CA[redacted] 11	21.0	4.3	57.0	6.5	640	48	0.0431 ± 0.0059	46.9 ± 12.1
Sept. 6, 1970								
SA[redacted] 3	21.2	6.2	7.0	5.6		No Tigriopus observed		
CA[redacted] 1	19.2	4.2	41.0	6.1	1930	46	0.0301 ± 0.0049	24.0 ± 7.2
CA[redacted] 2	17.0	5.0	40.0	6.2	260	62	0.0288 ± 0.0073	25.0 ± 6.1
CA[redacted] 4	18.2	6.7	3.0	5.0		No Tigriopus observed		
CA[redacted] 6	18.3	6.5	8.0	5.5	30	56	0.0334 ± 0.0058	58.9 ± 20.8
CA[redacted] 8	17.6	5.8	30.0	6.0	2090	59	0.0250 ± 0.0018	24.0 ± 6.1
CA[redacted] 9	17.9	4.8	40.0	6.4	1370	57	0.0247 ± 0.0029	23.4 ± 5.1
Oct. 31, 1970								
SA[redacted] 2	17.9	5.8	30.0	6.6	10		0.0272 ± 0.0035	108.9 ± 14.2
CA[redacted] 1	14.5	5.6	43.0	6.6	80	52	0.0240 ± 0.0019	54.2 ± 14.6
CA[redacted] 2	13.0	5.8	41.0	6.0	240	75	0.0268 ± 0.0041	41.8 ± 6.3
CA[redacted] 4	18.5	6.3	16.0	5.6		Few animals present		

Table 13. (continued)

Sample	Temperature	Oxygen	Salinity	pH	Density	Sex Ratio	Body Size		Clutch Size	
CA 6	14.5	6.5	20.0	5.4	570	44	0.0244	0.0037	34.6	8.5
CA 7	15.0	5.6	40.0	6.5	20	45	0.0370	0.0018	109.8	11.2
CA 8	14.8	5.7	42.0	5.8	540	53	0.0253	0.0054	38.3	8.8
CA 9	15.0	5.6	41.0	5.9	280	32	0.0247	0.0051	35.2	16.3

a SA populations located at Shore Acres; CA pools located at Cape Arago

b During the period June 28, 1969 through Sept. 27, 1969, animals were observed for only clutch size.

Table 14. Components of hierarchial ANOVA of field brood size estimates made at three regional locations.

Source of Variance	df	SS	MS	F
Between regions	2	104,069	52,034	16.04 [a]
Between pools within regions	27	87,566	3,243	13.92 [a]
Between broods within pools	270	63,041	233	
Total	300	254,676	300	

[a] $p < 0.001$

Table 15. Components of three-way ANOVA of photoperiod, temperature and salinity effects on rate of egg production.

Source of Variance	df	SS	MS	F
Main Effects:				
Photoperiod	2	1.38	0.69	NS
Temperature	2	259.56	129.78	37.73 [a]
Salinity	3	1585.12	528.37	153.60 [a]
First Order Effects:				
Photoperiod-Temperature	4	9.74	2.44	NS
Photoperiod-Salinity	6	25.60	4.27	NS
Temperature-Salinity	6	155.42	25.90	7.53 [b]
Second Order Effects:				
Photoperiod-Salinity-Temperature	12	41.28	3.44	

a $p < 0.001$

b $p < 0.005$

Table 16. Components of three-way ANOVA of temperature, salinity and population effects on the number of clutches produced.

Source of Variance	df	SS	MS	F
Main Effects:				
Temperature	2	6.722	3.261	112.45 [a]
Salinity	2	13.448	6.724	231.86 [a]
Population	7	37.133	5.305	182.93 [a]
First Order Effects:				
Temperature-Salinity	4	26.289	6.572	226.62 [a]
Temperature-Population	14	42.829	3.059	105.48 [a]
Salinity-Population	14	28.290	2.021	69.69 [a]
Second Order Effects:				
Temperature-Salinity-Population	28	0.800	0.029	

[a] $p < 0.001$

Table 17. Components of three-way ANOVA of temperature, salinity and population effects on clutch size.

Source of Variance	df	SS	MS	F
Main Effects:				
Temperature	2	4987.20	2493.60	82.43 [a]
Salinity	2	107.94	53.97	NS
Population	7	2466.74	352.39	11.65 [a]
First Order Effects:				
Temperature-Salinity	4	651.62	162.90	5.39 [b]
Temperature-Population	14	2028.71	144.91	4.79 [a]
Salinity-Population	14	1209.15	86.37	2.86 [c]
Second Order Effects:				
Temperature-Salinity-Population	28	847.12	30.25	

a $p < 0.001$

b $p < 0.005$

c $p < 0.01$

Table 18. Components of three-way ANOVA of temperature, salinity and population effects on egg size.

Source of Variance	df	SS	MS	F
Main Effects:				
Temperature	2	0.07×10^{-8}	0.035×10^{-8}	NS
Salinity	2	0.02×10^{-8}	0.01×10^{-8}	NS
Population	7	0.32×10^{-8}	0.046×10^{-8}	NS
First Order Effects:				
Temperature-Salinity	4	0.08×10^{-8}	0.02×10^{-8}	NS
Temperature-Population	14	0.10×10^{-8}	0.007×10^{-8}	NS
Salinity-Population	14	0.18×10^{-8}	0.013×10^{-8}	NS
Second Order Effects:				
Temperature-Salinity-Population	28	5.55×10^{-8}	0.198×10^{-8}	

Table 19. Components of three-way ANOVA of temperature, salinity and population effects on sex ratio.

Source of Variance	df	SS	MS	F
Main Effects:				
Temperature	2	0.0152	0.0076	NS
Salinity	2	0.1118	0.0559	2.79 [a]
Population	7	0.0487	0.0070	NS
First Order Effects:				
Temperature-Salinity	4	0.1230	0.0308	NS
Temperature-Population	14	0.1592	0.0114	NS
Salinity-Population	14	0.1912	0.0137	NS
Second Order Effects:				
Temperature-Salinity-Population	28	0.5608	0.0200	

[a] $p < 0.10$

Table 20. Components of three-way ANOVA of temperature, salinity and population effects on developmental time.

Source of Variance	df	SS	MS	F
Main Effects:				
Temperature	2	1937.5	968.8	968.8 [a]
Salinity	2	5.0	2.5	NS
Population	7	20.5	2.9	2.9 [b]
First Order Effects:				
Temperature-Salinity	4	9.8	2.4	2.4 [c]
Temperature-Population	14	22.2	1.6	NS
Salinity-Population	14	19.8	1.4	NS
Second Order Effects:				
Temperature-Salinity-Population	28	28.2	1.0	

[a] $p < 0.001$

[b] $p < 0.025$

[c] $0.05 < p < 0.10$

Table 21. Components of three-way ANOVA of temperature, salinity and population effects on *r*.

Source of Variance	df	SS	MS	F
Main Effects:				
Temperature	2	0.0331	0.01655	40.32[a]
Salinity	2	0.0001	0.00005	NS
Population	7	0.0128	0.00183	4.46[b]
First Order Effects:				
Temperature-Salinity	4	0.0023	0.00058	NS
Temperature-Population	14	0.0174	0.00124	3.02[b]
Salinity-Population	14	0.0020	0.00014	NS
Second Order Effects:				
Temperature-Salinity-Population	28	0.0115	0.00041	

[a] $p < 0.001$

[b] $p < 0.005$

Table 22. Components of completely randomized ANOVA of density effects on clutch size.

Source of Variance	df	SS	MS	F
Between densities	4	6143	1536	12.19 [a]
Within densities	348	44,266	127	
Total	352	50,409		

[a] $p < 0.001$

Table 23. Components of hierarchial ANOVA of number of clutches produced per female, with respect to treatment, population and individual.

Source of Variance	df	SS	MS	F
Between series	2	126	63.0	3.20 [a]
Between populations within series	21	414	19.7	2.43 [b]
Between females within populations	336	2728	8.1	
Total	359	3268	9.1	

[a] $0.05 < p < 0.10$

[b] $p < 0.001$

BIBLIOGRAPHY

Allard, R.W. and A.D. Bradshaw. 1964. Implications of genotype-environment interactions in applied plant breeding. Crop Science. 4:503-508.

Bagenal, T.B. 1966. The ecological and geographical aspects of the fecundity of the plaice. J. Mar. Biol. Ass. U. K. 46:161-186.

Barnes, H. and M. Barnes. 1965. Egg size, nauplius size, and their variation with local, geographical, and specific factors in some common cirripedes. J. Anim. Ecol. 34:391-402.

__________. 1968. Egg numbers, metabolic efficiency of egg production and fecundity; local and regional variations in a number of common cirripedes. J. Exp. Mar. Biol. Ecol. 2:135-152.

Birch, L.C. 1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. 17:15-26.

__________. 1960. The genetic factor in population ecology. Amer. Nat. 94:5-24.

Birch, L.C., T. Dobzhansky, P.O. Elliot, and R.C. Lewontin. 1963. Relative fitness of geographic races of _Drosophila_ _serrata_. Evolution. 17:72-83.

Bishop, J.A. 1969. Changes in genetic constitution of a population of _Sphaeroma_ _rugicauda_ (Crustacea:Isopoda). Evolution. 23:589-601.

Blaxter, J.H.S. and G. Hempel. 1963. The influence of egg size on herring larvae (_Clupea_ _harengus_). J. Cons. Perm. Int. Explor. Mer. 28:211-240.

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13:115-155.

Brewer, R.H. 1964. The phenology of _Diaptomus_ _stagnalis_ (Copepoda: Calanoida): The development and the hatching of the egg stage. Physiol. Zool. 37:1-20.

Brooks, J.L. 1946. Cyclomorphosis in _Daphnia_. I. An analysis of _D._ _retrocurva_ and _D._ _galeata_. Ecol. Monogr. 16:409-447.

Chapman, A. 1969. The bionomics of _Diaptomus_ _gracilis_ Sars (Copepoda: Calanoida) in Loch Lomond, Scotland. J. Anim. Ecol. 38:257-289.

Chitty, D. 1960. Population processes in the vole and their relevance to general theory. Can. J. Zool. 38:99-113.

Cody, M. 1966. A general theory of clutch size. Evolution. 20:174-184.

Cole, L.C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29:103-137.

Comita, G.W. and J.J. Comita. 1966. p. 171-185, In H. Barnes (ed.). Some Contemporary Studies in Marine Science. Allen and Unwin, Ltd. London.

Corkett, C.J. and I.A. McLaren. 1969. Egg production and oil storage by the copepod Pseudocalanus in the laboratory. J. Exp. Mar. Biol. Ecol. 3:90-105.

Deevey, E.S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283-314.

Dobzhansky, T., R.C. Lewontin, and D. Pavlovsky.1964. The capacity for increase in chromosomally polymorphic and monomorphic populations of D. pseudoobscura. Heredity. 19:597-614.

Doty. M.S. 1957. Rocky intertidal surfaces. p. 535-585, In J.W. Hedgpeth (ed.). Treatise on Marine Ecology and Paleoecology. Geol. Soc. Amer. Mem. 67.

Dunham, H.H. 1938. Abundant feeding followed by restricted feeding and longevity in Daphnia. Physiol. Zool. 11:399-407.

Edmondson, W.T. 1945. Ecological studies of sessile Rotatoria, Part II. Dynamics of populations and social structures. Ecol. Monogr. 15:141-172.

Egloff, D.A. 1967. Ecological aspects of sex ratio and reproduction in experimental and field populations of the marine copepod Tigriopus californicus. Doctoral Dissertation. Stanford Univ. 141 pp.

Ehrlich, P.R. and P.H. Raven. 1969. Differentiation of populations. Science. 165:1228-1232.

Eisenberg, R.M. 1966. The regulation of density in a natural population of the pond snail, Lymnaea elodes. Ecology. 47:899-906.

Emery, K.O. and R.E. Stevenson. 1957. Estuaries and lagoons. p.673-750, In J.W. Hedgpeth (ed.). Treatise on Marine Ecology and Paleoecology. Geol. Soc. Amer. Mem. 67.

Epling, C., D.F. Mitchell, and R. Mattoni. 1953. On the role of inversions in wild populations of Drosophila pseudoobscura. Evolution. 7:342-365.

Fisher, R.A. 1929. The genetical theory of natural selection. Dover. New York. 287 pp.

Frank, P.W. 1952. A laboratory study of intraspecies and interspecies competition in *Daphnia pulicaria* and *Simocephalus vetulus*. Physiol. Zool. 25:178-204.

Fraser, J.H. 1936. The occurrence, ecology and life history of *Tigriopus fulvus* (Fischer). J. Mar. Biol. Ass. U. K. 20:523-536.

Gadgil, M. and W.H. Bossert. 1979. Life historical consequences of natural selection. Amer. Nat. 104:1-25.

Gause, G.F. 1934. The struggle for existence. Williams and Wilkins. Baltimore. 163 pp.

Gibor, A. 1956. Some ecological relationships between phyto- and zooplankton. Biol. Bull. 111:230-234.

* >

Harper, J.L., P.H. Lowell, and K.G. Moore. 1970. The shapes and sizes of seeds. p. 327-356, *In* R.F. Jonhston (ed.). Annual Review of Ecology and Systematics. Vol. 1.

Hutchinson, G.E. 1951. Copepodology for the ornithologist. Ecology. 32:571-577.

Igarashi, S. 1963. Developmental cycle of *Tigriopus japonicus* Mori. Sci. Rep. Tohoku Univ. Ser. 4 (Biol.). 29:59-72.

Janzen, D.H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. Evolution. 23:1-27.

Johnson, M.P. and S.A. Cook. 1968. "Clutch size" in buttercups. Amer. Nat. 102:405-411.

Kinne, O. 1964. The effects of temperature and salinity on marine and brackish water animals. Oceanogr. Mar. Biol. Ann. Rev. 2:281-339.

Krogh, A. 1939. Osmotic regulation in aquatic animals. Cambridge Univ. Press. 242 pp.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press. Oxford. 343 pp.

________. 1956. Variations in the reproductive rates of birds. Proc. Roy. Soc. Lond. B. 145:329-333.

Leslie, P.H. and R.M. Ranson. 1940. The mortality, fertility, and rate of natural increase of the vole (*Microtus agrestis*) as observed in the laboratory. J. Anim. Ecol. 9:27-52.

Levine, R.P. 1952. Adaptive responses of some third chromosome types of *Drosophila pseudoobscura*. Evolution. 6:216-233.

* Hairston, N.G., D.W. Tinkle, and H.M. Wilbur. 1970. Natural selection and the parameters of population growth. J. Wildlife Man. 34:681-690.

Levins, R. 1968. Evolution in changing environments. Princeton Univ. Press. Princeton. 120 pp.

Lewontin, R.C. 1955. The effects of population density and composition on viability in *D. melanogaster*. Evolution. 9:27-41.

________. 1956. Studies on homeostasis and heterozygosity. I. Amer. Nat. 90:237-255.

________. 1958. The adaptations of populations to varying environments. Cold Spring Harbor Symp. Quant. Biol. 22:395-408.

________. 1965. Selection for colonizing ability. p. 79-92, *In* H.G. Baker and G.L. Stebbins (ed.). The genetics of colonizing species. Academic Press. New York. 588 pp.

Lotka, A.J. 1924. Elements of physical biology. Williams and Wilkins Co., Inc. Baltimore. 465 pp.

Lynch, R.S. and H.B. Smith. 1931. A study of the effects of modifications of the culture medium upon length of life and fecundity in a rotifer, *Proales sordida*, with special relation to their heritability. Biol. Bull. 60:30-59.

MacArthur, R.H. 1962. Some generalised theorems of natural selection. Nat. Acad. Sci. Proc. 48:1893-1897.

________. 1965. Patterns of species diversity. Biol. Rev. 40:510-533.

MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press. Princeton. 203 pp.

Margalef, R. 1969. Diversity and stability: A practical proposal and a model of interdependence. p. 25-37, *In* Brookhaven Symposia in Biology. No. 22. Diversity and stability in ecological systems.

Marshall, S.M. and A.P. Orr. 1952. On the biology of *Calanus finmarchicus*. VII. Factors affecting egg production. J. Mar. Biol. Ass. U. K. 30:527-547.

________. 1961. On the biology of *Calanus finmarchicus*. XII. The phosphorus cycle:Excretion, egg production, autolysis. J. Mar. Biol. Ass. U. K. 41:463-488.

McLaren, I.A. 1965. Some relationships between temperature and egg size, body size, development rate and fecundity, of the copepod *Pseudocalanus*. Limnol. Oceanogr. 10:528-538.

Monk, C.R. 1941. Marine harpacticoid copepods from California. Trans. Amer. Microsc. Soc. 60:75-99.

Mullin, M.M. and E.R. Brooks. 1970. The effect of concentration of food on body weight, cumulative ingestion, and rate of growth of the marine copepod *Calanus helgolandicus*. Limnol. Oceanogr. 15:748-755.

Murdoch, W.W. 1966. Population stability and life history phenomena. Amer. Nat. 100:5-12.

Murphy, G.I. 1968. Pattern in life history and the environment. Amer. Nat. 102:391-403.

Nicholson, A.J. 1950. Population oscillations caused by competition for food. Nature. 165:476-477.

Paine, R.T. 1966. Food web complexity and species diversity. Amer. Nat. 100:65-76.

Pannikar, N.K. 1940. Influence of temperature on osmotic behavior of some Crustacea and its bearing on problems of animal distribution. Nature. 146:366-367.

Park, T. and N. Woollcott. 1937. Studies in population physiology. VII. The relation of environmental conditioning to the decline of *Tribolium confusum* populations. Physiol. Zool. 10:197-212.

Park, T., E.V. Gregg, and C.Z. Lutherman. 1941. Studies in population physiology. X. Interspecific competition in populations of granary beetles Physiol. Zool. 14:395-430.

Pearl, R. 1932. The influence of density of population upon egg production in *Drosophila melanogaster*. J. Exp. Zool. 63:57-84.

Pearl, R. and L.J. Reed. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc. Nat. Acad. Sci. 6:275-288.

Perrins, C.M. 1965. Population fluctuations and clutch size in the great tit, *Parus major* L. J. Anim. Ecol. 34:601-647.

Pianka, E.R. 1970. On r- and K-selection. Amer. Nat. 104:592-597.

Poulson, P.L. and W.B. White. 1969. The cave environment. Science. 165:971-981.

Puckeridge, D.W. and C.M. Donald. 1967. Competition among wheat plants sown at a wide range of densities. Austr. J. Agr. Res. 18:193-211.

Ranade, M.R. 1957. Observations on the resistance of *Tigriopus fulvus* to changes in temperature and salinity. J. Mar. Biol. Ass. U. K. 36:115-119.

Ravera, O. and V. Tonolli. 1956. Body size and number of eggs in diaptomids as related to water renewal in mountain lakes. Limnol. Oceanogr. 1:118-122.

Ricklefs, R.E. 1968. On the limitation of brood size in passerine birds by the ability of adults to nourish their young. Proc. Nat. Acad. Sci. 61:847-851.

Sacher, G. 1966. The complementarity between development and aging--experimental and theoretical considerations. N.Y. Acad. Sci. Conf. on Interdisciplinary Persp. of Time. Jan 17-20, 1966.

Salthe, S.N. 1969. Reproductive modes and the numbers and sizes of ova in the urodeles. Amer. Midl. Nat. 81:467-490.

Scott, D.P. 1962. Effect of food quantity on fecundity of Rainbow Trout Salmo gairdneri. J. Fish. Res. Bd. Can. 19:715-731.

Slobodkin, L.B. 1954. Population dynamics in Daphnia obtusa. Ecol. Monogr. 24:69-88.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry. W.H. Freeman &&Co. San Francisco. 776 pp.

St. Amant, J.L.S. 1970. The detection of regulation in animal populations. Ecology. 51:823-828.

Strong, D.R. 1971. Differentiation of reproductive characteristics among populations of the freshwater amphipod, Hyalella azteca. Doctoral Dissertation. University of Oregon.

Thoday, J.M. 1953. Components of fitness. Symp. Soc. Exp. Biol. 7:96-113.

Tinkle, D.W. 1969. The concept of reproductive effort and its relation to the evolution of life histories in lizards. Amer. Nat. 103:501-516.

Waddington, C.H. 1957. The strategy of the genes. Allen & Unwin, Ltd. London. 262 pp.

Walker, I. 1967. Effect of population density on the viability and fecundity in Nasonia vitripennis (Hymenoptera:Pteromalidae). Ecology. 48:294-301.

Williams, G.C. 1966. Adaptation and natural selection. Princeton Univ. Press. Princeton. 307 pp.

Wright, S. and T. Dobzhansky. 1946. Genetics of natural populations. XII. Experimental reproduction of some of the changes caused by natural selection in certain populations of Drosophila pseudoobscura. Genetics. 31:125-156.