

LIFE HISTORY VARIATION IN Neomysis mercedis HOLMES (CRUSTACEA,
MYSIDACEA)

by

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ABSTRACT

This thesis examines the relationship between demographic parameters and patterns of energy allocation in a brackish water mysid to test several predictions of life history theory. Populations of N. mercedis subject to different regimes of age-specific mortality allocated energy to reproduction in a manner consistent with predictions based on the maximization of individual fitness. The mechanism by which reproductive allocation was varied was largely through temperature dependent phenotypic variation in the size at maturity which altered size-related components of fitness such as clutch size.

N. mercedis in the tidal marshes of the Fraser River delta produced three generations per year which differed in their demographic and life history traits. Summer generations matured at smaller size, carried fewer embryos, had larger eggs, reduced fertility rates, and more even sex ratios than the overwintering generation. Seasonal changes in body size were shown to result from the effects of temperature.

Instantaneous per capita birth rates were greatest in the spring and declined to low relatively constant values throughout the summer. Fecundity varied directly with measures of food availability. Size-specific instantaneous mortality rates were higher on small mysids than on larger animals during the spring breeding period but were higher on large animals during the late summer. The mortality rates of neonates were directly related to the abundance of predatory salmon fry and inversely related to food availability, while those of several larger size classes

varied inversely with food. Fish predation was generally strongly selective for large mysids. For the mature size classes, the increment in mortality rate with increasing size was positively correlated with environmental temperature, which provided a mechanism through which temperature dependent phenotypic variation in adult size could be selected.

The lifetime energy budgets of females from the W, S1, and S2 generations were about 690, 195, and 175 J respectively. The summer and overwintering females differed significantly in their patterns of allocation of assimilated energy. The reproductive effort of the summer females was about 50% greater than that of the W females (12-13% versus 8.5% of the energy budget).

My results were in agreement with several of the predictions of life history theory. Reproductive effort was increased when adult mortality rates were high. Reproduction in N. mercedis imposed a real cost in terms of reduced future fecundity and decreased survivorship. Age at maturity decreased and reproductive effort increased during the growth phase of the population. However, no evidence of genetic differentiation was found between the estuarine population and an upriver freshwater population which differed in reproductive characteristics.

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GENERAL INTRODUCTION

Introduction

This work deals principally with the question "Do populations in which adult mortality rates exceed juvenile mortality rates allocate a greater proportion of their total energy budget to reproduction than populations in which juvenile mortality exceeds adult mortality?". Interest in this question arises because it is one of the major qualitative predictions of life history theory (Stearns 1976; 1983a) and one which has been inadequately tested to date. Consideration of the above question necessarily focusses attention on factors which influence mortality rates or patterns of energy allocation and thus gives rise to a number of ancillary questions such as (1) what are the proximate factors that determine age-specific patterns of mortality? How do mortality rates vary temporally and spatially? (2) what are the proximate factors which influence patterns of energy allocation by the organism? (3) do populations which diverge in life history characteristics also diverge genetically?

The Problem

Life history theory deals primarily with two sets of traits: (1) the amount and timing of reproductive effort, and (2) the number and size of young. Within the constraints imposed by the genetics and physiology of the organism, selection is expected to shape the above factors to maximize "fitness". Attempts to account for variation in reproductive pattern have generated an enormous literature which is reviewed in Giesel (1976), Stearns (1976, 1977, 1980), and Calow (1977). Stearns (1977, 1980) has critically assessed the data and the ideas underlying the theory; the viewpoint is implicitly adaptionist and thus susceptible to the criticisms of Gould and Lewontin (1979). Mayr (1983) has defended the adaptionist paradigm implicit in life history theory.

Theories which deal with the optimal allocation of reproductive effort (Schaffer 1974; Taylor et al. 1974; Pianka and Parker 1975) take as their starting point the concept of reproductive value, the contribution that a female of age x makes relative to her newborn contemporaries to the ancestry of future generations (Fisher 1930):

$$[1] \quad V(x) = [\exp(r \cdot x)/l(x)] \sum_{y=x}^{\infty} [\exp(-r \cdot y) \cdot l(y) \cdot b(y)]$$

where r is the intrinsic rate of natural increase under the stable age distribution defined by the age-specific schedules of survivorship $l(x)$ and fecundity $b(x)$. Maximizing individual fitness using r as a fitness measure is equivalent to maximizing

the reproductive value at every age (Schaffer 1974; Yodzis 1981). But the reproductive value can be partitioned (Williams 1966; Pianka and Parker 1975) into components which represent current reproduction and the expectation of future reproduction:

$$[2] \quad V(x) = b(x) + [l(x+1)/l(x)] \cdot V(x+1)$$

The current level of reproduction, however, imposes costs in terms of decreased survival or decreased future fecundity (Calow 1979; Bell 1980) which are assumed to increase with the current reproductive effort. Thus the optimal allocation of age-specific reproductive effort is determined by trade-offs resulting from the interaction of the fecundity and survivorship schedules.

Reproductive effort is measured as the proportion of its total energy budget that the organism allocates to reproduction (Hirshfield and Tinkle 1975; Tuomi et al. 1983). This definition is favoured over measures such as clutch weight, the ratio of clutch weight to body weight (Tinkle and Hadley 1975), or various physiological indices (Calow 1979) because it appears straightforwardly to link cost to effort and because it largely eliminates the confounding effects of animal size and of resource intake from comparisons of levels of effort (Hirshfield and Tinkle 1975). With current reproductive effort defined in this manner, both (1) the physiological mechanisms by means of which resource allocation is altered and (2) the circumstances under which re-allocation increases fitness become questions of

interest (Fisher 1930).

Numerous authors have addressed the question of the evolution of "optimal" life history strategies; their work is exhaustively reviewed in Stearns (1976). Attempts to "predict the direction and magnitude of changes in phenotypic traits when specified changes are made in the environment" (Stearns 1980, p.275) have resulted in a recurring set of predictions connecting reproductive pattern and mortality:

(1) "high, variable, or unpredictable adult mortality rates select for increased reproductive effort early in life" whereas "high, variable, or unpredictable juvenile mortality will favour decreased reproductive effort and longer adult life" (Stearns 1983a, p.60),

(2) "where adult mortality exceeds juvenile mortality, the organism should reproduce only once in its lifetime. Where juvenile exceeds adult mortality, the organism should reproduce several times" (Stearns 1976, p.3),

(3) increases in current reproductive effort will reduce future reproductive effort, through decreased survivorship or through decreased future fecundity (Pianka and Parker 1975).

The derivation of the first two of the above predictions is virtually free of restrictive assumptions (Horn 1978). Thus, the predictions should be of wide application and comprise a strong test of life history theory.

These predictions are generally tested by comparing the

predicted and observed phenotypes in different populations, that is, by correlating reproductive patterns and environmental conditions (Stearns 1976; Caswell 1983). Phenotypic differences in life history traits between populations have often been assumed to result from the fixation, under selection, of genotypes yielding the appropriate life history strategy. However, life history theory as formulated above is wholly strategic (Caswell 1983); it makes no reference to the mechanisms by which the appropriate strategy will be implemented. Giesel (1976, p.58) has suggested that "environment-dependent phenotypic plasticity in reproductive patterns are important components of reproductive strategy". The phenotypic norm of reaction may itself evolve (Futuyma 1979); phenotypic plasticity in some traits is genetically controlled (Gupta and Lewontin 1982). It has been argued that developmental plasticity in reproductive traits will evolve (Kaplan and Cooper 1984). Thus either genotypic change or phenotypic plasticity could be a source of variation in life history traits.

The level at which adaptation to spatial or temporal environmental heterogeneity occurs may depend on the frequency of environmental change, that is, on whether the organism sees heterogeneity as a mean environment or as alternate environments. Depending on environmental "grain" (Levins 1968), adaptation may occur as "easily reversible behavioral and physiological changes, as developmental changes which are irreversible within the lifetime of an individual, or genetic

adaptation reversible only over generations" (Caswell 1983, p.37). In rapidly fluctuating environments, phenotypic plasticity is favoured over genetic polymorphism (Giesel 1976) provided there is a sufficiently strong correlation between developmental plasticity and the future environment (Caswell 1983). An experimental study of evolution in heterogeneous environments (Mark 1982) confirmed the expectation that adaptation to environmental heterogeneity depended on the temporal predictability of the environment.

Comparisons between separate populations of a relatively short-lived organism living in seasonally-variable environments may be useful in testing the predictions of life history theory. Predictable seasonal variation in factors such as predation, weather, and the quantity and quality of food, which may directly affect the survival of adults and young or the production of young, should generate the contrasts in life history traits predicted by life history theory. I have used the brackish water mysid Neomysis mercedis Holmes 1897 to test the predictions summarized (p. 4) above.

The Animal and its Environment

Mysids are small, shrimp-like, predominantly marine, peracaridan crustaceans which are widely distributed and often extremely abundant in nearshore marine waters (Mauchline 1980). Brackish water estuaries and the lower reaches of coastal rivers in the north temperate zone usually have dense populations of mysids of the genus Neomysis of which a single species dominates

over a wide area: N. integer in Europe (Tattersall and Tattersall 1951); N. americana along the east coast of North America (Wigley and Burns 1971); N. mercedis along the west coast of North America (Holmquist 1973); N. intermedia along the north Pacific coast of Asia and Alaska (Ii 1964; Holmquist 1973); and N. awatschensis along the central Pacific coast of Asia (Ii 1964). These species seem to be ecological equivalents: they are similar in size, morphology, feeding, habitat use, and life histories (Tattersall and Tattersall 1951; Kinne 1955; Hulbert 1957; Murano 1964; Heubach 1969; Mauchline 1971; Wigley and Burns 1971; Williams 1972; Williams et al. 1974; Kost and Knight 1975; Pezzack and Corey 1979; Siegfried et al. 1979; Siegfried and Kopache 1980; Bremer and Vijverberg 1982; Toda et al. 1982, 1983, 1984; Knutson and Orsi 1983; Murtaugh 1983). A generalized life history would include marked seasonality in abundance with a summer maximum and 2-3 generations per year with noticeable size differences between generations.

N. mercedis is abundant in nearshore waters along the west coast of North America and especially in the lower reaches of Pacific coast rivers such as the Fraser (Northcote et al. 1976) and the Sacramento - San Joaquin (Heubach 1969; Siegfried et al. 1979) where it is a major prey item for fishes (Turner and Kelley 1966; Levy et al. 1979; Levy and Northcote 1981, 1982). Its life history has been described at the southern limit of its distribution, in the Sacramento - San Joaquin river system (Heubach 1969; Siegfried et al. 1979). Several studies have

correlated year-to-year fluctuations in its abundance to measures of food resources (Anonymous 1978; Knutson and Orsi 1983). There are, however, no detailed studies of demographic processes operating in N. mercedis populations.

In the lower Fraser River, a predictable sequence of changes in the physical and biological environments is driven by the annual temperature cycle. As temperatures rise in the spring, snowmelt from the interior drainage of the Fraser River produces a 10-fold increase in discharge which flushes the salt wedge out of the estuary, transforming the brackish water marshes into a freshwater environment. As a consequence, the species composition of the assemblage of fish predators changes seasonally (Levy et al. 1979). Moreover, in the early spring, several hundred million juvenile salmon move through the estuary over a period of a few months (Northcote 1974); a number of these rear in the estuary for a period of days to weeks (Levy and Northcote 1982) feeding on mysids and other organisms (Levy et al. 1979). Breeding and growth by fishes resident in the estuary throughout the summer, coupled with the above changes in the composition and abundance of the fish community, can be expected to produce significant seasonal changes in the intensity and size-distribution of predation on N. mercedis. At the same time, primary production by algae (Takahashi et al. 1973) and macrophytes (Kistritz and Yesaki 1979) generally increases in concert with temperatures. The abundance of benthic meiofauna, which is the principal food of N. mercedis in the Fraser River estuary (Johnston and Lasenby 1982), also

increases from spring to summer (Harrison 1981).

As a consequence, different generations of the mysid are likely to be exposed to quite different regimes of predation and food abundance, factors which will directly alter survivorship and fecundity. Variation in life history characteristics are expected and should conform to the predictions summarized above.

The Aims and Organization of the Thesis

This thesis deals with the population biology of Neomysis mercedis, especially with variation in life history traits such as size and age at maturity, frequency of breeding, and the size and number of young, and with the factors which may influence these traits. The work has three main goals: (1) to account for fluctuations in the numerical abundance of the mysid in terms of factors affecting birth and death processes within the population, (2) to examine the patterns of energy allocation by the mysid under varying demographic regimes, and (3) to relate observed life history variation to the extensive body of theory that attempts to predict how life history traits will vary under specified environmental conditions. My approach is comparative and descriptive, and involves contrasts within and between populations.

The first chapter documents the life history of an estuarine population of N. mercedis, and pays particular attention to variation in life history characteristics and in mortality rates. I also examine the proximate factors which influence birth and death processes in the population. The

second chapter examines the factors influencing the physiological processes which determine energy allocation patterns and compares the patterns seen under different demographic regimes with those predicted by life history theory. The final chapter examines differences in allozyme frequencies and in life history traits in a freshwater and a brackish water population of N. mercedis.

CHAPTER 1. THE POPULATION DYNAMICS OF Neomysis mercedis HOLMES
IN THE TIDAL MARSHES OF THE FRASER RIVER ESTUARY

Introduction

Neomysis mercedis is a brackish water mysid which is common in estuaries and the lower reaches of rivers along the Pacific coast of North America (Heubach 1969; Holmquist 1973; Northcote et al. 1976). It is an important prey item for many fishes in coastal rivers (Turner and Kelley 1966; Northcote et al. 1977; Levy et al. 1979). Its life history has been studied only in the Sacramento - San Joaquin River system, at the southern limit of its range, where it showed large seasonal fluctuations in abundance and size (Heubach 1969; Siegfried et al. 1979).

The factors which determine the abundance of mysids are wholly unknown. Several studies have suggested that year-to-year fluctuations in the abundance of N. mercedis are related to food levels (Anonymous 1978; Knutson and Orsi 1983). The mechanisms through which food would determine abundance have not been specified, however; these could be through fecundity or survival. There are no detailed studies of the factors influencing birth and death processes in mysid populations. A knowledge of the factors affecting demographic processes in N. mercedis populations should account for the fluctuations in abundance as well as suggest the factors driving seasonal changes in life history characteristics seen in the populations.

I have determined the life history of an estuarine population of N. mercedis in the tidal marshes of the Fraser

River delta. I measured instantaneous birth and death rates and related variation in the rates to the abundance of food and predators to assess the relative importance of these factors as agents of demographic change within the population. Variation in life history characteristics within the population were examined from the viewpoint of the predictions of life history theory (Stearns 1976).

Materials and Methods

Study Site Description

The life history and demography of an estuarine population of Neomysis mercedis were determined from bi-weekly or monthly collections made between October 1977 and March 1979 at a large, dendritic, tidal drainage channel on Woodward Island (49°06'N, 123°08'W), a small, relatively undisturbed intertidal island which forms part of the tidal marshes of the Fraser River estuary (Figure 1). The island is of low relief, with a plant community dominated by the sedge Carex lyngbyei (Kistritz and Yesaki 1979). Mixed, semidiurnal tides usually flood the island twice daily, to depths of about 0.5 m, depending on tide height and river discharge. Drainage is via a series of branching channels with well-defined banks, whose lower reaches may be several meters below the general elevation and up to 30 m wide. The centres of the channel bottoms and other areas of relatively higher current consist of fine sands, while the sides, upper reaches, and other low gradient areas are silts. The lower

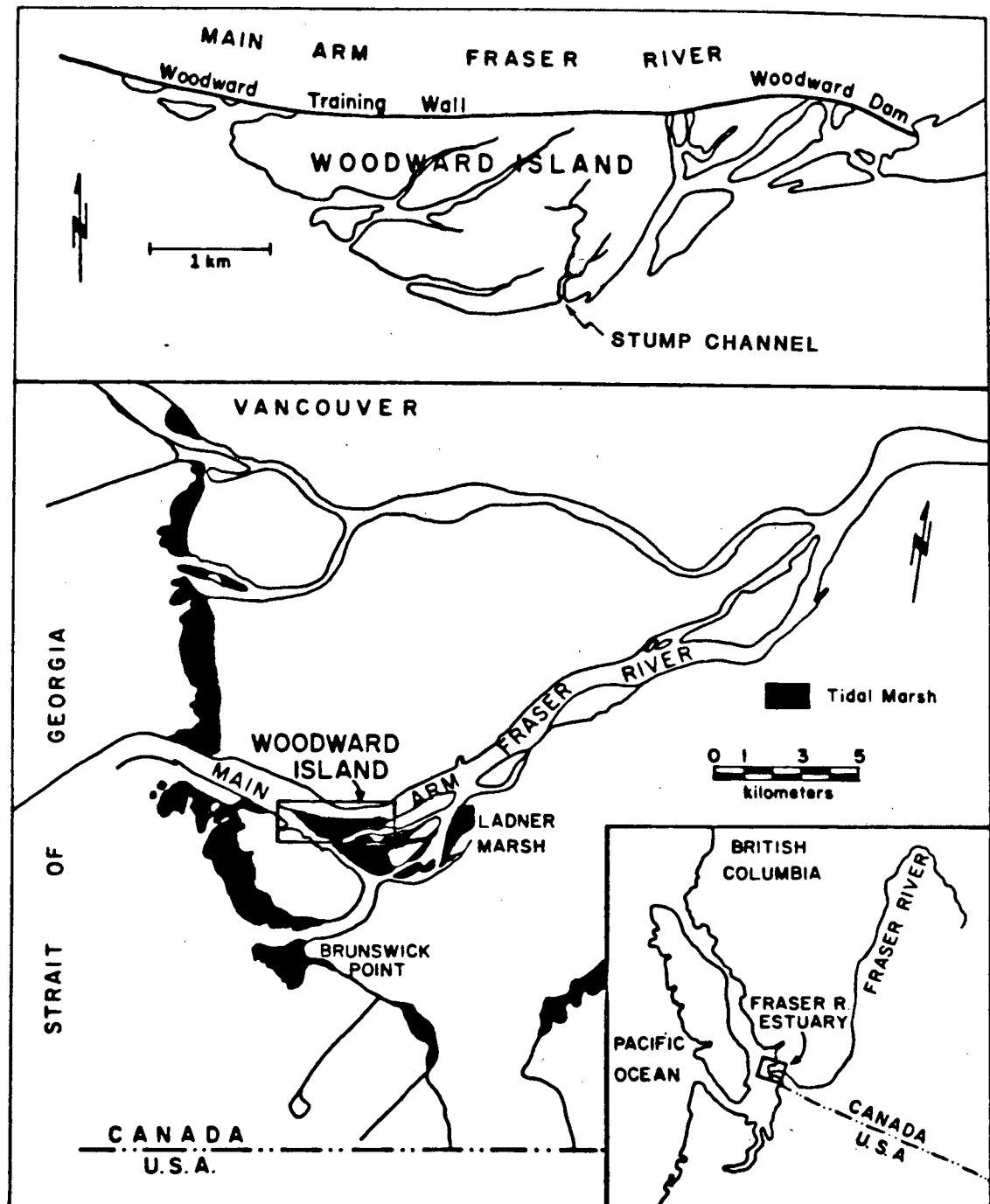


Figure 1. Map of the Fraser Estuary and Delta with insets showing general location of Estuary and details of Woodward Island.

reaches of the principal channels usually retain 0.3-1 m water depth at low tide, especially in the centre which is often scoured into a shallow trough, but may drain completely on exceptionally low tides. Although most of the channel is devoid of vascular plants, scattered stands of Potamogeton spp. occur in backwater areas in the lower reaches during midsummer. Diatom films are noticeable on the mudflats and filamentous green algae occur at times.

My sampling site ("Stump Channel") was 495 m long, with a mouth width of 20 m, an area of 4610 m², a maximum depth of about 2 m at the mouth, and a mid-channel mean sediment size of 192 μ m (Levy and Northcote 1981). Concurrent studies of the vascular plant (Kistritz and Yesaki 1979) and fish (Levy et al. 1979) communities provide further information about the site.

Collection Methods

The mysid population at the study site was sampled at or immediately before the daytime low tide by making 2-4 replicate 10 m long tows along the mid-channel bottom with a sled-mounted, rectangular, 1.1 mm mesh net which was 50 cm wide and 30 cm high. The net was 1 m long and ended in a detachable plankton cup with 116 μ m mesh screening. Light intensity and current speed are known to influence the vertical distribution of related mysids (Heubach 1969; Herman 1963). Preliminary studies of the mysid's pattern of outmigration from the dewatering channels (Appendix 1) showed that they emigrated from the upper reaches of the channel along the bottom just prior to the

draining of the channel. The sampling regime consequently ensured that the entire population in the channel was available to the sampling gear. The collections were made in the lowermost 100 m of the channel, which had a relatively flat bottom and which generally retained water at low tide. I assume that the population in Stump Channel did not change appreciably after the infrequent occasions that the channel drained completely since the whole population emigrated as a unit along the bottom and because the mysids should not be subject to net downstream transport within the estuary (Siegfried et al. 1979).

To minimize gear avoidance by the mysids, I placed the sled in mid-channel in front of me, returned to shore, walked downchannel along the edge of the bank, then quickly towed the sled to me with a 10 m line. Each tow sampled 5 m² of habitat.

Samples were usually frozen in the field with dry ice; one sample per collection was preserved in 10% formalin. Because the density (#·m⁻²) of the mysids in the channel might vary as the area of the channel accessible to them changed with tide height, I attempted to sample at the same water depth (0.3-0.7 m). The undrained area of the channel was roughly constant (about 1050 m²) over this depth range.

Towed nets are known to be size-selective, because of size-differential gear avoidance and mesh retention (Clutter and Anraku 1968; Vannucci 1968). The relative capturability of different size mysids was determined in the field (Appendix 2) and the results used to correct the density and size-frequency

data.

Vertical profiles of temperature and salinity were measured with a YSI model 33 T-S-C meter at intervals of 0.5 m from the surface and just above the channel bottom about one hour before the low tide.

Analysis of Field Samples

The mysids were identified as Neomysis mercedis Holmes using the descriptions and keys of Holmes (1897), Banner (1948), and Holmquist (1973). The identification was confirmed by Dr. Charlotte Holmquist of the Swedish Museum of Natural History, Stockholm.

Frozen samples were thawed into 10% formalin and the animals sorted from the debris in a shallow, white tray, against which the mysids were very conspicuous. Samples were counted in their entirety. Size-frequency distributions were determined by subsampling with a Folsom plankton splitter to obtain about 300-400 animals, or by measuring all animals if the total in the collection was less than this. Subsamples drawn from the same sample did not differ in their size-frequency rankings (Kendall's coefficient of concordance = 0.82, $p < 0.05$). Animals were sized by measuring the exopod of the uropod to the nearest 0.02 mm at 50X magnification. Sequential measurements on the same live, frozen, and formalin-preserved animals showed that measurements of the heavily sclerotized uropod did not change with the preservation technique for periods up to 1 year.

The biomass ($\text{mg dry weight} \cdot \text{m}^{-2}$) of the mysids on a given

date was estimated from the corrected size-frequency distribution using the measured length-weight relation. The length-weight relation was determined by killing freshly collected, live animals by immersion in warm water, measuring them, rinsing them with distilled water, drying them in pre-weighed aluminum pans at 60°C for 15-18h, and weighing them to the nearest μg . The dried animals were stored in a desiccator over calcium chloride to cool to room temperature and weighed immediately. Preliminary measurements showed the dry weight stabilized within the drying period.

Counts and mean dry weight measurements of embryos were made at intervals throughout the breeding season. Freshly collected gravid females were killed as above and the eggs gently removed from the marsupium with a stream of water from a pipette. Females used for embryo counts had closed marsupia and showed no signs of egg loss. Embryonic stages were categorized following Berrill (1969), except that his stage VI was combined with stage V. Clutch weights, mean egg weights, and the female somatic tissue weight (body weight) were determined as described above. Adult males in breeding condition usually ejaculated when immersed in warm water. The cottony sperm mass was easily collected and weighed, as above, as a minimal measure of the male's reproductive effort.

Animals were categorized as to sex and maturity using the following criteria (modified from Reynolds and DeGraeve 1972):

(1) juveniles - animals which lacked all secondary sex characteristics. Animals with uropod lengths < 1.35 mm could

not be sexed reliably and were therefore all classed as juveniles;

(2) immature males - animals which possessed any of:
(a) a male process on the antennules (Tattersall and Tattersall 1951, p.19), (b) a biramous fourth pleopod with the exopod not fully developed, or (c) paired cylindrical penes bearing scattered stout setae;

(3) mature males - animals possessing elongate fourth pleopods, extending beyond the tip of the fifth pleopod, and with the chelae fully developed and > 0.25 of the length of the rest of the exopod. Breeding males had sperm visible in the ampullae and penial sacs (not always visible in preserved specimens) as well as heavily setose male processes;

(4) immature females - animals possessing two pairs of laterally compressed, forward directed marsupial plates (oostegites) originating at the base of the last two pairs of thoracic appendages; marsupium incomplete; sternal processes (Tattersall and Tattersall 1951, p.14) on the posterior thoracic segments;

(5) mature non-breeding females - animals with large, rounded, closed marsupia, but without embryos;

(6) gravid females - animals with embryos present in the marsupium

Demographic Analyses

Instantaneous per capita birth rates were calculated using the egg ratio method (Edmondson 1974; Paloheimo 1974; Lynch 1982). Instantaneous mortality rates were calculated after Lynch (1983). Lynch's procedures for estimating instantaneous birth and death rates are applicable to continuously breeding populations in which females carry the developing embryos until they hatch as free-living young. All current methods for estimating demographic parameters in continuously breeding natural populations require a number of more-or-less restrictive assumptions (Seitz 1979; Taylor and Slatkin 1981). Lynch's techniques are more general than competing methods and furthermore they allow estimates to be made separately by size classes rather than yielding a single population-averaged estimate.

The instantaneous mortality rate, $m(i)$, for the i -th size class is approximately (Lynch 1983)

$$[3] \quad m(i) \approx [\ln\{N(i,0) + [G(i-1,1) + G(i-2,i)] \cdot \exp(-m(i) \cdot t/2) - [G(i,i+1) + G(i,i+2)]\} - \ln\{N(i,t)\}] / t$$

where $N(i,t)$ is the density of animals in the i -th size class at time t , and $G(i,j)$ is the number of animals initially in size class i which grow into size class j over the time interval t . The derivation of [3] requires that the size class width be much greater than the expected growth over the interval t . Thus uropod size classes of 0.5 mm between 0.3 and 3.8 mm were used.

The expected growth increments which determine $G(i,j)$ were derived from rearing experiments which are reported elsewhere (chapter 2). Prior to using [3] to estimate size specific mortality rates for N. mercedis, I assessed the accuracy of the estimator by applying it to simulated populations of known parameter values; the results are discussed in Appendix 3.

The instantaneous per capita birthrate for the population is (Lynch 1982)

$$[4] \quad b = \sum_{i=1}^{i_{\max}} P(i) \cdot b(i)$$

where $P(i)$ is the proportion of the total population in the i -th size class, and $b(i)$ is the size-specific instantaneous per capita birth rate,

$$[5] \quad b(i) = E(i) \cdot [r(i) + m(i)] / [\exp(D \cdot [r(i) + m(i)]) - 1]$$

where $E(i)$ is the number of eggs per individual for the i -th class (the egg ratio), $r(i)$ is the instantaneous rate of increase of the i -th class, and D is the egg development period. Lynch's birth rate estimator corrects the fraction of eggs hatching per day for changes in the egg age distribution which result from adult female mortality, but not for temporal variation in the rate of egg laying. The egg age distribution implied by the proportions of the different embryonic developmental stages in my samples was strongly skewed towards the youngest stages at all times. This suggested that adult mortality was the principal cause of non-uniform egg age

distributions, and that, therefore, adjustments beyond those implicit in Lynch's algorithm were unnecessary.

The egg development estimate and instantaneous mortality rates used in [5] were average values over the egg development period ending on the sampling date. Egg development was estimated from the temperature dependent relationship obtained in rearing experiments (chapter 2).

Approximate confidence limits for the birth and death rates were estimated by a Monte Carlo technique in which the rates were repeatedly ($n=100$) re-estimated after randomly drawing all parameters used in the estimation procedure from normal distributions within ± 1 standard error of the observed mean values of the parameters. The resulting central 95% quantiles of the distribution of estimates give measures of the precision of the estimates.

The influence of food resource availability on fecundity and instantaneous mortality rates was examined using correlation analysis and stepwise linear regression. If benthic meiofauna comprise the principal food of the estuarine population of N. mercedis (Johnston and Lasenby 1982), then several indices of food resource availability can be constructed using the meiofauna abundances reported by Harrison (1981) for contemporaneous sampling on similar substrates at a nearby site. Seasonal variation in food availability can be represented by: (1) the per capita standing stock, i.e., the meiofauna abundance divided by mysid abundance, or (2) the supply:demand index calculated as the ratio of meiofauna abundance to the daily

consumption C estimated for the mysid population from the ingestion equation (Johnston and Lasenby 1982) summed over size classes:

$$C = 24 \cdot \sum_{i=1}^{i_{\max}} 3.81 \cdot N(i) \cdot W(i)^{0.782} \cdot T^{0.515} / w(p)$$

where $N(i)$ is the abundance of the i -th size class, $W(i)$ is the average dry weight of a mysid in the i -th class, T is the temperature, and $w(p)$ is the average prey weight. The resulting supply:demand index incorporates seasonal variation in the mysid's requirements resulting from changes in the abundance and size structure of the mysid population and in ambient temperatures as well as variation in prey abundance. It may therefore better reflect the relative availability of food resources to the mysids.

Size-specific mortality rates resulting from fish predation were estimated directly from the stomach contents of fishes caught at the same time as the mysid samples (Levy et al. 1979). Bias in the fish samples was probably negligible since the technique used (blockage of the dewatering channel with a fine-meshed seine) caught most of the fish present. The abundances of those species not fully retained by the net have been adjusted for the measured gear efficiency (Levy et al. 1979). Subsamples of those fish species which were noted to contain N. mercedis or which were reported by Levy et al. as consuming N. mercedis were examined at monthly intervals from mid-October 1977 to October 1978. Fish of each species were

chosen to span the available size range in rough proportion to the occurrence of different sizes. Generally 10-20 fish of a species were examined on each date although more might be done if this was necessary to characterize the mysid size distribution. Stomachs were removed by means of incisions at the esophagus and the pyloric sphincter. The stomach contents were categorized and the percentage of each prey type estimated visually by displacement. All N. mercedis were measured and sexed as previously described.

The overall size frequency distribution of N. mercedis from fish stomachs on a given date was constructed by weighting the observed distributions for each fish species by the average abundance of each species in the two consecutive-day sampling series including my sampling date (D.A. Levy, unpublished). Size-specific instantaneous mortality rates were estimated as

$$[6] \quad m(i) = -2 \cdot \ln\{1 - S(i)/[A \cdot D(i)]\}$$

where $S(i)$ is the total number of mysids of size class i found in the stomachs, A is the channel area at the time of sampling, and $D(i)$ is the density of the i -th size class of mysids in the environment. Expression [6] arises simply from a consideration of the probability of a mysid being eaten over a day (2 tidal cycles). Let $p(i)$ be the probability of a mysid being eaten over one tidal cycle. Then the number surviving over one tidal cycle is $N(i,0) \cdot [1-p(i)]$ where $N(i,0)$ is the initial number of size class i mysids. The probability of surviving over 2 cycles

is $N(i,0) \cdot [1-p(i)] \cdot [1-p(i)]$. But,

$$N(i,1) = N(i,0) \cdot [1-p(i)] \cdot [1-p(i)] = N(i,0) \cdot \exp[-m(i)]$$

whence [6] is obtained by noting that the probability of being eaten is the proportion of mysids eaten over one cycle,

$$p(i) = [S(i) / A \cdot D(i)].$$

This derivation assumes that: (1) the probability of being eaten does not change over the tidal cycles, i.e., that a small proportion of the mysids are eaten, (2) all fish feeding in the channel are represented in the samples (which have been adjusted for differential gear efficiency, Levy et al. 1979), (3) all mysids found in the fish stomachs are consumed within the channel, and (4) all mysids eaten in the channel are found in the fish stomachs, i.e., the evacuation rate is less than the residence time in the channel. Most of these assumptions are reasonable since the fish are observed to migrate into the tidal channel on the rising tide and generally to remain in the channel until forced to emigrate by the ebbing tide, although there are species differences in the timing of outmigration (Levy et al. 1979).

The standard error of the mortality rates estimated from equation [6] is approximately (Baird 1962, p.64):

$$s(m) \approx \sqrt{(\partial m / \partial A)^2 \cdot s(A)^2 + (\partial m / \partial D)^2 \cdot s(D)^2 + (\partial m / \partial S)^2 \cdot s(S)^2}$$

where $s(A)$ is the standard error of A , etc.

Results

Physical Parameters

The temperature and salinity of the bottom waters in the tidal channel showed marked seasonal variation (Figures 2a and 2b). Temperatures cycled smoothly from midsummer maxima between 19 and 21°C, to midwinter minima of 3 to 4°C. Saline water occurred in the tidal channel only during the fall-early spring period; the channel was a freshwater environment during the summer. Brackish water intrusions were of low salinity, 6 ppt being the maximum value. The salinity changes largely resulted from the seasonal cycle of river discharge which regulates the upstream penetration of the salt wedge (Hodgins 1974).

The temperature cycle was characteristic of temperate latitudes. Although the surface waters showed considerable diel variation, the temperature and salinity of the bottom waters in the lower reaches of the channel were relatively slowly varying (K.J. Hall, unpublished data). Both the temperature and salinity cycles were therefore reasonably predictable seasonal occurrences (Northcote et al. 1975).

Abundance

Population densities of Neomysis mercedis fluctuated over a 25-fold range throughout the year. The abundance of N. mercedis declined sharply in the autumn, and continued to decline slowly throughout the winter to reach minimum densities of 30-40·m⁻² by

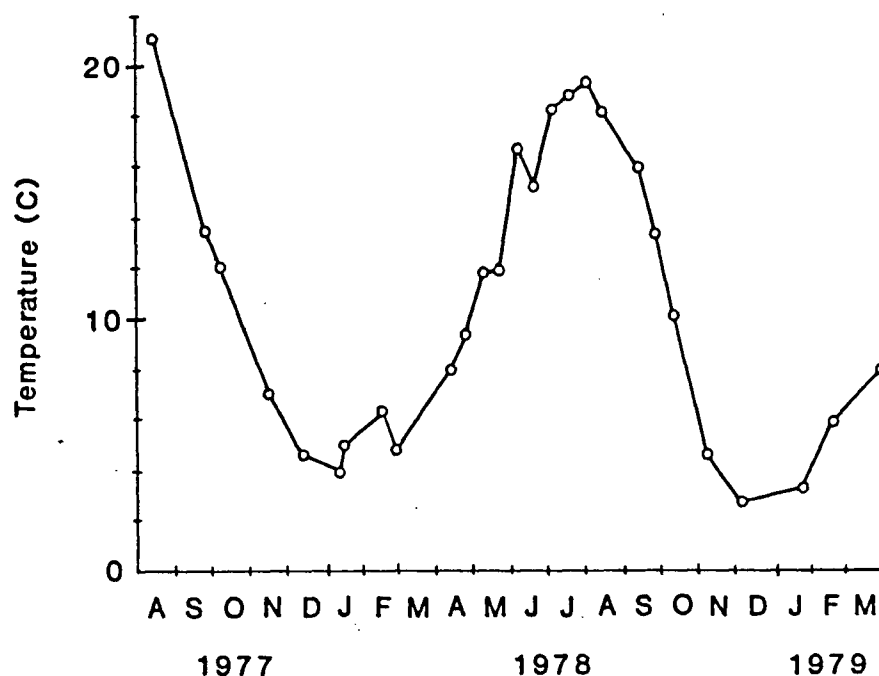


Figure 2a. Bottom water temperature at Woodward Island from 1977 to 1979.

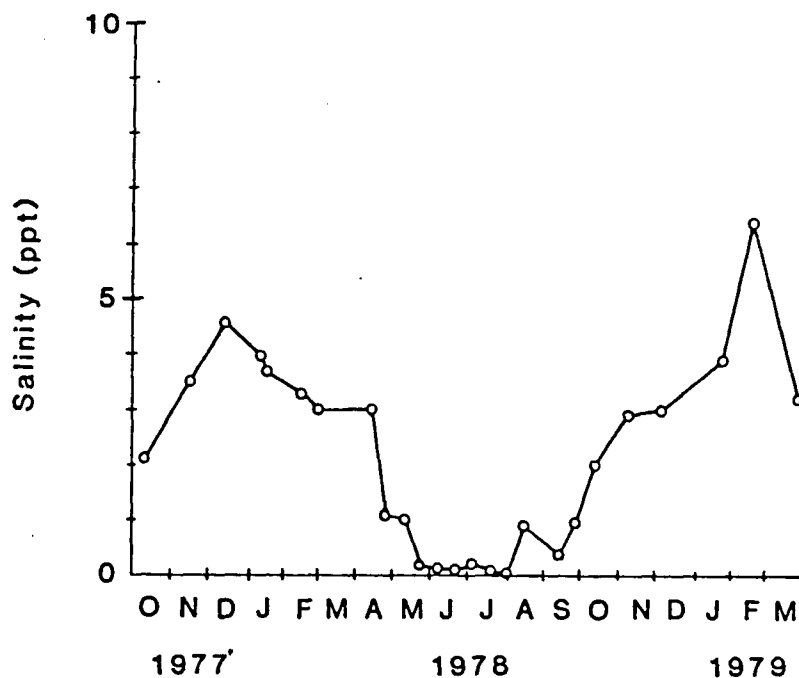


Figure 2b. Bottom water salinity at Woodward Island from 1977 to 1979. The tidal channel is a freshwater environment during the early summer.

spring (Figure 3a). Population levels increased rapidly in early summer and more or less stabilized at $900-1000 \cdot m^{-2}$ by midsummer. It should be noted that the density measurements refer only to the sidechannel habitat and were measured at low tide when the mysids could utilize only about 25% of the channel. Densities in the main river channels were considerably lower (Northcote et al. 1976). The summer maxima were statistically distinguishable from the spring minima (Anova, $p < 0.05$, Scheffe's test), but all other comparisons were non-significant. Variance-to-mean ratios were consistently greater than one, and implied that the population was contagiously distributed at the spatial scale of my sampling (Elliott 1977).

Egg bearing females were present continuously from mid-March to mid-October; newly hatched juveniles were found from the end of April until early November. Although breeding was continuous throughout the seven month period, the abundance of embryos showed pronounced maxima in early May, early August, and mid-October (Figure 4a). The successive appearances of maxima in the abundances of juveniles, immatures, and adults (Figure 4b,c,d) suggested that N. mercedis had three generations per year: (1) an early summer generation (S1) which hatched in late May-early June and grew rapidly to mature and breed in late July-early August; (2) a second summer generation (S2) which hatched in early August and bred in October; and (3) an overwintering generation (W) which consisted of the juvenile offspring of the S2 generation hatched in early autumn, together with that portion of the S2 generation which did not mature

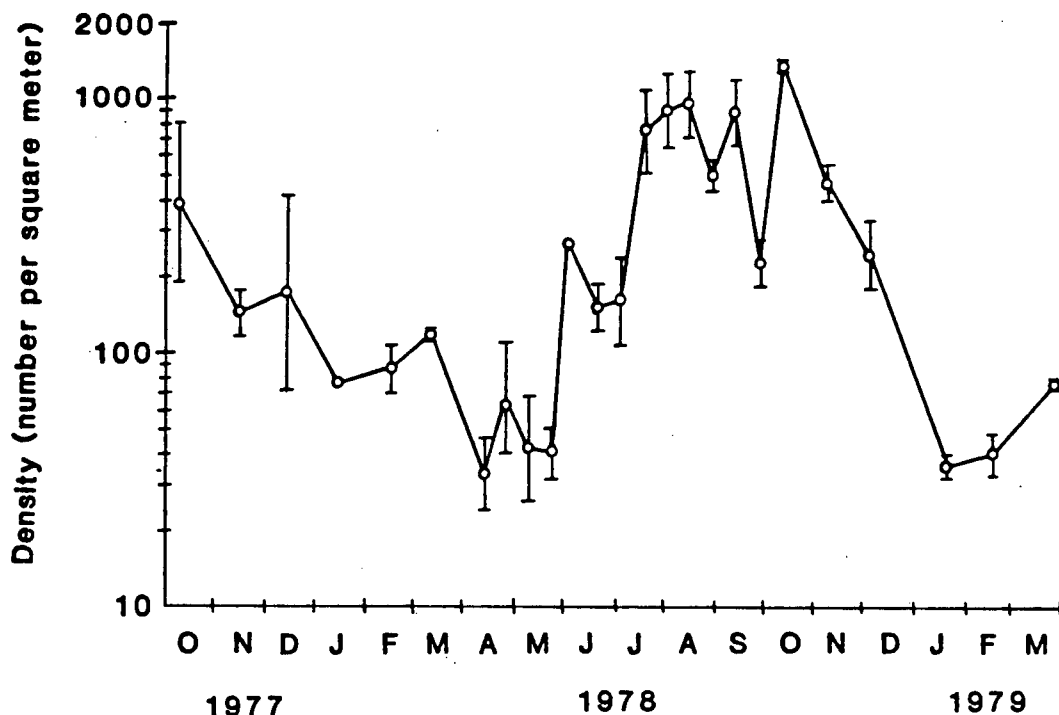


Figure 3a. The seasonal abundance of Neomysis mercedis at Woodward Island between October 1977 and March 1979. Vertical lines represent ± 1 standard error. The summer maxima are significantly different from the winter - spring minima ($p < 0.05$).

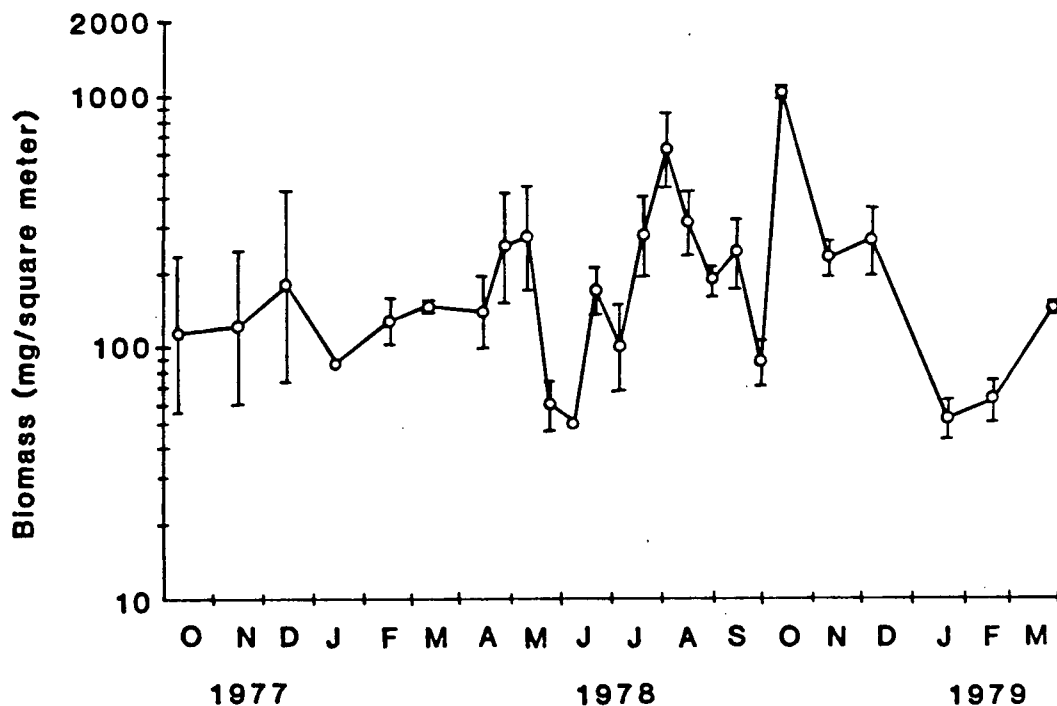


Figure 3b. The biomass (± 1 SE) of Neomysis mercedis at Woodward Island from 1977 to 1979.

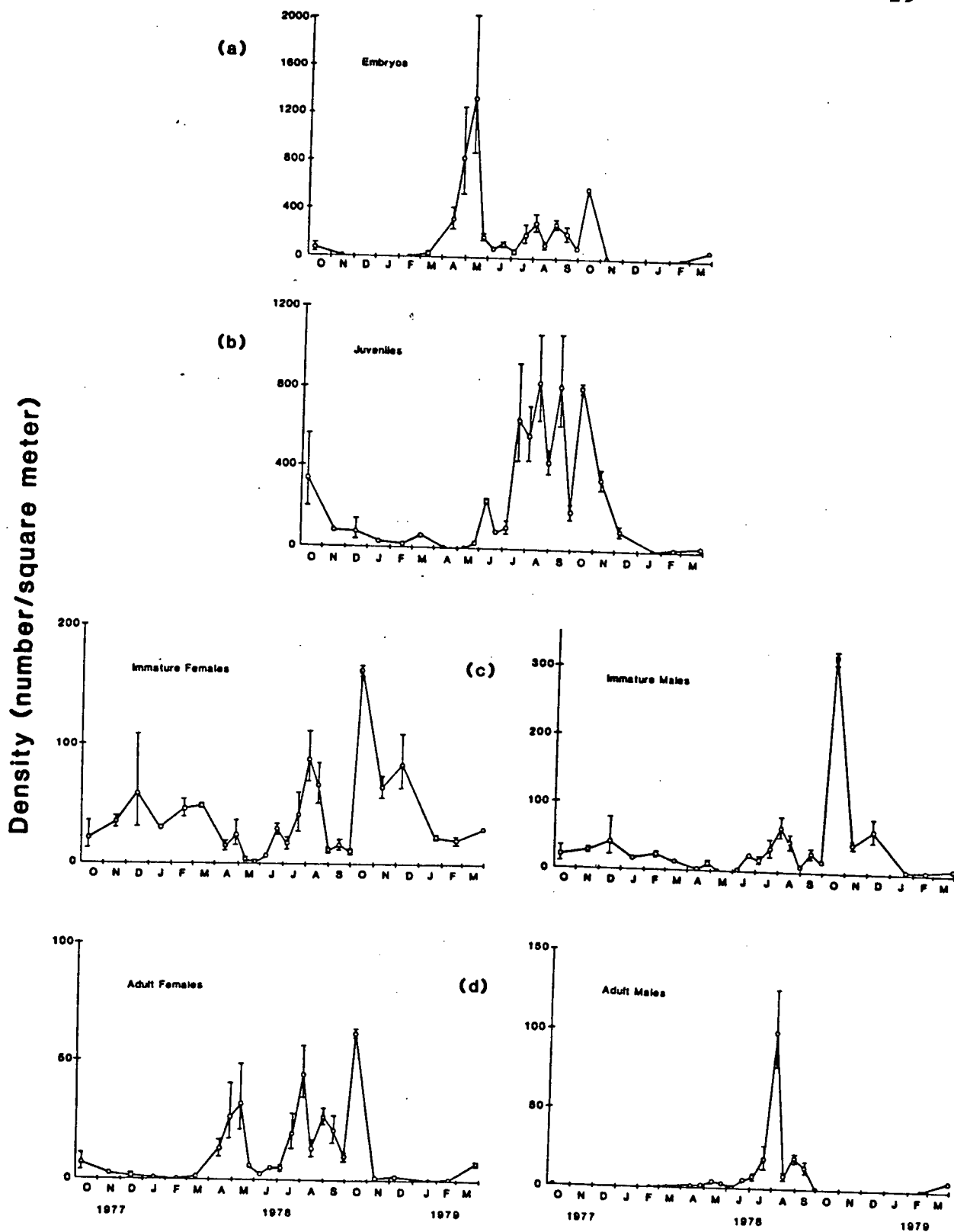


Figure 4. The seasonal abundance of female and male *Neomysis mercedis* at Woodward Island, 1977 to 1979. (a) eggs and embryos, (b) juveniles, (c) immatures, (d) adults. Note the different scales.

before falling temperatures curtailed breeding. The overwintering generation matured primarily in April to breed in April-May, giving rise to the next S1 generation.

The identities of the generations were somewhat blurred by continuous reproduction during the breeding season, by temperature induced changes in rates of development and maturation, and by temporal changes in size-specific mortality rates which led to overlap between components of successive generations. The broad size structure of the population when breeding was initiated in spring, together with the production of a second clutch by a small proportion of the W females, gave rise to a small but distinguishable secondary peak (S1b) in abundance which moved through the successive size classes (Figure 5). The average age at which females reproduced, which will approximate the generation time for this population (Ricklefs 1973), was estimated from the appearance of embryos as approximately 85 days for the S1 generation, 56+ days for the S2 generation, and 210+ days for the overwintering generation. The duration of the free-living stages were estimated (Figure 5) as approximately 57 days for the S1 generation, 43 days for the S2 generation, and 185+ days for the W generation.

The relative proportions of juveniles, immatures, and adults fluctuated seasonally as the various generations waxed and waned (Figure 5) but were relatively constant throughout much of the breeding season, with adult females comprising 3.2 (SE= ± 0.46 , n=10)% of the total population on average, and juveniles comprising 78.1 (± 4.22)%.

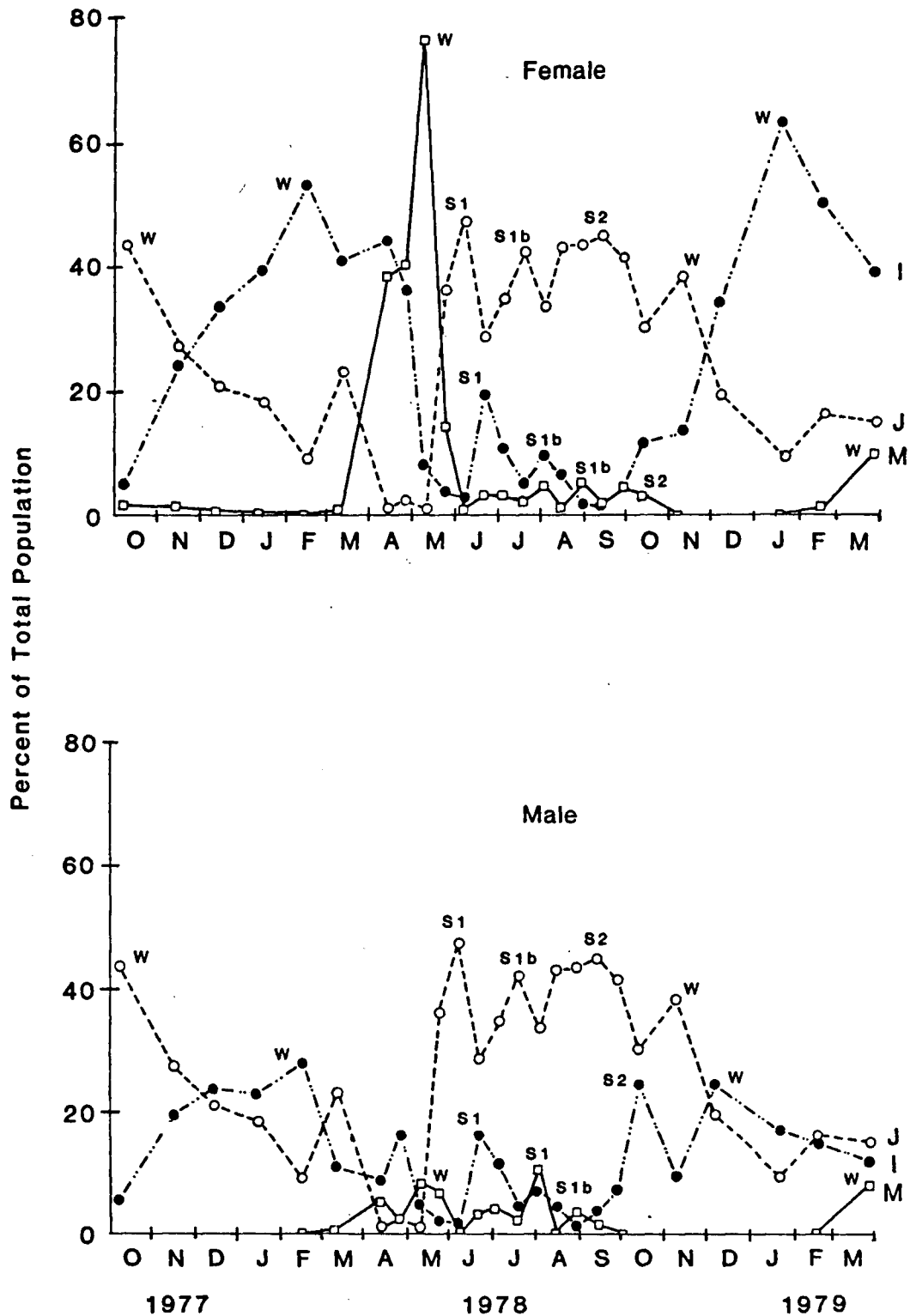


Figure 5. Relative proportions of juveniles, immatures, and adult *Neomysis mercedis* at Woodward Island between October 1977 and March 1979. (○) are juveniles, (●) are immatures, and (◻) are adults. Generations are designated as: (W) overwintering, (S1) first summer, and (S2) second summer. The S1 generation shows a small secondary group (S1b).

Peak biomass values were $0.6-1.0 \text{ g}\cdot\text{m}^{-2}$ (Figure 3b). Biomass increased and decreased successively as the S1 and S2 generations grew to maturity and died. It remained fairly constant at values near $100 \text{ mg}\cdot\text{m}^{-2}$ throughout the winter, increased slightly in the spring, then decreased as the W generation adults died in late May to June.

Body Size

The changes in generation time between the summer and winter generations were accompanied by changes in several life history parameters including size at maturity, fecundity, egg size, and sex ratio. The mean size of adult females (Figure 6a) and adult males (Figure 6b) decreased considerably in the summer, from near 2.9 mm uropod length to about 2.2 mm. This corresponded to a decline in the mean dry weight from about 5.4 mg to 2.3 mg. The 10 percent quantile of the adult females, which better approximates the size at first maturity, showed a similar change from about 2.8 mm to 2.0 mm (Figure 6c), which implied that the seasonal differences resulted from a reduction in the size at first reproduction rather from size-differential mortality. The proximate cause for these changes was probably the field temperature regime; the size at maturity of laboratory reared males and females (Figure 7a) generally decreased with increasing temperatures (Anova, $p < 0.01$). The smaller effect seen in the laboratory at 20°C may have resulted from prior temperature history (de March 1978) since some individuals were wild females that had not been at 20°C continuously over their

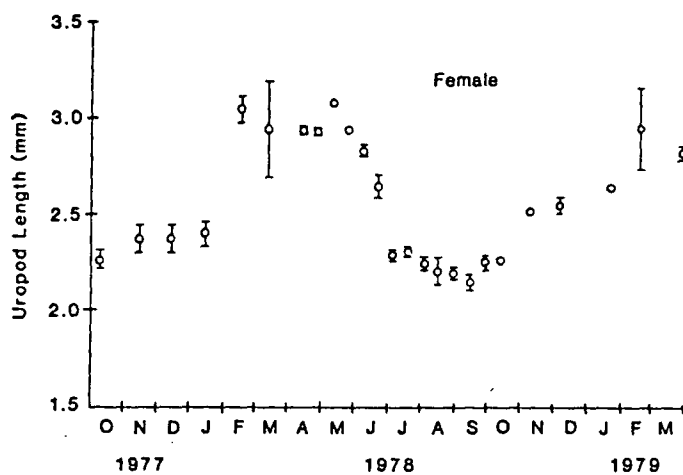


Figure 6a. Seasonal changes in the mean size (± 1 SE) of adult female *Neomysis mercedis* at Woodward Island, 1977 - 1979.

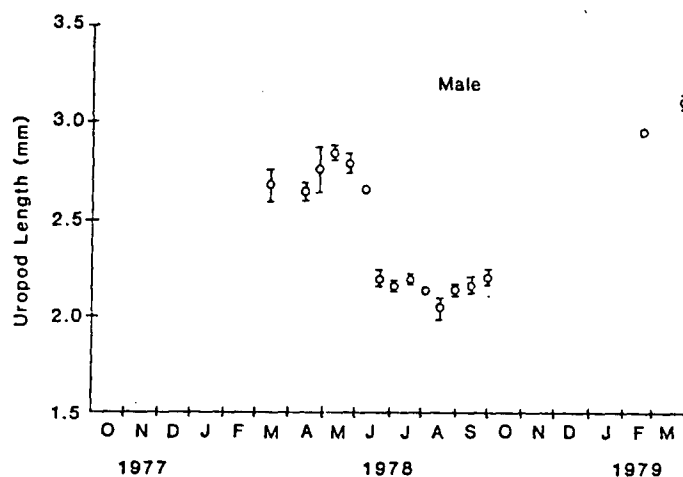


Figure 6b. The seasonal pattern of mean (± 1 SE) size of adult male *Neomysis mercedis* at Woodward Island.

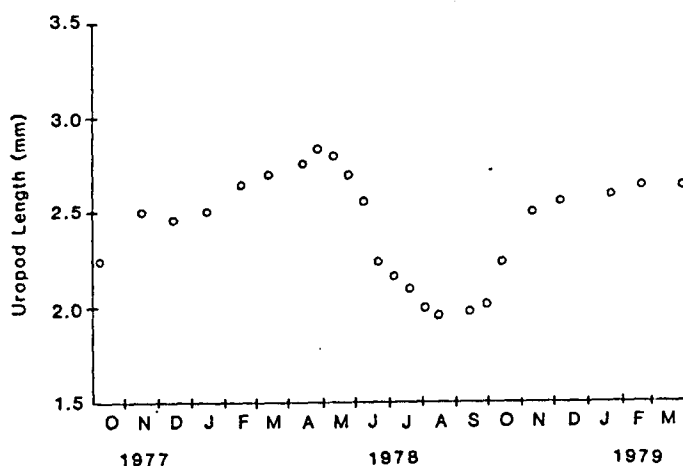


Figure 6c. The seasonal pattern of the 10 percent quantile size of adult female *Neomysis mercedis* at Woodward Island.

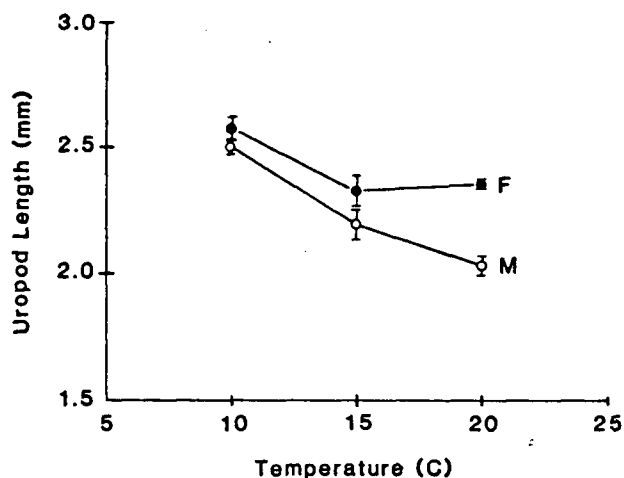


Figure 7a. The size at maturity (± 1 SE) of reared male (O) and female (●) *Neomysis mercedis* at different temperatures .

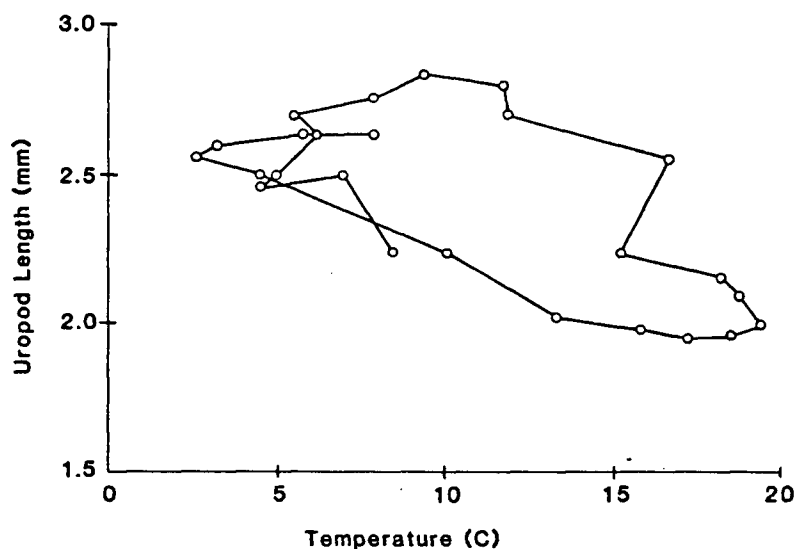


Figure 7b. The effects of prior temperature history on the size at maturity of female *N. mercedis* at Woodward Island . The data form a time series going clockwise from October 1977 (lower left) to March 1979. The size at maturity of females which mature at a given ambient temperature varies depending on the direction of temperature change.

lifespan. The effect of prior temperature history on the size of newly maturing animals was evident when the first decile size of mature females was plotted against the ambient temperature at the time of sampling (Figure 7b). There was a marked hysteresis associated with the direction of temperature change. Animals which experienced regimes of rising temperatures matured at larger size for the same ambient temperature (at the time of sampling) than those which experienced falling temperature regimes. The differences between the size at maturity at similar temperatures during rising and falling temperature regimes probably did not result from the effects of food availability (Figure 17a). In a regression of size against temperature and food availability, food did not further increase ($p=0.08$) the proportion of the variance explained beyond that accounted for by the significant temperature effect ($p<0.01$).

Egg Size

The frequency distributions of the mean size of eggs carried by individual females in the Woodward Island population changed seasonally during 1978. The frequency distribution of mean egg weights in the spring breeding generation was bimodal, with a major mode at 25-30 μg and a much smaller mode at 40-45 μg (Figure 8a). The summer generations had, on average, much larger eggs, the modal egg size being 35-40 μg (Figure 8b). There was little overlap in the spring and summer distributions; the most common egg size in the spring breeding animals did not occur during the summer. The spring and summer egg weight -

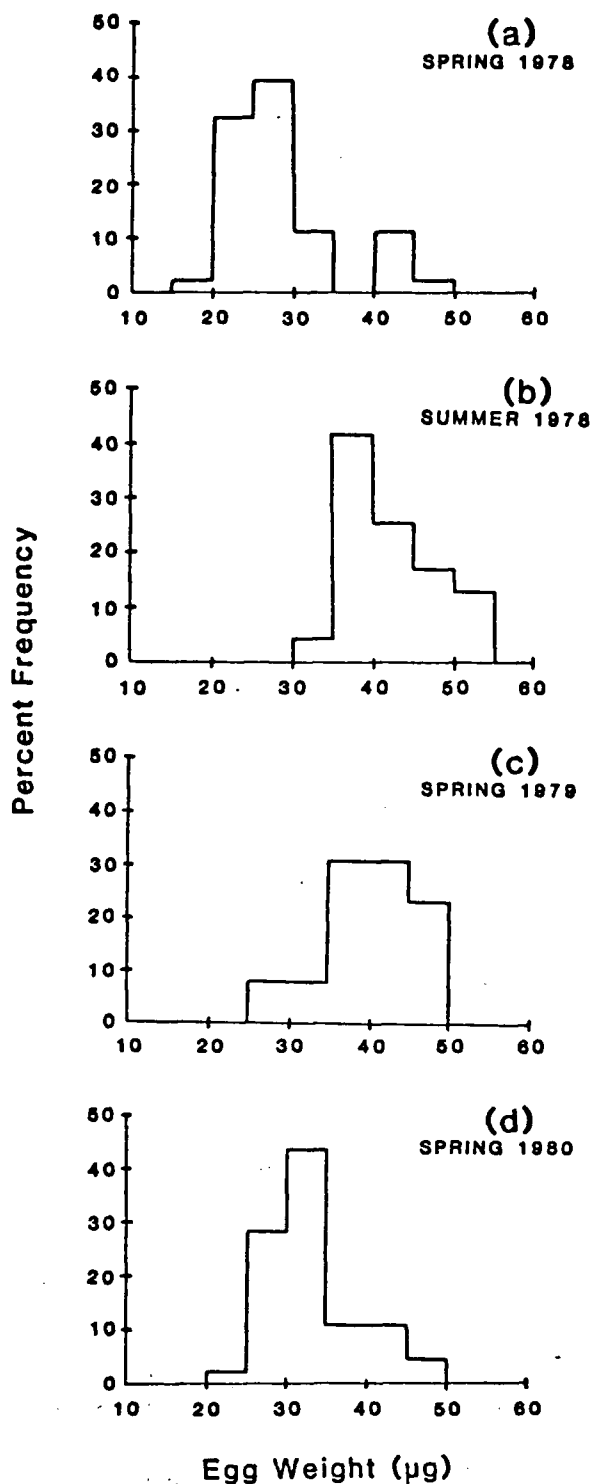


Figure 8. The frequency distributions of mean egg weights for *Neomysis mercedis* at Woodward Island, 1978-1980. (a) spring 1978 (n=39), (b) summer 1978 (n=26), (c) spring 1979 (n=13), and (d) spring 1980 (n=46).

frequency distributions differ significantly ($p < 0.01$, Kolmogorov Smirnov 2-sample test). The females appeared to be divided into small (egg weights $< 35 \mu\text{g}$) and large ($> 35 \mu\text{g}$) egg types, with the former predominant in the early spring breeders and the latter present in the summer. The average egg size for the small and large forms were 26.1 ($\text{SE} = \pm 0.51, n = 38$) and 42.5 ($\pm 0.95, n = 29$) μg respectively. Within-clutch variation in egg size was not examined but the average within-clutch coefficient of variation in the dry weight of newly hatched young, which should reflect egg weight, was 11.4 (± 0.94)%. Size at hatching was probably correlated with egg size as the range of dry weights of hatchlings (14 - $48 \mu\text{g}$) was similar to the range of mean egg weights (15 - $58 \mu\text{g}$). The frequency distributions of egg weights seen in the springs of 1979 and 1980 (Figure 8c,d) were significantly different from that of spring 1978 ($p < 0.05$, KS 2-sample test). In both 1979 and 1980 the egg weight distributions were unimodal and heavier than the 1978 distribution although the ranges of egg weights were similar. The mean egg weight in spring 1979 of ($39.8 \mu\text{g} \pm 1.61, n = 13$) was indistinguishable from the large egg mean for 1978 while the spring 1980 mean of $33.5 \mu\text{g}$ ($\pm 0.84, n = 46$) was intermediate in value.

Egg size was independent of female size for all cases except the 1978 small egg type where there was a weak inverse relationship which accounted for only 15% of the egg size variance.

Fecundity

The brood size (the number of eggs or stage I embryos) increased exponentially with increasing size of the mother, but during 1978 females carrying large and small eggs differed ($p < 0.05$, Ancova) in their size-fecundity relations (Figures 9a and 9b). The functional regression of $\log(\text{number of eggs})$ against $\log(\text{female size})$ is given in Table 1. Size accounted

Table 1. Summary of size dependent relations of the form $\log(y) = a + b \log(\text{uropod length in mm})$ for female Neomysis mercedis from Woodward Island, 1978.

y	a	b	(1 SE)	r^2	n
total weight (mg)	-0.547	2.79	(0.018)	0.99	195
body weight (mg)	-0.562	2.73	(0.016)	0.99	221
clutch weight (mg)	-1.294	2.80	(0.21)	0.62	67
egg number (<35ug)	-0.801	4.94	(0.57)	0.50	38
II,III embryos	-0.125	3.61	(0.48)	0.49	30
IV,V embryos	-0.903	4.96	(1.18)	0.27	15
egg number (>35ug)	0.0863	2.89	(0.41)	0.48	28
sperm weight (ug)	-4.99	6.65	(1.62)	0.53	10
body length (mm)	0.737	0.994	(0.005)	0.99	236

for 48-50 % of the variation in egg number. Although the slopes of the size-fecundity relations were statistically indistinguishable ($p > 0.05$), females carrying eggs with a mean dry weight $< 35 \mu\text{g}$ had about 1.56 as many eggs as similar sized females producing larger eggs. The ratio of the egg numbers for the two classes of females closely corresponded to the ratio of the mean egg weights for large and small eggs. The dependence of the total dry weight of the clutch on the size of the mother

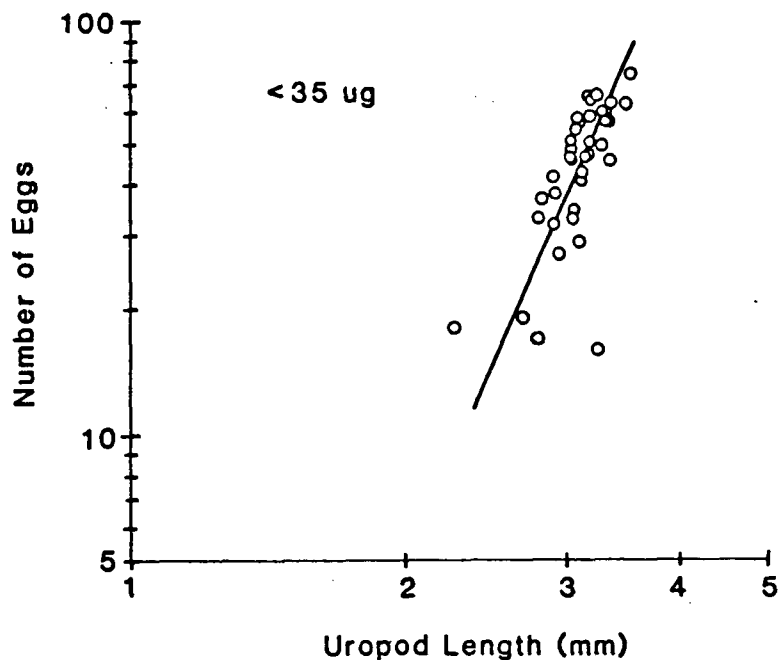


Figure 9a. The relationship between brood size and female size for females producing "small" eggs during 1978.

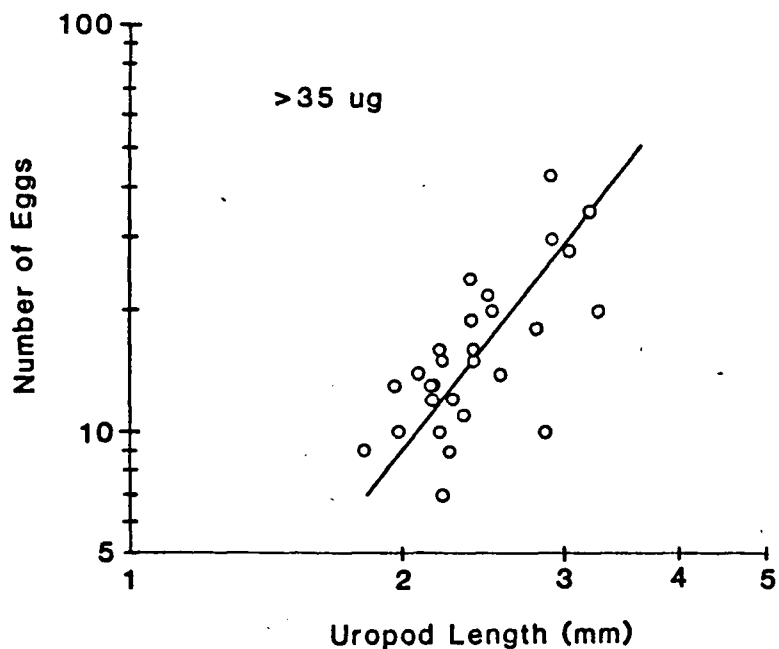


Figure 9b. The relationship between brood size and female size for females producing "large" eggs during 1978.

(Figure 10a) was identical ($p > 0.05$) for females with small and large eggs. Clutch weight increased exponentially with the size of the female (Table 1). Similarly, the dry weight of sperm produced by males increased exponentially with the size of the animal (Figure 10b, Table 1), but was only about 1-2% of the clutch weight of females of the same size.

Comparison of the embryo number-female size relations for successive embryonic stages (Figures 9a, 11a, 11b) suggested that there was pre-hatching mortality. Although the slopes of the lines did not differ ($p > 0.05$, Ancova), the number of old (stage IV and V) embryos was only about 75% the number of earlier stage embryos carried by similar sized females, which implied an instantaneous mortality rate for embryos of $0.005 - 0.009 \text{ day}^{-1}$ in late spring. Numbers of stage II and III embryos did not differ from those of eggs and stage I embryos ($p > 0.05$). The reduction in the number of late stage embryos carried by females reflected marsupial egg mortality rather than temporal changes in ovulation rates since the egg number - female size relation remained invariant over the samples for which the mortality was calculated (Ancova, $p > 0.05$).

The egg number - female size relations seen in spring 1979 and spring 1980 were indistinguishable from that seen in 1978 for N. mercedis carrying small eggs (Ancova, $p > 0.05$). There was, however, significant year-to-year variation in the clutch weight - female size relations. Although the slopes of the clutch weight relations remained constant, the 1979 broods averaged about 1.53 times heavier than those of equivalent sized females

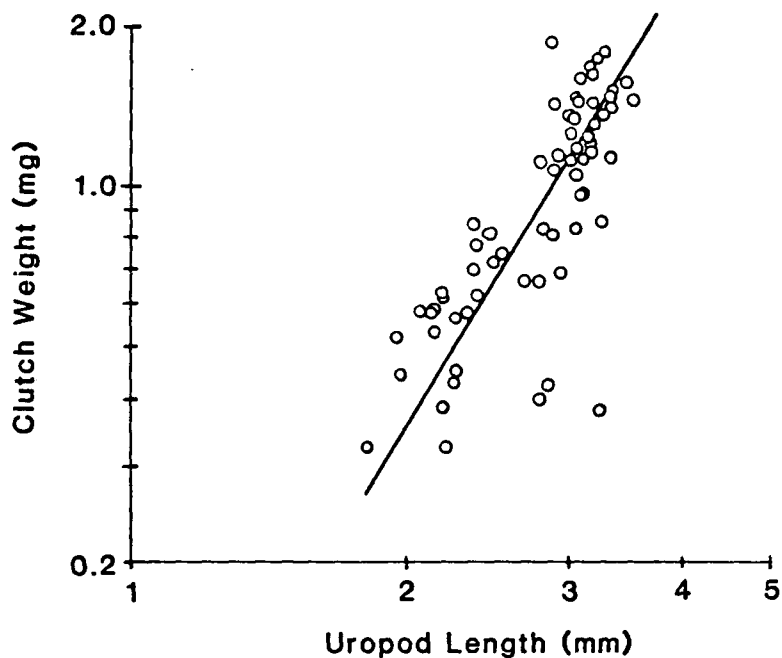


Figure 10a. The relationship between the clutch weight and female size for Neomysis mercedis at Woodward Island, 1978 .

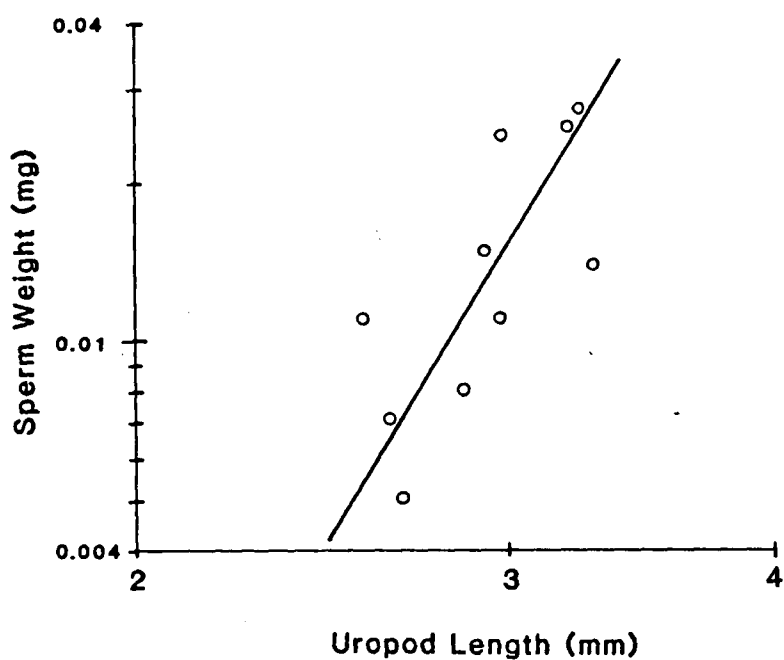


Figure 10b. The relationship between sperm weight and male size for Neomysis mercedis at Woodward Island .

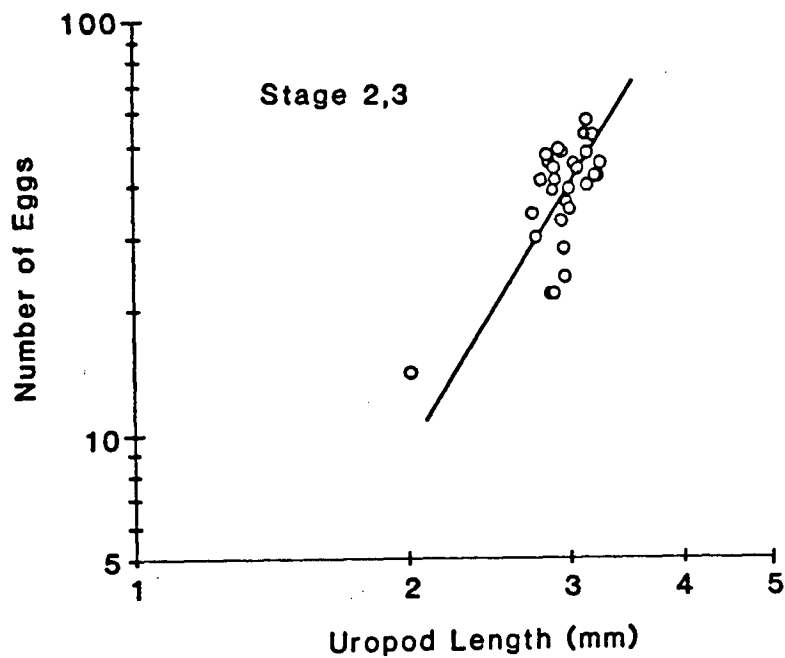


Figure 11a. The dependence of the number of stage II and III embryos on female size for females carrying "small" embryos, 1978.

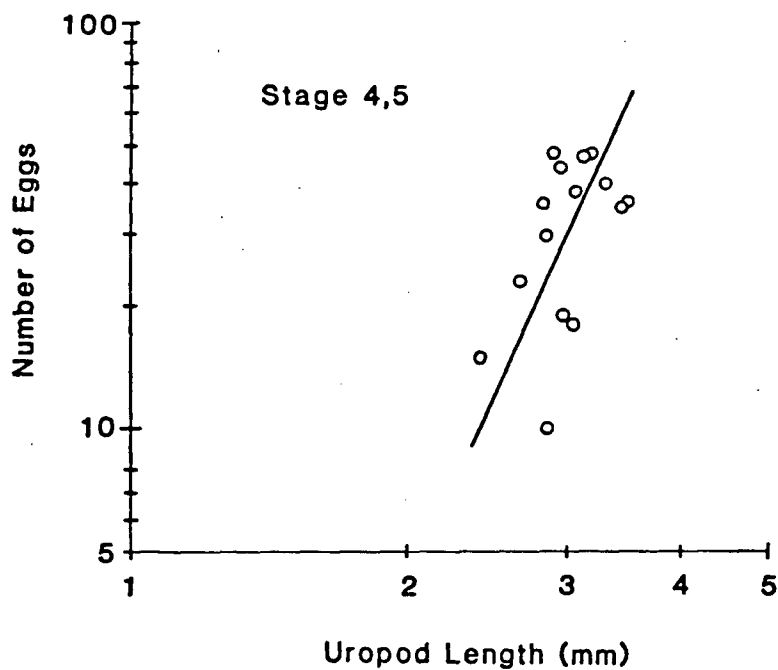


Figure 11b. The dependence of the number of stage IV and stage V embryos on female size, 1978.

in 1978 while the 1980 broods averaged about 1.27 times heavier than the 1978 clutches. The differences correspond closely to the differences in mean egg weights between years.

Thus, during 1978, the spring breeding generation consisted predominantly of large females producing large clutches of small eggs with a few females producing clutches of large eggs. The summer breeding generations consisted of small females which produced small numbers of large eggs but the same total clutch weight on a size-adjusted basis. The 1979 and 1980 spring breeding generations consisted of large females who produced the same numbers of young as the 1978 spring generation females but who laid significantly larger eggs which shifted the clutch weight - size relation upward relative to the 1978 animals without affecting the slope of the line. Variation in size-related measures of reproductive output and female condition are summarized in Table 2.

Sex Ratio and Fertility

The male:female ratio of the whole population fluctuated about one during the summer but declined steadily to 0.2-0.3 during the winter (Figure 12). The percentage of adult females in the population also decreased (Figure 5a), to $< 1\%$, during the winter as the mature females died after breeding in October while no females matured at the low winter temperatures. As the W generation matured in the spring the percentage of adult females increased quickly, and reached 76% by late April. This

Table 2. Homogeneous groupings of size-adjusted measures of reproductive output and female condition. Bracketted groups do not differ significantly at the 0.05 probability level (Scheffe test). Variables have been log-transformed to homogenize variances.
 1 = 1978 small egg type, 2 = 1978 large egg type,
 3 = spring 1979, 4 = spring 1980.

variable	groupings
egg weight	1 < 4 < (2, 3)
size-adjusted:	
a) fecundity	2 < (1, 3, 4)
b) clutch weight	(1, 2) < 4 < 3
c) body weight	(1, 2, 4) < (1, 3, 4)
d) total weight	2 < (1, 4)

reflected the low numbers of males in the population at that time. The proportion of adult females then declined rapidly as the spring brood hatched and the W generation females died. The percentage stabilized in the range from 2-5% for the balance of the summer, and averaged 3.2%.

The percentage of the adult females which were gravid increased from zero to about 80% as the W generation matured in the spring, declined rapidly to about 40% by July as these females died and increased again to stabilize between 60-70% in late summer (Figure 13). The seasonal reduction in the size of breeding females combined with the decrease in the proportion that were breeding to lower the average brood size per adult female from about 30 eggs per adult female in the W generation to about 10 per adult female throughout the summer (Figure 14).

Although multiple broods were produced by about 21% of the

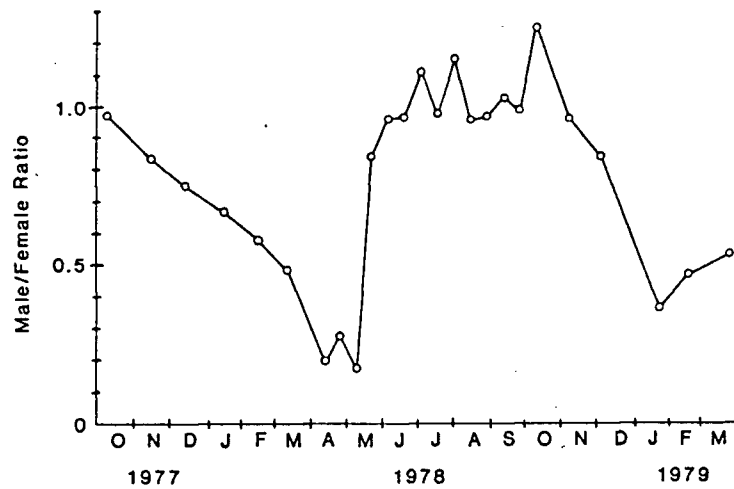


Figure 12. The seasonal pattern of the ratio of males : females at Woodward Island, 1977 to 1977.

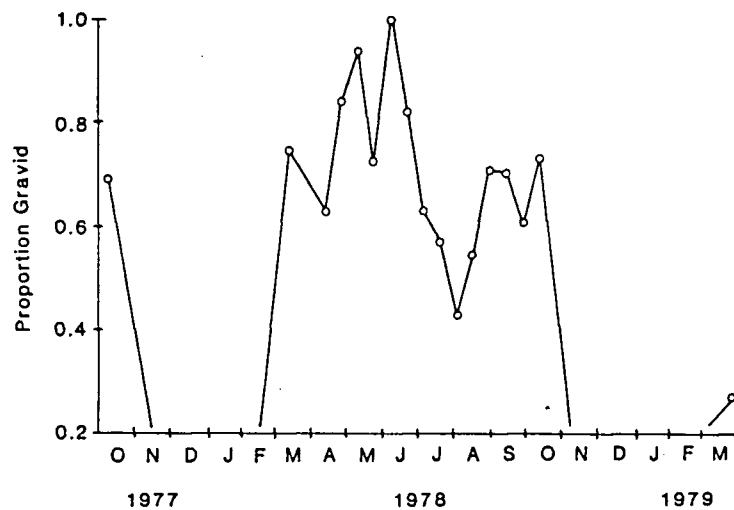


Figure 13. The seasonal pattern of the proportion of adult female Neomysis mercedis that are gravid .

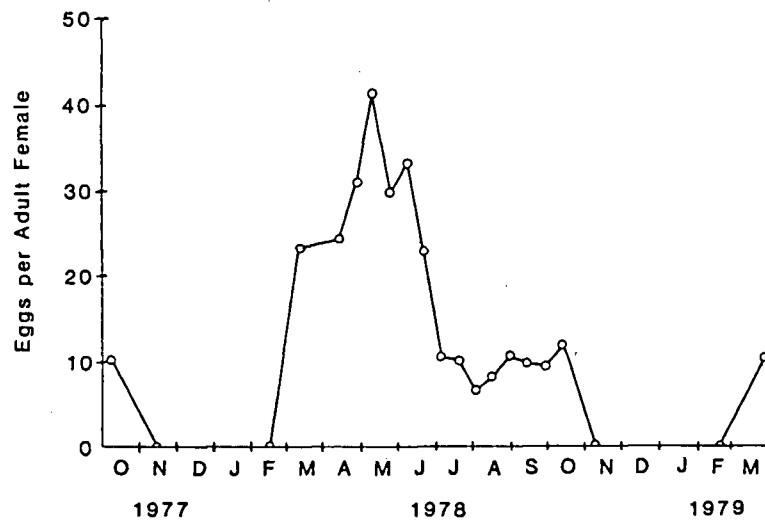


Figure 14. The seasonal pattern at Woodward Island of average number of eggs per adult female Neomysis mercedis, 1977 - 1979 .

females reared in the laboratory (chapter 2), the mortality rates calculated for adult females in the natural population made it unlikely that many produced a second clutch, and improbable that any females successfully brooded more than two clutches. The persistence of large gravid females until late June, well after the first decile adult size had decreased, suggested that a small proportion ($< 10\%$) of the W generation produced multiple clutches.

The reproductive characteristics of the three generations of N. mercedis are summarized in Table 3.

Table 3. Summary of the reproductive characteristics of the three generations of Neomysis mercedis at Woodward Island during 1978.

parameter	W	S1	S2
size at breeding (mg)	5.44	2.25	2.89
mean egg size laid (ug)	26.1	42.5	42.5
clutch weight / body weight	0.19	0.19	0.19
average # eggs / brood	25	9	12
percentage gravid	>80	<60	70
number of broods	1 - 2	1 - 2	1
generation time (days)	210+	85+	56+
population density ($\#/m^2$)	40	900	1400

Demography

Instantaneous per capita birth rates showed considerable variation over the 1978 breeding season (Figure 15). Birth rates were highest in the late spring as the offspring of the W generation hatched. Maximum rates of about 0.27 day^{-1} were

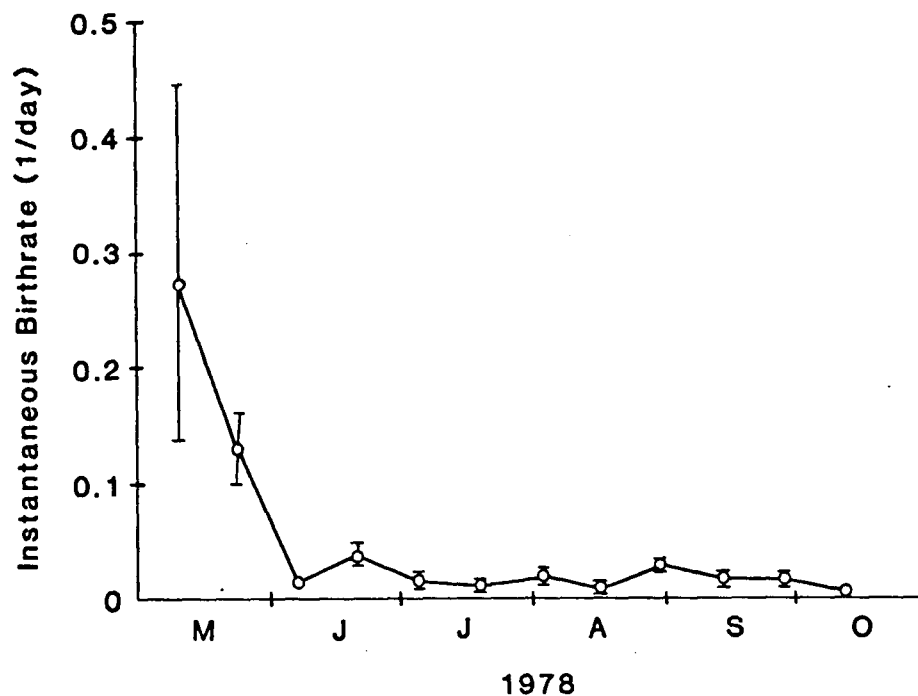


Figure 15. Per capita instantaneous birth rates for Neomysis mercedis at Woodward Island, 1978 . Vertical lines represent 95% distribution limits from repeated re-estimation of the birth rates.

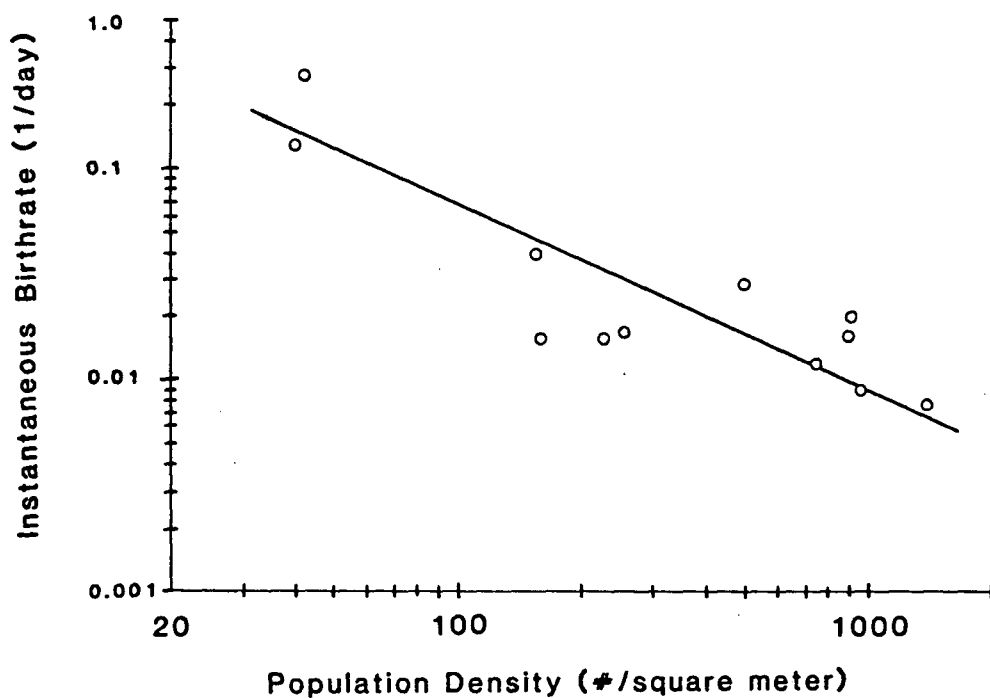


Figure 16. Dependence of per capita instantaneous birth rates of Neomysis mercedis at Woodward Island on population density .

found in late May. The birth rate then fell to rather constant low values ($0.01 - 0.03 \text{ day}^{-1}$) throughout the summer. Although three size classes bred until late June the 2.8-3.5 mm uropod length class accounted for 60 - 83% of the total birth rate. Thereafter, as reproduction shifted to smaller animals, the reproducing size range narrowed to two classes (1.8-2.8 mm) which made approximately equal contributions to the overall birth rate. Breeding ceased after mid-October.

Birth rates showed a strong inverse variation with population density (Figure 16; $r^2=0.74$, $p<0.01$, $n=12$) which suggested that some density-dependent process, such as competition for food resources, was an important determinant of the birth rates. Measures of food availability such as the food supply:demand ratio (Figure 17a) peaked in late spring and rapidly declined to much lower values throughout the summer. Egg production, measured as the mean number of eggs per adult female (Figure 14), was positively correlated ($r=0.57$, $p<0.05$, $n=13$) with the food supply:demand ratio. Birth rates were positively correlated with meiofauna standing crop ($r=0.75$, $p<0.05$, $n=12$) although not with the food supply:demand ratio. Correlative evidence of this sort is weak and potentially biased by intercorrelations with other variables. Nevertheless, there is at least the suggestion that food levels play a major role in determining birth rates in N. mercedis at Woodward Island.

Instantaneous mortality rates for specific size classes of N. mercedis varied considerably throughout time (Figure 18a-g). Because the mortality rates were estimated using the Lynch

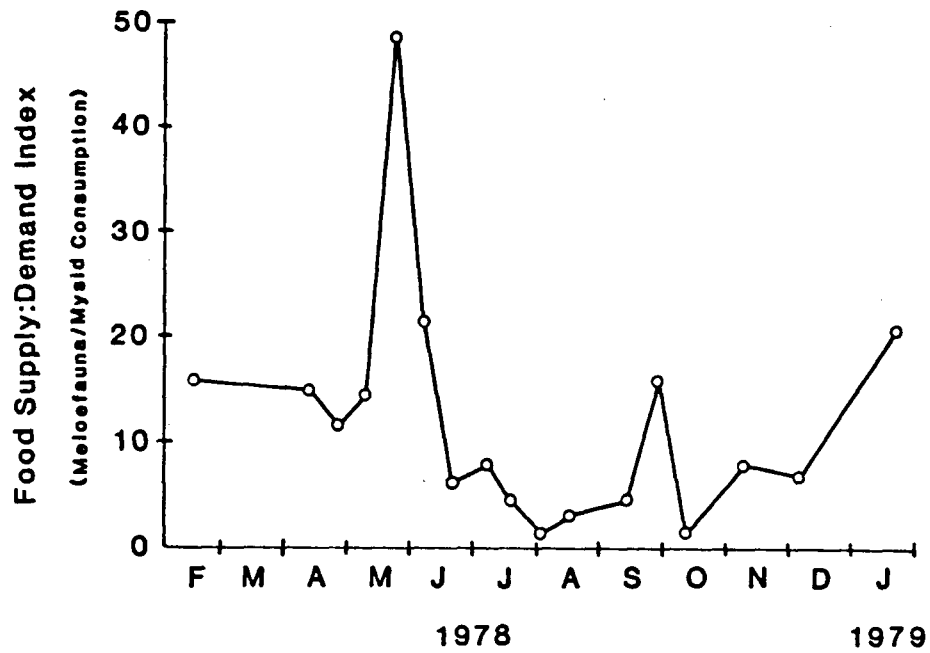


Figure 17a. Food resource supply:demand index for *Neomysis mercedis* at Woodward Island .

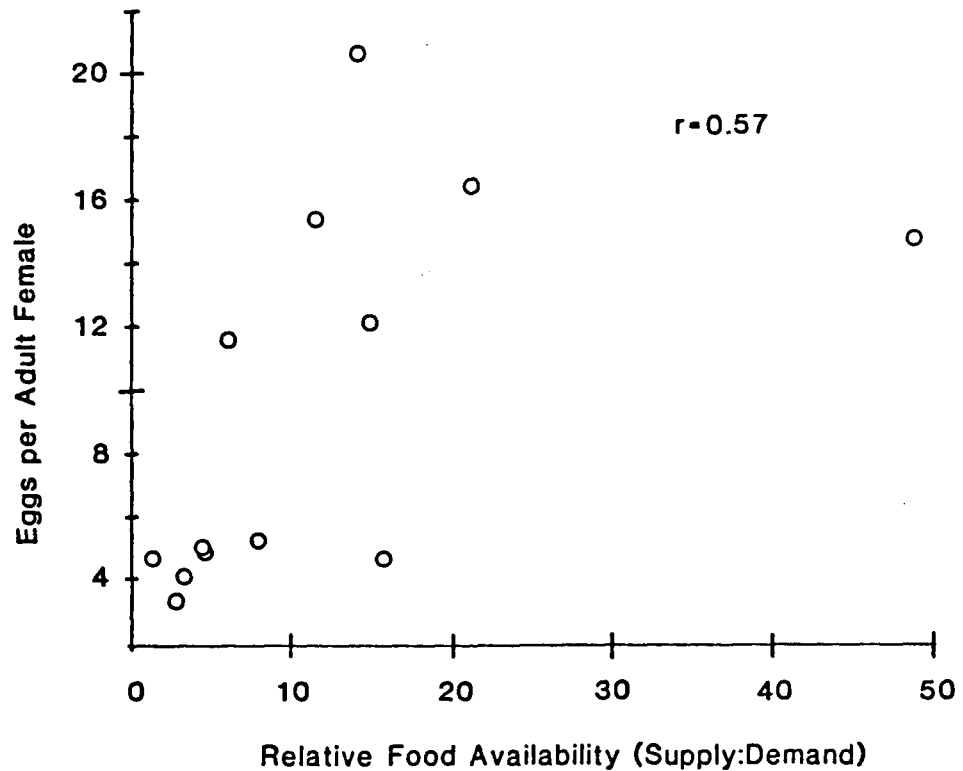


Figure 17b. Correlation between egg production (measured as the average number of eggs per adult female, and food availability).

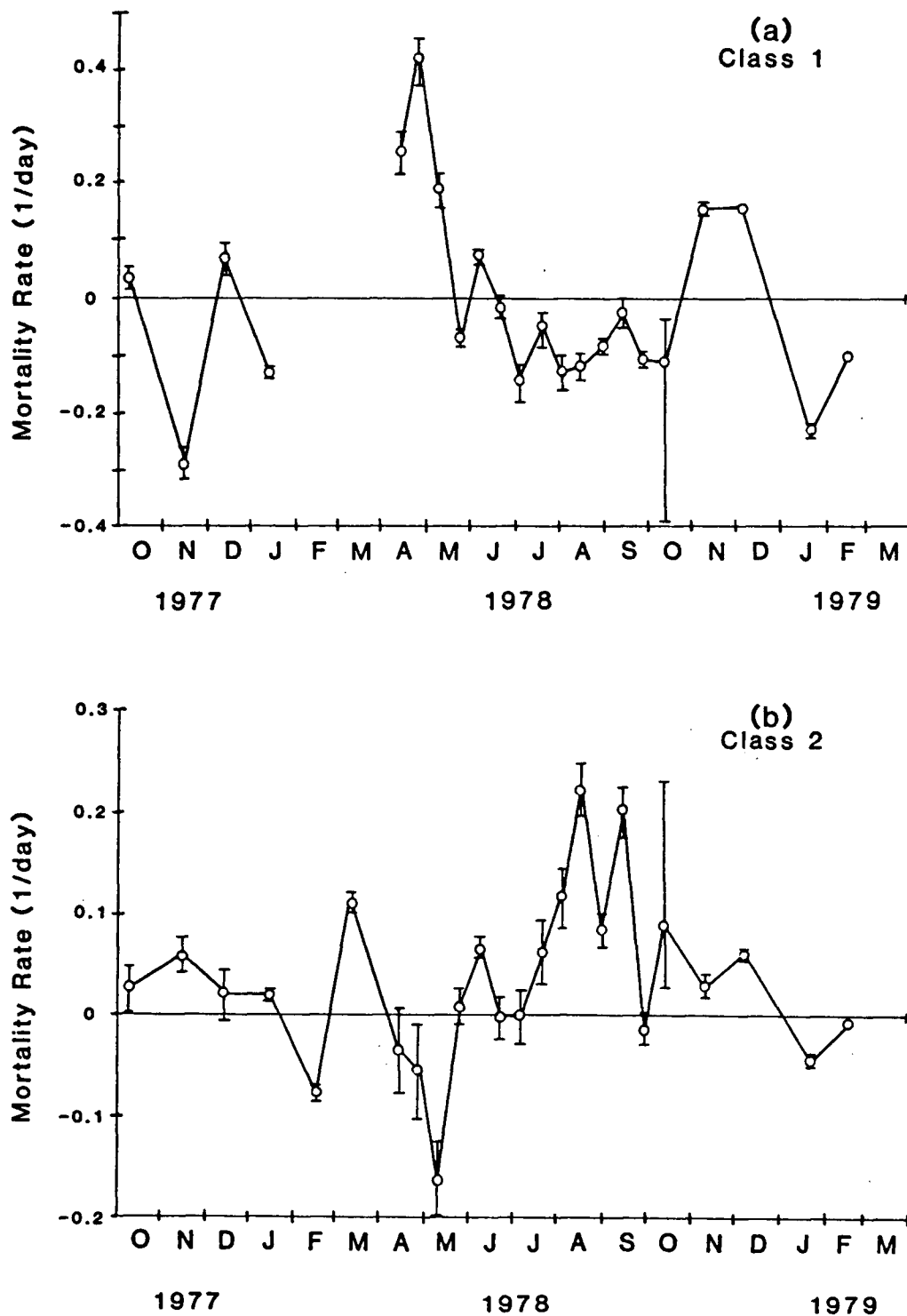


Figure 18. Seasonal variation in instantaneous death rates (and 95% distribution limits) of *Neomysis mercedis* at Woodward Island, 1977-1979. Vertical lines represent the 95% distribution limits from repeated re-estimation of the mortality rates. (a) = class 1 (0.3-0.8 mm uropod length), (b) = class 2 (0.8-1.3 mm),

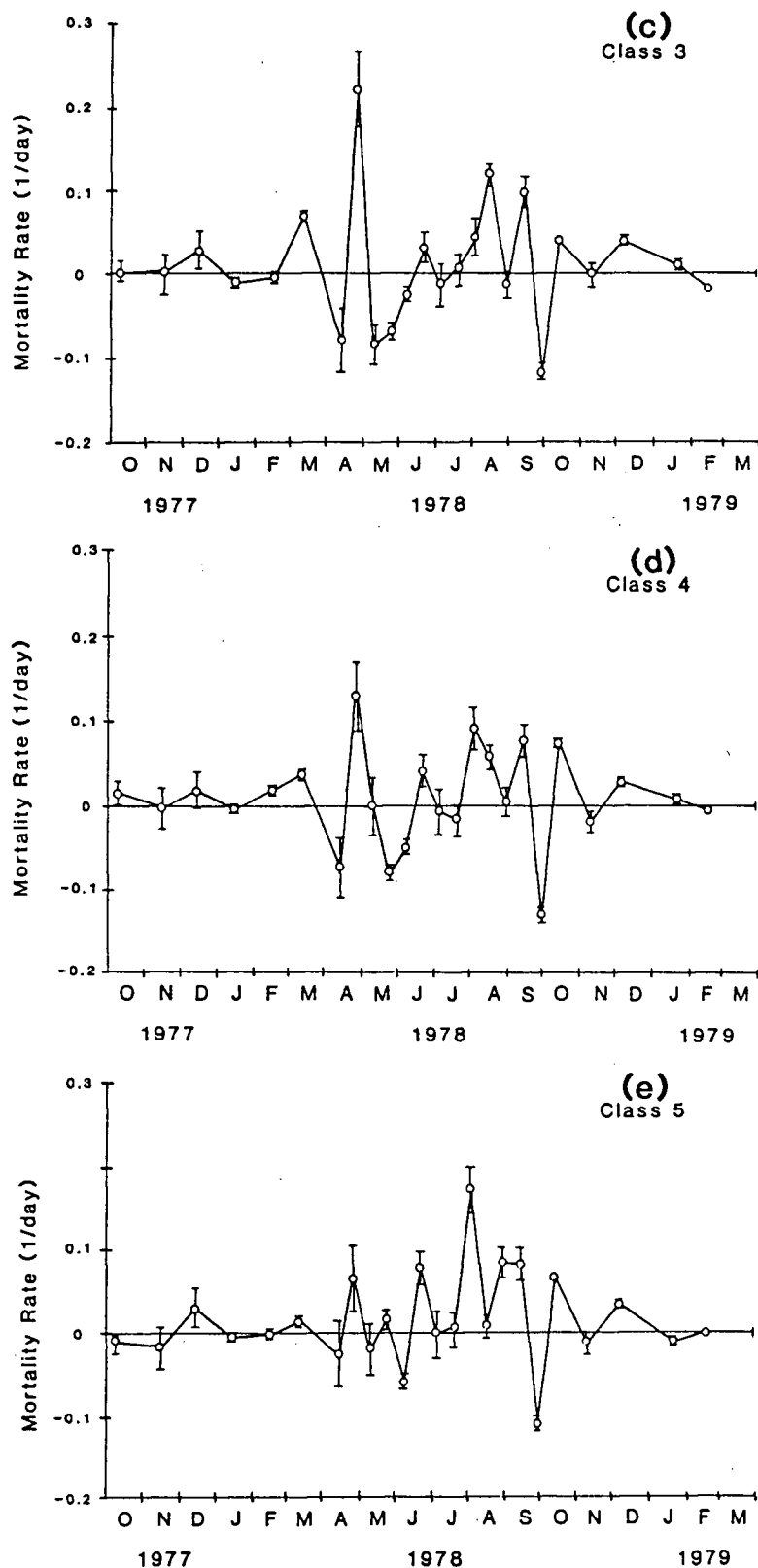


Figure 18. Seasonal variation in instantaneous death rates (and 95% distribution limits) *Neomysis mercedis* at Woodward Island, 1977-1979. Vertical lines represent the 95% distribution limits from repeated re-estimation of the mortality rates. (c) = class 3 (1.3-1.8 mm), (d) = class 4 (1.8-2.3 mm), (e) = class 5 (2.3-2.8 mm),

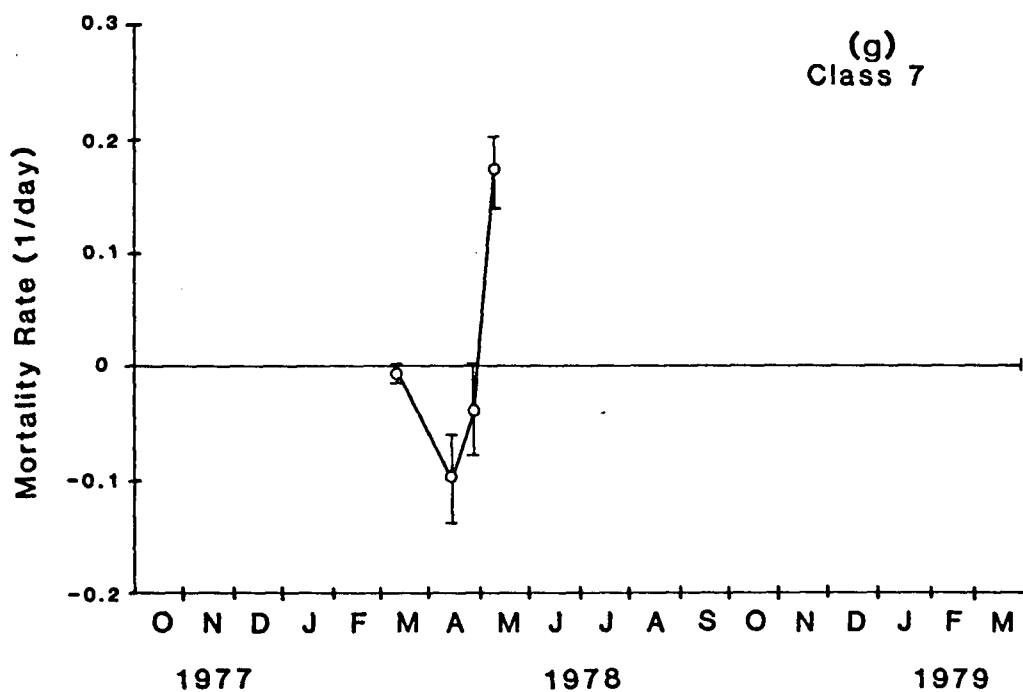
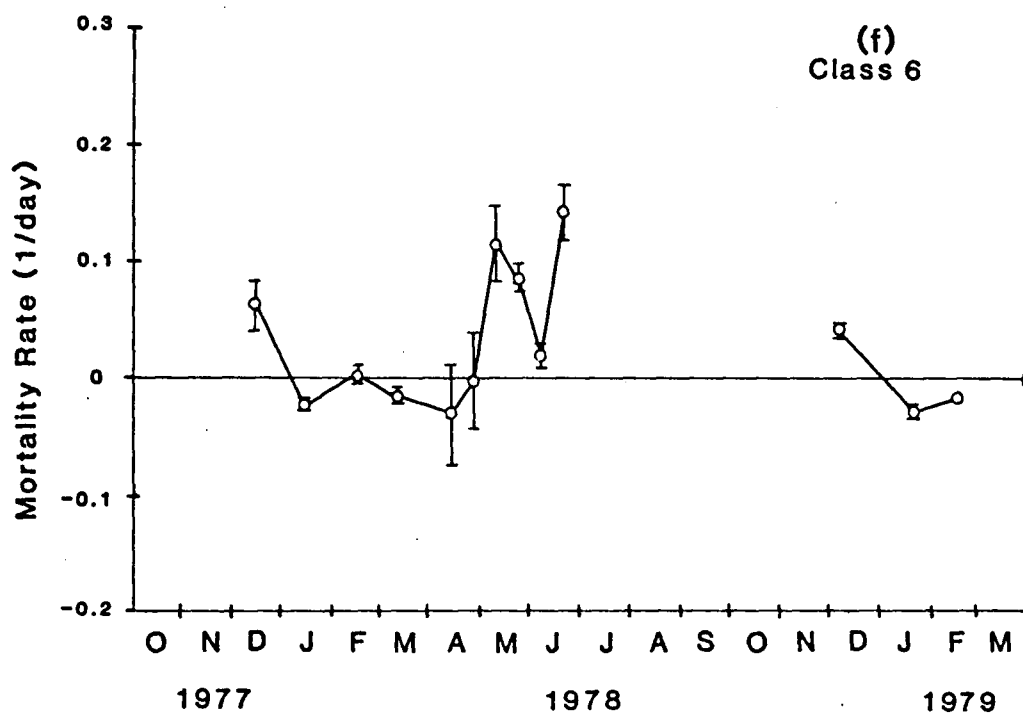


Figure 18. Seasonal variation in instantaneous death rates (and 95% distribution limits) *Neomysis mercedis* at Woodward Island, 1977-1979. (f) = class 6 (2.8-3.3 mm), (g) = class 7 (3.3-3.8 mm)

algorithm, it is likely that they slightly underestimate the true values (see Appendix 3). The degree to which the true mortality rates are underestimated depends upon (1) the magnitudes of the rates, (2) the rate of change of mortality between size classes, (3) the initial size-frequency structure of the population, and (4) the duration of the estimation interval. For the Woodward Island data, true values could be underestimated by about 30% for the smallest size class to about 50% for the largest (see Tables A2 and A3). However, the 95% confidence limits on the mortality rates would generally encompass the true values if bias were of the magnitude suggested in Appendix 3. Uncertainties in the population density estimates were a major cause of uncertainty in the absolute magnitude of the mortality rates. Nevertheless, the relative rates of the different size classes should be correct (Lynch 1983).

The consistently negative mortality rates estimated for class 1 animals during the late summer period may have arisen from (1) inaccuracies in the density estimates (which were subject to large adjustments for gear selectivity for the smallest animals, Appendix 2), (2) from the effects of underestimates of the hatching or growth rates on the expected densities (as, for example, from the effects of diel temperature fluctuations, Meyers 1984), or (3) from immigration. Non-uniformities in the egg age distribution other than those resulting from adult mortality (which is incorporated in the algorithm) are unlikely to account for the period of negative

mortality estimates since this would require a continuous increase in the rate of egg production over the period, which is not evident (Figure 14).

In general, the magnitudes of seasonal fluctuations were greater for smaller size classes than for the larger classes. Newly hatched mysids (class 1, Figure 18a) showed the largest seasonal variation in death rates. Animals born early in the breeding season experienced very high mortalities ($0.18 - 0.42 \text{ day}^{-1}$). Mortality rates declined considerably through the late May to late June period and remained at low, relatively constant levels throughout the remainder of the breeding season. The death rate of class 1 animals rose at the onset of winter but declined over the winter.

Classes 2 - 5 all showed a similar pattern of seasonal variation, but with the magnitude of seasonal variation decreasing in the larger animals. Mortality rates were relatively constant at low values during the winter and declined slightly between March and May. The decline occurred somewhat later in the two largest classes. Death rates generally increased steadily from mid-May to September and then declined to low, winter values. Late summer peak mortalities were about 0.20 day^{-1} for class 2, 0.12 day^{-1} for class 3, 0.09 day^{-1} for class 4, and 0.17 day^{-1} for class 5.

The two largest size classes were present only in the winter to spring period. They showed a pattern of temporal variation which was quite different from the intermediate size classes. Death rates were low and quite constant until May when

they increased greatly and remained considerably above the winter levels until the classes disappeared from the population in late June (Figures 18f and 18g).

Throughout the winter there was little variation in mortality rates with size. During the April - early June period, when the overwintering generation was breeding, the death rates of the smallest, newly hatched animals were greater than those of larger animals; the pattern of size-specific mortality tended to be U-shaped, with high rates for the largest and smallest mysids. During the summer the mortality rates were generally lowest for the class 1 animals, but varied little for the intermediate size animals. The overall temporal variation in size-specific mortality rates can therefore be summarized as two rather distinct mortality regimes: (1) during the spring breeding period when the death rates of newly hatched animals exceeded those of larger immatures and adults, and (2) during the summer breeding period when the death rates of newly hatched juveniles were less than those of larger animals (Figure 19).

For the range of body sizes over which N. mercedis matured, the size-specific mortality rates generally increased with increasing body size during May to October, when breeding occurred (Figure 20a,b). The increase in instantaneous mortality rates with increasing body size implied selection against larger adults. The per day survival of the larger classes would be reduced by Δm (since $S_2 \approx S_1(1 - \Delta m)$ for small Δm). The increase in mortality rate with increasing size was positively correlated with the average ambient water temperature

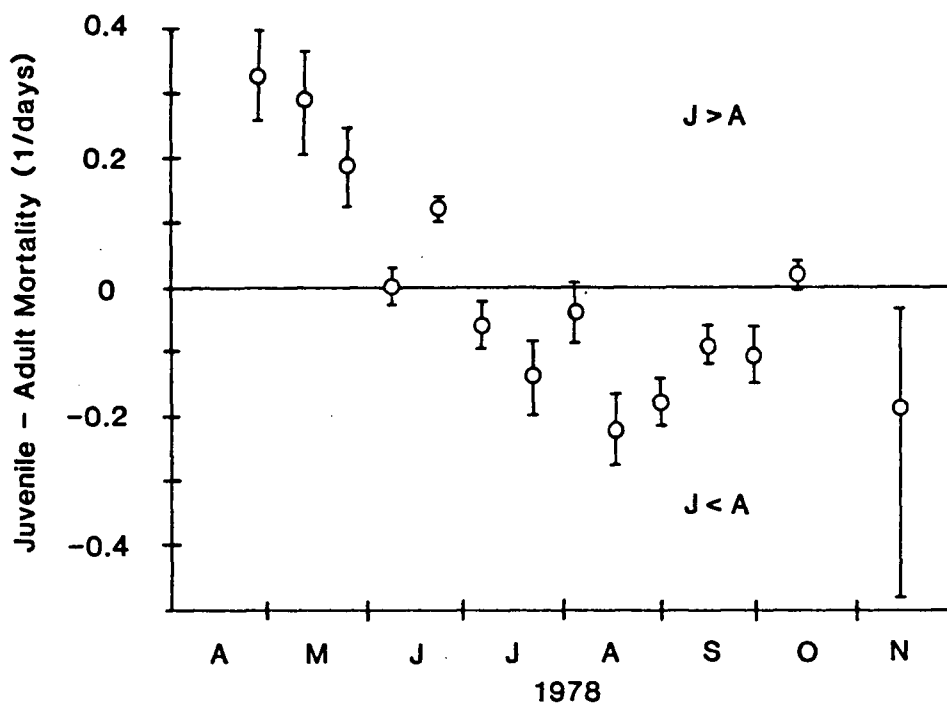


Figure 19a. Difference in mortality rates between neonates (class 1) and adult (class 4) animals. Positive values indicate that juvenile mortality rates exceed those of adults.

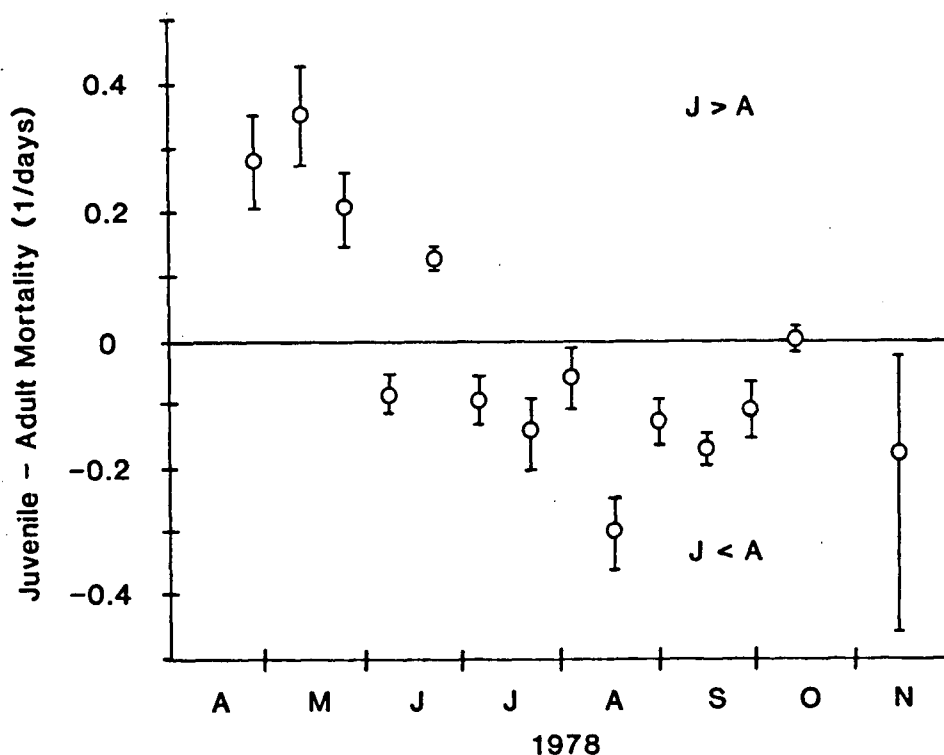


Figure 19b. Difference in mortality rates between neonates (class 1) and adult (class 5) animals. Positive values indicate that juvenile mortality rates exceed those of adults.

over the estimation interval ($r=0.58$, $p<0.05$, $n=13$ for the increase in mortality rates from class 5 to class 6; $r=0.35$, $p=0.10$, $n=24$ for the increase between classes 4 to 5). Thus, the ambient water temperature could be a predictor of the relative intensity of selection against further increases in adult body size.

Stepwise linear regression models for size-specific mortality rates suggested that mortality rates were inversely related to food levels (Table 4). Fifty - one percent of the variance in the mortality rates of class 2 mysids and 34% of that of class 4 animals were accounted for by measures of food availability. Mortality rates of class 1 mysids varied inversely with food availability and directly with the abundance of chinook and sockeye salmon fry and smolts. The density of the salmon predators accounted for most (74%) of the 83% of the total variance explained by the regression model. However, neither food levels nor predator densities were significant predictors of mysid death rates for other size classes. The magnitudes of the standardized regression coefficients suggested that the effect of fluctuations in food resources on mortality rates was similar for all sizes of immature animals.

Fish Predation

N. mercedis was preyed upon by a variety of fishes (Table 5) as well as the shrimp Crangon franciscorum Stimpson. The importance of N. mercedis as a dietary item for its predators varied considerably, both between fish species and between

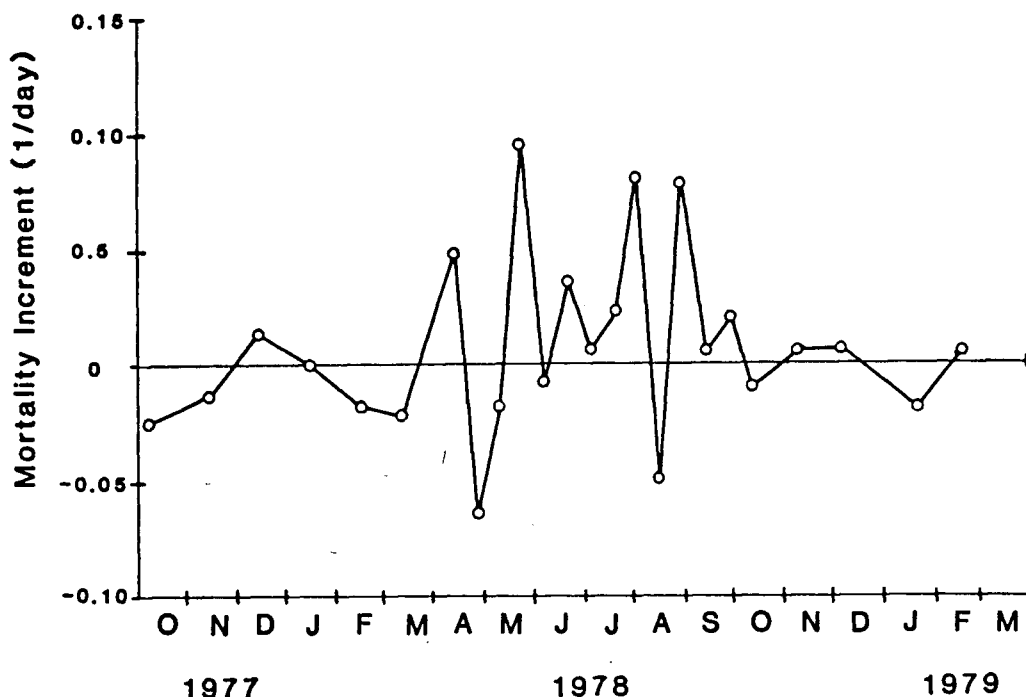


Figure 20a. Seasonal variation in the increment in the probability of death per unit time with increasing size from class 4 to class 5 for Neomysis mercedis at Woodward Island. Positive values indicate increasing mortality rates with an increase in size. The values are generally positive throughout the period from May to September.

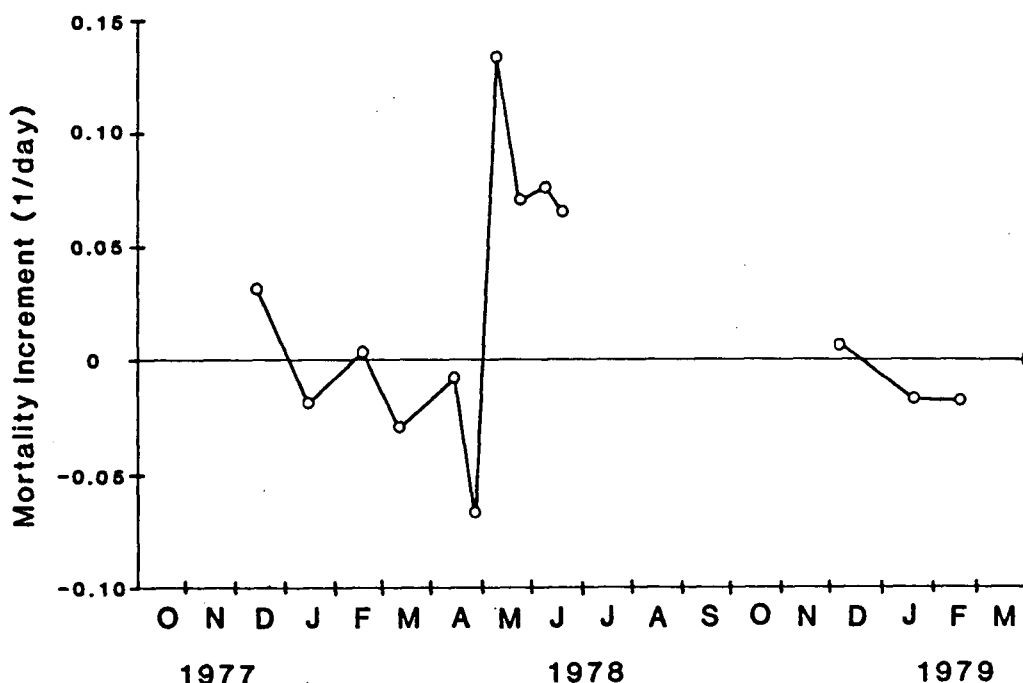


Figure 20b. Seasonal variation in the increment in the probability of death per unit time with increasing size (from class 5 to class 6) for Neomysis mercedis at Woodward Island. Positive values indicate increasing mortality rates with an increase in size.

Table 4a. Coefficients of the multiple regression model
 death rate = b per capita food resources +
 c predator abundance for class 1 N. mercedis
 (n=13).

variable	standardized coefficient	+-	SE	R ² added
salmon fry density	1.324	+-	0.240	0.74
per capita food	-0.551	+-	0.240	0.09
R ²				0.83

Table 4b. Coefficients of the multiple regression model
 death rate = b supply:demand index for class
 2 N. mercedis (n=15).

variable	standardized coefficient	+-	SE	R ² added
supply:demand index	-0.714	+-	0.194	0.51

Table 4c. Coefficients of the multiple regression model
 death rate = b supply:demand index for class
 4 N. mercedis (n=15).

variable	standardized coefficient	+-	SE	R ² added
supply:demand index	-0.581	+-	0.226	0.34

sampling dates. There was no obvious relation between the proportion of N. mercedis in the diet of its fish predators and its seasonal abundance (Table 5). The relative importance of particular fish species as predators on N. mercedis also changed seasonally (Figure 21) in response to changes in the species composition, abundance, and size structure of the fish community. During the fall - winter period sculpins, smelt, herring, and especially starry flounders accounted for most of

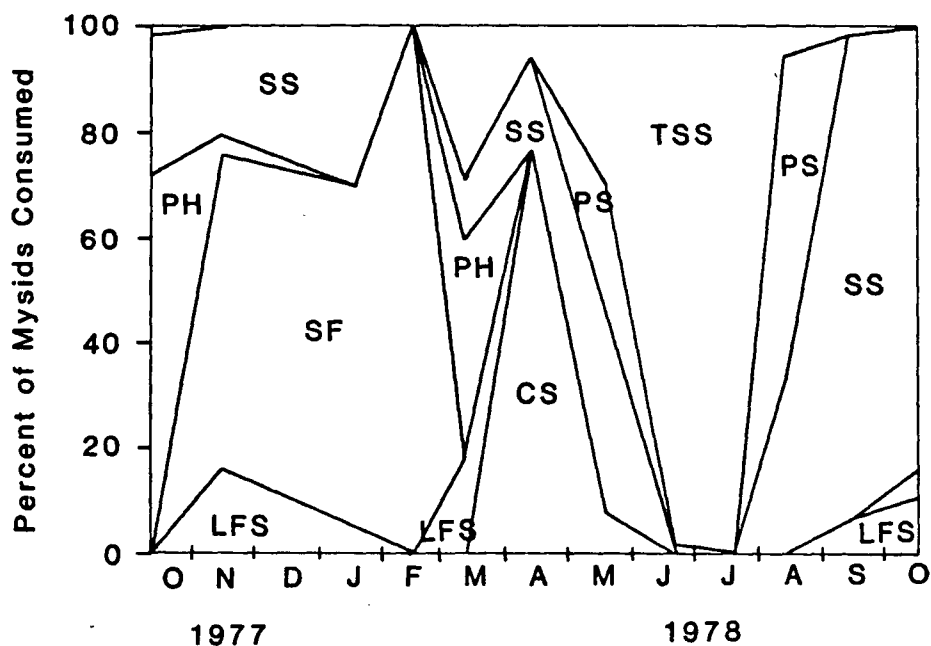


Figure 21. Seasonal changes in the proportion of *Neomysis mercedis* consumed by particular fish species, 1977 - 1978. LFS = long-finned smelt, PH = Pacific herring, SF = starry flounders, SS = staghorn sculpins, PS = prickly sculpins, CS = chinook salmon, and TSS = threespined stickleback.

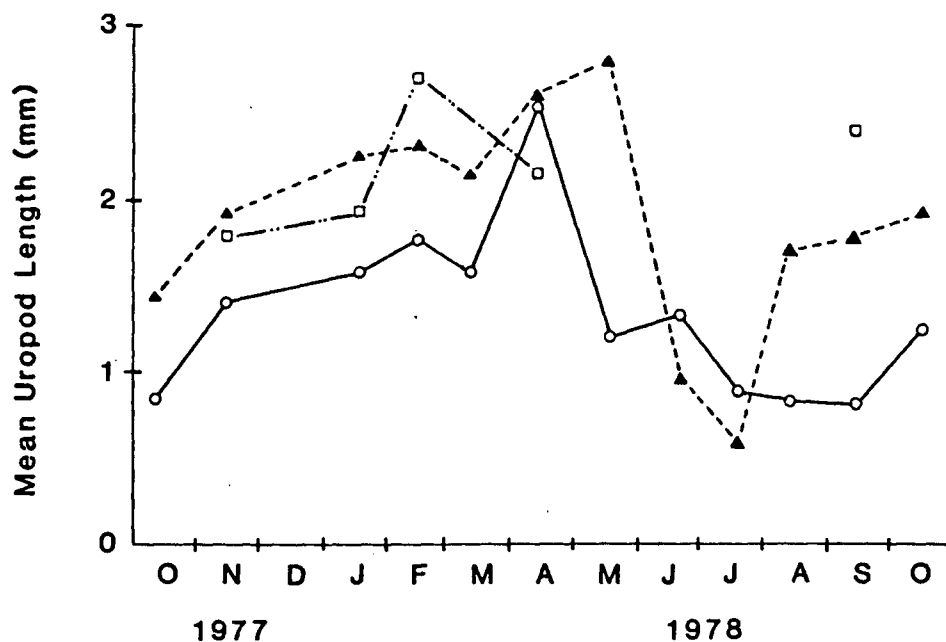


Figure 22. Seasonal changes in the mean size of *Neomysis mercedis* consumed by fish at Woodward Island, 1977 - 1978. (Δ) is the mean size from fish stomachs, (□) is the mean size from *Crangon* stomachs, and (O) is the mean size in the population.

Table 5. Contribution of N. mercedis (average % volume \pm SE) to the diets of fishes at Woodward Island, 1977 - 1978. SS=staghorn sculpin, PS=prickly sculpin, PH=Pacific herring, TSS=three spined stickleback, LFS=long finned smelt, SF=starry flounder, CS=chinook salmon, and CF= Crangon franciscorum

date	SS	PS	PH	TSS	LFS	SF	CS	CF
12-13/X/77	21.7 (1.8)	11.3 (2.8)	94.3 (2.2)	2.5 (2.5)				
16/XI/77	9.6 (4.1)		16.5 (2.0)		3.5 (1.1)	3.6 (3.6)		67.4 (2.8)
19-20/I/78	2.8 (0.3)			1.1 (1.1)		18.6 (5.4)		86.3 (2.1)
15-17/II/78						6.5 (6.5)		9.6 (9.6)
12-13/III/78	0.5 (0.5)		52.2 (15.5)	5.6 (0.9)	34.8 (21.2)			
12-13/IV/78	40.0 (0.0)			4.4 (0.9)	100.0 (0.0)		7.1 (1.2)	14.8 (2.4)
19-20/V/78	2.3 (0.3)	15.5 (1.9)		9.0 (0.7)			0.3 (0.3)	
23-24/VI/78	0.1 (0.1)	4.5 (0.6)		14.0 (0.5)			3.0 (1.3)	
19-20/VII/78	19.7 (1.7)			17.0 (1.3)			1.2 (0.5)	
14-15/VIII/78	2.9 (0.9)	5.4 (0.7)		0.8 (0.3)				
14-15/IX/78	36.0 (1.3)			8.3 (1.4)	100.0 (0.0)			12.8 (5.1)
18-19/X/78	4.5 (1.2)		33.8 (4.8)		31.0 (2.8)			

the N. mercedis consumed. However, as juvenile salmon moved through the estuary in spring, chinook salmon fry and smolts became the major predators on the mysids. The impact of the salmon was through their numerical abundance since N. mercedis

never comprised more than about 7% of the salmon's diet (Table 5). Levy et al. (1979) also found that N. mercedis was a relatively small component of the diet of chinook salmon (averaging 9.1% of volume). In early summer small stickleback consumed most of the mysids lost to fish predation, once again as the result of the greatly increased numerical abundance of the fish. In late summer sculpins became the dominant fish predator on N. mercedis. The role of C. franciscorum was difficult to assess. Although N. mercedis was an important prey item for the shrimp (Table 5), especially during the winter, the shrimp was not quantitatively sampled by the collection methods used. Elsewhere it is known to be an important predator on N. mercedis (Siegfried 1982).

Changes in the nature of the fish community interacted with changes in the size structure and abundance of the mysid population to shift fish predation pressure to different mysid size classes at different times. The mean and median size of mysids consumed by fish increased between late fall and spring (Figure 22), fell dramatically in June and July because of selection for the smallest mysid size classes by the numerically dominant small sticklebacks, and then increased again to the previous fall values. The size - frequency distributions of mysids from fish stomachs differed significantly from those of the mysid population on all occasions ($p < 0.05$, Kolmogorov Smirnov 2-sample test). In June and July the mean size of N. mercedis from the fish stomachs was less than that of the mysid population, in April there was no difference in the

means, and in all other cases the mean size from the fish stomachs was greater than that of the population ($p < 0.05$, t -test). Gravid females, whose broods rendered them very visible, were usually represented in the fish stomachs in the same proportion as they occurred in the population ($p > 0.05$, chi-squared test), although in one case they were overrepresented and in 2 cases they were underrepresented.

Size-specific instantaneous mortality rates resulting from fish predation are given in Table 6. Except in early summer, mortality rates from fish predation generally increased with increasing mysid size. The largest size classes often had greatly elevated mortality rates. Mortality rates on the 2 smallest mysid classes were greatest (maximum of 0.07 day^{-1}) in early summer but declined thereafter to extremely low values ($< 0.001 \text{ day}^{-1}$) and remained at low values while the classes were present in the population. Mortality rates on classes 3 - 5 from fish predation showed little temporal variation. Maximal rates (about 0.012 day^{-1} , 0.030 day^{-1} , and 0.045 day^{-1} respectively) were observed in the fall but generally the rates ranged between 0.005 and 0.015 day^{-1} . Class 6 mysids had high mortality from fish predation during the winter but mortality was fairly low in the spring and early summer, with a slight increasing trend until the size class was eliminated in June. The large class 7 animals, which were found only in spring and early summer, showed very high losses to fish predation in April; however the death rate declined between April and June as the class became less abundant.

Table 6. Size specific instantaneous mortality rates on *N. mercedis* from fish predation (\pm 1 SE).

Sampling Date	Uropod Length Class						
	0.3-0.8mm	0.8-1.3mm	1.3-1.8mm	1.8-2.3mm	2.3-2.8mm	2.8-3.3mm	3.3-3.8mm
10 October 1977	0.0041 (0.0025)	0.086 (0.054)	0.22 (0.14)	0.36 (0.25)	0.089 (0.056)		
16 November 1977	0.0057 (0.0012)	0.0011 (0.0002)	0.0089 (0.0018)	0.029 (0.006)	0.043 (0.009)	0.14 (0.03)	
15 January 1978		0.00030 (0.00001)	0.0037 (0.0001)	0.0130 (0.0003)	0.036 (0.001)	0.28 (0.01)	
17 February 1978		0.00010 (0.00002)	0.00025 (0.00005)	0.0027 (0.0006)	0.0058 (0.0012)	0.0087 (0.0019)	
14 April 1978			0.012 (0.004)	0.0079 (0.0027)	0.0084 (0.0029)	0.0064 (0.0022)	0.17 (0.06)
25 May 1978			0.0018 (0.0004)	0.017 (0.004)	0.013 (0.003)	0.014 (0.003)	0.028 (0.006)
22 June 1978	0.074 (0.016)	0.028 (0.006)	0.015 (0.003)	0.011 (0.002)	0.012 (0.003)	0.028 (0.006)	0.010 (0.002)
20 July 1978	0.012 (0.005)	0.0041 (0.0016)	0.0029 (0.0011)	0.0013 (0.0005)	0.0030 (0.0011)		
17 August 1978	0.000042 (0.000014)	0.00045 (0.00015)	0.0027 (0.0009)	0.0061 (0.0020)	0.0093 (0.0030)		0.0011 (0.0003)
15 September 1978	0.000095 (0.000031)	0.0011 (0.0004)	0.0098 (0.0033)	0.026 (0.009)	0.045 (0.015)		
13 October 1978	0.000046 (0.000002)	0.00050 (0.00002)	0.0026 (0.0001)	0.0060 (0.0003)	0.0097 (0.0004)		

Discussion

N. mercedis in the tidal marshes of the Fraser River delta appears to produce three generations per year. Breeding is initiated in late March - early April as water temperatures increase above 6-8°C, and continues until mid October when temperatures decline sharply. Newly hatched juveniles appear in the population in mid-late May. These animals (the S1 generation) grow quickly to mature in late July and early August at 2.0-2.1 mm uropod length. Young produced by the S1 generation appear in early August and mature by mid October at 2.0-2.1 mm. The production of young is continuous throughout the summer period because of multiple brooding by a small proportion of females in each generation and because of the range of sizes initially present in the overwintering (W) generation, which spreads breeding over an extended period in the spring. Animals hatched in the late summer (S2) and early fall (W) grow rapidly until the temperature decreases in November, and overwinter as slowly growing juveniles or immatures. These animals grow rapidly when temperatures again increase in the spring, and mature between April and early June at sizes which decrease from 2.8-2.6 mm uropod length; the smaller sizes of the later maturing females result from the higher temperatures during the maturation period.

The failure of eggs and embryos to develop at temperatures below about 6°C (chapter 2) results in a cessation of breeding between November and March. This, in turn, imposes a marked seasonality on the abundance of the mysid. Standing crops

($\# \cdot m^{-2}$) decline continuously during the winter to minimum values of 30-40 $\cdot m^{-2}$ in late winter and early spring. Abundance increases quickly in the early summer as recruitment of young to the population commences, and stabilizes at densities near 1000 $\cdot m^{-2}$ in the late summer - early fall period.

In conjunction with the seasonal changes in abundance there occur changes in the life history traits of the mysids, the most evident of which are a decreased size at maturity and an increased egg size in the summer generations.

Body Size Variation

Variation in adult body size is fairly common in crustaceans (e.g. Hutchinson 1967, p. 856; Kinne 1970, p. 511; Nelson 1980; Culver 1980) and has variously been attributed to the effects of temperature (Corkett and McLaren 1978, p. 115; de March 1978; Culver 1980; Armitage and Landau 1982), nutrition (Richman 1958; Deevey 1960; Vijverberg 1976; Brambilla 1980; Evans 1981; Elmore 1982), predation (Strong 1972; Northcote and Clarotto 1975; Stenson 1976), or intrinsic differences (Corkett and McLaren 1978, p. 123; Klein Breteler and Gonzalez 1982) acting singly or in combination (Vidal 1980a; Klein Breteler and Gonzalez 1982; Sheader 1983). Maturation at smaller body size during the summer has frequently been reported in mysids (Mauchline 1980, p. 204,211) and, in Neomysis, has been ascribed to temperature (Heubach 1969; Toda et al. 1982, 1983). Seasonal variation in the size of Leptomysis lingvura has been attributed to temperature effects on metabolism (Gaudy and

Guerin 1979). Interpopulation differences in the size at maturity in Mysis relicta within Lake Tahoe were attributed to regional differences in food levels (Morgan 1980).

Variation in life history traits may be discussed in terms of both proximate and ultimate causes. Temperature may be the most important proximate factor inducing the summer reduction in size at maturity in the Woodward Island population of N. mercedis since the size at maturation of well-fed laboratory reared animals decreased similarly with increasing temperature. Although the decrease in adult body size at 20°C was less than that at corresponding temperatures at Woodward Island, the difference may result from the early thermal histories of wild animals reared to maturity at 20°C. The field derived temperature - size relation (Figure 7b) showed a marked hysteresis depending on the direction of temperature change. A similar dependence of adult size on temperatures experienced during early life has been reported for the amphipod Hyalella azteca (de March 1978) and was discussed by her as a mechanism to optimize reproduction in fluctuating thermal environments. Seasonal variation in food availability did not account for a significant amount of the variation in size at maturity of N. mercedis at Woodward Island beyond that attributable to temperature effects. Temperature may generally be a more important determinant of adult body size in aquatic crustaceans than food levels. Daphnia reared at a fixed temperature matured at the same body size over a wide range of food levels by varying the number of prereproductive instars (Anderson 1932;

Neill 1981a). However, such a response may not be general (W.E. Neill, pers. comm.).

Inadequate nutrition in the field population is unlikely to have been an important modifier of adult size in the present case since: (1) growth rates were similar to those of laboratory reared animals (chapter 2), and (2) the clutch weight - female size relation did not vary between the 1978 generations. Growth and reproductive output are commonly regarded as sensitive indicators of the nutritional state of an animal. However the fact that animals which matured at small size during the summer apparently had sufficient food resources for normal growth and reproduction does not necessarily imply that larger animals with greater metabolic requirements would also find adequate food levels. Both per capita food levels and supply:demand indices declined throughout the summer.

From May to October there was strong selection against large body size (Figure 20). Mortality rates (from all sources) consistently increased with increasing size during summer. Because the increment in probability of death with increasing size for the mature size classes of N. mercedis was correlated with temperature, temperature could be a predictor of the intensity of selection against further increase in body size. Thus a physiological response to increased temperature that led to a reduced body size at maturity would result in a higher probability of survival. Seasonal variation in the intensity of selection against large animals which was correlated with environmental temperatures may promote genetic mechanisms

underlying a temperature-dependent phenotypic plasticity in size at maturity.

Egg Size Variation

Variation in egg size has been reported for several mysids (Wigley and Burns 1971; Lasenby and Langford 1972; Mauchline 1973a; Brattegard 1974; Baychorov 1979) including N. americana and N. integer. Seasonal changes in egg size within a population are known for N. integer (Mauchline 1973a) and Leptomysis lingvura (Wittmann 1981b). In these two cases, however, the larger winter generation females carried larger eggs than the smaller summer females, in contrast to the situation seen for N. mercedis at Woodward Island. Changes in egg size may be commonly overlooked because the customary measurement of egg diameters rather than egg weights reduces the magnitude of differences relative to measurement error: the 1.56 times change in mean egg weights which I observed would change the egg diameters only by about 1.17 times. The ratios of egg volumes calculated for the ranges of egg diameters reported for N. integer and N. americana vary from 1.35 to 2.25 times which are similar to the variation which I observed. The seasonal changes in size-adjusted fecundities reported for most Neomysis species (Kinne 1955; Murano 1964; Heubach 1969; Mauchline 1971; Siegfried et al. 1979) may represent changes in mean egg size if the total clutch weight remains constant between generations as in N. mercedis. Thus seasonal variation in egg size may be quite common in the Mysidacea.

Seasonal egg size cycles within populations have been reported for numerous other crustacean groups including cladocerans (Green 1966; Kerfoot 1974; Culver 1980; Brambilla 1982), copepods (Hutchinson 1967, p.659; Hart and McLaren 1978), amphipods (Steele and Steele 1975a; Sheader 1983), and isopods (Brody and Lawlor 1984). Seasonal variation in environmental temperatures and/or food levels are often regarded as the proximate factors inducing egg size variation while (predictable) seasonal variation in size differential mortality on juveniles from size-selective predation or size-related competition are invoked as the ultimate causes (Cody 1966).

The occurrence of larger eggs in the summer generations of N. mercedis at Woodward Island is in contrast to the data for most crustaceans where smaller eggs are associated with higher temperatures (Steele and Steele 1975; Hart and McLaren 1978; Nelson 1980; Culver 1980; Brambilla 1982; Sheader 1983). Latitudinal comparisons similarly associate larger eggs with colder environments (Nelson 1980; Van Dolah and Bird 1980). However field data confound the simultaneous effects of temperature, food, and interpopulation differences. The relative magnitudes of different factors are difficult to assess. In laboratory experiments the direct effects of temperature on egg size in Daphnia accounted for only a small portion of the observed seasonal variation (Brambilla 1982). Diet is known to affect egg number in the mysid Mysidopsis bahia (Johns et al. 1981) and in numerous other crustaceans (Smyly 1973; Vijverberg 1976; Lampert 1978; Sheader 1983) but food

effects on egg size are less commonly reported. Food limitation resulted in smaller size at birth in Daphnia (Green 1956; Brambilla 1980) but in larger young in the isopod Armadillium (Brody and Lawlor 1984). The production of larger young under adverse conditions is known in other organisms such as aphids (Dixon and Wellings 1982) and fish (Stearns 1983a,b), and is often discussed as an adaptive response to factors influencing the survival of young (Hutchinson 1951; Smith and Fretwell 1974)

The factors which induce seasonal egg size variation in N. mercedis remain obscure. Neither a direct physiological response to varying resource levels nor intrinsic differences between generations is wholly consistent with the data.

Food availability might directly influence egg size in Neomysis. The decrease in the growth rate preceding sexual maturity in N. mercedis (chapter 2) and in other mysids (Clutter and Theilacker 1971; Gaudy and Guerin 1979) suggests that vitellogenesis is accomplished by the diversion of energy from somatic growth to reproductive products in the period immediately before egg laying. Vitellogenesis occurs over the last several intermolts preceding the first clutch in Leptomysis lingvura (Wittmann 1981a). In N. integer it is accompanied by a decrease in body lipid stores (Raymont et al. 1966). Since N. integer has rather low lipid reserves (13% of the body weight, Raymont et al. 1964), it is likely that food availability immediately preceding egg extrusion influences egg size. In N. mercedis the dry weight of the clutch averages about 19% of the female's total weight so much of the animal's

energy stores would be utilized for vitellogenesis.

The invariance of the fecundity - body size relation in the spring generations despite considerable year-to-year variation in egg size provides the strongest suggestion that egg size differences may be, in part, a physiological response to the maternal nutritional state, as it implies that differences in reproductive effort are reflected in variation in egg size rather than egg number. However, the size-adjusted mean body weights, which can be interpreted as condition factors, do not vary between the spring generations nor do the mean gravid female sizes, as might be expected if the egg size differences resulted from differences in maternal nutrition. Moreover the occurrence of both large and small egg forms in the 1978 spring generation is inconsistent with an environmental determination of egg size unless different females have experienced quite different environments. Although this is possible, as for instance through immigration from upriver populations, the fact that the 1979 and 1980 spring generations do not show bimodal egg size distributions, despite similar river discharge patterns, argues against immigration as the mechanism generating the 1978 bimodality. The broad range of egg sizes seen at all periods implies that there is considerable intrapopulation variability in egg size under similar environmental conditions.

The constancy of the clutch weight - body size and body weight - body size relationships throughout 1978 imply that the differences in egg size and fecundity seen between the 1978 spring and summer generations represent variation in the

allocation of equivalent resources among young rather than differences in the availability of energy for reproduction. Egg size differences could result from intrinsic differences between individuals in different generations or from differences in the provisioning of eggs under different environmental conditions. Indices of food availability decrease in summer so the increase in mean egg size seen during summer may be a physiological response to a (predictable) decrease in food availability, such as seen in the isopod Armadillium (Brody and Lawlor 1984).

Intraspecific variation in egg size has several important demographic consequences. Because females producing small and large eggs in 1978 had the same clutch weight - body size relation, the production of large eggs reduced the female's fecundity by 35%. McLaren (1965) reports a similar situation in the copepod Pseudocalanus minutus. Moreover, since the egg development period increases as the 0.31 power of the egg weight (Wittmann 1981b), the larger egg increases the incubation time by about 16%. If adult mortality is less than that of neonates, larger eggs would, on average, improve survivorship. However, small eggs were produced during the early part of the breeding period when the mortality rates of adults were generally less than those of neonates. Since larger eggs result in larger hatchlings, the interval from hatching to sexual maturity is reduced if sexual maturity occurs at a specific size at a given temperature. Although the difference in mean egg size ($16\mu\text{g}$) appears too small to significantly affect the age at maturity, growth in weight is exponential at a constant rate, so small

initial differences are greatly amplified as time progresses (Lawlor 1976; Kaplan 1980). Simultaneous reduction in the size at maturity as temperatures rise will further reduce the age at maturity. Reductions in the age at maturity may increase survival by decreasing the duration of exposure to mortality agents such as predation.

Variation in egg size can therefore influence the rate of population increase through changes in fecundity, through changes in the age at first reproduction, and through changes in survivorship. The effects of egg size on the potential rate of population increase can be roughly estimated from (McLaren 1963)

$$[7] \quad r = [1/D] \cdot \ln(E \cdot S)$$

where D is the generation length, E is the number of eggs produced per female, and S is the survivorship. Equation [7] assumes non-overlapping generations but will be approximately correct in the present case, although there is continuous breeding, since the overlap between successive generations is low (Figure 4) and most females reproduce only once. The generation length may then be approximated by the sum of the egg development period and the pre-reproductive period. Variation in generation length resulting from the egg size from which the generation is produced results in small increases in r, of about 0.001-0.002 day⁻¹, for large eggs in the W and S2 generations but no difference in r with egg size for the S1 generation. Variation in fecundity and in generation length resulting from

the egg size from which the generation is produced causes small increases in r , of about $0.001-0.005 \text{ day}^{-1}$, for small eggs in all generations (Appendix 4). Thus, the survival of young from large eggs must exceed that of young from small eggs for r to be increased. This result could suggest that seasonal differences in size-specific mortality on young is the ultimate cause of egg size variation in N. mercedis. However, the differences in r are quite small. Relatively small increases in the survivorship of young from large eggs relative to those from small eggs can compensate for the concomitant reduction in egg number. Thus, if the mortality rates of neonates from different egg sizes varied little, then r would be largely independent of egg size.

Seasonal variation in temperature may have much larger effects on r than does egg size variation. The temperature dependence of growth rates (chapter 2) and of adult size reduces the age at maturity of the summer generations to one-third that of the overwintering generation, but also, because of the exponential dependence of fecundity on female size, reduces the average number of young per brood to 10 from 25-30 (Table 3). The potential average rate of increase of the summer generation females ($0.025-0.030 \text{ day}^{-1}$) is about 1.6-2.2 times that of the winter generation (0.015 day^{-1}), assuming no mortality. Thus the reduction in generation length more than compensates for the concomitant reduction in fecundity. Lewontin (1965) has argued that, in general, r is more sensitive to changes in the age at first reproduction than to changes in fecundity and MacArthur and Wilson (1967, p.85) claim that "in general small changes in

developmental rates of the order of 10% are roughly equivalent to large increases in fertility of the order of 100%." However the effect may be dependent on the magnitude of fecundity (Cole 1954).

Demography

Maximum per capita instantaneous birth rates (0.27 day^{-1}) occur in the spring, but quickly decline to values near 0.01 - 0.03 day^{-1} for the rest of the summer. Several factors combine to reduce the per capita birth rate:

(1) a decrease in the size of females at maturity, with a corresponding decrease in clutch size,

(2) an increase in the mean egg size, which also decreases the clutch size,

(3) a decrease in the proportion of the adult females that are gravid,

(4) a reduction in the proportion of the population comprised by the adult females.

Decreases in the incubation period with increasing temperature and a reduced age at maturity offset the preceding factors to a degree, but nevertheless the birth rate declines.

Although the mechanisms through which the decline in the birth rate during the high density summer period occurred are clear (see above), the proximate factors inducing the changes are not. In particular, the role of food limitation remains ambiguous. Evidence that the birth rates of N. mercedis during the higher density summer period are limited by decreases in the

relative availability of food remains weak, although numerous mechanisms through which such an effect could occur remain possible.

Food availability is known to affect fecundity in numerous crustaceans (e.g. Vijerberg 1976; Lampert 1978; Checkley 1980; Durbin et al. 1983). The relative availability of food for N. mercedis at Woodward Island declined from spring to summer (Figure 17a) and was positively correlated with the average number of eggs per adult female; the birth rate was positively correlated with meiofauna standing crop. The change in the average number of eggs per adult female results partly from the decrease in the size at maturity, which appears to be primarily a temperature response with no additional effect due to food variation. Moreover, the body size at maturity began to decline in early June when relative food availability was still high. Further, the growth rates of that component of the field population which matured was in good agreement with the growth rates of well-fed laboratory reared animals (chapter 2).

Although food levels are expected to influence clutch size, the decrease in size-adjusted clutch sizes in the summer breeding females appears due to the increase in the mean egg size, since the size-adjusted clutch mass remained constant. The constancy of the clutch weight relation, however, merely indicates that those animals which were able to breed were able to allocate similar amounts of energy to reproduction. It does not rule out other effects of food limitation. The reduction in the proportion of adult females which were breeding may be such

an effect. The proportion of adult females which were gravid was not correlated with food availability at the sampling date, but was strongly positively correlated to food availability at the preceding sampling date ($r=0.74$, $p<0.05$, $n=13$) as might be expected if the mysids largely depended on the acquisition of energy over the molt preceding egg laying to produce eggs. The reduction in growth rates immediately prior to sexual maturity is sufficient to accumulate most of the energy expenditure on the first clutch through the diversion of energy to vitellogenesis (see chapter 2), which makes plausible the observed correlation between the proportion breeding and prior food availability. The lack of seasonal variation in size-adjusted clutch weight may imply a contest competition for food resources at the higher population densities, in which successful individuals obtain sufficient resources to breed while unsuccessful individuals do not breed. The generally higher mortality rates during the high density period are consistent with this speculation. However, in laboratory studies of feeding in N. mercedis (Johnston and Lasenby 1982), there was no obvious interference between feeding mysids at densities similar to those in the field.

If year-to-year variation in the size-adjusted clutch weight of the low density spring breeding animals can be interpreted as reflecting the general level of food abundance, then the invariance of the size-adjusted clutch size in these animals suggests that the observed variation in mean egg size between the spring and summer breeding females in 1978 does not

represent a direct response to food availability. The summer breeding females in 1978 partitioned similar size-adjusted amounts of reproductive energy quite differently from the low density spring-breeding animals. An inverse dependence of egg size on food is reported for an isopod (Brody and Lawlor 1984), so a direct physiological response to food availability cannot be ruled out but this begs the question of the adaptive significance of the resulting reduction in clutch size. The simple analysis discussed above (see also Appendix 4) suggests that r would be largely independent of egg size unless survivorship varied considerably with egg size. During the early summer, the mortality rate from fish predation increased on the smallest size class of mysids (Table 6) but mortality rates from all sources decreased (Figure 18). The methods used to estimate mortality rates cannot resolve differences in rates on a size scale fine enough to differentiate between the survival of hatchlings from large and small eggs. Thus, although mortality rates were generally lower on neonates during the period when large eggs were produced, the available data suggests no obvious advantage for large eggs, although the customary speculations regarding increased ability to avoid predators or to acquire food (Cody 1966) may apply.

Multiple regression suggested that the instantaneous mortality rates of juveniles were related to measures of food availability (Table 4). However, most of the variation in the death rates of neonates was accounted for by the abundance of salmon fry rather than by food, and, although food accounted for

up to 50% of the variance in mortality of larger juveniles, substantial amounts of the variance remained unaccounted for. Although the mechanisms responsible for the observed temporal pattern of size-specific mortality cannot be exactly specified, biological rather than environmental factors were probably the main mortality agents. Temporal variation in one component of size-specific mortality, that resulting from fish predation, was evident as the fish community changed seasonally. Temperature and oxygen levels at Woodward Island did not reach values known to be lethal to N. mercedis (Wilson 1951; Hair 1971).

Changes in the age structure of the mysid population which result from recruitment and from seasonal variation in the age-specific mortality rates reduce the proportion of the population comprised by adult females, and therefore lower the per capita birth rate through a reduced egg ratio. Lower food availability during the summer may contribute to the reduced proportion of adult females through reduced survivorship. However, since in most cases the mortality rates cannot be partitioned into the effects of specific factors such as food or predation, the importance of food availability to the process remains ill-defined.

The estimates of instantaneous natality and mortality rates for N. mercedis are in the range commonly found for crustacean zooplankton (e.g. Neill 1981b). The maximum birth rates (0.27 day^{-1}) for N. mercedis are slightly higher than the few estimates available for other north temperate mysids, but the mean summer birth rates (0.03 day^{-1}) are similar to the 0.023 -

0.044 day⁻¹ that Fager and Clutter (1968) estimated for Metamysidopsis elongata and to the 0.10-0.15 day⁻¹ that Toda et al. (1981) calculated for Neomysis intermedia. Similarly, the death rates that I obtained are comparable to those estimated for M. elongata (0.019-0.10 day⁻¹) and N. intermedia (0.15-0.20 day⁻¹).

In general, the mortality rates from fish predation (Table 6) were in poor agreement with the total mortality rates estimated using the Lynch method (Figure 18). Lack of agreement between the two sets of estimates was not unexpected since they estimate different quantities. Fish predation was only one component of mortality and therefore would be expected to be lower than estimates of mortality from all sources. Moreover, the estimates of mortality rates from predation do not include all known predators, since Crangon predation could not be estimated. The estimates of mortality from fish predation were point estimates which referred to a specific sampling date whereas the Lynch method estimated average mortality over the (approximately 14 day) interval between samples. Temporal variation in mortality rates would reduce agreement between the two sets of estimates. Sequential estimates of mortality rates suggested considerable temporal variation in the death rate.

One of the assumptions in the estimation of mortality from fish predation, that all material found in the fish stomachs was consumed within the channel, was violated on one occasion (November 1977). Herring caught within the channel contained a lophogastrid mysid never found in the channel. Failure of this

assumption would inflate the apparent mortality estimates of those size classes actually consumed outside the channel. The resulting bias is unassessable.

Life History

Most of the life history traits displayed by Neomysis mercedis in the Fraser River estuary are also present in populations in the Sacramento-San Joaquin estuary (Heubach 1969; Siegfried et al. 1979), at the southern limit of its geographic distribution (Holmquist 1973). Similar life histories are reported for Neomysis integer (Vorstman 1951; Kinne 1955; Mauchline 1971; Beattie and de Kruijf 1978), Neomysis americana (Wigley and Burns 1971; Pezzack and Corey 1979), and Neomysis intermedia (Murano 1964; Toda et al. 1981, 1982). Indeed, the pattern of 2-3 generations per year, distinct winter and summer generations with marked differences in size at maturity, seasonal variation in size-adjusted fecundity, and strong seasonality in abundance seems characteristic of the genus.

The temperature dependence of the rates of growth and maturation, coupled with size-dependent fecundity, provides a mechanism for generating "environment dependent phenotypic plasticity in reproductive patterns" (Giesel 1976, p.58) which may allow N. mercedis to exploit the favourable environmental conditions that regimes of increasing temperatures may generally indicate in north temperate latitudes. In the Fraser River estuary, primary production by phytoplankton (Takahashi et al. 1973) and macrophytes (Kistritz and Yesaki 1979) show increases

in the May-August period that closely parallel the changes in water temperature. In the Sacramento-San Joaquin River estuary, year-to-year variation in the abundance of N. mercedis is highly correlated with indices of primary production (Anonymous 1978). The set of life history traits which Neomysis displays would allow the mysid to exploit the strong seasonality in primary production typical of the north temperate estuaries which form its habitat.

CHAPTER 2. THE UTILIZATION OF ASSIMILATED ENERGY BY Neomysis mercedis IN THE FRASER RIVER ESTUARY

Introduction

Life history theory attempts to account for variation in reproductive pattern by assuming that reproductive traits such as age and size at maturity, the amount and timing of reproductive effort, and the number and size of young are the results of selection acting to maximize individual fitness. If the intrinsic rate of increase r is an appropriate fitness measure, then fitness maximization is equivalent to maximizing the individual's reproductive value

$$V(x) = [\exp(r \cdot x) / l(x)] \sum_{y=x}^{\infty} [\exp(-r \cdot y) \cdot l(y) \cdot b(y)]$$

at every age (Schaffer 1974; Taylor et al. 1974; Yodzis 1981). This leads directly to the inter-dependence of the age-specific fecundity ($b(x)$) and survivorship ($l(x)$) schedules, and as a consequence, to the importance of trade-offs between present and future reproductive efforts in determining the "optimal" set of reproductive tactics (Pianka and Parker 1975).

Two questions, both first raised by Fisher (1930), then become of interest: (1) what are the physiological mechanisms by means of which reproductive effort is varied? and (2) under what circumstances is it advantageous to vary reproductive effort? Numerous authors have addressed the last question (for reviews see Giesel 1976; Stearns 1976, 1977; Calow 1977) to generate a

more-or-less agreed upon set of predictions (Hirshfield and Tinkle 1975; Stearns 1976) regarding the allocation of reproductive effort:

(1) increases in current reproductive effort will reduce future reproductive effort, either through decreased survivorship or through decreased future fecundity,

(2) adult mortality rates which are high, variable, or unpredictable will favour increased reproductive effort early in life whereas juvenile mortality rates which are high, variable or unpredictable should result in decreased reproductive effort and longer adult life (Stearns 1983a),

(3) semelparity should be favoured when the adult mortality rate exceeds the juvenile mortality rate and iteroparity favoured when juvenile mortality exceeds adult mortality,

(4) in expanding populations the age at maturity should be decreased, reproductive effort should be concentrated early in life, and brood size increased.

I attempted to test the above predictions by examining patterns of energy allocation in the brackish water mysid Neomysis mercedis. Reproductive effort was measured as the proportion of the animal's total energy budget that was devoted to reproduction (Hirshfield and Tinkle 1975; see also Bell 1980). I first measured the dependence on environmental variables of the physiological rates that determine the components of the energy budget (i.e., the mechanisms through which reproductive effort may be varied), and then applied the relationships to estimate energy budgets from field conditions

for populations at Woodward Island in the Fraser River estuary. Successive generations of the mysid in the Fraser River experience very different environmental and demographic regimes (chapter 1). The overwintering generation which breeds in the spring has adult mortality rates that are lower than juvenile rates while the converse is true of the summer generations. Population densities are low and food availability high when the overwintering (W) generation matures, the population is growing and food decreasing when the first summer (S1) generation breeds, and the population is stationary at a high density and food resources low when the second summer generation (S2) breeds. Reproductive patterns are expected to vary among the generations in accordance with the above predictions.

Methods and Materials

Molting and Growth

Reliable growth estimates could not be obtained from the time series of field data because of temporal variation in size-specific mortality rates (chapter 1). Therefore I determined growth rates and molt frequencies from individual mysids in laboratory rearing experiments. Individuals of known age were obtained by holding gravid females until hatching occurred. Newly hatched mysids were isolated in 300 ml clear plastic containers with 250 ml of water, and were fed to excess on newly hatched Artemia salina nauplii at intervals of 2-3 days, depending on temperature. The containers and water were changed

at least weekly; water levels were topped up as required between changes. Faecal pellets and dead prey were pipetted off daily. Measurements were made at 5, 10, 15, 20°C and at salinities of 10 ppt, 1 ppt, and freshwater. Temperatures were generally stable to within $\pm 0.5^{\circ}\text{C}$. Solutions of appropriate salinity were made by diluting seawater with aged wellwater. Photoperiods roughly corresponded to the natural daylengths appropriate to the rearing temperature (16 h at 20°C; 16 h at 15°C; 12 h at 10°C ; and 8 h at 5°C).

Initially I examined the containers for molts twice daily. When it became apparent that most molting occurred overnight, I reduced this to daily examinations immediately after "daybreak". The small size and transparency of the molts of the newly hatched animals meant that I undoubtedly missed molts for some animals. Mysids may also ingest their molts occasionally. Growth was determined from measurements of the length of the uropod on the molt, which is a measure of the size of the animal at the beginning of the intermolt period. Successive measurements of the uropod on both the animal and its molt confirmed that the uropod length changed only at molting, unlike the body length which shows intermolt growth (Mauchline 1973b). The size dependence of the molt weight was determined by measuring the molt, rinsing with distilled water, drying overnight at 60°C, and weighing to the nearest μg . Although individuals were reared for periods up to 280 days, substantial mortality occurred at molting and especially from animals injuring themselves when disturbed. Accordingly it was

necessary to supplement the growth rate data with measurements on field collected animals of unknown age in order to determine the growth rates of the larger (older) animals. I minimized the effects of prior history by matching the rearing temperature to the ambient field temperatures. Growth in weight, which was the variable of interest, was estimated from the uropod lengths using the size-weight relation obtained for wild animals (chapter 1). The number of broods produced by gravid females held in the laboratory was also noted.

Female mysids do not molt while carrying embryos (Mauchline 1973b). The intermolt interval of gravid females is therefore determined by the egg development period, with the molt usually occurring the same night that the young are hatched. I determined egg development times at 10, 15, and 20°C by pairing mature males with maturing females whose enlarging ovaries were visible through the transparent body. I did not directly observe copulation, but assumed that fertilization occurred when the female molted. Copulation occurs within a few minutes of the female molt in mysids (Nair 1939; Clutter and Theilacker 1971; Mauchline 1980, p.43). Eggs were extruded into the marsupium within a day of the molt, often even by unfertilized isolated females.

Energy Content

The energy content of somatic tissue, eggs, and molts were determined from the combustion of known amounts of material in a Phillipson-type microbomb calorimeter. The material was dried

as described in chapter 1, ground to a fine powder with a mortar and pestle, and compressed into pellets of 10-20 mg dry weight which were stored at -10°C to retard oxidation. Schindler et al. (1971) found that extended storage at low temperatures had no effect on caloric values. The pellets were re-dried at 60°C immediately before use. The calorimeter was calibrated with benzoic acid ($26.462 \text{ J}\cdot\text{mg}^{-1}$) after every 2-3 combustions. No corrections were made for acid formation or firing wire combustion; the latter was largely eliminated by adjusting the firing current.

Oxygen Uptake

Oxygen uptake was used as a measure of routine metabolic rate. Oxygen consumption was measured using a closed bottle technique similar to that described by Foulds and Roff (1976) and by Gaudy et al. (1980). Kamler (1969) discussed some of the problems associated with closed bottle measurements. The chief objections are the incorporation of the elevated oxygen consumption of the disturbed newly-introduced animals into the average uptake determination and possible changes in oxygen uptake as the oxygen concentration declines throughout the experiment. Sandemann and Lasenby (1980) have shown the oxygen uptake of Mysis relicta to vary with oxygen concentration but the variation was very slight above 6 ppt oxygen. Nevertheless the closed bottle technique seems appropriate to the estimation of routine metabolism in mysids. The container size and the measurement period can be chosen to allow the organism scope for

activity, incorporating any endogenous rhythms, without reducing the accuracy of the oxygen level determination. The effects of the initial, high oxygen uptake can be reduced by extending the length of the measurement period and in any event may approximate natural conditions where a variety of stresses may induce a similar response. Jawed (1973) showed that N. mercedis regulates its oxygen consumption above oxygen tensions of 50 mm Hg at 10°C; final oxygen concentrations in my experiments were always much greater than that level.

Measurements were made at nominal temperatures of 5, 7, 10, 15, and 20°C and at salinities of 10 ppt, 1 ppt, and freshwater to span the range normally encountered by the mysids. The animals were collected in late winter and early spring of 1979. They were held at 5 or 10°C and were acclimated to test conditions by sequentially raising the temperature over a period of several days. The rate of temperature change did not exceed a few degrees per day, a rate similar to natural temperature fluctuations in the animal's environment. Animals were usually held at test conditions for 4-5 days before being used. Simmons and Knight (1975) showed that oxygen consumption in N. mercedis stabilized within 2 days under similar rates of change.

In most cases individual animals were enclosed in acid-cleaned, ground glass stoppered bottles for a period of 24±2 h. The duration was chosen to include any potential diel activity cycles. Bottle sizes (30-300 ml) were large enough to permit the animal to swim normally. The typical behavior was an irregular pattern of swimming alternating with resting on the

bottom. Resting animals were not inactive as respiratory currents were generated by the thoracic appendages which are also used in more active swimming (Foulds and Roff 1976; Mauchline 1980, p.140). The mysids were fed Artemia nauplii several hours prior to the experiments and had prey in the crop and foregut. All measurements were done in the dark.

The mysids were chosen to span the largest possible size range (0.024-7.136 mg dry weight). This necessitated using several animals per bottle for the smallest animals to obtain precise uptake measurements. Although Kuz'micheva and Kukina (1974) showed the uptake rate of Neomysis mirabilis to be independent of mysid density over a broad range, I ran several samples with varying number of similar size mysids to confirm the density independence of the rates.

Oxygen partial pressures were measured with polarographic oxygen electrodes (Radiometer E5046) coupled to a Radiometer PMH-71 acid-base analyzer by a PMA 930 oxygen module. The electrode was mounted in a 70 μ l test cell cooled to the sample temperature by circulating water. The closed sample bottle was inverted several times and 2 ml subsamples removed by drawing a syringe up through the bottle. Replicate subsamples were slowly injected across the electrode to determine the oxygen tension. The electrode was calibrated against water saturated air at known temperature and pressure. The volumes of all bottles were found by weighing distilled water at 20°C. Oxygen consumption by the mysid was estimated from the difference in oxygen levels between the sample and the mean of 3 control bottles. Animals

were sexed and weighed as in chapter 1. Oxygen consumption rates were converted to $\mu\text{g O}_2 \cdot \text{animal}^{-1} \cdot \text{h}^{-1}$. Animals which molted during the measurements were analyzed separately.

Temperatures were found to fluctuate slightly over the incubation period, the mean difference from the nominal level being 0.3°C . Average temperatures over the 24 hour interval were used in regression analyses.

Results

Growth

The time pattern of uropod lengths for individual Neomysis mercedis was roughly rectilinear, with growth occurring in several distinct phases within each of which the uropod length changed linearly in time at a constant rate (Figure 22). Thus, the growth curve could be well approximated by a series of 2 or 3 straight line segments. Although the uropod length changed discontinuously, at molting, weight addition was probably a continuous process as in other crustaceans (Carlisle and Knowles 1959). Because of the relationship of weight to length, the linear change in uropod length implies an exponential rate of increase in body weight. At temperatures below about 10°C , the growth of newly released young was slow initially but increased considerably as the animals attained sizes of 0.7-0.9 mm uropod length. This increase may be related to the ability of small animals to capture or handle prey. The higher rate was maintained until the animal neared sexual maturity, when the

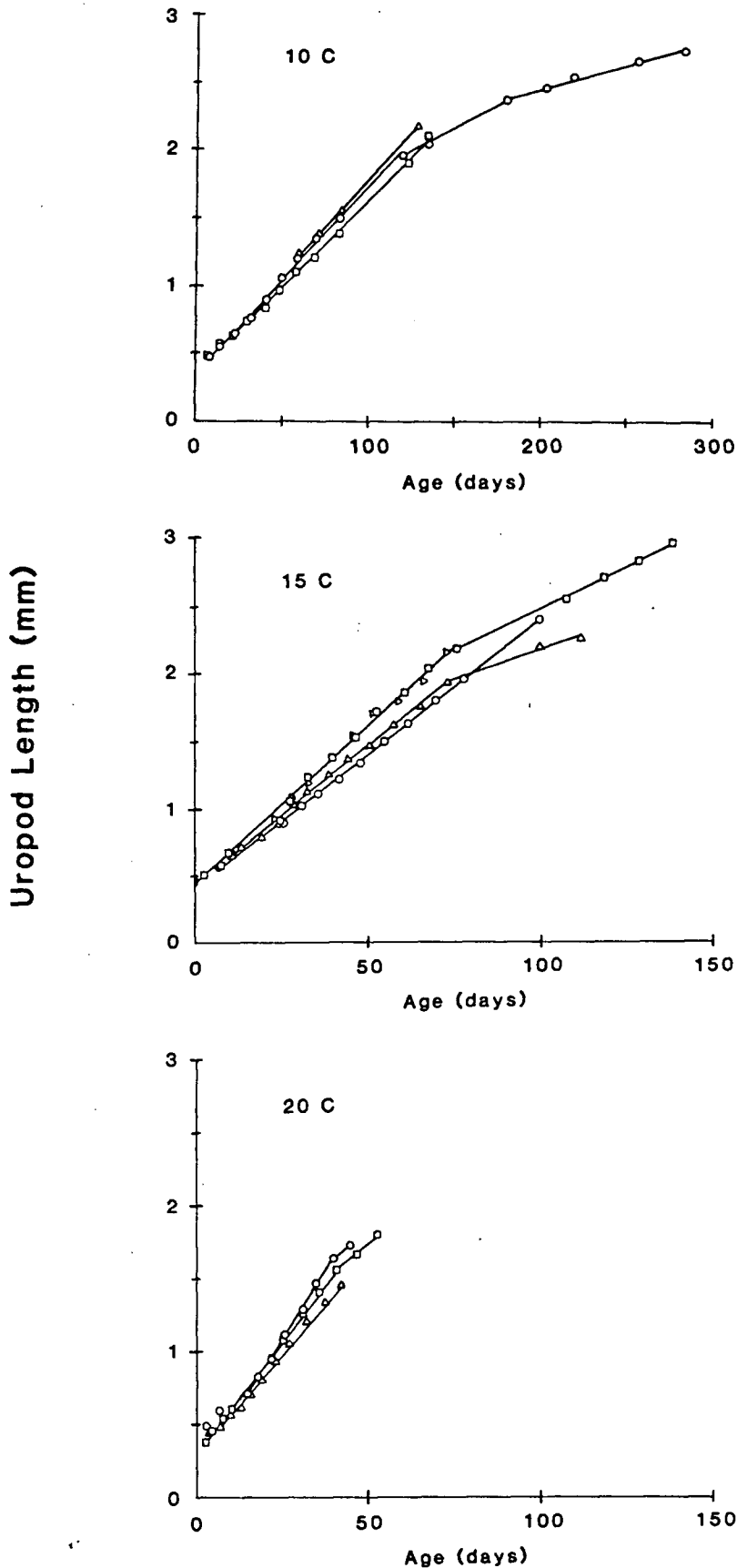


Figure 23. Representative growth curves for *Neomysis mercedis*: three sets of siblings at (a) 10°C, (b) 15°C, and (c) 20°C. Note that the size of individual mysids increases linearly in time over much of the animal's life.

rate of change of uropod length decreased. Thus the growth rate of an animal was constant over much of its life (Figure 23). At higher temperatures the initial low growth rate phase was reduced or absent and growth could be well described by two straight lines.

There was considerable variation in growth rates at a given temperature. Within-clutch variation in growth rate was high (see Figure 23), the coefficient of variation (CV) for siblings averaging 15% and reaching 38% in some clutches. Consequently there were no differences ($p > 0.1$, Anova) in the mean growth rates of the broods of different females. Within-clutch variation in growth rates was similar in magnitude to that of the size at hatching (chapter 1), but the growth rate did not vary significantly with size for those animals whose size at hatching was known ($r = 0.27$, $p > 0.05$, $n = 19$). However, the relative imprecision and small range of neonate sizes possible with the size measure (uropod length) used may have obscured the effects of neonate size on growth rates, which are expected to be exponential in weight. Similarly no major differences were found in the growth rates of animals reared at different salinities or between wild and laboratory hatched animals at the same temperature. Temperature did, however, have a significant effect on growth rates, which increased linearly with increasing temperature over the range (5-20°C) examined (Figure 24). A curvilinear relationship (quadratic in temperature) did not improve the fit to the data.

A marked reduction in the growth rate approximately

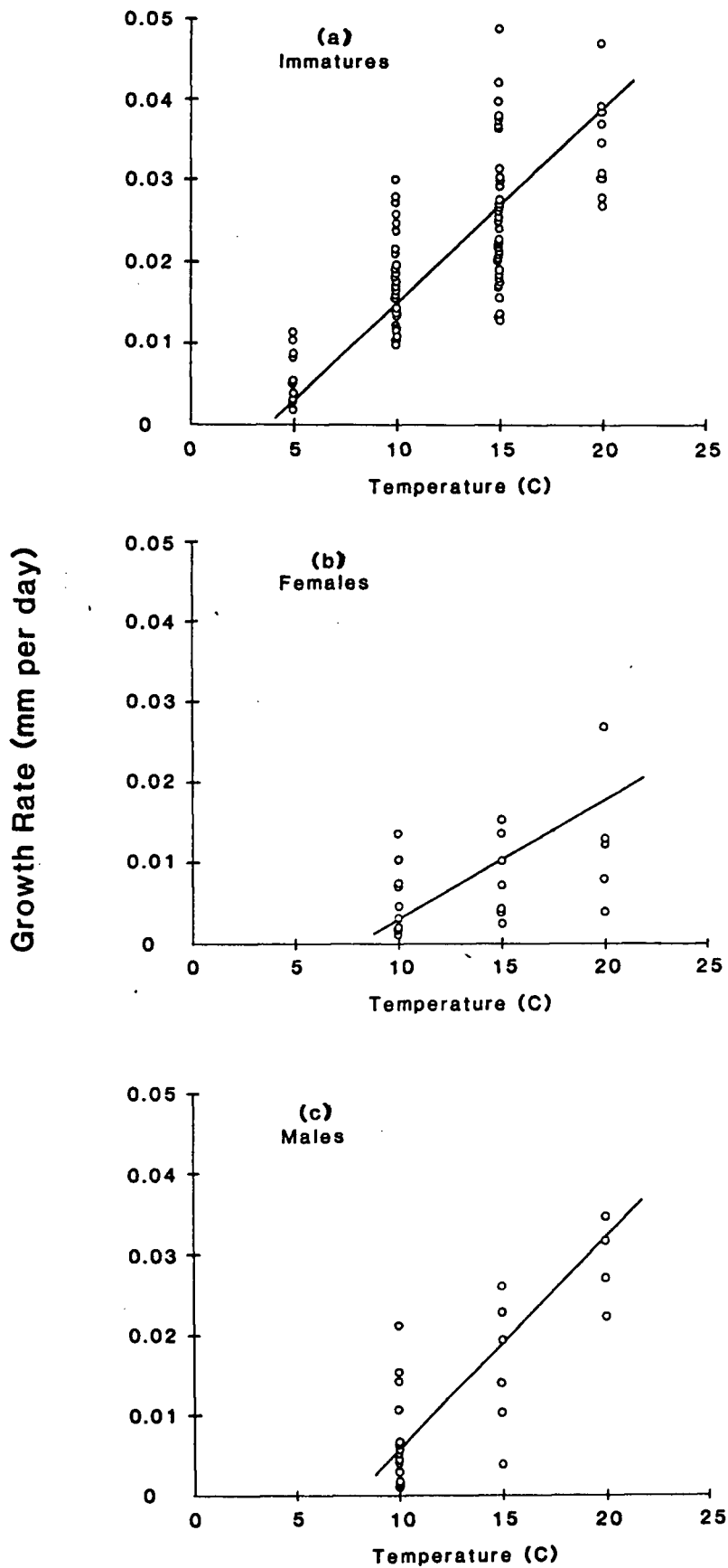


Figure 24. The dependence of the growth rates of *Neomysis mercedis* on temperature. (a) = immatures, (b) = mature females, (c) = mature males.

coincided with sexual maturity. The slopes of the growth rate-temperature relations were identical for immature animals and mature males, but the rates were lowered by about $0.4 \text{ mm} \cdot \text{day}^{-1}$ for the mature males ($p < 0.05$, Ancova). The slope of the relation was lowered for mature females ($p < 0.05$, Ancova) with the result that the growth rates of mature females (Figure 24b) were considerably less than those of either immature animals (Figure 24a) or mature males (Figure 24c). The reduction in growth rate usually was evident at the molt preceeding egg production. The temperature dependence of growth rates for both mature males and females extrapolated to zero growth at temperatures near 8°C ; animals in the Woodward Island population did not mature at temperatures much below this. The temperature dependence of the growth rates is given in Table 7.

Table 7. Coefficients of the linear relation $y = a + b T$ between growth rate (mm uropod length/day) and temperature for immature, mature female, and mature male Neomysis mercedis.

category	a	b	+ - 1 SE	r^2	n
immatures	-0.0088	0.00238	+ - 0.00013	0.59	142
mature males	-0.0208	0.00265	+ - 0.00030	0.66	29
mature females	-0.0117	0.00147	+ - 0.00028	0.22	24

When the growth rate data summarized in Table 7 were applied to the field temperature data for Woodward Island, the occurrence of peaks in the abundance of mature females were correctly predicted starting from the peaks in abundance of newly hatched animals. The intervals calculated for the S1, S2,

and W generations were 58 days, 46 days, and 257 days respectively while those estimated from the size-frequency data (Figure 5) were 57 days, 43 days, and 185+ days. This result suggested that the growth rates of that segment of the field population which managed to breed was similar to those of well-fed laboratory reared animals.

Multiple clutches were produced by about 21% of the mature females held in the laboratory (Figure 25). In most cases of multiple brooding, two clutches were laid but up to 5 broods were produced by a single female. N. mercedis is physiologically capable of iteroparity.

Molting

Molting generally occurred at night but I observed portions of the molting process on two occasions. The molt split dorsally, backward from the anterior region of the animal, and was removed by vigorous flexing of the body in the dorso-ventral plane as the animal swam or rested on the substrate. Convulsions occurred at intervals of about 3 seconds until the animal was free of the exuvium. The animal was swimming normally within 5 minutes after the molt.

At a given temperature, the duration of the intermolt period increased with the size of the animal (Table 8). There was a slight suggestion of reduced intermolt periods for small males in the 10°C data. The molt frequency (intermolt period⁻¹) increased linearly with increasing temperature (Figure 26a) for each size category; functional regressions of the molt rate are

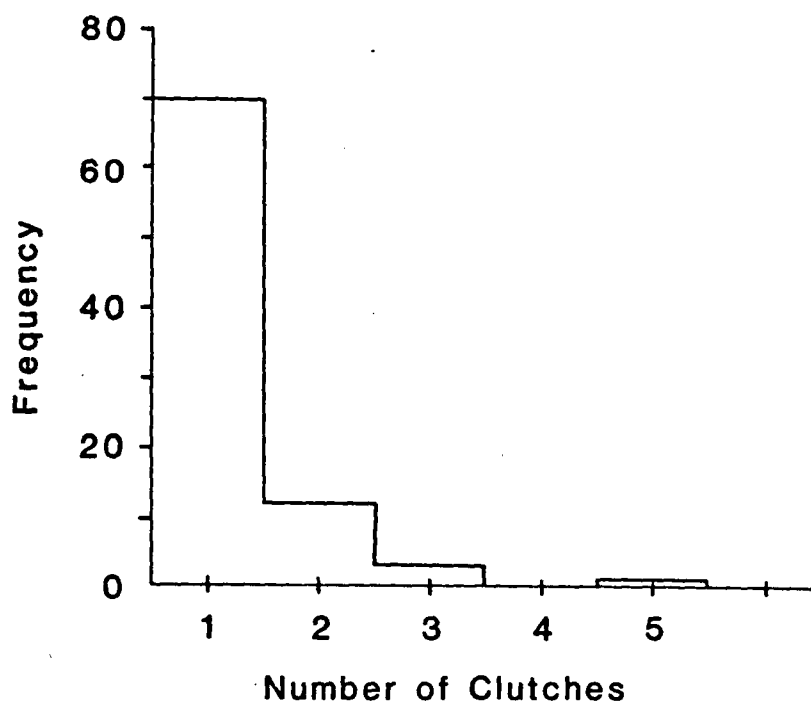


Figure 25. The frequency of clutches produced by mature Neomysis mercedis held under laboratory conditions .

Table 8. Average intermolt period in days (\pm 1 SE) for Neomysis mercedis of different sizes at 5, 10, 15, and 20 C.

size (mm)	5 C	10 C		15 C	20 C
		males	females		
0.4-0.6	19.3 \pm 1.5	6.5 \pm 0.3	7.8 \pm 0.4	3.7 \pm 0.3	2.8 \pm 0.2
0.6-0.8	18.0 \pm 0.9	7.0 \pm 0.3	7.5 \pm 0.5	4.4 \pm 0.2	3.3 \pm 0.1
0.8-1.0	22.0 \pm 2.0	7.3 \pm 0.3	8.2 \pm 0.2	5.3 \pm 0.2	3.9 \pm 0.1
1.0-1.2	18.2 \pm 1.8	8.8 \pm 0.3	9.2 \pm 0.4	5.9 \pm 0.2	4.5 \pm 0.2
1.2-1.4	24.0 \pm 3.0	9.6 \pm 0.4	10.7 \pm 0.5	6.3 \pm 0.2	4.6 \pm 0.2
1.4-1.6	28.5 \pm 4.0	10.3 \pm 0.3	10.7 \pm 0.2	6.8 \pm 0.2	5.0 \pm 0.2
1.6-1.8	24.7 \pm 2.9	11.2 \pm 0.3	11.2 \pm 0.3	7.0 \pm 0.2	5.5 \pm 0.3
1.8-2.0		11.8 \pm 0.3	11.5 \pm 0.3	7.6 \pm 0.2	6.1 \pm 0.3
2.0-2.2		12.8 \pm 0.3	12.9 \pm 0.4	7.8 \pm 0.2	6.2 \pm 0.3
2.2-2.4	28	13.0 \pm 0.4	13.8 \pm 0.7	8.7 \pm 0.5	6.7 \pm 0.3
2.4-2.6		15.1 \pm 0.6	16.6 \pm 0.6		
2.6-2.8		16.7 \pm 0.8	18.5 \pm 3.5		

given in Table 9. The slopes of the relation between the molt frequency and temperature were strongly dependent on the size of the animal (Figure 26b) as were the constant terms of Table 9. The dependence of the molt frequency on body size and temperature becomes

$$[8] \quad \text{molt rate} = -0.00782 \cdot W^{-0.70} + 0.00971 \cdot W^{-0.24} \cdot T$$

Egg development periods were considerably greater than the normal intermolt intervals for animals of the same size. Egg development periods declined at higher temperatures with the development rate (development period⁻¹) increasing linearly with temperature (Figure 26c). A curvilinear (quadratic) function gave a marginally better fit ($r^2=0.96$ for the quadratic polynomial against 0.95 for the linear relation), however the difference in predictive ability between the two is negligible, especially since the development periods were only recorded to the nearest day. The maxima of the range of incubation periods

Table 9. Functional regressions of mean molt frequency (day^{-1}) against temperature for different size classes of Neomysis mercedis.

uropod size (mm)	a	b	+ - 1 SE	r^2	n
0.4-0.6	-0.0625	0.0212	+ - 0.0014	0.98	5
0.6-0.8	-0.0303	0.0170	+ - 0.0005	0.99	5
0.8-1.0	-0.0170	0.0140	+ - 0.0008	0.99	5
1.0-1.2	0.0007	0.0111	+ - 0.0002	0.99	5
1.2-1.4	-0.0181	0.0117	+ - 0.0004	0.99	5
1.4-1.6	-0.0160	0.0109	+ - 0.0003	0.99	5
1.6-1.8	-0.0064	0.0096	+ - 0.0003	0.99	5
1.8-2.0	0.0066	0.0080	+ - 0.0004	0.99	4
2.0-2.2	-0.0060	0.0085	+ - 0.0007	0.99	4
2.2-2.4	-0.0021	0.0077	+ - 0.0002	0.99	5

observed (27-38 days at 10°C , 17-23 days at 15°C , and 10-11 days at 20°C) were about 1.1-1.4 times the minimum values. If egg development were proportional to the 0.31 power of egg weight (as in Leptomysis lingvura, Wittmann 1981b), then the ratio of incubation times expected from the range of possible egg weights (about 20-50 μg) would be about 1.3 times. Thus egg size variation could account for much of the observed variation in egg development times. The incubation rate extrapolated to zero, indicating that eggs fail to develop, at 5.9°C . Gravid females were not present in the natural population at temperatures below this.

The dry weight of the molts increased with uropod size (Figures 27a and 27b). However the relations were different for males and females, the slope of the female's regression being significantly greater than that of the male's ($p < 0.05$, Ancova). The difference in slope was probably related to the development of the large marsupial plates in maturing females.

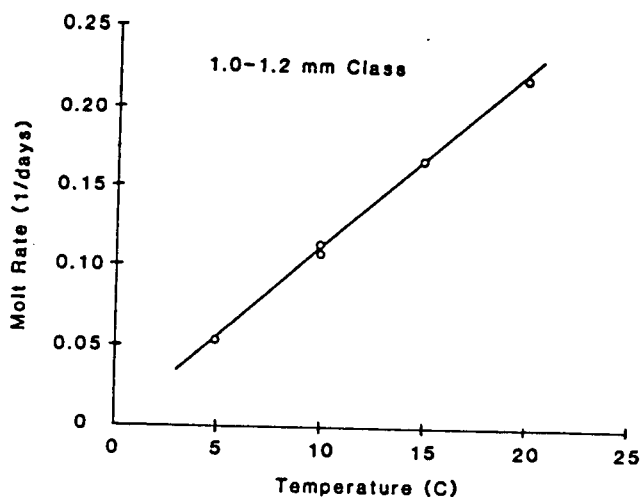


Figure 26a. The dependence of the molt frequency on temperature. Similar linear relationships were obtained for all size classes.

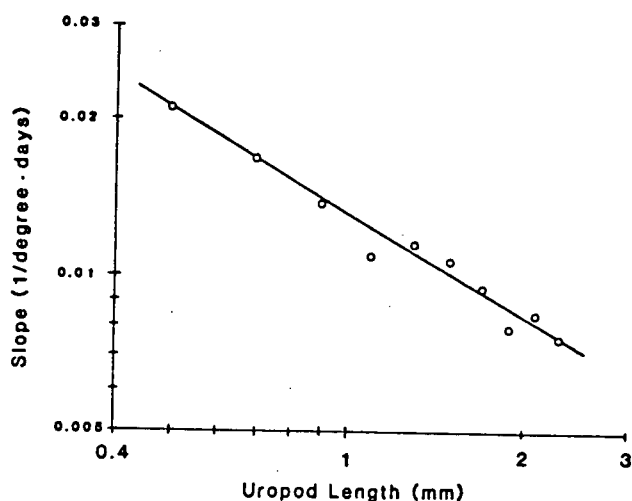


Figure 26b. The dependence of the slopes of the molt frequency - temperature relations on body size.

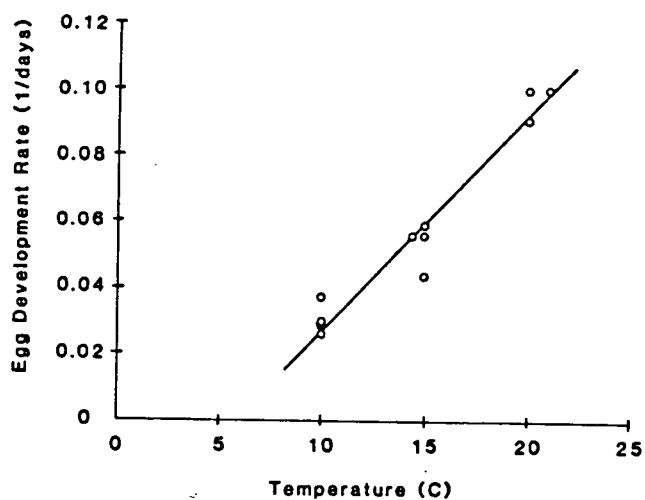


Figure 26c. The dependence of the egg development rate on temperature.

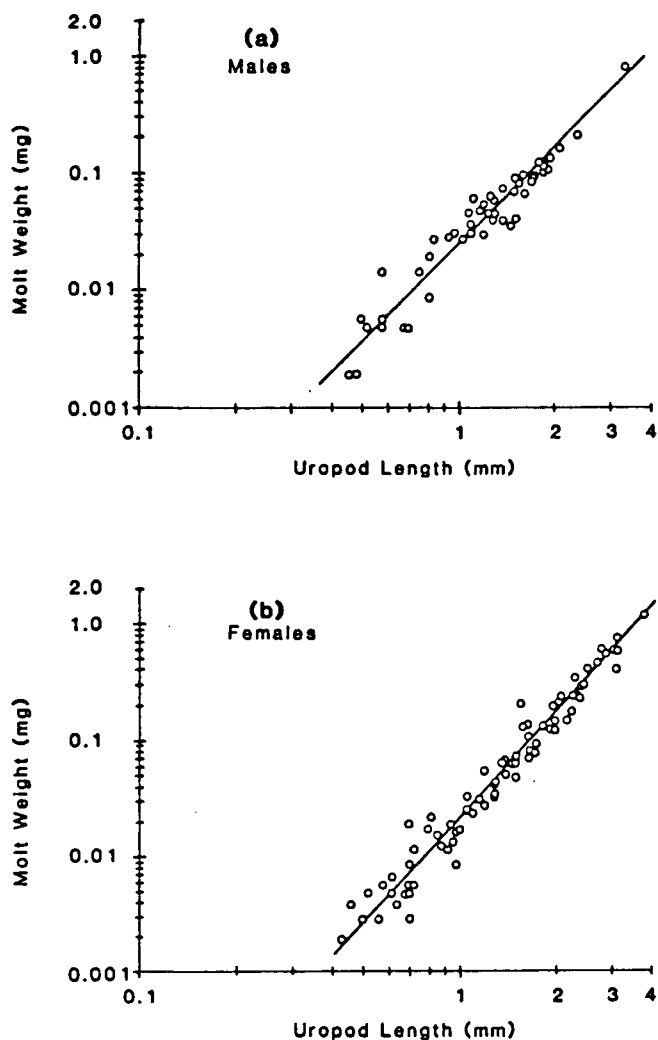


Figure 27. The dependence of the weights of molts from Neomysis mercedis on animal size .

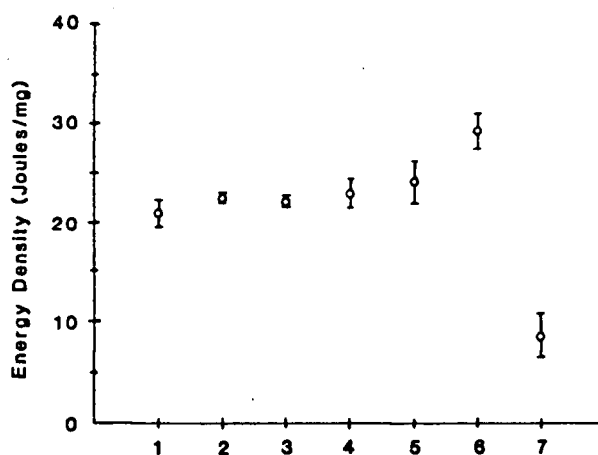


Figure 27c. The energy content (± 1 SE) of body tissue, eggs, and molts of Neomysis mercedis . 1=immatures, 2=mature nongravid females, 3=gravid female somata, 4=whole gravid females, 5=mature males, 6=eggs, 7=molts

Energy Content

The energy densities (Figure 27c) of the body tissues of immature, mature nongravid female, gravid female, and male N. mercedis did not differ significantly ($p > 0.05$, Anova) and averaged 22.35 ($SE = \pm 0.61$) $J \cdot mg^{-1}$ dry weight. Eggs had an energy content of 29.26 (± 1.76) $J \cdot mg^{-1}$ while molts averaged 8.69 (± 2.14) $J \cdot mg^{-1}$.

Oxygen Uptake

There was no systematic variation in rates of oxygen consumption with the number of animals enclosed in a sample ($p > 0.05$, Wilcoxon signed rank test). Consequently all multiple animal data were used in the analyses. The expected log-log relationship between oxygen consumption and dry weight was found for all temperature and salinity combinations (Figure 28a-e). All subsequent analyses use the logarithm of the measured uptake rate as the dependent variable.

Interpretation of the simultaneous effects of temperature and salinity on oxygen consumption by N. mercedis was complicated by the fact that the slopes of the uptake-weight relations varied among the temperature-salinity treatments ($p < 0.05$, Ancova). However multiple range tests (Scheffe's test) on the slopes failed to resolve differences. Inspection of the slope values (Table 10) suggested the $20^{\circ}C - 10$ ppt treatment may have had a higher slope value than the other treatments. Since my purpose was to generate an empirical predictor of

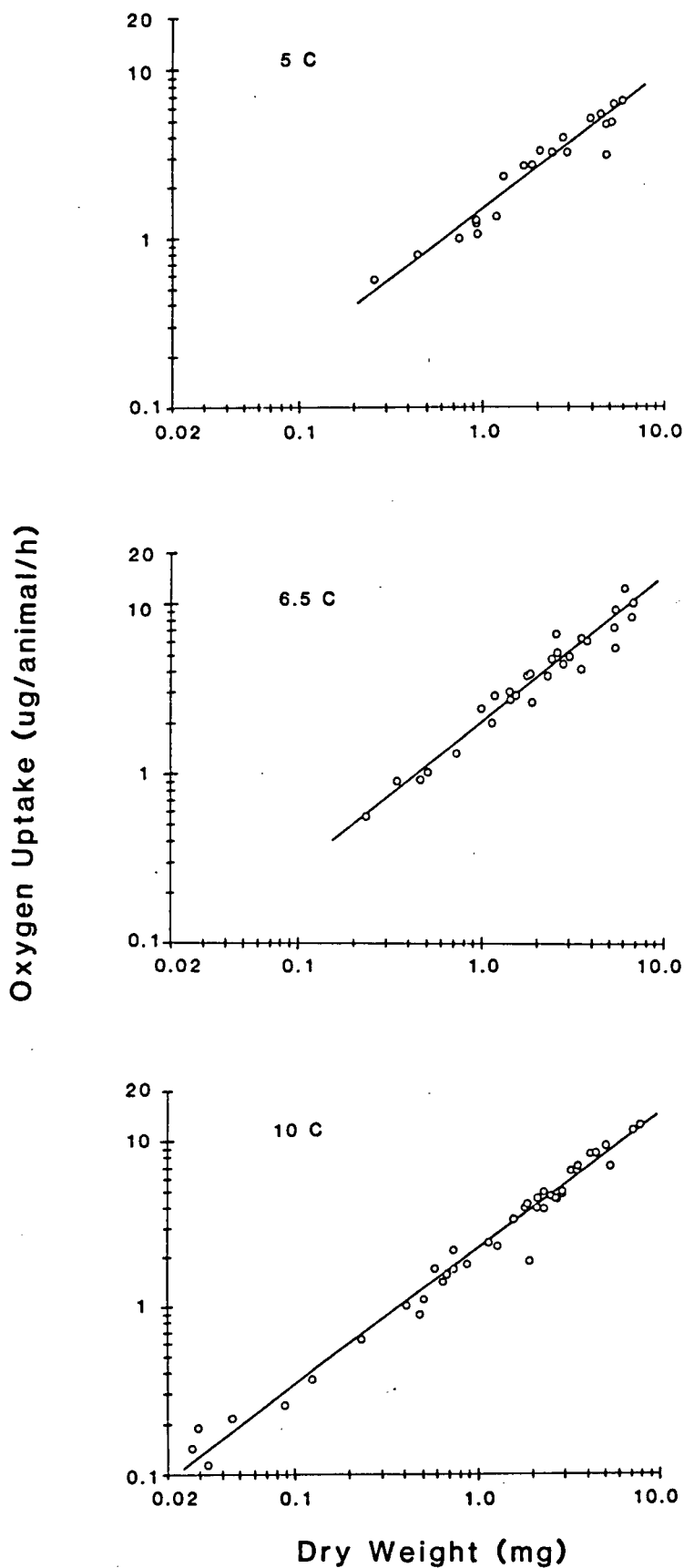


Figure 28. The dependence of oxygen uptake by Neomysis mercedis at 5, 6.5, 10, 15, and 20°C on body weight .

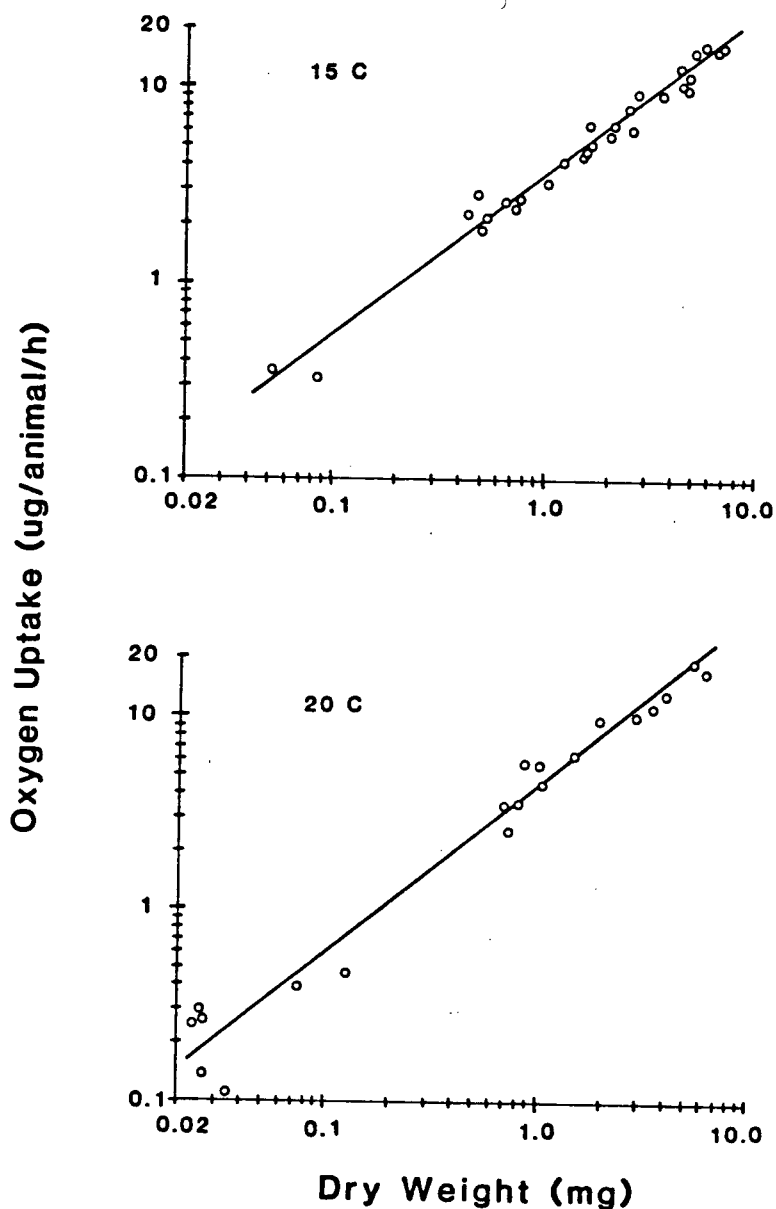


Figure 28. The dependence of oxygen uptake by Neomysis mercedis at 5, 6.5, 10, 15, and 20°C on body weight .

routine metabolism and the 20°C - 10 ppt conditions did not occur at Woodward Island (chapter 1), a change in slope under such conditions has no effect on the energy budget calculations. Moreover, salinity effects on oxygen uptake in N. mercedis are small or non-existent over the range below 10 ppt (Simmons and Knight 1975). The slope values obtained for the different treatments (0.72-0.95) were similar to those found for other mysids (Table 15).

Table 10. Slopes (and 95% confidence limits) of functional regressions of log(oxygen uptake) against log(weight) under various temperature and salinity combinations.

		Salinity (ppt)		
		freshwater	1 ppt	10 ppt
		-----	-----	-----
Temperature (C)	5	0.832 (0.71-0.95)	0.810 (0.59-1.03)	0.894 (0.56-1.21)
	6.5		0.835 (0.71-0.96)	0.915 (0.81-1.01)
	10	0.769 (0.67-0.87)	0.881 (0.81-0.95)	0.866 (0.83-0.90)
	15	0.902 (0.83-0.97)	0.733 (0.62-0.84)	0.784 (0.70-0.87)
	20		0.787 (0.74-0.83)	0.962 (0.86-1.07)

It is known that weight, temperature, and salinity interact to modify the oxygen uptake rate of N. mercedis (Simmons and Knight 1975). A simple regression model of the form

$$\log(\text{oxygen uptake rate}) = a + b \cdot \log(W) + c \cdot \log(T) + d \cdot \log(S)$$

(where the oxygen uptake is in $\mu\text{g O}_2 \cdot \text{animal}^{-1} \cdot \text{h}^{-1}$, W is the dry weight in mg, T is the temperature in $^{\circ}\text{C}$, and S is the salinity in ppt) accounted for 98% (n=139) of the variance in my data (Table 11). The salinity term made a non-significant reduction to the sum of squares and could be deleted without affecting the fit to the data. The coefficients of the reduced model are given in Table 11. Inspection of the raw residuals for the

Table 11. Coefficients of the multiple regression model
 $\log(\text{uptake}) = a + b \log(W) + c \log(T) + d \log(S)$
 for oxygen consumption by Neomysis mercedis.

variable	full model coefficient \pm 1 SE		reduced model coefficient \pm 1 SE	
constant	-0.334	\pm 0.041	-0.331	\pm 0.041
weight	0.837	\pm 0.013	0.837	\pm 0.013
temperature	0.738	\pm 0.040	0.735	\pm 0.040
salinity	-0.008	\pm 0.007		
r^2	0.98		0.98	

reduced model did not suggest any systematic deviations from the model structure. A similar logarithmic dependence of metabolism on temperature has been found in some fishes (Brett and Groves 1979) and copepods (Vidal 1980c).

The oxygen uptake rates of animals which molted during the measurement period were compared against the rates predicted using the reduced regression model. Oxygen consumption was somewhat greater in molting animals ($p=0.10$, sign test), and

averaged 1.32 times the predicted value for non-molting animals.

Energy Budgets

The allocation of assimilated energy to growth, molting, routine metabolism and reproduction was calculated for the W, S1, and S2 generations at Woodward Island using the above relationships between physiological rates and environmental variables. The initial size of the mysid was determined by the egg size of the parent generation. Growth was calculated daily over intermolt intervals which were estimated by averaging the temperature dependent molt rates over the interval predicted from the initial temperature. The use of the growth relation from well-fed laboratory reared animals assumed no food limitation for those animals which mature in the field. Changes in uropod length were converted to weight using the body weight - uropod length relation reported in chapter 1. Metabolism was converted to energy equivalents assuming a conversion factor of $14.15 \text{ J} \cdot \text{mg}^{-1} \text{ O}_2$ (Lasenby and Langford 1972). Measurements of oxygen uptake:carbon dioxide evolution in Neomysis integer (Raymont and Krishnaswamy 1968) and O:N ratios in N. rayii (Jawed 1969) suggest that this is a reasonable value; in any event, the possible range of values introduces an uncertainty of less than 4% (Elliott and Davidson 1975). Metabolism was increased by 1.32 times on the day of molting. Size at maturity was that observed at the nearest sampling date. If the animal reached maturity, growth over the preceding intermolt period was recalculated using the adult growth rate.

The allocation of energy to reproduction was assumed to commence with the reduction in growth rate one molt before egg laying. Yolk formation in Metamysidopsis elongata occurs in the intermolt period immediately before molting and copulation (Clutter and Theilacker 1971), and over several molts preceding laying in Leptomysis lingvura (Wittmann 1981b). Because reared females produced successive clutches, I assumed that the allocation of energy to reproduction continued during the incubation period although this energy may not produce young if the female did not survive to breed a second time. The reproductive effort of males was ignored because of the small weights of sperm produced and the probable small numbers of copulations undertaken by an individual; the number of copulations was crudely estimated from the ratio of gravid females to mature males.

Excretory losses of assimilated energy were estimated from the oxygen consumption rate using a conversion factor of $2.59 \text{ J} \cdot \text{mg}^{-1} \text{ O}_2$ (Elliott and Davison 1975), which is appropriate for ammoniotelic animals. Ammonia and small amounts (10-15%) of free amino acids are the principal excretory products of Neomysis rayii and N. integer (Jawed 1969; Raymont et al. 1968). Excretory losses of assimilated energy were about 18% of the metabolic rate of heat production.

Cumulative energy allocations over the lifetimes of individual animals are summarized in Tables 12 and 13. Approximate confidence limits for the components of the energy budget were estimated using a Monte-Carlo procedure in which the

budget was repeatedly ($n=100$) re-estimated randomly drawing all parameters from normal distributions within ± 1 standard error of the mean value. The resulting central 95% quantiles of the distribution of energy budgets gave estimates of the precision of the budgets.

Table 12. Lifetime allocation of energy (J) to growth, molting, metabolism, excretion, and reproduction for female Neomysis mercedis producing one clutch (mean and 95% distribution limits).

	W	S1	S2
growth	120.1 (17.4%) (113.4-124.0)	55.6 (28.3%) (52.8-59.4)	44.7 (25.6%) (41.9-50.3)
molts	29.0 (4.2%) (27.4-29.9)	7.0 (3.6%) (6.7-7.4)	5.6 (3.2%) (5.1-6.8)
reproduction			
offspring	27.3 (3.9%)	11.3 (5.8%)	9.4 (5.4%)
ovaries	31.4 (4.6%)	14.4 (7.3%)	11.8 (6.7%)
total	58.7 (8.5%) (54.6-61.0)	25.7 (13.1%) (23.7-28.1)	21.2 (12.1%) (19.0-24.3)
metabolism	407.7 (59.1%) (378.5-436.9)	91.4 (46.5%) (79.1-102.8)	87.4 (50.0%) (73.3-110.0)
excretion	74.6 (10.8%) (69.3-80.0)	16.7 (8.5%) (14.5-18.8)	16.0 (9.1%) (13.4-20.1)
total	690.1 (650.2-725.5)	196.4 (178.0-215.8)	174.9 (155.0-210.9)

The general pattern of energy allocation was similar for females in all three generations. Most (45-60%) of the assimilated energy was required for routine metabolism. This was especially true of the W generation where low winter temperatures reduced growth and inhibit maturation, greatly increasing the lifetime maintenance costs. Energy lost in molts was a small proportion of the total budget. Reproduction

Table 13. Lifetime allocation of energy (J) to growth, molting, metabolism, and excretion for male Neomysis mercedis (mean and 95% distribution limits).

	W	S1	S2
growth	140.6 (20.8%) (126.5-148.9)	72.8 (37.0%) (68.9-76.3)	62.5 (31.8%) (59.9-64.2)
molts	34.5 (5.1%) (32.3-36.2)	9.3 (4.7%) (8.8-10.0)	9.4 (4.8%) (8.8-9.7)
metabolism	422.5 (62.6%) (387.2-462.2)	96.7 (49.2%) (85.0-109.3)	105.3 (53.6%) (91.6-115.3)
excretion	77.3 (11.5%) (70.9-84.6)	17.7 (9.0%) (15.6-20.0)	19.3 (9.8%) (16.8-21.1)
total	675.0 (617.2-727.2)	196.5 (179.3-214.2)	196.4 (178.7-209.1)

accounted for 8-13% of the energy budget, but energy allocated to reproduction and not producing young, that is, the energy shunted to the ovaries during the last incubation period, was an appreciable proportion (about 55%) of the total reproductive effort. Growth accounted for a large fraction of the available energy for immature animals but became a progressively smaller component after the start of breeding.

The lifetime total assimilated energy was similar for males and females in the same generation (Tables 12 and 13). This implied that the reduction in the growth rate of females at sexual maturity represented a re-channeling of energy from growth to reproduction and that the allocation of energy to reproduction continued during the incubation period since the amount of energy so allocated closely balanced the male and female budgets.

Females in the W generation used 3-4 times as much energy

over their lifetime as summer generation females. Although the larger size at maturity and smaller egg size of the winter females resulted in more young per female, the lifetime cost of producing each young remained somewhat higher (25 J as compared to about 20-22 J for young from summer females). Since each egg had an energy content of about 0.76-1.2 J, the energy efficiency was about 6% for the S generations and 3% for the W generation. The net energy efficiency (production/assimilation) was highest (45%) in the growing S1 generation and lowest (30%) in the declining W generation. The stationary S2 generation also had a high net energy efficiency (41%).

The proportion of the total energy budget allocated to reproduction was about 8.5% (95% limits of 8.0-9.0%) in the W generation. The summer generations made significantly larger reproductive efforts: 13.1% (12.2-13.9%) in the S1 generation and 12.1% (11.4-13.1%) in the S2 generation (Table 12). However, when expressed as a proportion of production, the reproductive efforts were similar in all generations (about 28-29% of production). The energy content of offspring comprised 3.9% of the total budget of the W generation, 5.8% for the S1 generation, and 5.4% for the S2 generation.

Some females in the W and S1 generations may produce several clutches. Energy budgets for females producing two clutches are given in Table 14. The regime of increasing temperatures experienced by these animals altered the relative amount of the budget expended on metabolism but the lifetime energy cost per young was greatly reduced, to 13 J per young for

both the W and S1 females.

Table 14. Lifetime allocation of energy (J) to growth, molting, metabolism, excretion, and reproduction in female Neomysis mercedis which produce two clutches (mean and 95% distribution limits).

	W	S1
growth	140.3 (16.4%) (129.3-146.4)	69.9 (24.8%) (65.7-75.2)
molts	34.0 (4.0%) (31.8-35.4)	9.3 (3.3%) (8.7-10.2)
reproduction		
offspring	58.4 (6.8%)	25.8 (9.2%)
ovaries	36.9 (4.4%)	18.2 (6.4%)
total	95.3 (11.2%) (87.7-99.2)	44.0 (15.6%) (40.7-47.9)
metabolism	493.7 (57.8%) (451.1-535.2)	134.1 (47.6%) (116.8-151.3)
excretion	90.4 (10.6%) (82.6-97.9)	24.5 (8.7%) (21.4-27.7)
total	853.7 (795.3-909.3)	281.8 (255.0-309.5)

Discussion

Physiological Rates

The growth in size of N. mercedis could be represented by several phases within each of which the average daily increment in uropod length was constant in time but varied directly with temperature. A linear dependence of growth rates on temperature

was also noted by Gaudy and Guerin (1979) for Hemimysis speluncola and Leptomysis lingvura and by Lasker (1966) for the euphausiid Euphausia pacifica while Toda et al. (1984) found a weak exponential dependence on temperature in Neomysis intermedia as did Pezzack and Corey (1979) for N. americana. Because of the exponential relationship between body weight and uropod length, constant growth of the uropod length implies that the specific growth rate, expressed as the % change in body weight per day, has the form

$$[9] \quad G = dW/Wdt = (-0.01526 + 0.004047 \cdot T) \cdot (W^{-0.366})$$

The specific growth rate increases with increasing temperature over the range from 5 to 20°C but declines with increasing weight, as is commonly the case (Shushkina 1972; Brett 1979; Vidal 1980a). The allometric weight dependence of the specific growth rate found for N. mercedis is common in fish and the weight exponent is in the range (-0.33 to -0.41) reported (Brett 1979). However this relationship is not general in poikilotherms (Vidal 1980a).

The qualitative form of the specific growth rate function follows from the dependence of the consumption (Johnston and Lasenby 1982) and metabolic rates on size and temperature. The assumption that the growth rate is proportional to the difference between the ingestion rate and the metabolic rate leads to a specific growth rate of the form

$$[10] \quad G = \{0.003132 \cdot H \cdot T^{0.515} - 0.007097 \cdot T^{0.735}\} \cdot W^{-0.20}$$

where H is the number of hours per day that the mysid feeds. While this predicts a curvilinear dependence on temperature, in fact it is virtually indistinguishable from a linear dependence over the temperature range at which the data were obtained; between-individual variability in growth rates would improve the "linearity" of the observed relation. However, the observed rates of change of the specific growth rate with temperature are less than those predicted by equation 10, especially for large animals. The observed (equation 9) and predicted (equation 10) growth rates only agree within a factor of 1.5-3.

In several copepods, the different effects of temperature on the body-size dependence of growth and development rates account for the observed inverse relationship between temperature and body size (Vidal 1980b). Adult body size also decreases with increasing temperature in N. mercedis (chapter 1) and in other mysids (Gaudy and Guerin 1979; Matsuidara et al. 1952; Toda et al. 1984). The growth rate expression derived from the observed consumption and metabolic rates (equation 10) predicts a decreased size at maturity for N. mercedis at increased temperatures if the number of molts to maturity is fixed or decreases with increasing temperature. Equation 9 predicts reduced size at maturity only if the number of molts to maturity decreases with rising temperatures. Many crustacea, such as copepods, have a fixed number of molts to maturity (Hartnoll 1982). Based on my rearing data, the number of post-

embryonic molts to first reproduction seems to be about 14-15 in N. mercedis. Gaudy and Guerin (1979) also suggest a fixed number of molts to maturity for the two species which they studied. Berrill and Lasenby (1983) suggest that Mysis relicta matured after 12-13 molts at two temperatures. However, Toda et al. (1984) found an inverse relation between the number of molts to maturity and temperature in Neomysis intermedia; these are by far the most comprehensive data and very likely apply to other mysids in the genus Neomysis. Thus energetic considerations correctly predict the observed qualitative temperature dependence of the size at maturity in N. mercedis.

Temperature and food concentration interact with body size to vary growth rates in a complex fashion (Vidal 1980a). Vidal found that the critical food concentration for growth of several copepods increased with body size proportionally more at high temperatures than at low. Consequently maximum growth rates of small copepods were more strongly influenced by temperature than food concentration while the growth rates of larger copepods were relatively more dependent on food levels. If similar results obtain for N. mercedis the progressive reduction in adult body size observed in the natural population during the summer would permit the maintenance of high growth rates under declining food resources, such as might occur as the population density increased. The smaller reduction in adult body size with increased temperature noted in well-fed laboratory reared animals as compared to field animals at similar temperatures may then represent the effect of resource levels while the general

correspondence of the growth rates would follow from the relative independence from food concentration of the growth rates of small animals. This speculation cannot be tested with my data since I did not examine the effects of resource levels on growth. However the growth rates of immature mysids are generally more strongly temperature dependent than those of adults (Table 7).

Changes in the growth rate of N. mercedis resulted partly from changes in molt frequency, which increased with rising temperature and decreased with increasing size (equation 7). The temperature and size dependences of the molt frequency were qualitatively similar to those of other mysids (Mauchline 1980, p.210), but the temperature dependence was better described by a linear relation than by the logarithmic relation advocated by Mauchline (1977, 1980).

The slopes of the body size dependence of the molt and body weights were the same in male N. mercedis, so that the molt weight was a constant proportion (9.2%) of the body weight, or about 3.5% of the energy content. In females the development of the large brood pouch altered the body form so that the molt weight was an increasing fraction of the body weight. Molt weights in N. mercedis are similar to those (13%) of Metamysidopsis elongata (Clutter and Theilacker 1971), but are considerably less than those of cladocera (10-30%, Bottrell 1975).

Similarly to the intermolt period, the duration of embryonic development was strongly temperature dependent in

N. mercedis but was much greater than the intermolt interval for nongravid females of similar size. The increased intermolt duration in brooding females probably results from hormonally induced anecdysis which is known in other crustacea that carry their eggs (Lawlor 1976). The observed linear dependence of egg development rates on temperature is common, although curvilinear relations are known (Bottrell 1975; Meyers 1984). The duration of embryonic development is correlated with egg size in some peracaridan crustaceans (Steele and Steele 1975b; Wittman 1981b) so that the variations in egg size observed in N. mercedis (chapter 1) may alter generation times.

Metabolic rates of aquatic invertebrates are influenced by a multiplicity of factors including present and previous environmental conditions, size, ontogenic stage, nutrition, level of activity, and behavior (Kinne 1971, p.874). In general the body size dependence of metabolism is little affected by environmental variables which instead alter the level of metabolism (Vidal 1980c). Sex, maturity, and season slightly influence oxygen consumption in N. mercedis (Simmons and Knight 1975) but their effects are largely negligible compared to those of body size and temperature. My measurements of the "routine" metabolism of acclimated, normally active, fed animals are well described by a model of the form

$$\log(M) = a + b \cdot \log(W) + c \cdot \log(T)$$

which assumes that the body size dependence of the metabolic rate is indeed independent of temperature, as is often found (Comita 1968; Vidal 1980c). The above allometric model gave a

weight exponent of 0.837 ± 0.013 which is very close to Winberg's value of 0.81 for crustacea (Duncan and Klekowski 1975). Similar weight exponents obtain for other mysids (Table 15).

Table 15. Exponents for the weight dependence of metabolic rates in mysids.

species	b	reference
<u>Neomysis mercedis</u>	0.837	this study
	0.774	Simons and Knight 1975
	0.62	Jawed 1973
<u>N. mirabilis</u>	0.81	Shushkina et al. 1971
<u>N. integer</u>	0.58-0.83	Vlasblom & Elgershuizen 1977
<u>Mysis relicta</u>	0.75	Lasenby and Langford 1972
	0.778	Foulds and Roff 1976
<u>Leptomysis lingvura</u>	0.55-0.72	Gaudy et al. 1980
<u>Hemimysis speluncola</u>	0.38-0.70	Gaudy et al. 1980

The level of metabolism in N. mercedis increased with increasing temperature but salinity had little effect. Simmons and Knight (1975) and Vlasblom and Elgershuizen (1977) noted that salinity altered oxygen uptake in N. mercedis and in N. integer. However the range of salinities which I used (0-10 ppt) was much smaller than the preceding studies. Simmons and Knight also found no salinity effect at salinities below 30‰ seawater (about 10 ppt). Because of the variety of effects which may result from internal ion changes, it is difficult to predict the changes in oxygen uptake of varying osmotic loads. Indeed, no changes in oxygen uptake may occur if growth rates or fecundity are reduced, as in Artemia (Lockwood 1976). Estuarine mysids osmoregulate at salinities above or below normal (Dormaar and Corey 1973; Lockwood 1976). Osmoregulation in N. integer

and N. rayii is thought to involve the excretion or production of free amino acids by protein catabolism (Raymont et al. 1968; Jawed 1969), but evidently the metabolic cost is slight.

Temperature and body size had similar effects on metabolic rates. A doubling of the body weight increased the metabolic rate by a factor of 1.79 while a doubling of the temperature increased the rate by 1.66 times.

Metabolic rates in mysids may only weakly depend on activity levels. Foulds and Roff (1976) showed that oxygen uptake in Mysis relicta did not differ between routinely active animals and those swimming at speeds similar to observed vertical migration rates, and increased only by a factor of 1.2 at speeds of 2-4 body lengths per second. The relative independence of metabolic rates from activity levels at normal swimming speeds probably results from the continuous use of the thoracic appendages to generate respiratory and feeding currents as well as for locomotion (Cannon and Manton 1928; Foulds and Roff 1976).

My data on the routine metabolism of N. mercedis incorporates digestive metabolism since the measurements were made on recently fed animals. The effects of ration level on the metabolic rates of poikilotherms are ambiguous. Studies on copepods (Vidal 1980c) have found the level of metabolism to be independent of food concentrations whereas fish show a direct relation between metabolic rate and rations (Brett and Groves 1979). I assume that the metabolic rate of N. mercedis changes little with the quantity of ration.

In several rearing studies (Gaudy and Guerin 1979; this study) considerable mortality has occurred at molting. Lasker (1966, p.1298) observed that non-growing euphausiids continued to molt, but became progressively shorter, leading him to conclude that "molting is a metabolic necessity and continues at the expense of the organic reserves of the animal". The metabolic rates of molting N. mercedis averaged 1.32 times higher than those of non-molting animals over the 24 h period. Mysids have low body concentrations of storage products such as carbohydrates (Linford 1965; Raymont et al. 1966; Clutter and Theilacker 1971); Linford suggests that N. integer lives largely on its daily ingestion. If so, the moderate increase in metabolism associated with molting may impose a considerable stress on the organism, especially if feeding is depressed on the day of the molt as in euphausiids (Lasker 1966).

The energy densities of molts, eggs, and whole N. mercedis are very similar to values obtained for other mysids (Table 16). While the energy values of mysids are within the range reported for crustacea, they lie somewhat above the modal value (Griffiths 1977). The lipid fraction in mysids is small (10-15%, Raymont et al. 1966; Clutter and Theilacker 1971; Johnson and Hopkins 1978) and shows no significant seasonal variation (Linford 1965; Johnson and Hopkins 1978). Because most mysids are omnivores and many inhabit relatively food-rich areas such as estuaries, the energy densities of mysids may indicate that, as a group, they are rarely resource limited.

The preceding data suggest the importance of the animal

Table 16. Energy densities (J mg^{-1} whole animal) of mysids.

species	body	eggs	molt	reference
<u>Neomysis mercedis</u>	22.35	29.26	8.69	this study
<u>N. mirabilis</u>	22.89	-	-	a
<u>Metamysidopsis elongata</u>	19.25	29.96	10.38	b
<u>Mysis relicta</u>	22.59	-	-	c
	20.91-28.03	-	-	d
<u>M. stenolepis</u>	19.72	-	-	e
<u>Taphromysis bowmani</u>	18.52-19.72	-	-	f

references a : Shushkina et al. 1971
 b : Clutter and Theilacker 1971
 c : Lasenby and Langford 1972
 d : Hakala 1979
 e : Tyler 1973
 f : Johnson and Hopkins 1978

size and the temperature dependence of physiological rates in controlling the allocation of assimilated energy among components of the energy budget. Differences in the size and temperature dependences of rates of molting and somatic growth lead to a reduction in the size at maturity as temperature rises. The change in the somatic growth rate is a consequence of the different responses of ingestion and metabolism to variation in temperature and body size. The size and temperature dependence of growth and egg development limits the rate at which energy can be accumulated over successive interbrood intervals for reproduction and thus influences both reproductive effort and the survivorship of adults. Because selection against large animals is positively correlated with temperature (chapter 1), the variation in size with temperature is intimately tied to variation in the age-specific survivorship schedule.

Life History Theory

The abrupt decline in the growth rate of females at sexual maturity has been observed in several mysids (Clutter and Theilacker 1971; Gaudy and Guerin 1979; Cuzin-Roudy et al. 1981; Toda et al. 1984) and probably represents a re-allocation of energy from somatic growth to the formation of reproductive material. The decrease in somatic growth rates of mature females relative to immatures is sufficient to accumulate the energy content of the clutch over the intermolt preceding egg laying at 10°C, and to accumulate 75-80% of the energy content of the clutch at 15 and 20°C. The close agreement, despite different growth rates, of the total energy budgets of females and males (the latter making little direct allocation of energy to reproduction) suggests that the reduced growth rate of females represents the energetic "cost" of reproduction. Since fecundity is strongly dependent on body size, the reduction in somatic growth imposes a real cost to current reproduction in terms of decreased future reproductive potential.

Current reproduction may also impose a second direct reproductive cost in terms of reduced survivorship. Although the presence of a developing brood in the marsupium renders the largely transparent animal quite visible, increased predation by fish on gravid females, such as reported for some copepods (Feifarek et al. 1983), was not observed (chapter 1). However, the low incidence of females surviving to produce second or subsequent broods suggests that the energetic costs of reproduction may affect longevity.

Energy allocated to successive broods seems largely to be accumulated over the preceding intermolt. If the reduction in growth rates at sexual maturity represents the diversion of energy from somatic growth to reproductive products then the potential rate of accumulation of energy for reproduction will be the difference between the growth rates of immature and mature females. The amount of energy accumulated for successive clutches will be this difference times the duration of the intermolt, which, for a brooding female, is the egg development period. Thus, the dependence of the growth rates on size and temperature, in concert with the temperature dependence of egg development, will control the amount of energy available for successive clutches.

Because the specific growth rate varies inversely with weight (equation 9) while the egg development period is independent of maternal size, larger females accumulate proportionately less energy over each successive brood period. That is, the potential accumulation of energy over an intermolt, expressed as a proportion of body weight, will also vary inversely with body size. But the clutch weight is observed to remain a constant fraction of the body weight since both show the same size dependence (chapter 1). As the acquisition of surplus energy lags behind the requirements of reproduction, because of continued growth or of temperature regimes, successive broods will impose increasingly severe stresses on the animal.

The optimality arguments which underlie much of life

history theory require that current reproductive effort impose "costs" in terms of deleterious effects on subsequent fecundity or survival (Schaeffer 1974; Bell 1980). The experimental demonstration of such costs in this and other studies (Snell and King 1977; Hirshfield 1980; Browne 1982; Brody et al. 1983; Feifarek et al. 1983; Reznick 1983) strengthen the underpinnings of life history theory.

The proportion of the total energy budget allocated to reproduction differed significantly between the winter and summer generations and the difference was in the direction predicted by theory: the summer generations, in which adult mortality rates exceeded juvenile rates, made about 1.5 times the reproductive effort of the overwintering generation where adult mortality was less than juvenile mortality rates. The difference in reproductive effort resulted from the increased maintenance costs associated with delayed maturation at winter temperatures. The cessation of breeding which resulted in the additional maintenance costs in the overwintering generation of N. mercedis in the Fraser River is not universal under low temperature winter conditions. Several populations of Neomysis integer breed throughout the winter (Mauchline 1971; Parker and West 1979) although others do not (Kinne 1955; Bremer and Vijverberg 1982). The inferences are that there is no developmental constraint to winter breeding in Neomysis and that the differences in reproductive effort seen in N. mercedis are at least potentially responses to selection.

The arguments for measuring reproductive effort as the

proportion of the animal's total energy budget allocated to reproduction focus on mechanisms which could increase its reproductive effort. In theory, reproductive effort could be varied by (1) altering the allocation of production between growth and reproduction for a fixed total budget, (2) by increasing the total budget with the increase going primarily to reproduction, or (3) by reducing the total budget with the reduction coming from growth and maintenance (Hirshfield and Tinkle 1975; Tuomi et al. 1983). Experiments which control energy intake have demonstrated that reproductive effort varies with the total energy budget (Hirshfield 1980; Browne 1982), and that the costs of a given level of effort vary with resource availability (Browne 1982). Thus it seems necessary to take account of the total energy budget in comparing levels of reproductive effort.

Nevertheless the measurement of reproductive effort as the proportion of production allocated to reproduction has considerable intrinsic appeal since variation in the amounts of energy allocated to reproduction can only come from production. Moreover, animals do alter the allocation of production between growth and reproduction in some cases: medakas reared at different temperatures partition similar amounts of total production increasingly into reproduction at higher temperatures (Hirshfield 1980). However this measure of reproductive effort ignores the fact that animals may require very different total energy budgets or take very different times to accumulate identical allocations to production and reproduction (Hirshfield

and Tinkle 1975).

The three generations of N. mercedis allocate the same proportion of their production (29%) to reproduction. The constancy of the ratio arises from the facts that both clutch weight and total weight (i.e., production) show identical dependence on body size (chapter 1) and the clutch weight - body size relation was invariant during 1978 when the data were collected. The clutch weight - body size relation does vary between years so that the proportion of production allocated to reproduction must also vary between years.

Neither of the above measures of "reproductive effort" is wholly satisfactory. Each attempts to reflect both the benefit and cost of reproduction in a single measure and each assumes that energy allocation is a reasonable correlate of effective fecundity, that is, the lifetime number of offspring surviving to breed. Effective fecundity clearly depends on the inter-relation of the fecundity and survivorship schedules. Although an increasing energetic commitment to reproduction may imply greater effective fecundity, the use of energy units begs the question of how that energy should be partitioned into young and how the age-specific survivorship schedule will vary with size and number of young. Summer and winter generations of N. mercedis divide the same weight-specific clutch mass into very different sized young but this difference is not reflected in the above measures of reproductive effort. Perhaps a more useful approach would be to attempt direct measurements of the effective fecundity of individuals.

The predictions of life history theory regarding the frequency of breeding are difficult to test with my data. N. mercedis is physiologically capable of iteroparity: females produced up to 5 broods in the laboratory. However only a small proportion of the females produced multiple broods and the high mortality rates on adults in the field make it unlikely that many females would produce more than two clutches. The rather broad size range of gravid females in the field suggest that some multiple breeding occurred in each generation although the conditions of juvenile mortality exceeding adult mortality for which iteroparity is predicted only occurred in the overwintering generation. The disagreement between theory and nature in the summer generations is not unexpected: the physiological mechanisms determining the semelparity/iteroparity dichotomy are unlikely to change between successive generations.

Energy Budgets

The lifetime energy budgets of the three generations of Neomysis mercedis (Table 12) have not been adjusted to account for the leakage of soluble organic compounds. Hargrave (1971) suggested that the excretion of dissolved organic matter by aquatic animals may be a large fraction (36%) of their total energy budget. Dagg (1976) separately measured the excretion of metabolic end products and the leakage of organic compounds in the amphipod Calliopius and found leakage to be about 30% of the metabolic carbon use. The extent to which the budgets for N. mercedis underestimate the total assimilated energy is

difficult to establish. Hargrave and Geen (1968) reported the "excretion" of organic compounds by an unidentified mysid. If the leakage of dissolved organic compounds in mysids also represents 30% of the metabolism, the above energy budgets may underestimate the assimilated energy by about 15%.

The lifetime energy budgets of N. mercedis (Tables 12 and 14) can be compared to those of other mysids (Table 17) whose size and longevity bracket those of N. mercedis. There is

Table 17. Lifetime allocation of energy (%) for females of several populations of mysids. Excretion is estimated as 18% of metabolic heat loss (Elliott and Davison 1975).

	<u>Metamysidopsis</u> <u>elongata</u>	<u>Mysis</u> <u>relicta</u> Char Lake Stoney Lake
growth	17.2%	11.8%
molts	6.4%	
metabolism	50.0%	71.7%
excretion	9.2%	13.1%
reproduction	17.2%	3.4%
total budget (J)	84.8	992.3

data: Metamysidopsis elongata (Clutter and Theilacker 1971)
Mysis relicta (Lasenby and Langford 1972)

considerable interspecific and interpopulation variation (3.4-17.2%) in the proportion of the total energy budget allocated to reproduction. Mortality rates for the small, short-lived Metamysidopsis elongata were higher for juveniles than for adults (Fager and Clutter 1968). As predicted, the mysid made a large reproductive effort (17.2%) and was iteroparous (Clutter and Theilacker 1971). The large, long-lived Mysis relicta made

low reproductive efforts (3.4-5.9%) and was physiologically iteroparous (Lasenby 1971). The lower reproductive effort of the arctic population resulted partly from slowed rates of growth and development under low temperatures (Berrill and Lasenby 1983) and/or low food, which increased maintenance costs, and partly from the much smaller egg size produced (0.12 mg as compared to 0.20 mg for the temperate population).

The large (1.7 times) differences in reproductive effort between the arctic and temperate M. relicta populations disappeared when the allocation of production was compared. The Char Lake population devoted 22% of its total production to reproduction while the Stoney Lake population allocated 26%. These values were similar to the 29% measured for N. mercedis. Metamysidopsis elongata allocated 42% of its lifetime production to reproduction while the semelparous giant, long-lived (7 yr), abyssal Gnathophausia ingens shunted 61% of its production into young (Childress and Price 1983). Semelparity was correctly predicted for G. ingens since juvenile mortality rates were generally less than those of later instars (Childress and Price 1978).

These data agree with the prediction that semelparous organisms will show greater reproductive efforts than iteroparous organisms (Hirshfield and Tinkle 1975); however the great range of effort shown by the iteroparous species is noteworthy. The lower efforts made by species that are physiologically iteroparous but effectively semelparous because of poor survival is of interest. One might expect a low

probability of producing a second clutch to favour high reproductive effort as in semelparity but such is not the case. Temporal variability in factors affecting survivorship might favour such a "bet-hedging" strategy.

The net energy efficiencies of the summer generations of N. mercedis were relatively high but were similar to those of N. mirabilis (0.43, Shushkina 1972) and M. elongata (0.41, recalculated from Table 17). The net energy efficiency of the winter generation was similar to the average net energy efficiency for invertebrates (0.32, Banse 1979) but was much greater than those of the two M. relictata populations (0.15 and 0.19).

CHAPTER 3. LIFE HISTORY VARIATION IN A FRESHWATER POPULATION OF
Neomysis mercedis HOLMES

Introduction

Spatially separated populations may diverge in their life history traits if environmental factors which directly affect the survival or the production of young differ between habitats. The fecundity of the brackish water mysid N. mercedis is strongly dependent on food levels while the survival of young is influenced by food availability and the abundance of fish predators, especially juvenile salmon (chapter 1). Freshwater habitats near the upstream limit of the mysid's distribution in the Fraser River differ from estuarine habitats in both the above factors: standing crops of periphyton and benthic invertebrates are lower and the abundance of downstream migrating juvenile salmon slightly higher at upriver sites (Northcote et al. 1975, 1976, 1978). Seasonal variation in fish predation on mysids is expected to be reduced in upriver habitats compared to the estuary because of minimal seasonal changes in fish species composition (Northcote et al. 1978) and the short term residence of juvenile salmon migrating to rearing sites in the estuary. Consequently, differences in life history traits are possible between freshwater and estuarine populations of N. mercedis, depending on the relative magnitudes of natural selection and gene flow (Futuyma 1979).

I have determined the life history of a freshwater population of N. mercedis to test the existence and nature of

life history variation between freshwater and estuarine populations. I have also examined the two populations for differences in the frequencies of electrophoretically detectable enzyme polymorphisms which might suggest genetic differences underlying life history differences between the populations.

Materials and Methods

Study Site and Collection Methods

The life history of a freshwater population of N. mercedis was studied at Nicomen Slough, a large sidechannel of the Fraser River located about 70 km upriver from the estuary (at about 122°10'W, 49°08'N) near the upstream limit of the mysid's distribution (Northcote et al. 1976). The site is located well upstream of the maximum penetration of the salt wedge. Collections were made as described in chapter 1 from September 1977 to March 1979 except that sampling was stratified by depth. Nearshore samples were taken at 0.5-1 m depth while midchannel samples were collected at 4-5 m. Sampling was done without reference to tidal fluctuations which are of small amplitude (about 0.5 m) at the site. Vertical profiles of temperature and conductivity were measured at midchannel. Samples were preserved, sorted, and analyzed as described in chapter 1 for the estuarine population.

Electrophoresis

Mysids collected at Nicomen Slough and at Woodward Island in December 1977 and mid-May 1978 were assayed for enzyme polymorphisms at 16 loci (Appendix 6) using horizontal starch gel electrophoresis. Individual whole animals were homogenized and processed as described in Parkinson (1981). All 16 loci were examined for each animal. Frequencies of enzyme variants were compared between populations.

Results

The life history of N. mercedis at Nicomen Slough was broadly similar to that of the estuarine population; details are given in Appendix 5. Two differences were noted however. First, breeding at Nicomen Slough commenced later in the spring than at Woodward Island. Very few gravid females were found before late April and the first newly-hatched juveniles did not appear until the end of May. Although gravid females were found until early November, only a small portion of the S2 generation matured and bred in 1978; the majority overwintered as immatures. Second, the mysid population at Nicomen Slough was separated into nearshore and midchannel components whose fluctuations suggested seasonal onshore-offshore movement and which differed in abundance and in size.

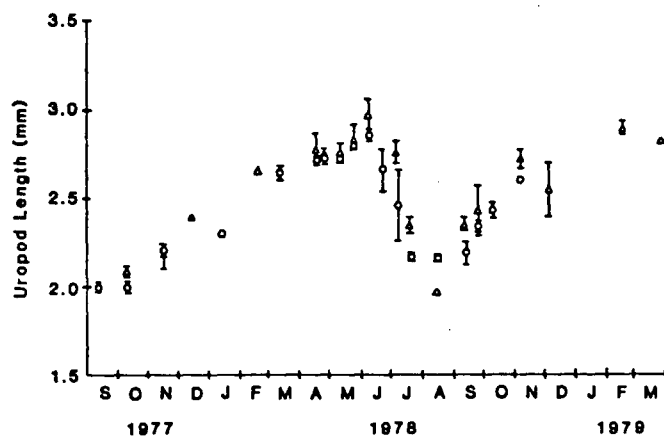


Figure 29a. The mean size (± 1 SE) of adult female *Neomysis mercedis* at Nicomen Slough, 1977-1979. (Δ) = midchannel, (O) = nearshore. Note the abrupt decrease in mean body size in early summer.

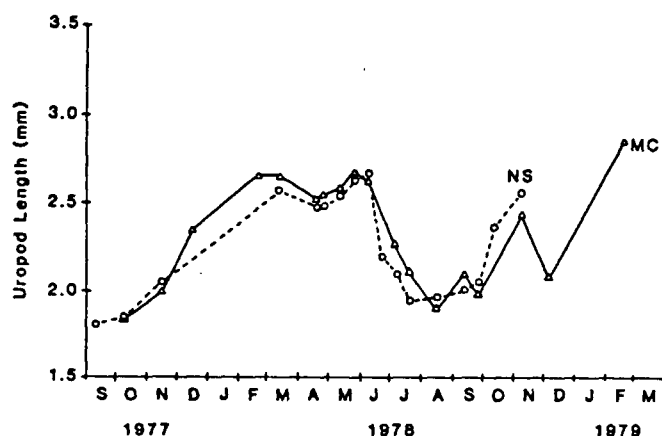


Figure 29b. The first decile size of adult female *Neomysis mercedis* at Nicomen Slough, 1977-1979. (Δ) = midchannel, (O) = nearshore. The first decile size approximates the size at maturity. Note the seasonal changes in size at maturity.

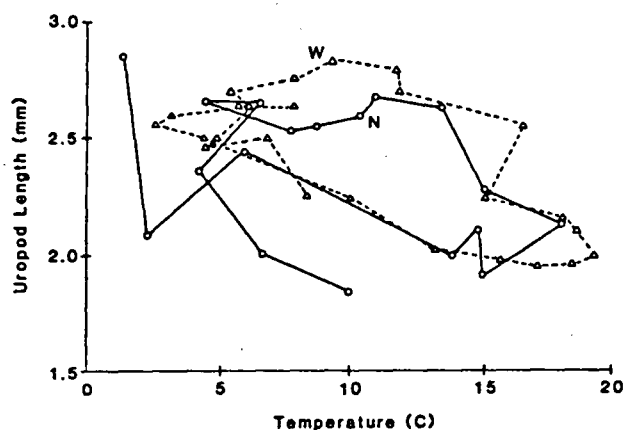


Figure 29c. The effects of ambient temperatures on the size at maturity of female *Neomysis mercedis* at Nicomen Slough (O) and Woodward Island (Δ). Note that, in the spring, females at Nicomen Slough mature at smaller body size than do females at Woodward Island at the same ambient temperatures (upper centre).

Body Size

The mean size and size at maturity of adult females at Nicomen Slough (Figure 29a,b) varied seasonally. The mean size of adult females decreased from 2.8 mm uropod length in the spring breeding generation to about 2.2 mm during the summer and increased again in the fall. The changes in mean size resulted from an abrupt decrease in the size at maturity from about 2.6 mm in the spring to about 2.0 mm in the summer, presumably as a response to seasonal temperature changes (chapter 1). The segment of the population in the cooler midchannel waters matured at a slightly larger size, as would be expected. The size at maturity during the summer was very similar to that of the estuarine population (chapter 1) but the spring breeding females at Nicomen Slough matured at a smaller size (2.6 mm) than the estuarine population (Figure 29c).

Egg Size and Fecundity

In contrast to the estuarine population, the frequency distribution of the mean size of eggs carried by females did not change seasonally at Nicomen Slough (Figure 30a,b). The frequency distribution was unimodal with a range from about 35 μ g to 55 μ g dry weight. The mean egg weight was 44.4 (SE= \pm 0.51, n=93) μ g which is indistinguishable from the average weight of the large-type eggs at Woodward Island. Fecundity increased exponentially with female body size (Figure 31a) and the fecundity - size relation was identical to that of the estuarine

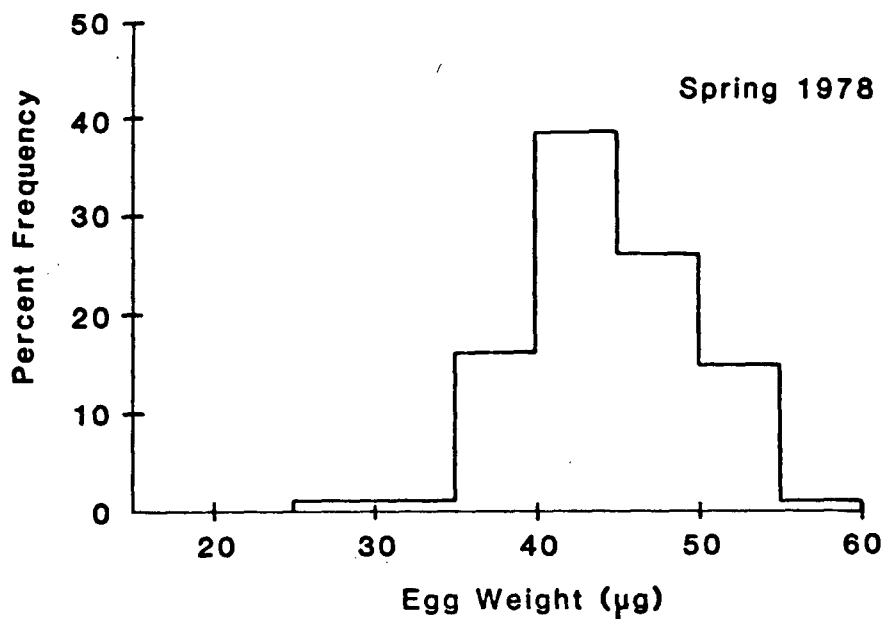


Figure 30a. The frequency distribution of mean egg weights at Nicomen Slough in spring 1978. ($n=78$).

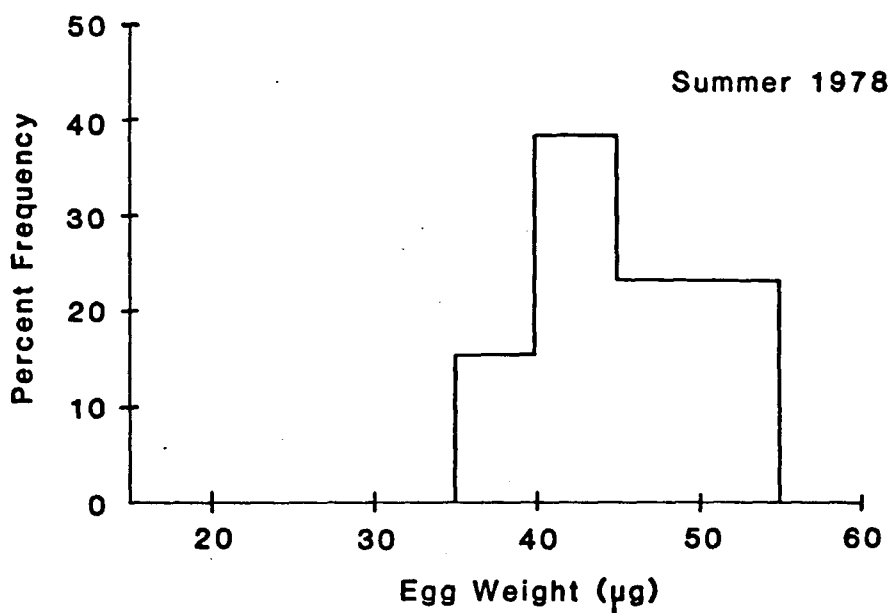


Figure 30b. The frequency distribution of mean egg weights at Nicomen slough in summer 1978. ($n=13$).

large egg animals (Ancova, $p > 0.05$).

Clutch Weight

The dry weight of clutches carried by females at Nicomen Slough increased exponentially with body size (Figure 31b). The slope of the clutch weight - body size relation was the same as that of the estuarine population, but clutches were about 20% heavier at the freshwater site (Table 18). The total weight -

Table 18. Comparison of size-adjusted measures of reproductive output and female condition in freshwater (Nicomen Slough) and estuarine (Woodward Island) populations of Neomysis mercedis. Bracketted groups do not differ significantly at the 5% probability level. Data have been log-transformed to homogenize variances. 1=Woodward Island 1978 small egg type, 2=Woodward Island 1978 large egg type, 3=Nicomen Slough 1978.

variable	groupings
egg weight	1 < (2, 3)
size-adjusted:	
a) fecundity	(2, 3) < 1
b) clutch weight	(1, 2) < 3
c) body weight	(2, 3) < 1
d) total weight	(1, 2, 3)

body size relations were identical at the freshwater and estuarine sites (Table 18). Within each population the slopes of the clutch weight - body size and total weight - body size relations were the same. Clutch weights were about 21% of the total weight for Nicomen Slough females but were only about 16%

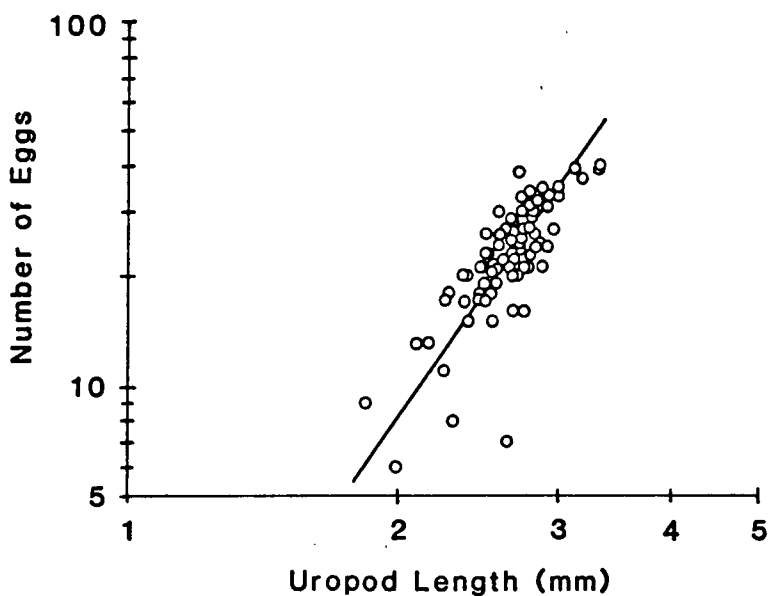


Figure 31a. The relation between fecundity and female body size at Nicomen Slough, 1978.

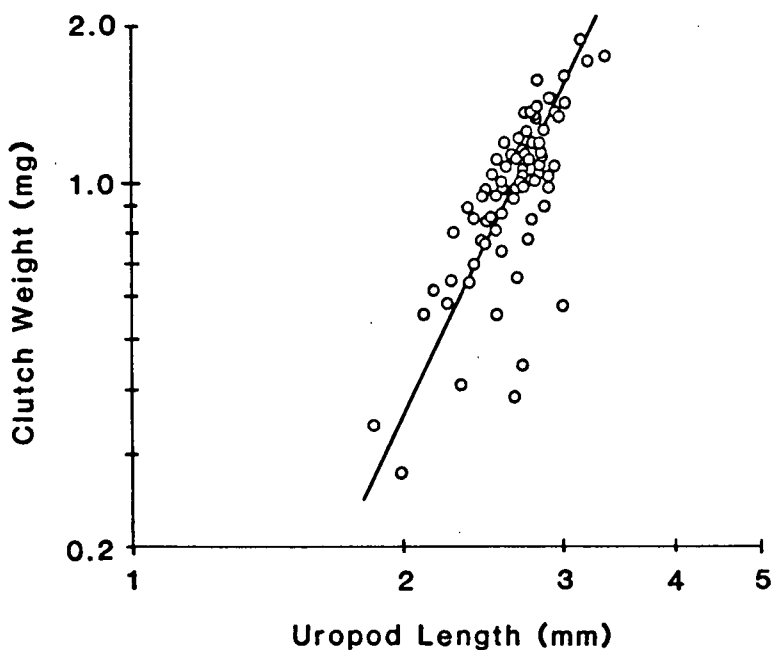


Figure 31b. The relationship between clutch weight and female body size at Nicomen Slough, 1978.

of the total weight for Woodward Island females in 1978.

Electrophoresis

Electrophoretically detectable enzyme polymorphisms were found at only two of the 16 loci surveyed. Maltase dehydrogenase (MDH) showed two variants which corresponded to one homozygous and the heterozygous genotype at a dimeric two allele locus while phosphoglucose isomerase (PGI) showed three variants which corresponded to one homozygous and two heterozygous genotypes at a dimeric three allele locus. The frequencies of the variants (Table 19) did not differ between populations (chi-squared test, $p > 0.05$).

Table 19. (a) The frequency of PGI protein variants in Neomysis mercedis .

	AB	BB	BC
Woodward Island	2	41	13
Nicomen Slough	1	42	12

(b) The frequency of MDH protein variants in Neomysis mercedis .

	AA	AB
Woodward Island	17	3
Nicomen Slough	16	4

Discussion

The most noticeable difference in life history traits between the freshwater population of N. mercedis at Nicomen Slough and the estuarine population at Woodward Island was the 20% increase in the size-adjusted clutch mass at the freshwater site despite identical size-adjusted total weights. Differences in the allocation of equal production between somatic and reproductive biomass could result from a developmental sensitivity to freshwater or from intrinsic differences between the populations. However, differences in the size-adjusted clutch weights were maintained between the estuarine and upriver populations during the summer when both sites were freshwater environments; thus direct effects of fresh and saline waters on the partitioning of production are unlikely although differential osmoregulatory costs might alter production. Size-adjusted clutch mass might also merely reflect differences in food availability. If so, then either the total weight - body size relation would be elevated, or the animals would mature at a larger size, or the animals would mature earlier at the richer site. The total weight - size relation was invariant between sites, the Nicomen Slough population matured at the same or smaller sizes as did equivalent generations at the estuarine site, and the age at maturity was similar or longer at Nicomen Slough. Food effects did not account for the observed differences. Intrinsic differences between the populations thus seem possible.

However no differences in genotype frequencies were found

between the populations when 16 electrophoretically detectable allozymes were surveyed. Although intrinsic differences between the populations are still very possible, since only a small portion of the genome was surveyed, there was no direct evidence that the observed differences in energy allocation patterns were associated with genetic differentiation between the populations. Interpopulation differences in the frequencies of esterase isozymes have, however, been found in Mysis relicta (Furst and Nyman 1969). In other aquatic crustaceans, certain life history traits have been shown to be heritable (Strong 1972; McLaren 1976; Doyle and Hunte 1981a,b) and rapid genetic change has been documented (Doyle and Hunte 1981a). Cody (1966) argued that selection should result in the allocation of an organism's limited time or energy resources in a manner which maximized the contribution of the genotype to following generations. Genetic-based differences in energy allocation patterns between populations, as postulated above, are not unreasonable.

Although the Nicomen Slough population made a larger energetic investment in reproduction, size-adjusted fecundity did not increase, since the mean egg size also increased. Interpopulation differences in egg size are known in many crustaceans (Hynes 1954; Strong 1972; Corkett and McLaren 1978; Van Dolah and Bird 1980; Mashiko 1982) and have been attributed to the physiological effects of temperature, food, and salinity or to the evolutionary effects of levels of predation and food availability (see discussion, chapter 1). Temperature is unlikely to be an important factor in the present case since

temperature differences between the upriver and estuarine sites were very slight in the spring when egg sizes differed greatly. Identical size-adjusted total weights imply that food availability did not differ greatly between sites despite the observed differences in mean egg size. The production of larger eggs could have been induced by freshwater since animals which experienced freshwater environments carried large eggs at either site. Freshwater populations of other crustaceans are known to produce larger eggs than adjacent brackish water populations (Hynes 1954). However, year-to-year variation in the egg size of spring-breeding estuarine animals which experienced saline conditions (chapter 1) suggest that other factors must also modify egg size.

The differences in environmental conditions existing between estuaries and adjacent waters are thought to promote genetic differentiation between adjacent populations (Levinton 1980). Although the differences in life history traits between freshwater and estuarine populations of N. mercedis may represent genetic adaptations, there was little evidence to make the claim probable. Nevertheless, there were obvious differences in life history traits between the two populations.

GENERAL DISCUSSION

A striking feature of the biology of N. mercedis is the variability in life history traits which is exhibited by the mysid. The variability manifests at two levels. There is firstly a seasonal variation in the size at maturity, which appears to result largely from the influence of temperature on physiological rates, and which carries with it a concomitant variation in size-related life history traits such as brood size and clutch mass. Secondly there is considerable between-individual variation in traits such as fecundity and egg size. Both levels of variation will strongly influence the relative production of offspring by individuals. Furthermore, such traits as size at maturity and fecundity commonly are heritable and thus potentially subject to selection. Seasonal variation in size-differential mortality rates, which result from seasonal changes in the abundance, species composition and size of predatory fishes and in per capita food levels, provide a mechanism through which selection could act.

The variation in life history traits seen in N. mercedis is largely in agreement with the predictions of life history theory. Current reproductive effort imposed costs in terms of decreased future fecundity and decreased survivorship; reproductive effort, measured as a proportion of the energy budget, increased when adult mortality rates were high; and both the age at maturity and reproductive effort occurred earlier in life in an expanding population. These results support the view that the life history characteristics of organisms can be

considered as an integrated set of adaptations resulting from natural selection.

Although the observed variation in life history traits agreed with theoretical predictions, the mechanism of change was probably phenotypic plasticity resulting from temperature variation rather than genetic change such as polymorphism. This result is not necessarily inconsistent with the assumptions implicit in life history theory since plasticity may itself be a genetically controlled trait subject to selection. The temperature dependence of the physiological rates which determine size and age at maturity synchronizes the variation in life history traits with seasonal variation in size-differential mortality and in food levels. The observed correlation between environmental temperatures and the increase in mortality with increasing size provides a mechanism through which selection could operate on the physiological rates. Thus, physiological responses to temperature which resulted in the size at maturity being a decreasing function of temperature would increase the survivorship of the individual possessing the trait. Temperature-dependent seasonal variation in the size at maturity also influences the rate of population increase through changes in size-dependent fecundity and in rates of development as well as through shifts in the size structure of the population which alter survivorship. The temperature dependences of the rates of growth and maturation observed in N. mercedis clearly are adaptive: the potential rate of increase for the summer generations was greater than that of the overwintering

generation because of a proportionally greater change in the generation length than in the concomitant reduction in fecundity.

Interpopulation differences in traits such as size-adjusted fecundity and clutch mass and in egg size may represent genetically based adaptations to specific environmental conditions, although no genetic differences were specifically demonstrated. Genetically based interpopulation differences in life histories are known in Mysis relicta which has sympatric summer breeding and winter breeding populations in some Swedish lakes (Furst 1972). Other interpopulation differences in life histories of M. relicta have been explained as the effects of food levels (Morgan 1980). A portion of both the inter- and intra-population variation seen in N. mercedis in life history traits such as clutch mass may reflect the varying conditions of food or temperature experienced by individuals. Although much of the intrapopulation variation in life history traits is accounted for by size variation, there remains considerable unexplained variation in brood size, clutch mass, and egg size. Nevertheless life history theory successfully accounts for the qualitative pattern of life history variation seen in N. mercedis.

Appendix 1: The Outmigration of *Neomysis mercedis* from Tidal Channels

The pattern of outmigration of mysids from the upper reaches of the tidal channel as the tide receded was examined using a vertical series of four drift samplers (30 cm X 30 cm, 0.47 mm mesh) placed at the confluence of a secondary channel which drained into the main channel about 60 m above the regular sampling site (Figure 1). Drift was sampled at alternate 0.5 h intervals continually from high slack water to low tide on the night of 11 January 1978 and at mid-day on 15 January 1978. Water depth, surface current speed, and temperature were measured at the beginning and the end of each 0.5 h sampling period. Samples were preserved in 10% formalin and counted as described above.

In both the day and night time series, a small pulse of mysids emigrated from the channel concurrently with an abrupt increase in current speed (Figure A1) to about $0.2 \text{ m} \cdot \text{s}^{-1}$ as the water level dropped below the bank height, confining flow to the channel. The proportion of the mysids caught in the upper nets during this pulse was much larger in the night sample than in the day sample. Moreover, the night samples showed a large increase in the drift in the interval immediately before the channel completely dewatered. This second peak was not present in the daytime series, in which the channel did not drain dry. Indeed, the drift rates in the daytime series were generally much lower than those in the nighttime series.

These results imply that outmigration is a passive response

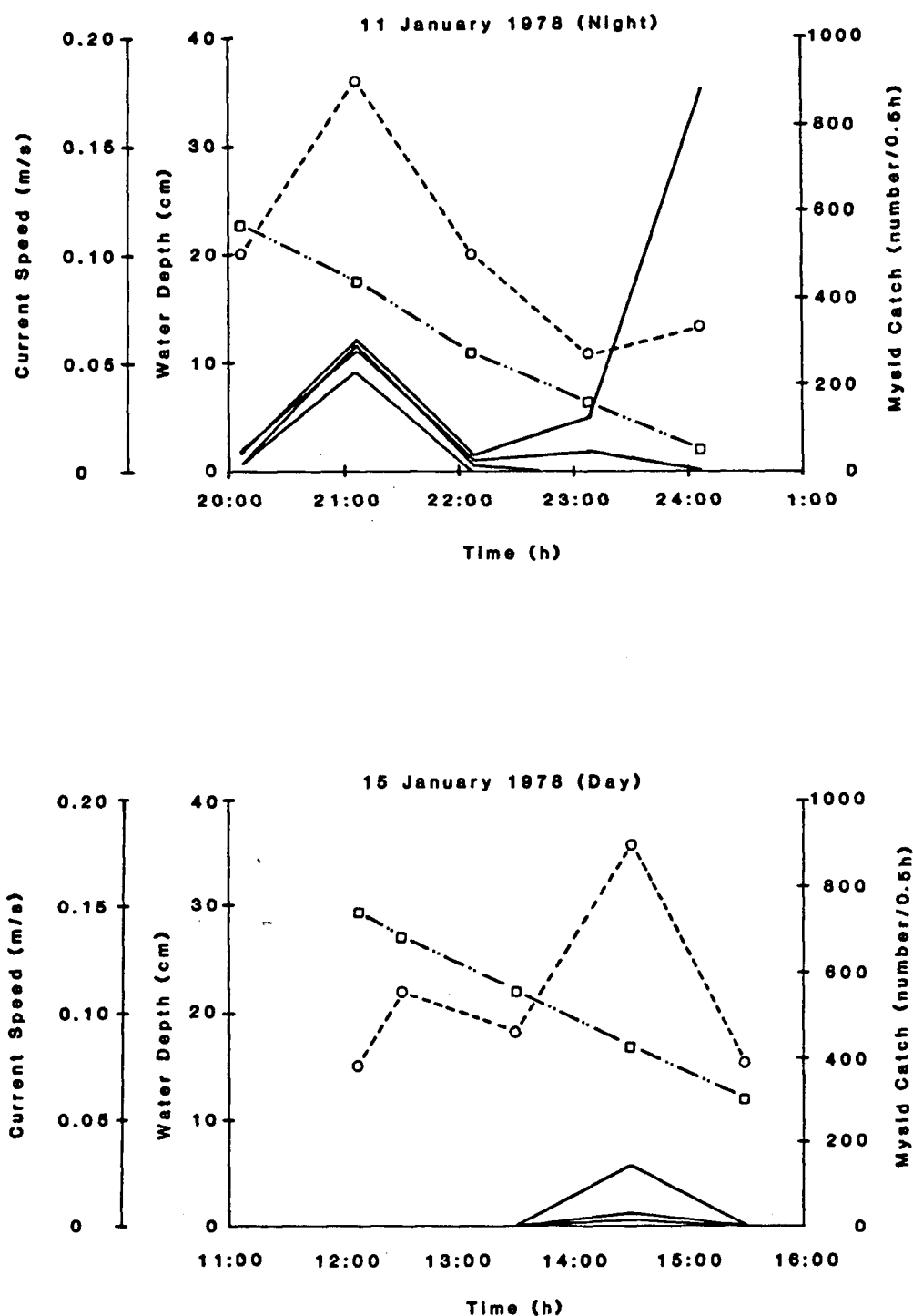


Figure A1. The emigration rate (numbers per 0.5 h) of *Neomysis mercedis* on falling tides at night and mid-day. (□) = water depth in dm, (o) = current speed in $\text{m}\cdot\text{s}^{-1}$, (—) = the vertical series of drift net catches with the top curve being the bottom net.

to physical transport processes rather than being a behavioral mechanism. I observed mysids to be oriented upstream and swimming vigourously while being swept out of the channels. Much of the emigration occurred just at low water when the draining of the channel forces the animals out. Much of the outmigration occurred along the bottom of the channel rather than in the water column. There were more mysids drifting in the water column at night than in the day. This is consistent with studies of the light and current responses of N. mercedis and related mysids (Heubach 1969; Herman 1963).

Appendix 2: The Selectivity of the Sled-Towed Net

Towed nets are known to be selective by size, both because of size based differential gear avoidance and because of mechanical mesh retention. I determined the relative catchability of different sized mysids by my gear on two occasions by comparing the size distribution of the sled-towed net to an unbiased sample of the true size distribution of the population. The latter was obtained as the concurrent catches of drift samplers placed at a constriction of the channel through which the entire mysid population must pass as the channel drained. I assumed that the drift net was non-selective; this is reasonable since: (1) the current speed at the constriction was sufficiently high that mysids (and fish!) could not avoid the net; (2) the mesh size was small enough (0.47 mm) to retain the smallest size classes of mysids; and (3) the channel above the drift net drained dry.

The drift net was set about 1.5 h before low tide and sled samples taken. The samples were preserved and analysed as described previously.

Small mysids were under-represented in the sled samples as compared to the drift samples (Figure A2). The relative proportion of N. mercedis in the sled samples increased with the size of the mysids, and became roughly constant above 1.0 mm uropod length.

This gives a measure of the relative rather than absolute catchabilities. I have normalized the relative catchabilities to one at sizes above 1.0 mm on the assumption that the constancy of the relative proportions indicated that the large mysids are caught by the sled sampler in their true proportions. The catchabilities thus obtained were used to correct the observed size-frequency distributions for gear selection. It should be noted that these catchability corrections will incorporate both behavioral and mechanical selection.

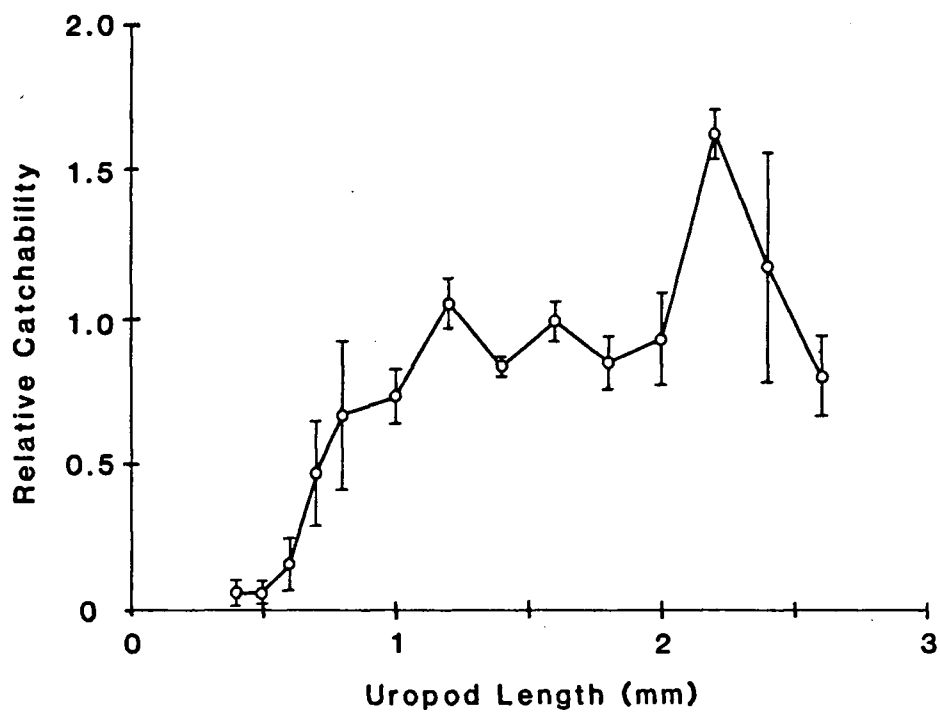


Figure A2. The relative catchability of Neomysis mercedis of different sizes by the sled-towed net .

Appendix 3: The Accuracy of Size-specific Mortality Rates
Estimated with the Lynch Algorithm

Lynch (1983) presented a technique to estimate size-specific mortality rates from periodic size-abundance data. He considered the precision of the estimates but not their accuracy. Here I examine the algorithm for bias by applying the method to a series of simulated populations of known characteristics.

If the flux of animals between size classes can be specified over the sampling interval t , then the size-specific mortality rate $m(i)$ can be calculated by comparing the expected and observed abundance at the end of the period. However, the expected number of animals in a given size class will depend on the mortality rate in the preceding size class as well as on the growth rate, as these determine the actual number of animals which survive to grow into the next class. This situation leads to an under-determined set of simultaneous equations in the mortality rates. Lynch reduced the problem to a set of independent equations in a single unknown, $m(i)$, by assuming that the mortality rate of the recruits to a given size class approximated that of the class considered, i.e., that the mortality rates were "slowly"-varying functions of size. The mortality rate for the i -th size class then becomes

$$[1] \quad m(i) = [\ln\{N(i,0) + [G(i-1,1) + G(i-2,i)] \cdot \exp(-m(i) \cdot t/2) \\ - [G(i,i+1) + G(i,i+2)]\} - \ln\{N(i,t)\}] / t$$

where $N(i,t)$ is the abundance of the i -th size class at time t and $G(i,x+1)$ is the flux of animals from class i to class $i+1$

over the interval t in the absence of mortality. Lynch gives expressions for the mortality rates of the first two size classes, which may be affected by recruitment during the intersample period.

The accuracy of the estimate will depend upon the ability of the approximation $[G(i-1,i) + G(i-2,i)] \cdot \exp(-m(i) \cdot t/2)$ to represent the actual time-pattern of transitions into the i -th class. The effects of errors in this approximation will depend on the magnitude of transitions into the class relative to the other terms in equation [1]. Therefore (1) the magnitude of the mortality rate, (2) the rate of change of mortality rates between size classes, (3) the time interval, and (4) the relative abundances of adjacent size classes may influence the accuracy of the mortality estimate.

I simulated a series of populations of known mortality rates to which Lynch's algorithm was applied. Each population consisted of 100 size classes at unit intervals. An initial distribution was specified for 20 classes of 5 unit intervals to represent an experimentally determined distribution. Transitions between classes were determined daily using the size- and temperature-dependent growth function measured for N. mercedis and were adjusted for mortality daily to yield the true final size distribution. The same function was used to calculate the G terms in equation [1] so that deviations of the estimated mortality rates from the true values reflect only inaccuracies in the approximation used in the derivation of equation [1].

The effects on the mortality rate estimates of the four factors listed above were examined by varying the initial size-frequency distribution, the magnitude of the mortality rates, the pattern of mortality with size, the percentage change in mortality rates between classes, and the duration of the sampling interval. The initial size-frequency distributions, which determined the relative importance of the approximation to the calculation of the mortality rate, were (1) a uniform distribution, (2) an approximately Gaussian distribution centred on the middle class, and (3) an approximately Poisson distribution centred on the first class. The estimated mortality rates are compared to the true values in Tables A1-A3.

Table A1. Ratios of (estimated·100% / actual) mortality rates calculated for a uniform initial size-frequency distribution using the Lynch algorithm.

(a) UNIFORM DISTRIBUTION		Mortality Rate					
		0.1 day ⁻¹			0.5 day ⁻¹		
Mortality Pattern	% Change	Time Interval			Time Interval		
		1 day	5 day	11 day	1 day	5 day	11 day
constant		95-96	76-86	67-100	96	82-90	66-100
increasing	10		76-85	63-95		80-89	63-95
	50	92-99	72-81	53-82			51-81
U-shaped	10	94-96	78-85	63-105		82-89	63-105
	50		73-92	53-126	92-100	74-94	52-122

The true mortality rates are consistently underestimated using Lynch's procedure. The accuracy of the estimate increased slightly as the true mortality rate increased, presumably

Table A2. Ratios of (estimated $\cdot 100\%$ / actual) mortality rates calculated for a Gaussian initial size-frequency distribution using the Lynch algorithm.

(b) GAUSSIAN DISTRIBUTION		Mortality Rate					
		0.1 day ⁻¹			0.5 day ⁻¹		
Mortality pattern	% Change	Time Interval			Time Interval		
		1 day	5 day	11 day	1 day	5 day	11 day
constant		91-99	77-92	66-100	91-99	80-94	66-100
increasing	10		77-92	63-97		78-94	63-97
	50	85-99	67-91	53-90			51-89
U-shaped	10	89-99	75-92	63-103		78-95	63-103
	50		67-93	53-115	85-100	69-98	52-114

because the $[G(i-1,i) + G(i-2,i)] \cdot \exp(-m(i) \cdot t/2)$ term became relatively smaller compared to the other terms in equation [1]. For the Gaussian and Poisson distributions, the least accurate estimates were obtained for classes with initial numbers that were small relative to the numbers growing into the class. The accuracy of Lynch's estimate decreased sharply with time as the magnitude of the approximation term increased. In general, the error in the estimate increased as the percentage difference in $m(i)$ between adjacent size classes increased. However, the direction of change in $m(i)$ between adjacent classes influenced the estimate. If $m(i)$ decreased from $i-1$ to i , then the estimate was larger in magnitude than when $m(i)$ increased by the same proportion between adjacent classes; this generally increased the accuracy of the Lynch estimate.

Lynch's mortality estimator was generally quite accurate under the conditions for which it was designed: short intervals

Table A3. Ratios of (estimated·100% / actual) mortality rates calculated for a Poisson-like initial size-frequency distribution using the Lynch algorithm.

(c) POISSON DISTRIBUTION		Mortality Rate					
		0.1 day ⁻¹			0.5 day ⁻¹		
Mortality pattern	% Change	Time Interval			Time Interval		
		1 day	5 day	11 day	1 day	5 day	11 day
constant		91-94	74-78	67-100	92-94	79-81	66-100
increasing	10		73-76	63-96		76-80	62-96
	50	86-92	65-72	51-84			
U-shaped	10	90-94	73-80	63-105		76-84	63-105
	50		65-91	52-123	86-100	66-93	51-126

and slowly changing $m(i)$ functions. However, it is clear that true mortality rates may be significantly underestimated when the sampling interval and inter-class transition rates are such as to make the magnitude of the term which represents transitions into the class large relative to the other terms in equation [1].

Appendix 4: The Effects of Egg Size on Rates of Population
Increase

The effects of egg size variation on the rate of population growth, r , can be examined using the following approximation (McLaren 1963):

$$[1] \quad r = [1/D] \cdot \ln(E \cdot S)$$

where D is the generation length, E is the number of eggs produced by a female, and S is the survivorship to maturity. Equation [1] can be re-written as

$$r = [1/D] \cdot \{ \ln(E) + \ln(S) \} = [1/D] \cdot \ln(E) + (-m)$$

where m is the average instantaneous mortality rate over the time to maturity. The effects of egg size are manifest through changes in the generation length which result from the dependence of the egg development period on egg size and through changes in fecundity.

First consider only the effects of generation length on r . The S1 generation originates from small (26.1 μg) eggs which are laid in late April - early May and hatch about 30-35 days later. The interval from hatching to maturity is about 57 days. The females mature at a size of 2.25 mg and produce 9 large (42.5 μg) eggs. The average instantaneous growth rate over the free-living stage is about

$$g_1 = [1/57] \cdot \ln(2.25 / 0.0261) = 0.0782 \text{ mg} \cdot \text{day}^{-1}$$

If the S1 generation had originated from large (42.5 μg) eggs, then the egg development period (EDP) would be increased by about 16% to $1.16 \cdot 35 = 40.6$ days and the free-living period (FLP) would be about

$$t = [1/g_1] \cdot \ln(2.25 / 0.0425) = 50.8 \text{ days}$$

The generation times are therefore $(35 + 57) = 92$ days for small eggs and $(40.6 + 50.8) = 91.4$ days for large eggs. Thus r will not vary with egg size.

The S2 generation hatches in early-mid August from large eggs laid in late July or early August, matures about 43 days later at 2.89 mg weight, and produces 12 large eggs per female. The calculated EDP is about 12 days at the field temperatures so that the EDP of large eggs would be $12 \cdot 1.16 = 13.9$ days. The instantaneous growth rate of the large egg neonates is

$$g_2 = [1/43] \cdot \ln(2.89 / 0.0425) = 0.0981 \text{ mg} \cdot \text{day}^{-1}$$

The FLP of small egg young would be

$$t = [1/g_2] \cdot \ln(2.89 / 0.0261) = 47.9 \text{ days}$$

Thus the generation lengths would be about $(13.9 + 43) = 56.9$ days for large eggs and $(12 + 47.9) = 59.9$ days for small eggs. The rates of population increase would be

$$r = [1/56.9] \cdot \ln(12) = 0.0437 \text{ day}^{-1} \text{ for large eggs}$$

$$\text{and } r = [1/59.9] \cdot \ln(12) = 0.0415 \text{ day}^{-1} \text{ for small eggs.}$$

The W generation hatches in mid-late October from large eggs laid in late September - early October, matures the next spring in late April at 5.44 mg weight, and produces about 25 small eggs per female. The EDP calculated at the field temperatures is about 35 days. Thus the EDP for large eggs will be $1.16 \cdot 35 = 40.6$ days. The average instantaneous growth rate for large eggs is

$$g_3 = [1/185] \cdot \ln(5.44/0.0425) = 0.0262 \text{ mg} \cdot \text{day}^{-1}$$

The FLP of neonates from small eggs would be

$$t = [1/g_3] \cdot \ln(5.44/0.0261) = 203.6 \text{ days}$$

The generation lengths would be $(40.6 + 185) = 225.6$ days for large eggs and $(35 + 203.6) = 238.6$ days for small eggs. The r values would be

$$r = [1/225.6] \cdot \ln(25) = 0.0142 \text{ day}^{-1} \text{ for large eggs}$$

$$\text{and } r = [1/238.6] \cdot \ln(25) = 0.0134 \text{ days for small eggs.}$$

Thus, large eggs result in slight increases in r in the S2 and W generations but not in the S1 generation, which may be why the egg weight distribution which gives rise to the S1 generation is bimodal for small and large eggs.

Fecundity effects can be examined by requiring females which hatch from a given size egg to produce the same size egg, i.e., by having egg size be highly heritable. Then the fecundity of small egg females in the S1 generation would be $1.56 \cdot 9 = 14$ eggs and r would be 0.0287 day^{-1} . The fecundity of S2 small egg females would be $1.56 \cdot 12 = 18.7$ eggs so that r would be 0.0488 day^{-1} . W generation females producing large eggs would have a fecundity of $25 / 1.56 = 16$ eggs so that r would be 0.0123 day^{-1} . The simultaneous effects of egg size on generation length and fecundity reduces the potential rate of population increase of large egg females. Large eggs then result in higher r values only if the average instantaneous mortality rate of large egg young over their lifetime is about 0.001 to 0.005 day^{-1} less than the death rate of small egg young. Seasonal changes in size-specific mortality rates of this magnitude are quite possible, and may be a factor inducing

the observed egg size variation.

Appendix 5: The Life History of *Neomysis mercedis* at Nicomen Slough

Physical Parameters

Midchannel and nearshore water temperatures (Figure A3) varied seasonally from about 2°C in the winter to 18-20°C in midsummer. Midchannel bottom water temperatures were 1-3°C cooler than temperatures at the 1 m site between late April and late September. In general temperatures were 1 or 2°C cooler at Nicomen Slough than at the estuarine site except in early fall when they were several degrees warmer.

Nicomen Slough was always a purely freshwater environment; salinity was not measurable. Conductivity was generally close to 100 $\mu\text{mho}\cdot\text{cm}^{-2}$ although there were small irregular fluctuations throughout the year.

Abundance

Population densities of *N. mercedis* fluctuated 30-40 fold throughout the year (Figure A4). For much of the year, densities were considerably lower in the deeper midchannel waters than at the nearshore site. Nearshore densities showed two peaks of about 600 $\cdot\text{m}^{-2}$, during the midsummer and in early autumn. As the densities at nearshore declined sharply in the late fall, there was a corresponding increase in the midchannel

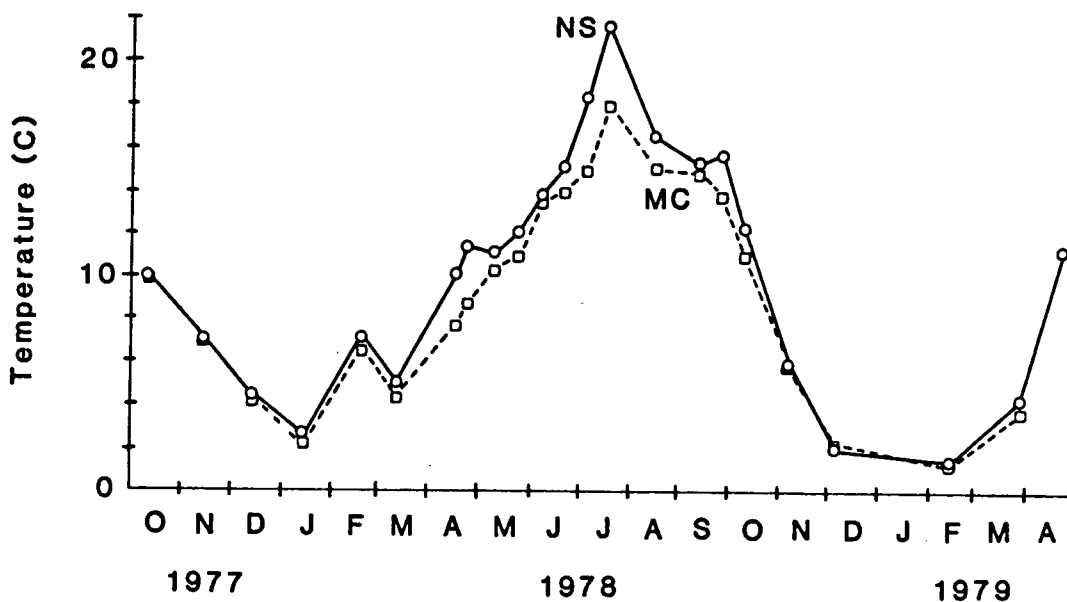


Figure A3. Bottom water temperatures at midchannel (\square) and at 1m depth (\circ) at Nicomen Slough from 1977 - 1979.

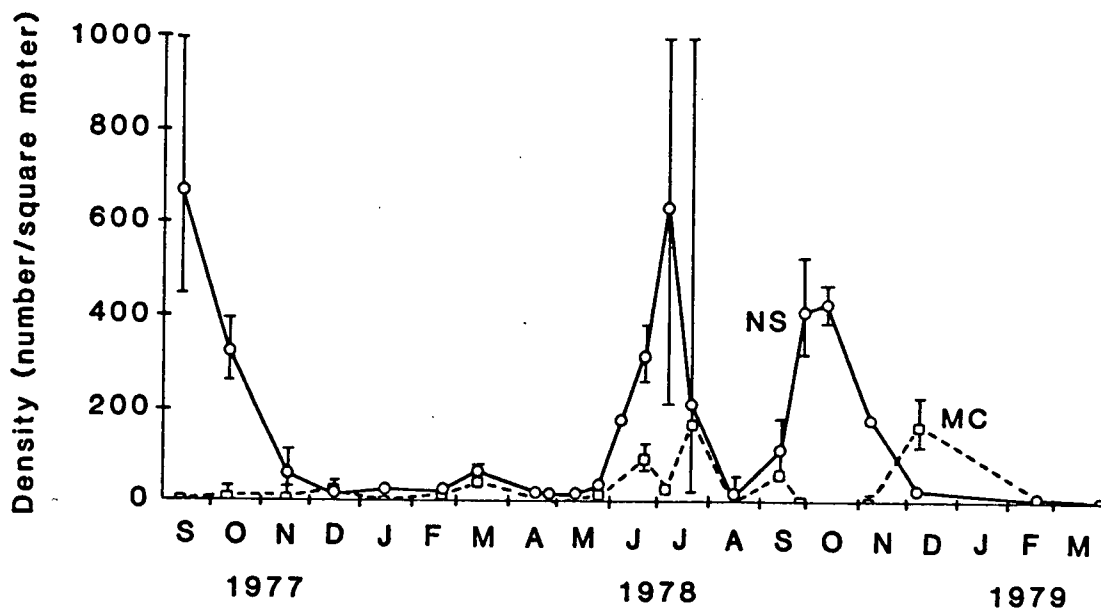


Figure A4. Population densities ($\# \cdot m^{-2}$) at the nearshore (\circ) and midchannel (\square) sampling sites at Nicomen Slough 1977 - 1979.

densities which suggested that part of the decline resulted from an offshore movement. Nearshore and midchannel densities were low (about $20 \cdot m^{-2}$) and similar from November to late May, when the nearshore segment began to increase rapidly. Midchannel densities increased more slowly and reached maximum densities only about one-third of the nearshore values. The midchannel midsummer maximum lagged the nearshore maximum and corresponded to a decline in the shallow-water density. Since nearshore water temperatures were approaching the upper lethal temperature for N. mercedis (Hair 1971), the change in densities may have represented an offshore movement to cooler midchannel waters. Densities declined precipitously in late summer at both locations but increased rapidly at the nearshore site in late September while midchannel abundance remained low until the autumn influx from the nearshore habitat.

Egg-bearing females were found from mid-April until early November (Figure A5a). Embryo densities and adult female densities increased at the nearshore site in May while they were decreasing at the midchannel site, which suggested that mature females moved onshore to brood their young. Juveniles first appeared in late May and increased rapidly in abundance thereafter. Successive peaks in the abundance of embryos, juveniles, and immatures at the nearshore site were seen in late May, early July, and late July respectively (Figures A5a,b,c). Nearshore adult density showed a broad maximum between late July and mid-August. The generation length for the first summer generation (S1) was thus about 85 days.

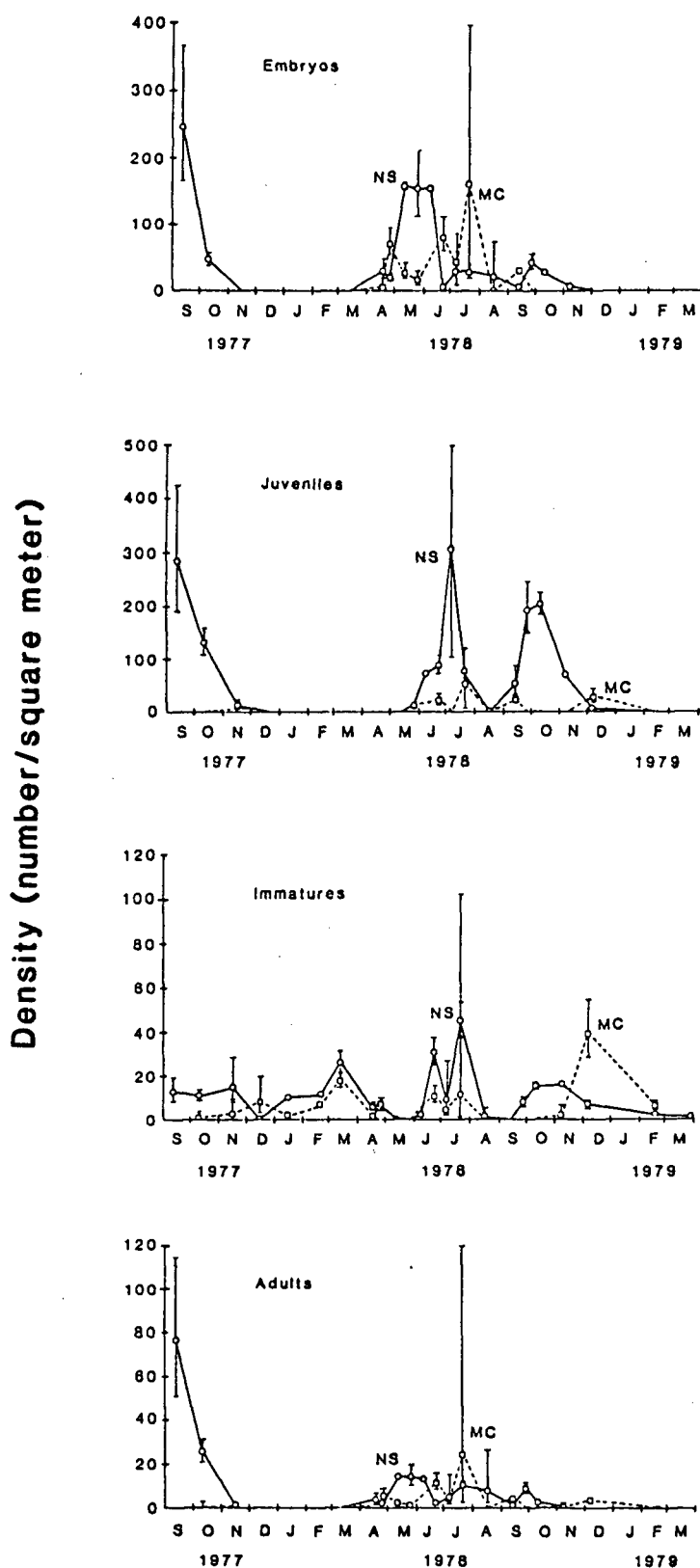


Figure A5. The densities (number per m^{-2}) of female (a) embryos, (b) juvenile, (c) immature, and adult Neomysis mercedis at Nicomen Slough from 1977 to 1979 .

Newly recruited animals appeared to rear in the warmer shallow waters; juvenile and immature mysids were much more abundant nearshore than at midchannel. After the initial pulse of breeding in May, however, adult females were more abundant throughout the summer at the midchannel stratum. The late July peak in adult and embryo densities at the midchannel location implied that the maturing S1 females moved to the deeper waters to breed.

The population apparently crashed in August despite the relatively high embryo abundance seen in July at the midchannel site. In mid-September and October embryo densities increased, first at midchannel and then near shore. Juveniles increased rapidly to a second peak (W generation) at the nearshore site, as did the immatures after a two week lag. Breeding ceased in November and both juveniles and immatures moved offshore in the November-December period to overwinter primarily as immatures.

Fecundity

The proportion of adult females breeding varied considerably over the year (Figure A6). Almost all adult females carried clutches during the spring and fall breeding peaks, but the proportion breeding fell to about 0.5 throughout the summer. During the fall breeding period, the proportion of females which bred increased first in the midchannel samples and declined as the proportion increased in nearshore samples, which implied that the gravid females moved onshore to breed.

The seasonal pattern was similar to that seen at Woodward

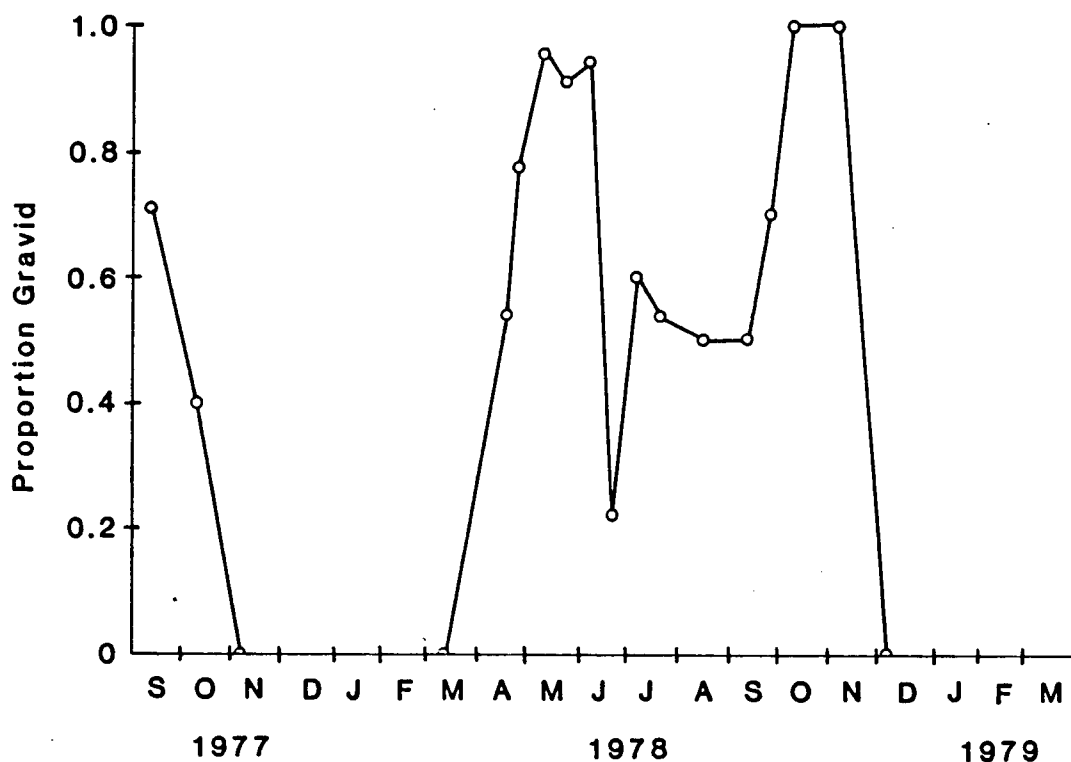


Figure A6. Seasonal variation in the proportion of gravid adult female Neomysis mercedis at Nicomen Slough, 1977 to 1979 .

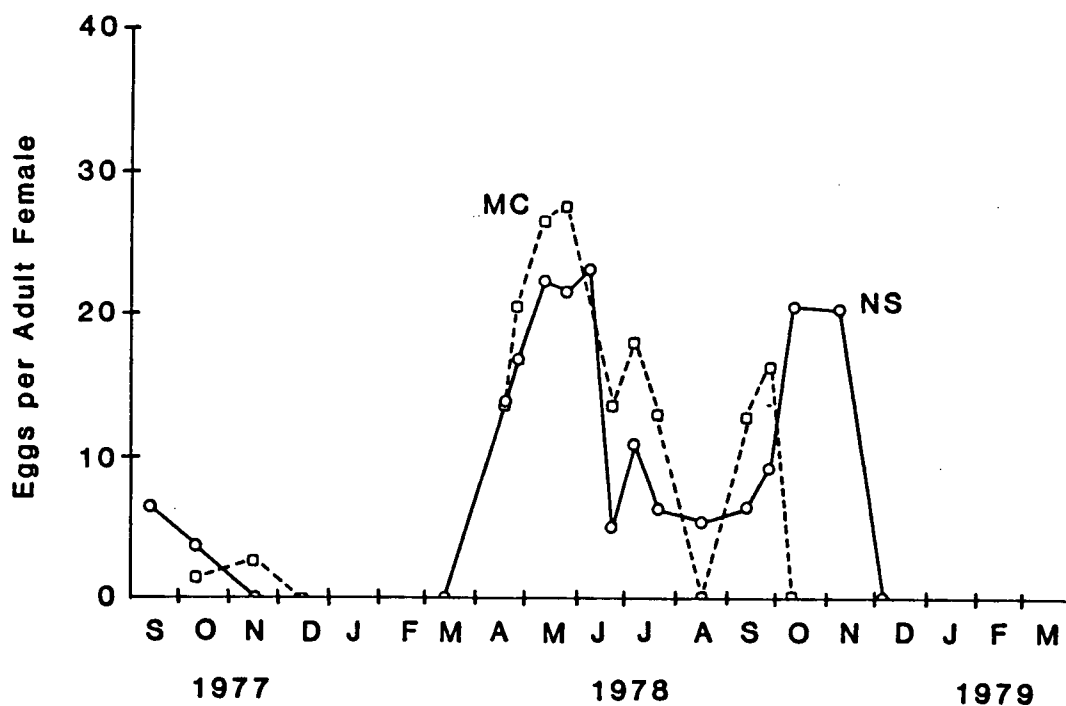


Figure A7. Seasonal variation in the average number of eggs per adult female Neomysis mercedis at Nicomen Slough 1977 to 1979 .

Island except that breeding commenced later and continued longer at Nicomen Slough, and a slightly higher proportion of females bred during the peak periods. The timing and extent of the midsummer decline in the proportion gravid was similar at both the freshwater and estuarine sites.

The number of eggs per adult female (Figure A7) was about 20 during the spring and fall breeding peaks but declined to about 5-6 during the summer as a result of the decreased proportion of females breeding and the smaller size of the summer-maturing females (chapter 3). The number of eggs per female was slightly higher in midchannel samples than in nearshore samples because of the larger size and slightly higher proportion breeding of the midchannel females. The average fecundity of Nicomen Slough females was about 20% lower than those of Woodward Island females in the spring (20 eggs per female versus about 25 per female). Fecundities were similar at both sites during the summer but the average fecundity of the upriver animals during the fall breeding peak was twice that of the estuarine animals (chapter 1). This difference resulted partly from the fact that the Nicomen Slough females matured later at a larger size (presumably because of cooler temperatures) and partly from the higher proportion breeding.

The male:female sex ratio fluctuated about one throughout much of the year (Figure A8). There was, however, a general decline in the ratio in late winter and early spring. The sex ratio was strongly skewed in favour of females at the time when the population density was beginning to increase from its winter

minimum.

Biomass fluctuated considerably as the generations waxed and waned (Figure A9). The midsummer maxima were about 160-180 $\text{mg}\cdot\text{m}^{-2}$ at both the nearshore and midchannel sites. Minimum values occurred in winter and were about 10 $\text{mg}\cdot\text{m}^{-2}$. The biomass values were much less than corresponding values at the estuarine site.

The total weight, body weight, clutch weight, fecundity, and total length of N. mercedis at Nicomen Slough were size dependent (Table A4). The regressions are compared with those of N. mercedis from the estuarine site in chapter 3.

Table A4. Summary of size-dependent functional regressions of the form $\log(y) = a + b \cdot \log(\text{uropod length in mm})$ for Neomysis mercedis at Nicomen Slough, 1978.

y	a	b +- 1 SE	r ²	n
total weight (mg)	-0.564	2.82 (0.016)	0.99	274
body weight (mg)	-0.578	2.74 (0.014)	0.99	274
clutch weight (mg)	-1.54	3.59 (0.24)	0.59	91
egg number	-0.157	3.55 (0.24)	0.61	89
body length (mm)	0.725	0.96 (0.007)	0.99	253

Thus, the freshwater population of N. mercedis at Nicomen Slough has two generations per year. The population overwinters as immatures in both the nearshore and midchannel habitats. As water temperatures rise in the spring, females mature and move into the nearshore areas. Breeding by the overwintering animals occurs from late April to early June and gives rise to a pulse of juveniles in the nearshore areas in early summer. Adults

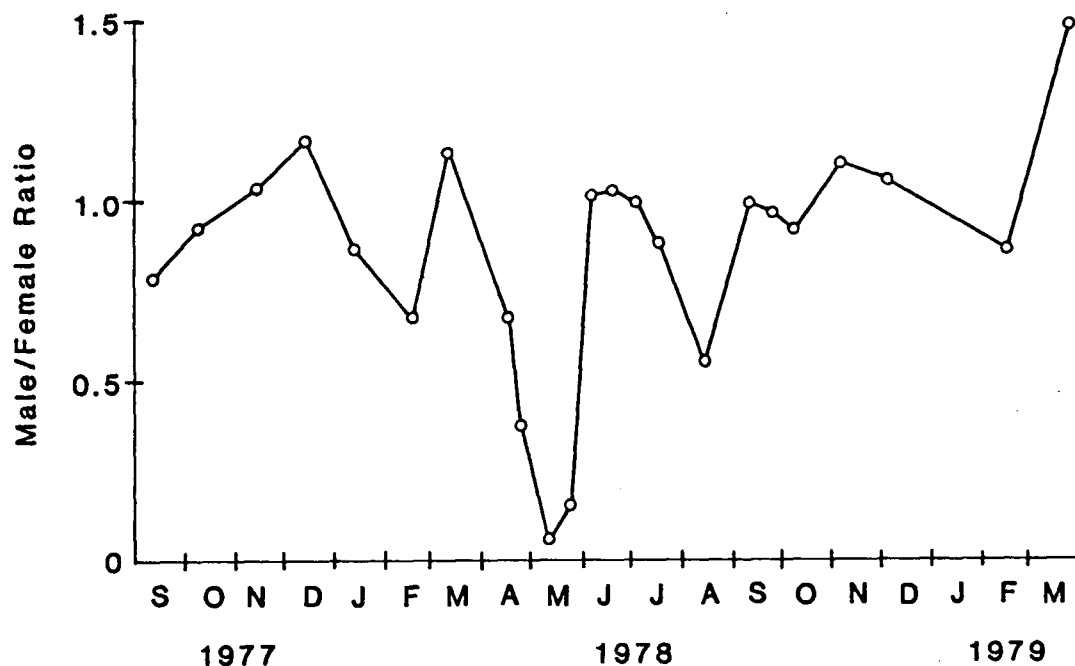


Figure A8. Seasonal variation in the male:female ratio of Neomysis mercedis at Nicomen Slough 1977 to 1979 .

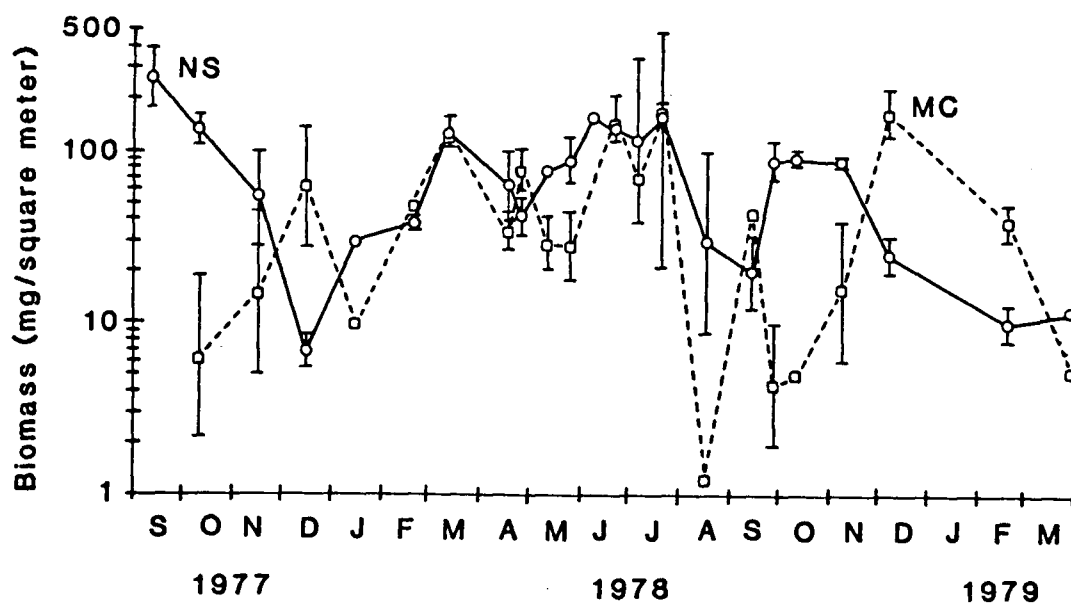


Figure A9. Seasonal variation in the biomass (mg dry weight per m²) of Neomysis mercedis at Nicomen Slough 1977 to 1979 .

mature at progressively smaller sizes as the temperature continues to increase throughout this early summer period but most adults remain in the midchannel habitat. The new-born mysids (S1 generation) rear in the shallows but move into the deeper waters when they mature in late July - mid August, possibly because of the extremely high water temperatures in the nearshore areas at this time. The population abundance decreases sharply in August despite the maturation of the S1 generation and remains low until a second pulse of breeding occurs in late September and early October. At this time mature females move to the nearshore habitat where the W juveniles are released. Breeding stops in November as temperatures fall and much of the W generation moves offshore to overwinter as immatures.

The life history of the freshwater population of N. mercedis at Nicomen Slough differed in several respects from that of the estuarine population at Woodward Island. First, the population of N. mercedis at Nicomen Slough apparently produced only two generations per year while the estuarine population produced three. The difference resulted from the sharp midsummer decline in abundance at the upriver site which, coupled with a concurrent reduction in the proportion of mature females breeding, effectively eliminated the midsummer generation corresponding to the S2 generation at the estuarine site. Second, population density at Nicomen Slough was lower than that at the estuarine site. Maximum densities at Nicomen Slough were about $600 \cdot m^{-2}$ while those at Woodward Island were

about $900-1000 \cdot m^{-2}$. Third, there were differences between the populations in the size at maturity, in fecundity, and in the allocation of assimilated energy (see chapter 3) .

The seasonal variation in abundance at Nicomen Slough differed from that at Woodward Island but was similar to that seen in N. intermedia (Toda et al. 1982). Although they suggested that the midsummer collapse of the N. intermedia population could result from fish predation or from fishing pressure, the decline corresponded to a period of very high temperature (above $25^{\circ}C$) just as did the decline seen at Nicomen Slough. Physiological stress may be a factor in the declines. Toda et al. discussed the differences in size and fecundity between the spring and fall breeding generations of N. intermedia as adaptations to increasing food resources in the spring and high predation pressure in the fall. The proximate cause was probably temperature, in both N. intermedia (Toda et al. 1983, 1984) and N. mercedis (chapter 2).

Appendix 6: Enzymes Surveyed Electrophoretically

The following enzymes were surveyed for electrophoretically detectable variants:

Abbreviation	Name
ADH	Alcohol dehydrogenase
AGP	a-glycerophosphate dehydrogenase
Fumerase	Fumerase
G6PDH	Glucose 6-phosphate dehydrogenase
HK	Hexokinase
IDH	Isocitrate dehydrogenase
IDH-NAD	Isocitrate dehydrogenase (b-diphosphopyridine nucleotide buffer)
LAP	Leucine aminopeptidase
LDH	Lactate dehydrogenase
MDH	Malate dehydrogenase
ME	Malic enzyme
PEP	Peptidase
PGI	Phosphoglucose isomerase
PGM	Phosphoglucomutase
SDH	Sorbitol dehydrogenase
TO	Tetrazolium oxidase

As no attempt was made to modify the procedures (Parkinson 1981) to improve the resolution, the results do not measure the extent of enzyme polymorphism in N. mercedis. In addition to MDH and PGI, several other enzymes (G6PDH; IDH; PEP) may have been polymorphic but the patterns were too blurred to be reliably interpreted.

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