AN ABSTRACT OF THE THESIS OF

Lynne D. Krasnow for the degree of Doctor of Philosophy in Oceanography presented on April 27, 1992 .

Title: Particle Selection for Tube Building and the Stabilization of Sediments by *Leptochelia dubia* (Crustacea, Tanaidacea): Interactions with Bacteria and Microalgae

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Abstract approved: _____

The population dynamics of the tubicolous tanaid crustacean *Leptochelia dubia* were examined for a population inhabiting intertidal fine sands in Yaquina Bay, Oregon. The effects of bacteria and microalgae on rates of tube building and particle sizes incorporated into tubes by *L. dubia* were also measured. Stabilization of sediments precultured with microbes and bound into tubes was tested in a seawater flume.

Two years of data, 1986-1987, demonstrate that population density rose from a low of 30,000 individuals m^{-2} during May to a high of approximately 300,000 m^{-2} during late September of each year. Reproduction was biannual; peaks of juveniles were recruited into the population during spring and fall. Reproductive male and female *L. dubia* were not present during the months of December or January during either year. Mean cohort growth rate was significantly lower from August-March than during the months April-July, indicating an effect of photoperiod, temperature, or some other factor related to season, such as food supply.

Laboratory experiments showed that the rate of tube building was a linear function of tanaid length. The presence of bacteria and microalgae in sediments had a positive effect on the rate of tube building, significantly increasing the magnitude of the intercept of the regression function over that measured in sterile sediment. The presence of bacteria and microalgae also appeared to increase the selection of silt-sized particles for tube building by large tanaids. A model incorporating the relationship between tanaid length, rates of tube building, and the density of the field population indicates that tanaids bind approximately 350 g sediment m^{-2} d^{-1} into tubes.

The stabilization of sediments by *L. dubia* was tested in a seawater flume, under turbulent hydraulically smooth conditions. At an imposed shear stress of $u_* = 2.22$ cm s^{-1}, the mean bedload transport rate of sterile sediment was 84.2 μg cm^{-2} min^{-1}. When sediment was precultured with microbes, bedload transport fell to 4.4 μg cm^{-2} min^{-1}. When tanaids were allowed to build tubes in sediment precultured with microbes, no bedload transport could be detected. Thus, under the hydraulic conditions imposed in the laboratory flume, tube building by *Leptochelia dubia* and the adhesive secretions of bacteria and microalgae interact to stabilize sediments against erosion.

Particle Selection for Tube Building and the Stabilization of Sediments by *Leptochelia dubia* (Crustacea, Tanaidacea): Interactions with Bacteria and Microalgae

by

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INTRODUCTION

Estuaries are temporary structures, filling with sediments over time scales of thousands to a few tens of thousands of years (Schubel and Carter 1984). An array of factors allows an estuary to act as filter for suspended materials received from its tributary river. Turbulence, mixing, non-tidal circulation, physicochemical flocculation, and biogenic aggregation all affect rates of sedimentation. The fate of particles after they reach the bottom also depends on a suite of physical, chemical, and biological factors. In some cases, biologically mediated processes overwhelm all others in the deposition and stabilization of sediments.

If silt- and clay-sized particles entering estuaries from rivers remained disaggregated, they would be kept in suspension by turbulent mixing and would rarely settle out. In a physicochemical model of particle flux, the behavior of particles is modified by flocculation. In river water, the surface of a negatively charged clay particle is covered with a double layer of hydrated cations (Knox 1986) and the positively charged particles repel each other. The thickness of the double layer depends on the ionic strength of the medium. In an estuary, increasing salinity has the effect of compressing the double layer, reducing the repulsive charge. Particles that collide stick together and form large networks or floccules up to 0.5 mm in diameter. Most flocculation occurs at 4 ‰, near the head of an estuary.

Eisma (1986) claims that for mineral particles >1 μm, physicochemical factors play a minor role in the process of

aggregation. Particles immersed in natural waters quickly acquire an organic coating that changes the surface characteristics of the particles, resulting in a negative surface charge (Neihof and Loeb 1974). The organic coating is composed of dissolved carbohydrates that originate from bacteria, algae, and higher plants. The coating acts as a "glue", holding the particles together (Eisma 1986). The "microflocs" thus formed fall through the water column and, in the region of viscous-dominated flow near the very bottom, combine into more fragile macroflocs.

Once these particles reach the bottom, they may be resuspended by turbulence associated with periodic tidal currents and high river flow. Under some conditions, however, the actions of biogenic adhesives may again overwhelm these physical forces. Fager (1964) observed that shallow-water sediments in La Jolla Bay colonized by dense aggregations of the tubicolous polychaete *Owenia fusiformis* were not resuspended by wave surge. Rhoads et al. (1978) reported that the stability of sediments from Long Island Sound increased after seeding with another tubicolous polychaete, *Heteromastus filiformis*. These authors, however, suggested that the effect was due to binding of the sediment surface by mucus films associated with enhanced microbial production.

The present study describes rates of tube building, particle-size selection, and stabilization of sediments by the tubicolous tanaid crustacean *Leptochelia dubia*. By virtue of its high abundance and extensive tube-building activities, *L. dubia* affects the granulometric and hydrodynamic properties of the sediments in which it lives. The activities of *Leptochelia* are, in turn, affected by the sediment-associated bacteria and microalgae which inhabit the surfaces of tubes and provide a source of food (Davis and Lee 1983). Even in the absence of tubes, the adhesives produced by microbes would play a role in the stabilization of sediments. Thus, the net effect of microbes and tanaids acting together in nature is the result of complex animal-microbe-sediment interactions.

The second chapter in this dissertation describes the life history of *Leptochelia dubia* from Yaquina Bay, Oregon. Estimates of density for this population exceed those published elsewhere by up to an order of magnitude, although this result may be due to the smaller sieve size used for sediment processing in the present study. The population in Yaquina Bay demonstrated a biannual pattern of reproduction. Peaks of juveniles were recruited into the population during the spring and fall in each of the two years of study. A different pattern of reproduction has been reported for a population in central California (Mendoza 1982), indicating a capacity to adapt to local environmental conditions.

Data on the density and size-structure of the tanaid population in Yaquina Bay were incorporated into a model of rates of tube building, described in Chapter III. Rates of tube building were derived from laboratory experiments with manipulated sediments. The effect of sediment-associated microbes was tested by comparing rates of tube building in sterile sediments with rates in sediments precultured with microbes. The presence of microbes in sediments increased the rate of tube building for a tanaid of a given size. The presence of microbes also increased the rate at which large tanaids incorporated silt-sized particles into tubes. In the latter case, it is hypothesized that aggregation of silts within extracellular microbial adhesives facilitated the handling of these small particles by large tanaids. However, these results may also be explained by an effect of organic coating on the selection of particles for feeding. Visual observations showed that, behaviorally, tube building and feeding are closely related.

Chapter IV describes measurement of the stabilization of sediments by *Leptochelia dubia* and sediment-associated bacteria and microalgae. Under conditions of turbulent but hydraulically smooth flow in a laboratory seawater flume, the bedload transport rate of sediments precultured with microbes was 95% less than that of sterile sediment. When tanaids were allowed to build tubes in sediment

precultured with microbes, no transport could be detected. These results confirm the predominant role of microbes in sediment stabilization at shear stresses near the critical level required for erosion of abiotic sediment. The effect of tanaids may become more important as shear stress is increased. It is clear that the combined activities of *Leptochelia* and sediment-associated microbes transform those particles which reach the bottom into a fabric of great intrinsic strength.

II. LIFE HISTORY AND POPULATION DYNAMICS OF THE GREEN TANAID, *LEPTOCHELIA DUBIA*, IN YAQUINA BAY, OREGON

INTRODUCTION

Approximately 800 living species of tanaid crustaceans inhabit the benthic littoral zone and the deep sea, world-wide (Sieg and Winn 1981, Holdich and Jones 1983, Sieg 1986). Although tanaids are often more abundant than amphipods, isopods, or cumaceans, advances in the study of this order of the Peracaridea have been relatively slow. Sieg and Winn (1978) suggest that investigators have been inhibited from undertaking studies of the ecology of this interesting group by the difficult task of identifying tanaids to species. The systematics of the Tanaidacea are complicated by sexual dimorphism, hermaphroditism, and the similarity of species within genera.

The taxonomy of the green tanaid, *Leptochelia dubia*, has only recently been resolved. *Tanais edwardsii*, *T. savignyi*, *T. dubia*, *Leptochelia dubia*, and *L. savignyi*, were described separately but are now reduced to one species under the senior synonym, *Leptochelia dubia* (Krøyer, 1842) (D. Holdich, The University, Nottingham, U.K., and J. Sieg, Universität Osnabrük, Germany, pers. comms.). In North America, *L. dubia* has been described as a grazer that effectively limits the production of benthic diatoms (Davis and Lee 1983), a predator that consumes the juveniles of competing species (Highsmith 1982), and a tube builder with an important role in the stabilization of sediments (Chapters III and IV). Further, *L. dubia* has been identified as an important prey of juvenile chum salmon (*Oncorhynchus keta*) in Netarts Bay, OR (J. Chapman, Hatfield Marine Science Center, Newport, OR, pers. comm.), English sole (*Parophrys vetulus*), starry flounder (*Platichthys stellatus*), and chinook salmon (*Oncorhynchus tschawytscha*) in Tillamook Bay, OR (Forsberg et al. 1977), staghorn

sculpins (*Leptocottus armatus*) in Tomales Bay, CA (Mendoza 1982), and small mojarras (Gerreidae), goatfish (*Pseudopeneus maculatus*), grunts (Haemulidae), and snappers (Lutjanidae) in Puerto Rico (Stoner 1986). Despite the cosmopolitan distribution of *L. dubia* and known abundances of up to 75,000 m^{-2} (Smith 1981) in soft sediments, only Mendoza (1982) has attempted to describe its population dynamics and life history.

The present study examines a population of *L. dubia* from an intertidal area in Yaquina Bay, OR. Data were collected as part of a larger study of tube building, particle-size selection, and sediment stabilization by this species. *Leptochelia dubia* demonstrated a biannual life cycle with two cohorts per year and peak densities of 300,000 m^{-2}. Observations showed that aspects of the reproductive behavior of this species are similar to those described for another paratanaid, *Heterotanais oerstedi*, and a member of the Family Tanaidae, *Tanais cavolinii* by Johnson and Attramadal (1982).

METHODS

I collected *L. dubia* from a sampling site on the intertidal sandflat just east of the Oregon State University, Hatfield Marine Science Center in Yaquina Bay (Fig. II.1). Yaquina Bay is a seasonally well-mixed estuary (Kulm 1965). Freshwater inputs to the bay are low during summer so that salinities of 30-33‰ are maintained (P. Henchman, Oregon State University, Hatfield Marine Science Center, Newport, OR, unpubl. data). During winter, rainfall and increased river flow reduces salinity in the bay to as little as 6‰ at low tide. Water and air temperature vary seasonally from 6-16°C and from 0-30°C, respectively (Davis 1981). Hours of daylight range from 12.2 d^{-1} in June to 6.0 d^{-1} in December. Sediments at the field site comprise a well sorted, very fine sand (2-3% silt/clay) with a median diameter of 96 μm (G. Ditsworth, U.S. Environmental Protection Agency, Newport, OR, unpubl. data).

I collected tanaids from a 60 x 60-m grid staked out on the intertidal flat. The grid was divided into three 20-m wide sections in the north-south direction at elevations of 1.1, 1.0, and 0.9 m above mean lower low water (MLLW). Tanaids were collected from one randomly chosen site within each section every two weeks between January 1986 and mid-March 1987. I sampled the sediment to a depth of 2 cm using the barrel of a 50-cc plastic syringe (surface area=5.31 cm^2). I collected duplicate samples, 10 cm apart, at each site. Before the mid-March 1987 collection period, the sampling area was expanded 10 m both to the north and south and 20 m to the east, creating an 80 x 80-m grid. The new grid was divided into four 20-m wide sections in the east-west direction to more accurately correspond with the dominant direction of tidal flow across the flats. On each sampling date, independent samples were taken from two randomly chosen locations within each of four tidal strata within the grid, increasing the number of independent samples for computation of means and standard errors from three to eight. I continued to collect biweekly samples through December 1987.

Fig. II.1. Location of study site in Yaquina Bay, Oregon. Small arrow points to the intertidal study site. Dashed lines indicate position of tide line at mean lower low water.

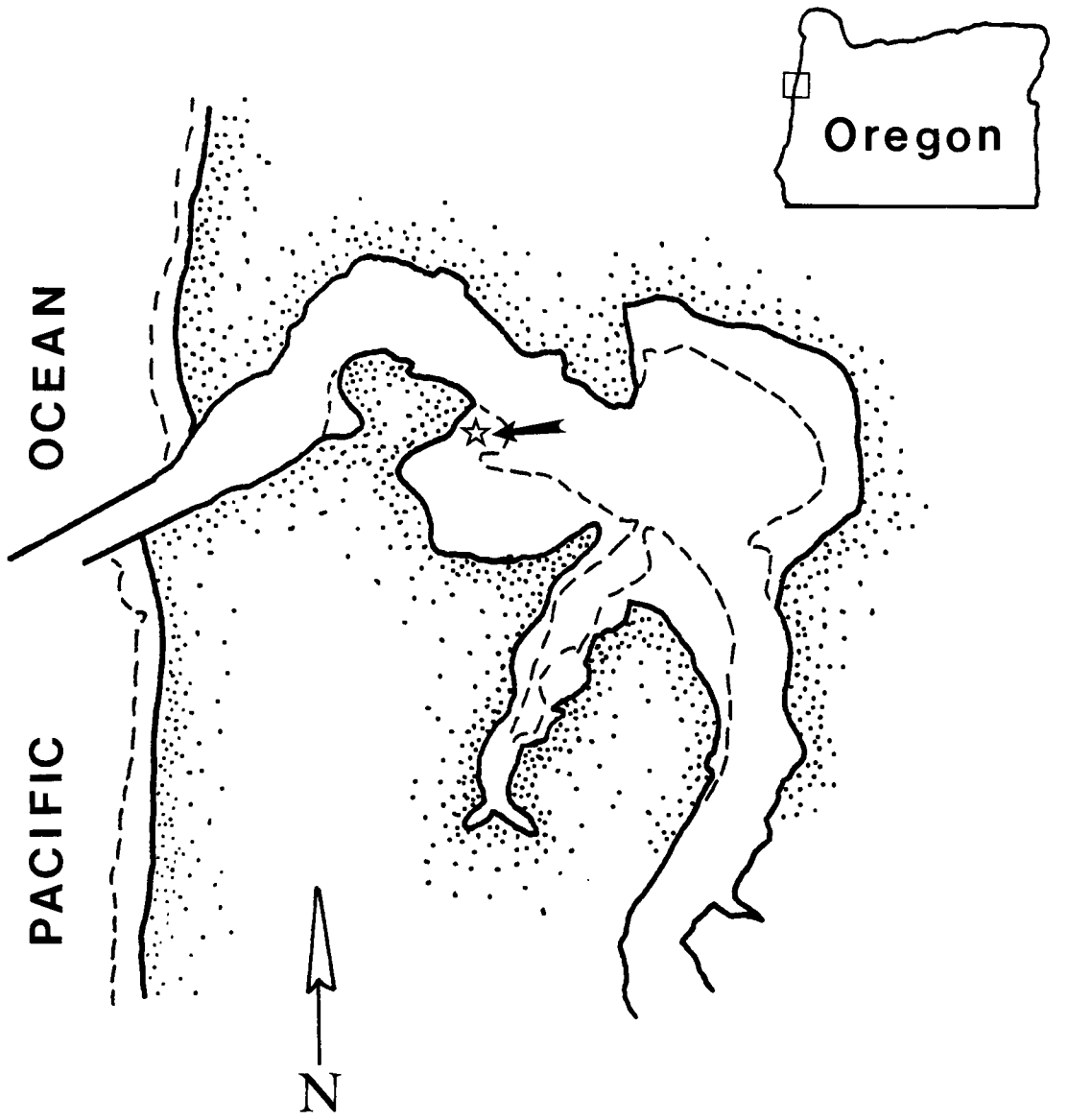


Fig. II.1

Sediment samples were placed in individual whirl-pack bags and were returned to the lab immediately after collection. Samples were fixed in a buffered 10%-solution of formaldehyde in seawater. After two weeks in formaldehyde, I rinsed each sample over a 63-μm mesh screen and then preserved it in 90% ethanol. Before sorting and counting, each sample was again rinsed on stacked 300-, 125-, and 63-μm sieves. Observations showed that all of the tanaid eggs and larvae were captured on the 125-μm sieve, so use of the 63-μm sieve was discontinued. The materials remaining on the 300- and 125-μm sieves were examined under a compound dissection microscope at 40X power. Macrofauna were removed, sorted, and stored in 90% ethanol. Carapace lengths were measured to the nearest 0.1 mm using a Zeiss Videoplan II Image Analysis System.

I conducted an experiment to determine the rate at which tanaids shrank after fixation in formaldehyde and storage in ethanol. The carapace lengths of live tanaids collected on 10 August 1988 were measured and the animals were then fixed in buffered 10% formaldehyde. After 18 d fixation, the tanaids were rinsed, remeasured, and stored in 90% ethanol. Tanaids were remeasured at 1, 2, 3, 6, and 12 month intervals thereafter. The shrinkage of a hypothetical 2.0-mm (carapace length) tanaid was estimated from linear regression equations for fresh length (Y) against length at time t (X). In fact, "length at time t" is a dependent function of the variable "fresh length". In this case, the dependent and independent variables were reversed to provide an assay for shrinkage over time.

For each bimonthly sampling date, a length frequency histogram was constructed from the lengths of 150 randomly selected female and juvenile tanaids. Lengths were adjusted to account for shrinkage, as described above. Cohorts were differentiated using the probability paper method of Harding (1949). Complete life cycles were observed for Cohorts 2-4 but not for Cohort 1, born three to four months prior to the initiation of sampling, and Cohort 5, which was likely to have

survived three to four months after sampling ended. Estimates of mean cohort length were plotted against Julian date to derive cohort growth curves.

Following the arguments of Bückle-Ramirez (1965, in Johnson and Attramadal 1982), Masunari (1983) describes three manca stages for *L. dubia* (identified as *L. savignyi*). Stage I and Stage II larvae develop within the female's marsupium. Late Stage II larvae emerge from the marsupium and moult to Stage III larvae, which develop in the tube nest. However, Messing (1981) states that because the first two "stages" are not separated by an ecdysis, "such a clear distinction as manca 1-manca 2 should not be applied". I have followed Messing in designating larvae that develop within the marsupium as Stage I and those that develop within the tube nest as Stage II individuals.

RESULTS

Although tanaids shrank over the entire 12.6 months of the preservation experiment, 93% of the observed reduction in carapace length occurred within the first six months (Fig. II.2). Because most of the tanaids collected for this study were stored in ethanol for over a year before they were measured, I used the equation for carapace length after 12 months storage in ethanol,

$$Y = 0.132 + 1.09\ X$$

$$r^2 = 0.98$$

where:

X = carapace length (mm) at time t

Y = fresh carapace length (mm),

to estimate fresh lengths for length frequency histograms.

In both 1986 and 1987, juvenile tanaids (individuals ≥1.3 mm) recruited into the population during both spring and fall (Fig. II.3). It is clear from the length frequency histograms that individuals born during spring grew over summer to reproduce during fall and those born during fall reproduced the following spring (Fig. II.4). Although there is reason to believe that individual females may have had more than one brood (see below), it is apparent that each cohort died at the end of its reproductive season. As a result, the population contained one (maturing) cohort during midwinter and midsummer and two overlapping cohorts (reproducing and newly recruited) during spring and fall.

The average density of the fall cohort declined over winter to approximately 30,000 m^{-2} by May of each year. Population density rose to 200,000 m^{-2} during the spring period of recruitment. Due to mortality of post-spawning adults and other losses from the population (predation, emigration, and mortality of non-reproductive individuals) over summer, density fell to 100,000 m^{-2}. Release of the fall cohort increased population density to approximately 300,000 m^{-2}. The lower standard errors for means derived from data collected

Fig. II.2. Shrinkage of a hypothetical 2.0-mm carapace length tanaid after 18 d fixation in formaldehyde and up to 12 months preservation in ethanol. Mean estimates of the carapace length of a tanaid of 2.0 mm fresh length were derived from Least Squares Linear Regressions of length at time = t (Y) as a function of fresh length (X). Vertical bars represent ± 1 SE. The number of replicates per treatment is indicated.

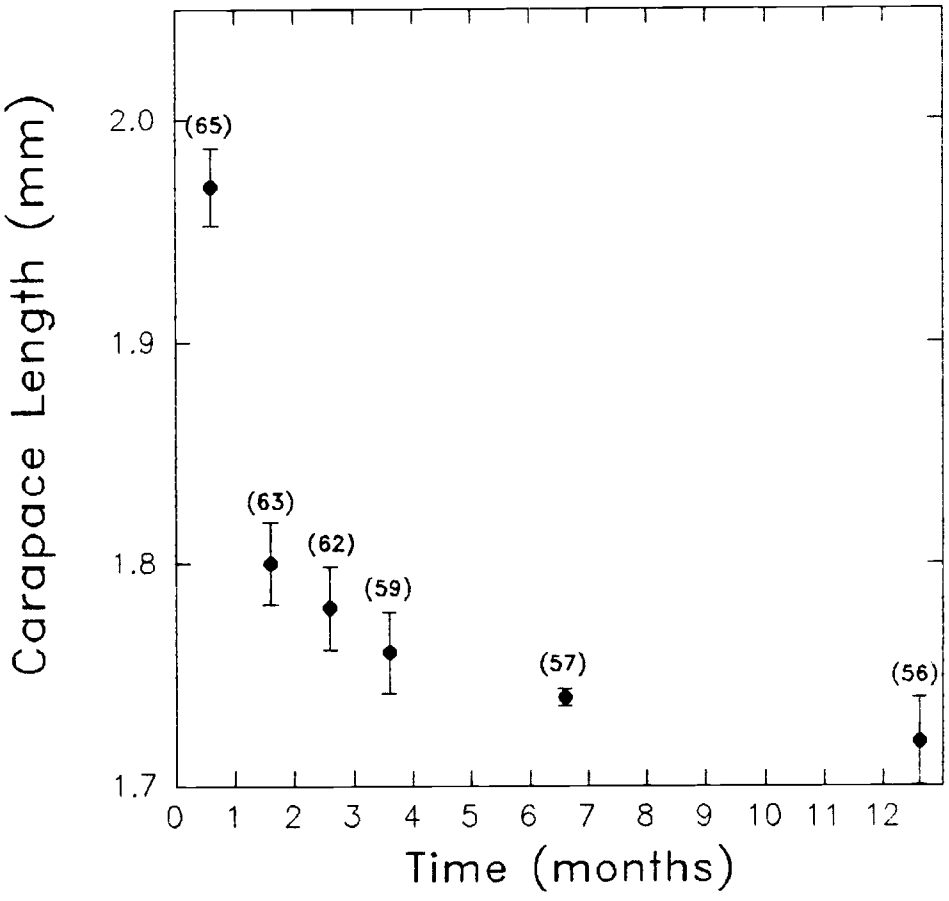

Carapace Length (mm)
2.0
1.9
1.8
1.7
(65)
(63)
(62)
(59)
(57)
(56)
0 1 2 3 4 5 6 7 8 9 10 11 12
Time (months)

Fig. II.2

Fig. II.3. Mean (± 1 SE) density of *Leptochelia dubia* at the intertidal study site in Yaquina Bay, 1986-1987. Tanaids < 1.3 mm carapace length were excluded from determinations of tanaid density.

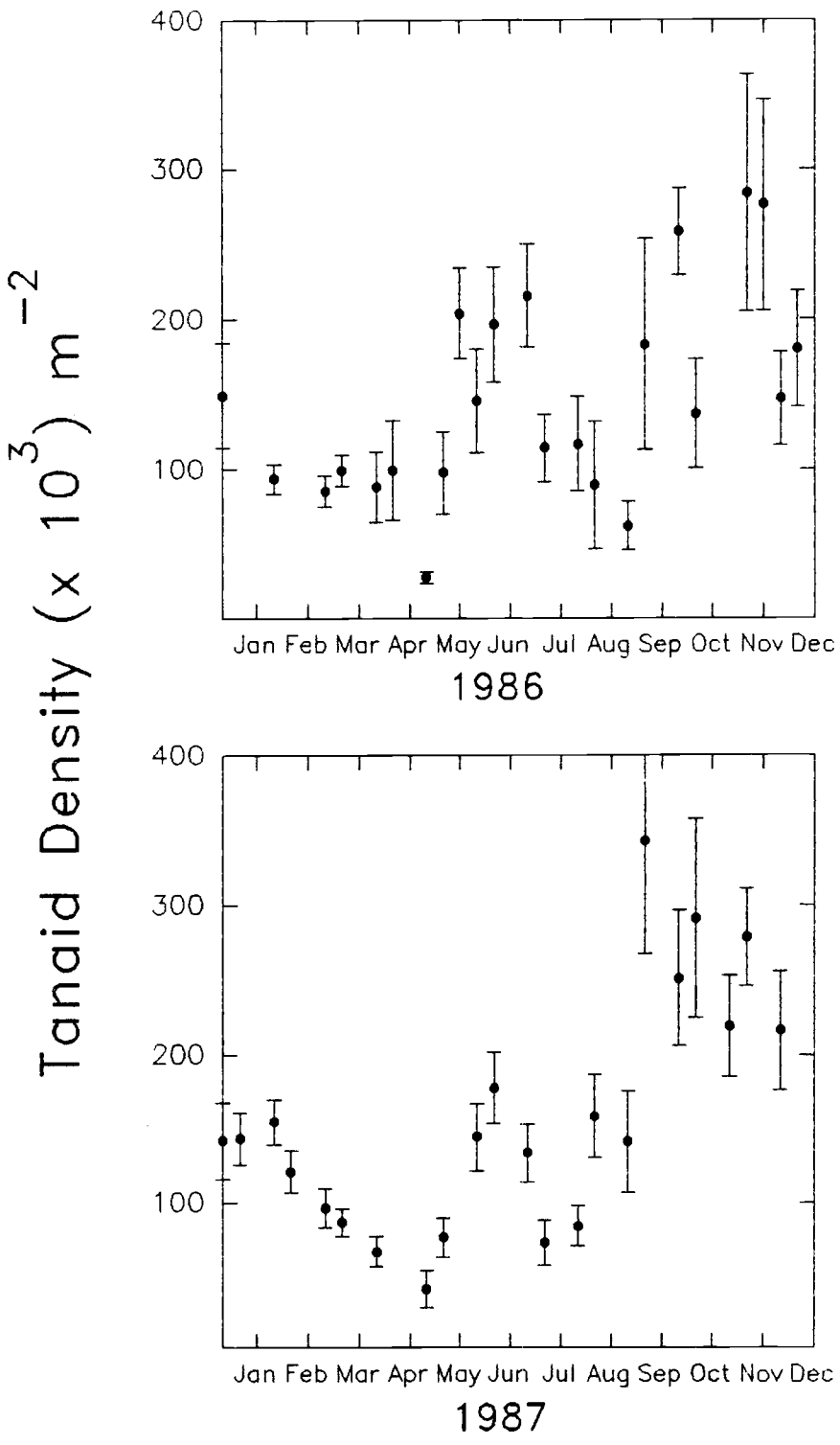

Tanaid Density (x 10^3) m^-2
400
300
200
100
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
1986
400
300
200
100
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
1987

Fig. II.3

Fig. II.4. Length frequency histograms for *Leptochelia dubia* at the intertidal study site in Yaquina Bay, 1986-1987. Dates of collection and the number of individuals measured for each date are indicated.

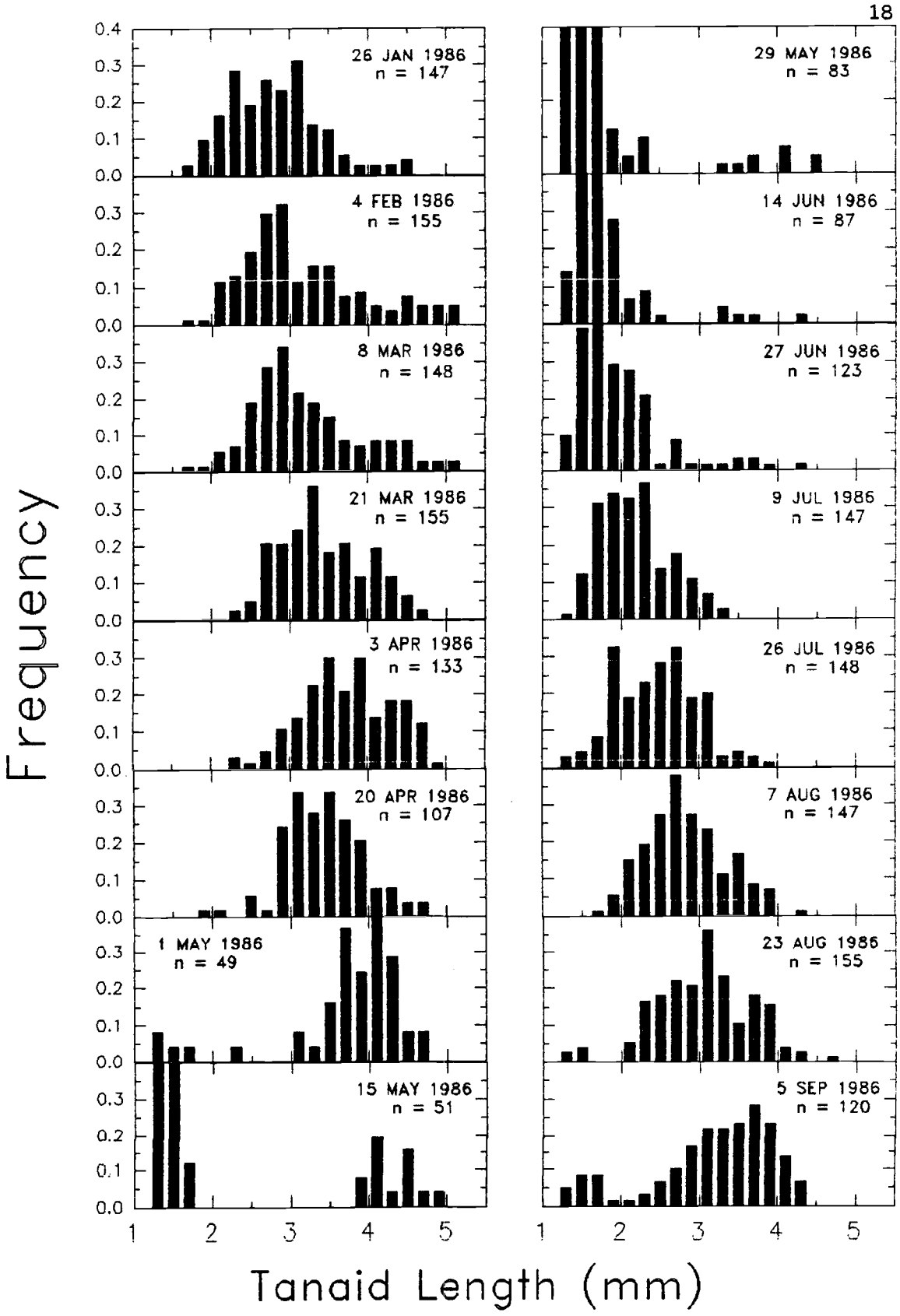

Frequency
Tanaid Length (mm)
26 JAN 1986
n = 147
4 FEB 1986
n = 155
8 MAR 1986
n = 148
21 MAR 1986
n = 155
3 APR 1986
n = 133
20 APR 1986
n = 107
1 MAY 1986
n = 49
15 MAY 1986
n = 51
29 MAY 1986
n = 83
14 JUN 1986
n = 87
27 JUN 1986
n = 123
9 JUL 1986
n = 147
26 JUL 1986
n = 148
7 AUG 1986
n = 147
23 AUG 1986
n = 155
5 SEP 1986
n = 120

Fig. II.4

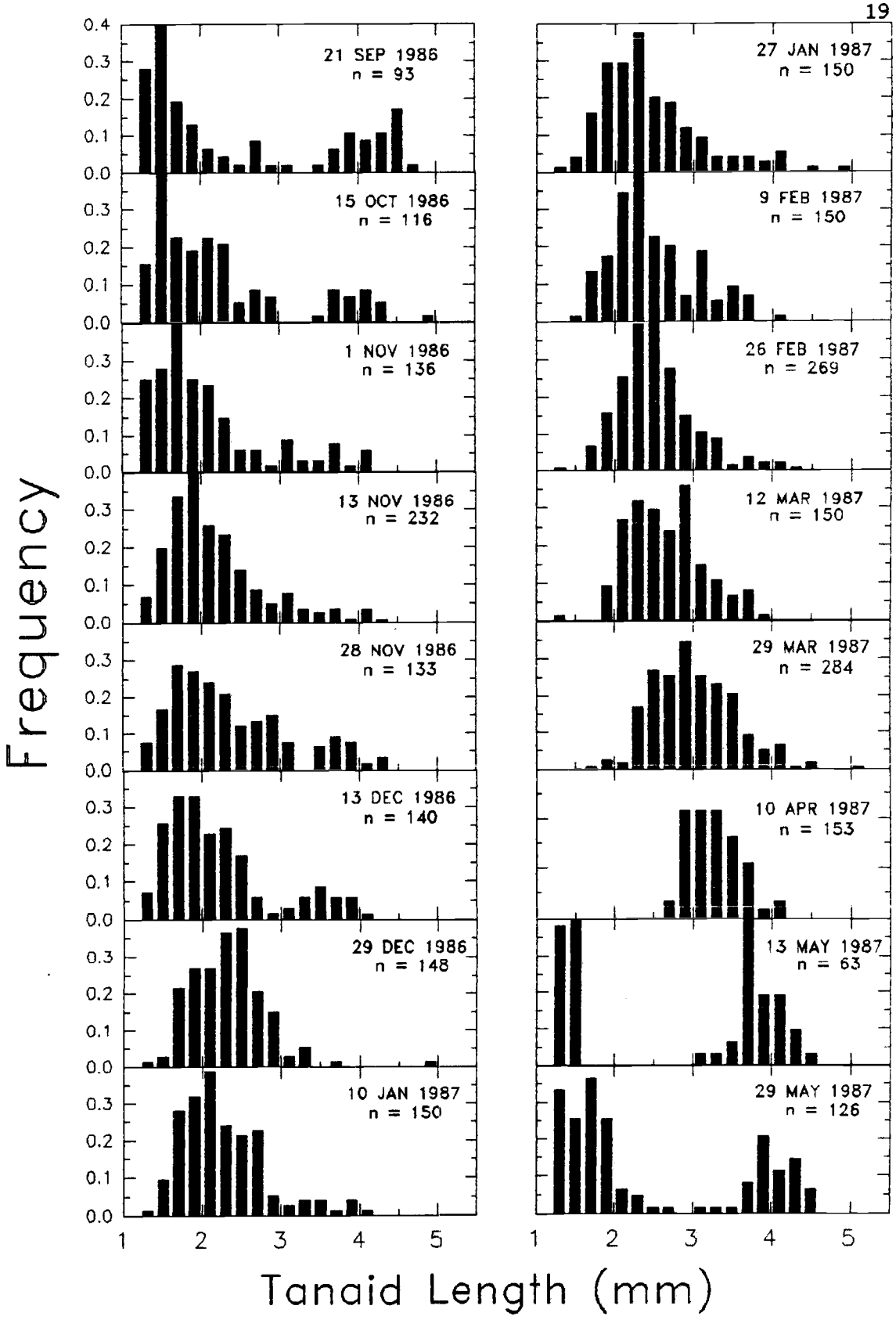


Fig. II.4 (continued)

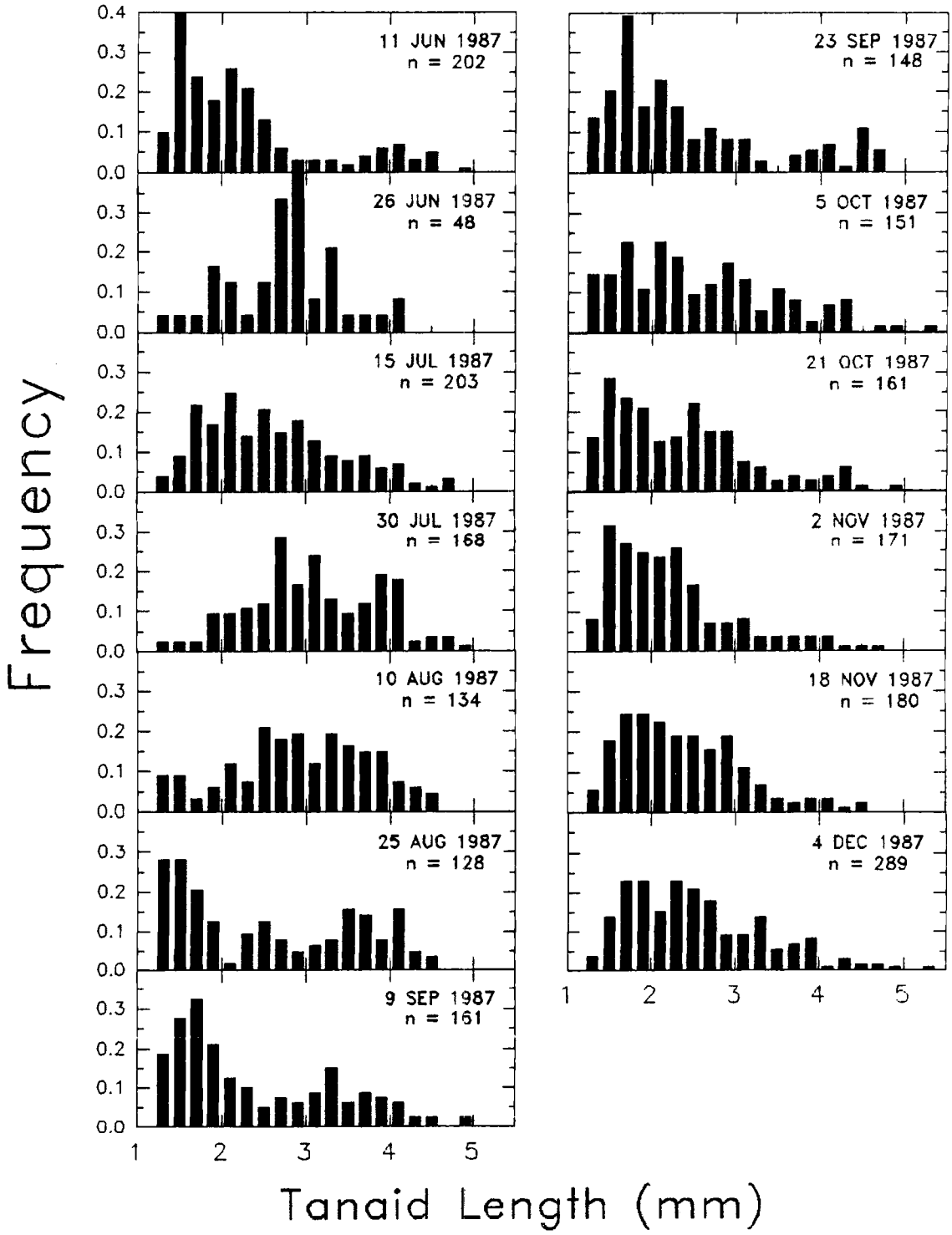


Fig. II.4 (continued)

during 1987 probably reflect the increase in sample size from three to eight during that year (see Methods).

Adult male *L. dubia* were not found in samples collected in December or January of either year (Fig. II.5). Males comprised <15% of the population during the rest of the year, except during spring 1986 when up to 48% of the population was male. Distinct peaks in the abundance of male tanaids (>13,000 m^{-2}) preceded peaks in the recruitment of juveniles by approximately three months during 1986. Male *Leptochelia* have no mouthparts and do not feed. Thus, the males that reproduced during spring died and were replaced by smaller males from the next cohort (Fig. II.6). The mean abundance of male tanaids remained below 10,000 m^{-2} in 1987 and the spring and fall peaks in abundance were less distinct than in the preceding year. The mean length of male tanaids ranged from approximately 2.5-3.5 mm. Males matured at a smaller size during summer than during winter/spring.

Reproductive females (with oostegites developing or overlapping to form a marsupium or with Manca Stage II larvae in a tube nest) were absent from samples collected during December-February of both years (Fig. II.7). During both April and September 1986, distinct peaks in the abundance of reproductive females preceded peaks in the recruitment of juveniles to the population by approximately two months. As observed for male tanaids, the spring and fall peaks in the abundance of reproductive females were less distinct in 1987 than in 1986. The mean length of female tanaids ranged from 3.8-4.4 mm (Fig. II.8).

The guts of 98% of 113 gravid *L. dubia* observed during the two year study were empty. As described for *Heterotanais oerstedi* (Bückle-Ramirez 1965, in Johnson and Attramadal 1982), the egg-filled ovaries almost fill the female's thorax, displacing the intestine. The guts of only 2 out of 14 females with Manca Stage I larvae in their marsupia contained food. However, 74% of 38 females with mancas in "tube nests" had been feeding.

Fig. II.5. Mean (± 1 SE) density of male *Leptochelia dubia* at the intertidal study site in Yaquina Bay, 1986-1987.

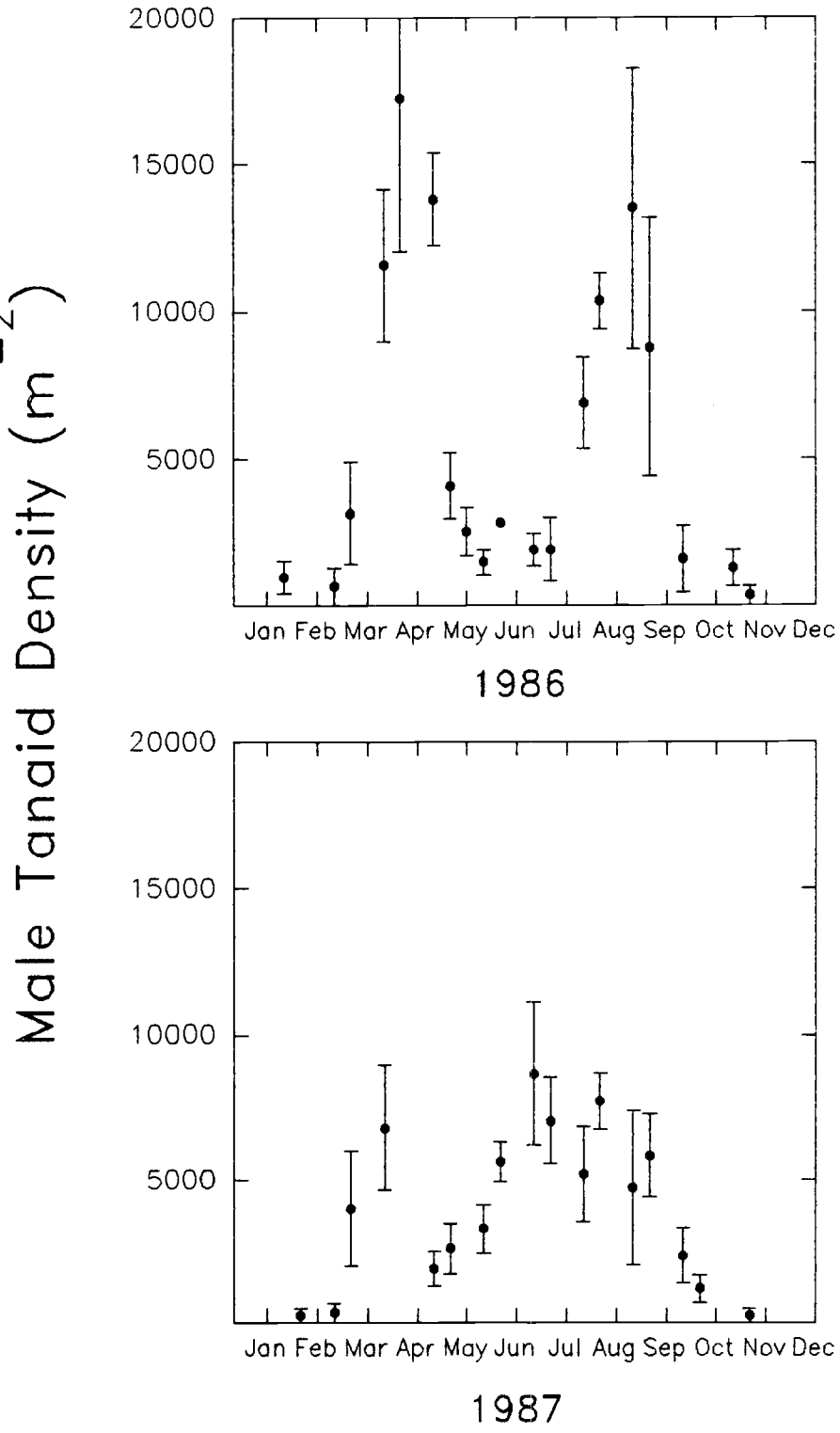

Male Tanaid Density (m^{-2})
20000
15000
10000
5000
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
1986
20000
15000
10000
5000
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
1987

Fig. II.5

Fig. II.6. Mean (± 1 SE) carapace lengths of male *Leptochelia dubia* in Yaquina Bay, 1986-1987.

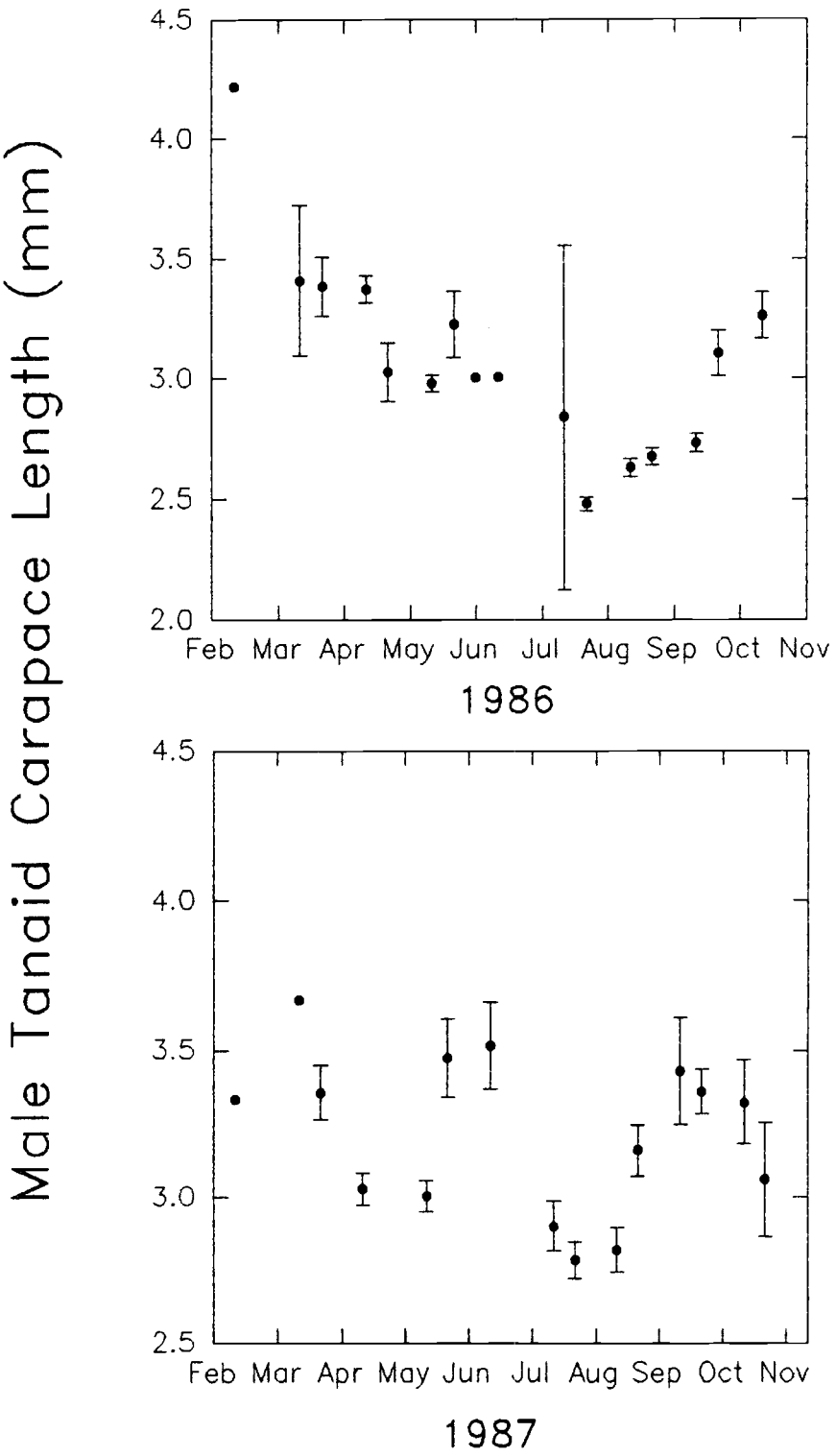

Male Tanaid Carapace Length (mm)
4.5
4.0
3.5
3.0
2.5
2.0
Feb Mar Apr May Jun Jul Aug Sep Oct Nov
1986
4.5
4.0
3.5
3.0
2.5
Feb Mar Apr May Jun Jul Aug Sep Oct Nov
1987

Fig. II.6

Fig. II.7. Mean (± 1 SE) density of reproductive female *Leptochelia dubia* (females with developing oostegites, marsupial eggs or larvae, or tube-nest larvae) in Yaquina Bay, 1986-1987.

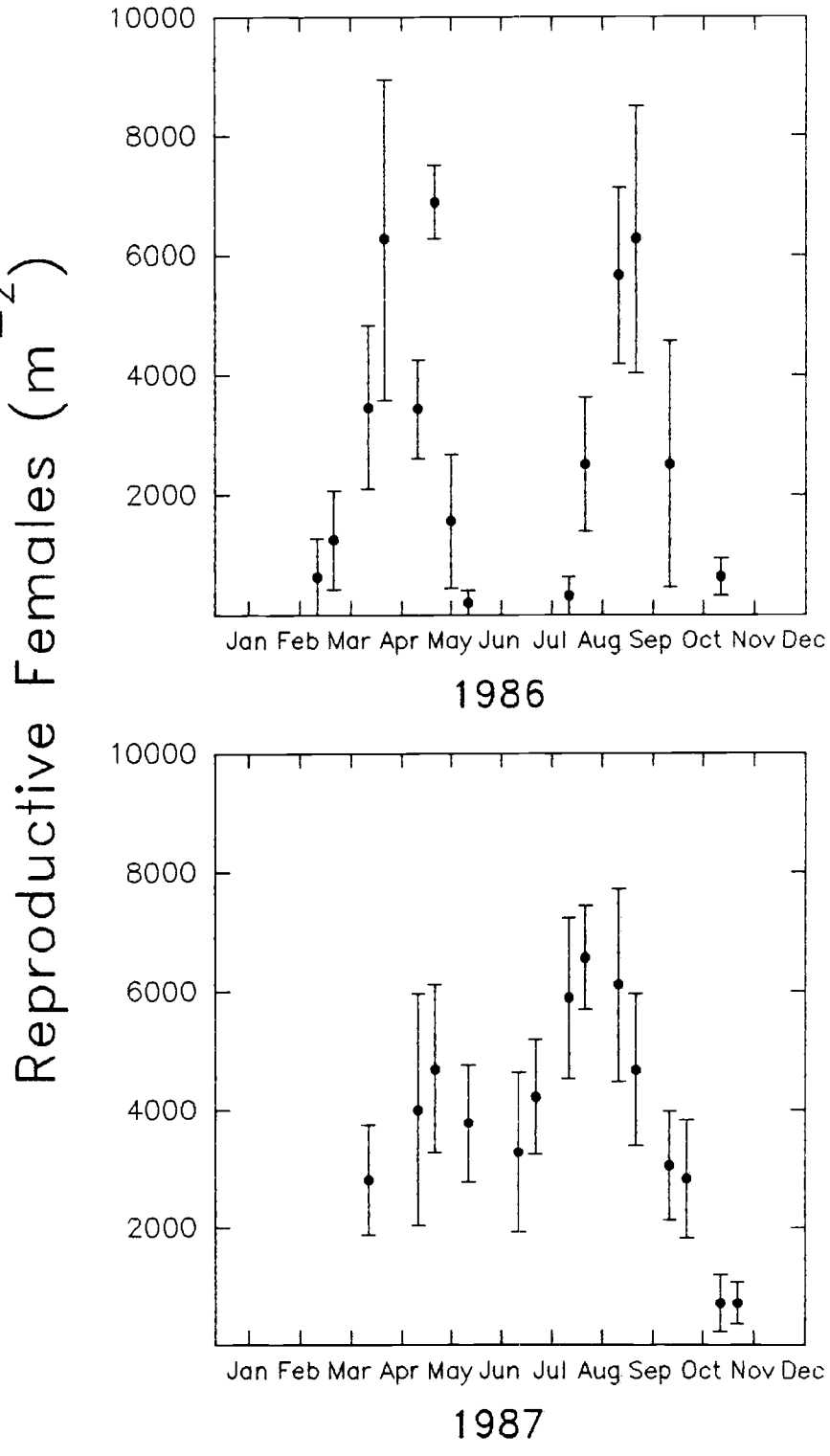

Reproductive Females (m^{-2})
10000
8000
6000
4000
2000
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
1986
10000
8000
6000
4000
2000
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
1987

Fig. II.7

Fig. II.8. Mean (± 1 SE) carapace lengths of female *Leptochelia dubia* in Yaquina Bay, 1986-1987.

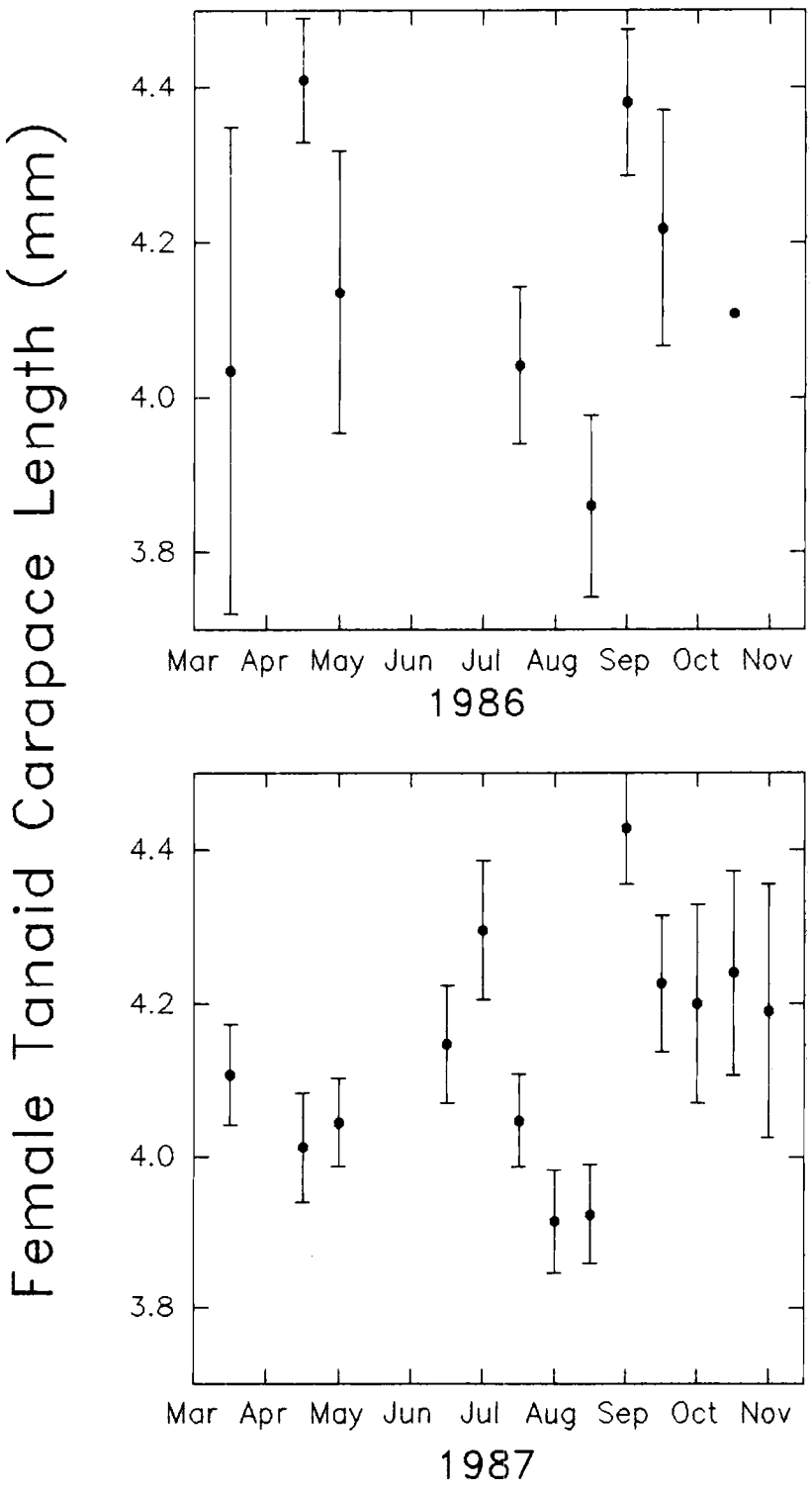

Female Tanaid Carapace Length (mm)
4.4
4.2
4.0
3.8
Mar Apr May Jun Jul Aug Sep Oct Nov
1986
4.4
4.2
4.0
3.8
Mar Apr May Jun Jul Aug Sep Oct Nov
1987

Fig. II.8

The mean length of marsupial (manca stage I) larvae was 0.90 ± 0.02 (SD) mm (n=125) during 1986 and 0.87 ± 0.07 mm (n=28) during 1987. The guts of only 2% of 130 stage I mancas examined contained food. Tube-nest (manca stage II) larvae averaged 1.11 ± 0.08 mm (n=364) and 1.32 ± 0.10 mm (n=189) during 1986 and 1987, respectively. Sixty-eight percent of 466 stage II mancas had material in their digestive tracts. Stage II larvae eventually cut through the wall of the female's nest and begin to build tubes of their own.

Plots of mean cohort length over time resulted in logistic growth curves for Cohorts 2-4 (Fig. II.9). The growth function for Cohort 3 appeared to be composed of two components, a period of relatively slow growth between August 1986 and March 1987 and a period of faster growth during March to May 1987 (cohorts "3a" and "3b", respectively). The slopes of these two portions of the curve for Cohort 3 can be compared with the slopes of the middle portions of the curves for Cohorts 2 and 4 (Table II.1). The growth rate for Cohort 3b was nearly identical to that of Cohorts 2 and 4 whereas the growth rate for Cohort 3a was an order of magnitude lower. Because Cohort 3a was present during the months of August through March, an effect of photoperiod, temperature, or some other factor related to season, such as food supply, on the rate of growth is indicated.

Fig. II.9. Mean (± 1 SD) cohort growth rates for *Leptochelia dubia* in Yaquina Bay, 1986-1987. Cohorts 1-5 are indicated by subscript and symbol.

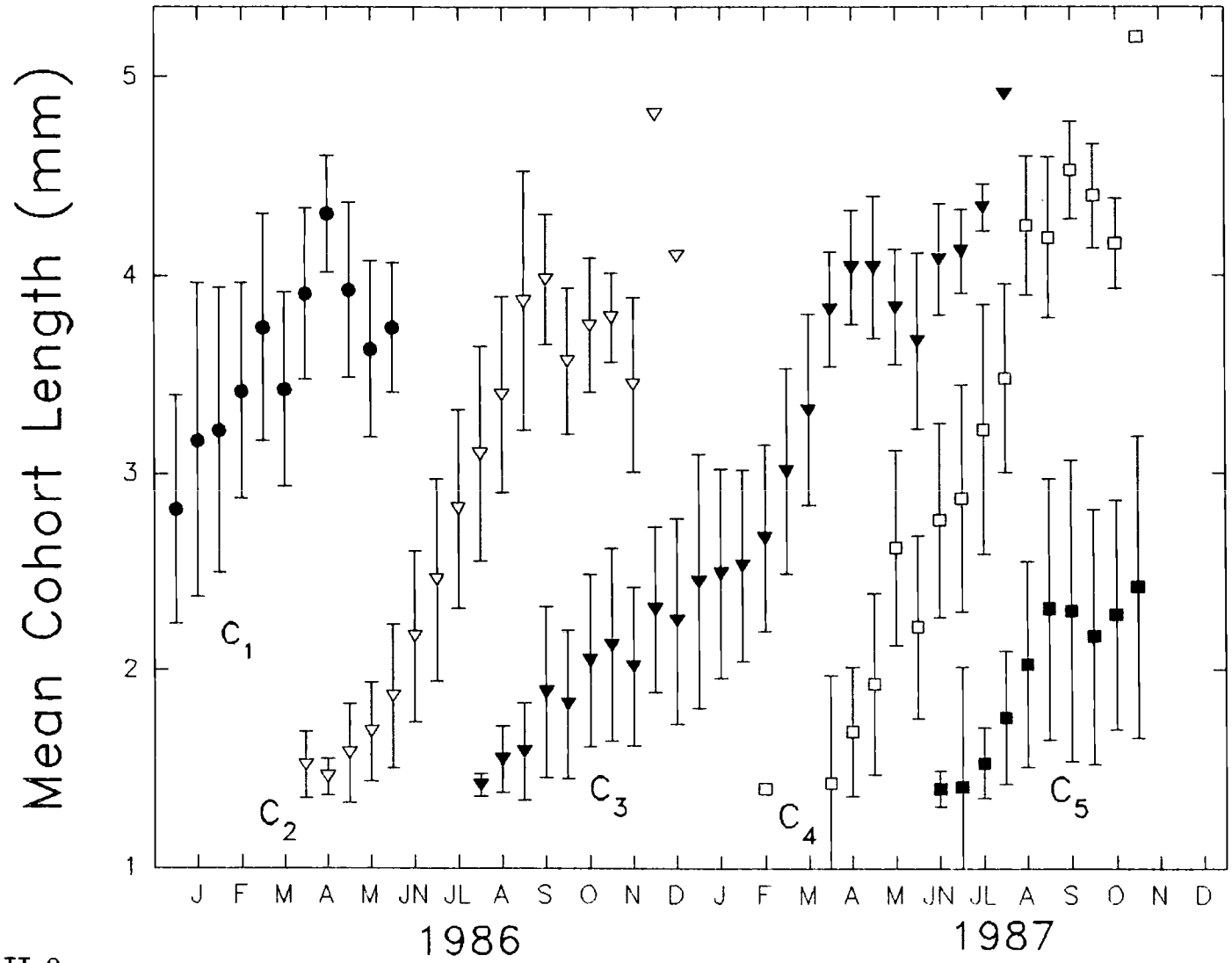

Mean Cohort Length (mm)
5
4
3
2
1
C1
C2
C3
C4
C5
J F M A M JN JL A S O N D J F M A M JN JL A S O N D
1986
1987

Fig. II.9

Table II.1. Regression functions for mean cohort length against Julian date. Data are for juvenile and female tanaids.

Cohort	Regression Function	n	P	r^2
2	Y = -0.971 + 0.0174 X	10	<0.001	0.95
3a	Y = 0.0684 + 0.00597 X	14	<0.001	0.97
3b	Y = -4.911 + 0.0175 X	5	<0.001	0.98
4	Y = -8.18 + 0.0192 X	12	<0.001	0.96

where:

Y = mean cohort length

X = Julian date.

DISCUSSION

The densities of *Leptochelia dubia* observed in this study ranged up to an order of magnitude higher than those reported by previous authors. Mendoza (1982) estimated year-round populations of up to 30,000 tanaids m^{-2} in Tomales Bay, CA, and Smith (1981) observed 75,000 m^{-2} during late summer at False Bay, British Columbia. Davis and Lee (1983) reported populations of 58,000 m^{-2} during June from the same intertidal sandflat as the present study. However, each of these authors rinsed sediment samples over a 0.5-mm (Smith 1981, Mendoza 1982) or 1.0-mm (Davis and Lee 1983) mesh sieve before sorting and counting. A 2.5-mm green tanaid measures less than 0.5 mm in diameter (pers. obs.). Thus, small individuals may have been lost through these relatively large-mesh sieves. Large, "unexplained" fluctuations in the density of the *Leptochelia* population in Tomales Bay (Mendoza 1982) may have resulted from the periodic recruitment of individuals to the 0.5-mm mesh sieve (Rees 1984).

Despite the large standard errors surrounding some of my estimates of tanaid abundance for 1986, I believe that my estimates are both accurate and conservative. I observed a peak abundance during fall of approximately 300,000 m^{-2} and a low density during late winter of 30,000 m^{-2} during both years. Further, I assumed that individuals less than 1.33 mm long were marsupial- or tube-nest larvae and omitted them from calculations of total population density.

The *Leptochelia* population sampled by Mendoza (1982) at Tomales Bay contained males and brooding females during all months of the year whereas reproductive individuals were absent during December and January in my study. This difference suggests plasticity in the ability of *L. dubia* to adapt its reproductive cycle to local environmental conditions and may, in part, explain the success of this species in colonizing littoral habitats around the world.

At the study site in Yaquina Bay, I observed different patterns in the abundances of reproductive individuals during summer 1986 than in 1987. In 1986, the spring and fall reproductive seasons were distinct, with a hiatus in June and July. In 1987, the abundances of both male and female tanaids decreased in April and May but then began to rise again in May and June. In effect, the fall reproductive season began two months earlier than during the previous year. As a result, the fall cohort began to recruit into the population as early as August 1987. It is likely that the acceleration of reproductive activity observed during 1987 was related to favorable environmental conditions. These were not addressed in the present study.

Masunari (1983) suggests that female *Leptochelia* reproduce more than once, either as secondary females or as secondary males. Highsmith (1983) and Stoner (1986) observed protogynous hermaphroditism in *L. dubia*; females kept in bowls with males remained female but, in some cases, females reversed sex when the males were removed. Although this behavior could not be observed by the methods employed in the present study, the presence of food in the digestive tracts of females with tube-nest larvae lends credence to the hypothesis that females reproduce more than once. The flocculent lining of the tube nest, rich in bacteria and microalgae (pers. obs., by epifluorescence microscopy), represents a potential source of food for both the female and her developing young. Nonetheless, it is apparent from the length frequency histograms that, except for the survival of adults of Cohort 3 into August and September 1987, all of the *L. dubia* in this study died by the end of their respective cohort's first reproductive season.

The mean growth rate of individuals maturing over summer was higher than that of individuals maturing during the winter months, indicating effects of photoperiod, temperature, and the abundance or quality of food. These factors were not addressed in the current study.

Aspects of the reproductive biology of *Leptochelia dubia* resemble those described for *Heterotanais oerstedi* and *Tanais cavolinii* (Johnson and Attramadal 1982). Females of all three species restrict the larvae to a "tube nest" in the latter stages of development. However, it is unclear whether female *Heterotanais* and *Tanais* feed during this period. According to Johnson and Attramadal, *H. oerstedi* females seal the tube as soon as the male leaves (after copulation) "and the tube remains sealed until the larvae have left the tube. The female cannot feed during this period". The female *T. cavolinii* is reported to build the brood nursery a few days before the release of her young and thus Johnson and Attramadal assume that she can feed only until that point in time. However, it was apparent that female *L. dubia* could feed inside the tube nest once the larvae had left the marsupium. The ability to feed appeared to be related to the return of the ovaries and digestive tract to the nonreproductive condition, not to the availability of food inside the tube nest. These observations suggest that the condition of the digestive tracts of brooding *H. oerstedi* and *T. cavolinii* should be reexamined.

It will be interesting to compare population parameters for *Leptochelia* in Yaquina and Tomales Bays with those of populations from other geographic regions. This versatile crustacean is known to live on a variety of plant and animal substrates (including sea grasses, macroalgae, soft muds, gorgonian corals, and sponges) in Brazil (Pires 1980) and Puerto Rico (Stoner 1986). Continuing studies will reveal more about the roles tanaids play and the influence of environment on the life history of this adaptable crustacean in littoral communities around the world.

III. RATES OF TUBE BUILDING AND PARTICLE-SIZE SELECTION BY THE TUBICOLOUS TANAID CRUSTACEAN *LEPTOCHELIA DUBIA*: INTERACTIONS WITH BACTERIA AND MICROALGAE

INTRODUCTION

The behavior of particulate material in estuaries, especially fluxes across the benthic boundary layer, is a critical gap in our understanding of estuarine function (National Environment Research Council, NERC, 1982, in Dyer 1989). An important component of the particle budget of any estuary is the degree to which particles that settle through the benthic boundary layer are stabilized against resuspension and erosion. The stabilization of deposited particles is relevant to the shallowing of harbors and navigational channels (Mehta 1986, Dyer 1989) and to the provision of food resources to benthic deposit-feeding organisms (Nowell et al. 1981, Geesy 1982, Luckenback et al. 1988, Miller and Sternberg 1988, Emerson 1989).

Interest in the role of the tubes of infaunal macroinvertebrates in the stabilization of sediments was stimulated by Fager's report (1964) that wave surge did not resuspend shallow-water sediments in La Jolla Bay colonized by dense aggregations of the tubicolous polychaete *Owenia fusiformis*. Rhoads et al. (1978) report that the stability of sediments from Long Island Sound increased after seeding with another tubicolous polychaete, *Heteromastus filiformis*, and suggest that the effect was due to binding of the sediment surface by mucous films associated with enhanced microbial production. Eckman et al. (1981) suggest that tubes foster microbial growth and promote mucous binding of sediments by enhancing diffusional fluxes of nutrients through the benthic boundary layer. Tubes may also enhance microbial production by reducing abrasion, which otherwise limits the distribution of microflora to cracks, crevices, and other surface concavities (Meadows and Anderson 1967, Weise and Rheinheimer 1978, DeFlaun and Mayer 1983, Krejci and Lowe 1986, Miller et al. 1987, Miller 1989). Irrigated tubes provide an oxygenated microhabitat

below the depth of the chemocline (Meyers et al. 1987) so that the inner walls of tubes are sites of intense microbial activity (Aller and Yingst 1978, Alongi 1985).

Where tubes form dense mats, tube building itself is a quantitatively important component of sediment stabilization. In the Bay of Fundy, maldanid and spionid polychaetes incorporate up to 50% of the upper 5 cm of intertidal sediments into tubes (Featherstone and Risk 1977). Resin casts of intertidal sediments from the Clyde Estuary, Scotland, reveal densely packed tubes of the amphipod *Corophium volutator* and the nereid polychaete *Nereis diversicolor* (Meadows et al. 1990). Aggregations of sabellariid worms create geological formations called "worm reefs". An example is the structure found off the southeast coast of Florida, described by Main and Nelson (1988). The types and sizes of materials captured in these formations depends on the availability of particles in the surrounding environment and on the selectivity and particle-handling capabilities of the species involved.

Polychaete worms and peracarid crustaceans (notably amphipods and tanaids) are numerically the most important tube-building macrofauna in most sedimentary habitats. Most studies of rates of tube building and of particle-size selection for feeding or tube building have focused on polychaetes (Brown and Ellis 1971, Featherstone and Risk 1977, Myers 1977, Taghon 1982, Whitlach and Weinberg 1982, Dobbs and Scholly 1986, Grémare 1988, Self and Jumars 1988, Main and Nelson 1988). Polychaetes select either large or small particles for tubes, depending on the species examined. In laboratory tests, the gammarid amphipod *Corophium salmonis* incorporated small particles into tubes (Self and Jumars 1988).

Tanaid crustaceans live in both deep and shallow benthic environments. On the high energy tidal flat of an Oregon estuary, the tube-building tanaid *Leptochelia dubia* achieves year-round densities of approximately 150,000 m^{-2} (Chapter II). By virtue of its high

abundance and extensive tube-building activities, *L. dubia* is expected to affect the granulometric and hydrodynamic properties of the sediment in which it lives. In the present study, I determined rates of tube building and particle-size selection by *L. dubia* as functions of animal size, experimental temperature, and the presence or absence of microbes in the sediment mix. I used these data to model seasonal patterns of sediment binding by a population of *L. dubia* in the field. Rates of tube building (dry weight of sediment per day) were found to be an increasing function of tanaid length. The model indicated that the field population of *L. dubia* in Yaquina Bay binds sediment into tubes at an average rate of 350 g m^{-2} d^{-1}, varying seasonally with tanaid abundance. The presence of microbes in sediments appeared to enhance the rate at which large tanaids incorporated silt-sized particles into tubes.

METHODS

Organisms and Sediments

I collected the tanaids used in the lab and field experiments from a study area on the intertidal sandflat just east of the Oregon State University Hatfield Marine Science Center in Yaquina Bay (Fig. II.1). The study site encloses an area of 640 m^2 and is located at an elevation of +1.0 m above MLLW. Yaquina Bay is a seasonally well-mixed estuary (Kulm 1965). Freshwater inputs to the bay are low during summer so that salinities of 30-33‰ are maintained (P. Henchman, Oregon State University, Hatfield Marine Science Center, Newport, OR, unpubl. data). During winter, rainfall and increased river flow reduce salinity to as little as 6‰ at low tide. Water temperature varies seasonally from 6-16^{0}C. Air temperature ranges from 0-30^{0}C (Davis 1981). Hours of daylight range from 12.2 d^{-1} in June to 6.0 d^{-1} in December. Sediments from the intertidal field site comprise a well sorted, very fine sand with a median diameter of 96 μm (G. Ditsworth, EPA, Newport, OR, unpubl. data). Pennate diatoms dominate the sediment microalgal community (Amspoker and McIntire 1978). Numerically abundant macroinfauna are tanaid (*Leptochelia dubia*) and amphipod (*Corophium salmonis* and *Eobrolgus spinosus*) crustaceans, bivalve molluscs (*Macoma balthica*), unidentified naidid oligochaetes, and polychaete worms (*Malacocerus glutaeus, Lumbrineris sp., Pygospio sp.*, and unidentified capitellids). Nematodes, harpacticoid copepods, and ostracods dominate the meiofaunal fraction of the community.

Tanaids chosen for tube building experiments were females and juveniles greater than 0.8 mm carapace length. Male *L. dubia* were excluded because they build tubes at a slower rate than do females or juveniles and appear to use their tubes for different purposes (Mendoza 1982). Male *L. dubia* have reduced mouthparts and do not feed. They spend some portion of their time walking across the surface of the sediment looking for mates (Highsmith 1983). Although

seasonally abundant, male *L. dubia* comprise less than 8% of the year-round population at the study site in Yaquina Bay (see Chapter II). Finally, to standardize the physiological condition of the experimental animals, I chose only tanaids with guts at least 50% full.

Visual Observations of Tube-Building Behavior and Tube Structure

I observed the tube-building behavior of *Leptochelia dubia* by placing animals in sand composed of crushed kryolite. Immersed in seawater, kryolite sand is virtually transparent and thus, the activities of animals below the surface can be observed.

Tube microstructure was studied using scanning electron microscopy. Tubes were fixed in 0.2 μm-filtered Grade I glutaraldehyde at a final concentration of 2.5%. Preparation of fixed samples for SEM followed standard procedures as described by Wardell (1988, pp.399-400).

Laboratory Experiment

I used a 3 x 3 factorial experimental design to estimate rates of tube building and particle-size selection by *Leptochelia dubia* (Fig. III.1). Factors investigated were temperature (5, 10, and 20^{0}C) and sediment treatment (sterile sediment and two different cultures containing sediment-associated microbes).

For each cell in the 3 x 3 experimental design, 40 tanaids built tubes in individual 60-mm diameter petri dishes, half-filled with experimental sediment, for 24 h. At the end of the experiment, I fixed the contents of each dish with buffered 0.2-μm-filtered formaldehyde in seawater (final concentration, 5%). After fixation, samples were rinsed on a 300-μm screen and examined under a dissection microscope. Tanaids picked from the samples were stored in 95% ethanol. Total carapace length was measured to the nearest

Fig. III.1. Matrix of temperature and sediment treatment combinations used in the 3 x 3 factorial laboratory experiment to determine rates of tube building and particle-size selection.

RATES OF TUBE BUILDING

LAB EXPERIMENT

Sediment Treatment:	Temperature 5°C	10°C	20°C
Sterile	Group A	Group D	Group G
I	Group B	Group E	Group H
II	Group C	Group F	Group I

Fig. III.1

0.01 mm using a Zeiss Videoplan II Image Analysis System. Tube material was ashed in glass cuplettes at 500°C for 4 h and weighed to the nearest 0.1 mg.

After weighing, I spread the mineral particles from each tube into casting resin on a glass microscope slide. Grain diameters were measured to the nearest 1 μm with the Zeiss image analyzer, attached by video camera to a compound microscope. Grains varied in shape from spherical to acicular and for many, I could find no obvious, single diameter to be measured. Therefore, I estimated the "projected diameter" of each grain: the diameter of a circle with the same area as that of the particle viewed normally to a plane surface on which the particle is at rest in a stable position (Allen 1975). The projected diameter estimates the true cross-sectional diameter of a particle but may not correspond to the diameter as determined by sieve analysis. Slides made from the tubes of large animals contained 100-500 particles. The first 100 particles encountered along a randomly chosen transect were measured on each of these slides. Small tanaids built smaller tubes. If slides made from these tubes contained fewer than 100 particles, all were measured.

The temperatures used in the lab experiment (5, 10, and 20°C) encompassed those measured at the study site during a calendar year (Davis 1981). Because only three cold rooms were available, I could not replicate this factor. A total of 120 dishes (40 per sediment treatment) was run at each temperature. These were placed, in random order, under a rack of four alternating standard and wide-spectrum Sylvania Gro-Lux fluorescent bulbs. Light intensity under each rack averaged 110 ± 18 $\mu E\ m^{-2}\ s^{-1}$ (Li-Cor LI-1000 Data Logger light meter, 4π model SPH Quantum sensor). Photoperiod for the 24-h experiment was 12L:12D.

I provided each tanaid with one of three experimental sediments in which to build a tube: sterile sand (ST), sand precultured at 17°C

for 6.5 wk and sand precultured at 10°C for 4 wk. I used commercial foundry sand, quarried from coastal dunes near Coos Bay, Oregon, as the substrate. Foundry sand ("sand") is predominately silica and is free of detrital organic material. Sand was separated into <63, 63-125, 125-250, 250-500, and >500 μm fractions by dry sieving. Grains 32-63 μm in diameter (coarse silt) were separated from the fraction less than 63 μm by beaker decantation (Wills 1988, pg. 183). (I omitted grains less than 32 μm in diameter from the experimental sediment for logistical reasons, cited below.) I remixed the fractions 32-63, 63-125, 125-250, 250-500, and >500 μm in lots of 600 g total weight in the proportions 3, 60, 30, 6, and 1%, respectively, to create a particle-size class distribution approximating that found in the field (G. Ditsworth, U.S. EPA, Newport, OR, unpubl. data). After the fact, a crack was discovered in the weld on the 125-μm screen. Tests revealed that as much as 50% of the sand on the 63-μm sieve consisted of particles that had leaked through the crack from the 125-μm sieve above. Thus, too many 125-250 μm and too few 125-250 μm particles were added to the experimental sediment mix. The true proportions of silts and sands, as determined by image analysis, differed between the three sediment treatments (Table III.1). Apparently, the crack in the sieve widened over time.

The 600 g lots of reconstituted sand were sterilized by ashing at 500°C for 4 h. The potential toxicity of ashed foundry sand to invertebrates was tested by assaying the development of mussel (*Mytilus trossulus*) larvae in beakers containing ashed sand and pathogen-free seawater. After 48 h, the mean percent normal larvae in beakers containing ashed sand (98.6 ± 0.01%, n = 3) did not differ significantly from the mean percent normal larvae in control beakers (95.3 ± 0.01%, P = 0.47, One Way Analysis of Variance). Thus, the ashed sand was assumed to be a suitable substrate for the tanaid experiments.

I cultured sediment-associated microalgae and bacteria on sterilized sand to create the two non-sterile sediment treatments.

Table III.1. Grain-size composition of sediments used in laboratory and field rate of tube building and particle-size selection experiments.

	Mean (±SE) Percent Number			
Size Class (μm)	<63	63-125	125-250	250-500
Laboratory Sediment Treatments:				
Sterile	10.6 ± 0.8	19.3 ± 0.6	61.2 ± 0.4	5.2 ± 0.5
Culture I	21.6 ± 0.7	34.5 ± 0.3	40.0 ± 0.7	1.3 ± 0.3
Field Sediment:				
	38.2 ± 0.3	28.8 ± 0.1	28.8 ± 0.4	2.5 ± 0.4

Mobile, epipelic diatoms and their associated microbial flora were isolated from field sediments by a modification of the method of DeJonge (1980). A layer of golden-brown sediment, 0.5-cm deep, was lifted from the surface of the flats with a plastic spatula and placed in a clean pyrex pan. The field sediment was covered with a 2-mm layer of sterile foundry sand. Two layers of lens tissue were gently pressed into the top of the sand. I covered the container with transparent plastic wrap and placed it under a rack of fluorescent bulbs at 20°C (110 $\mu m\ m^{-2}\ s^{-1}$, constant illumination). After 24 h, I removed the lens tissue and adherent material and gently agitated both of them in a beaker of sterile f/20 algal growth medium (Guillard 1975). I poured the suspension, which contained microbes, macro- and meiofauna, and sand grains, through 37-μm mesh Nitex® fabric. The lens tissue fibers, the macro-, and most of the meiofauna were filtered out of the suspension by the Nitex® cloth. The remaining suspension (diatoms, bacteria, small meiofauna, and silt particles) was poured onto the sterilized foundry sand in acrylic culture dishes. The culture medium (Guillard's f/2, diluted to f/20 to promote bacterial adhesion) was drained through the 20 μm Nitex mesh on the bottom of the dishes and refreshed every other day. At the same time that the culture medium was changed, the cultures were gently but thoroughly stirred with a plastic spoon to prevent the build up of anoxic conditions. Particles smaller than 32 μm diameter were omitted from the experimental sediment because some fraction of them would have been lost through the mesh during the drainage procedure.

It was my intent that the microbial culture reared at 17°C contain higher standing stocks of bacteria and microalgae than the culture reared at 10°C. Microalgal standing stocks were estimated as chlorophyll *a* content, measured by the method of Lorenzen (1967). Bacterial standing stocks were estimated by direct counts using epifluorescence microscopy (Fry 1988). Samples were prepared for counting following the procedure described by Montagna (1982). Sediments were diluted 500 times with sterile distilled water and

homogenized for 10 min in a Hamilton Beach commercial blender. The homogenate was allowed to settle for 60 s before a subsample was withdrawn by pipette. Subsamples were stained with 4'-6'-Diamidino-2-phenylindole (DAPI, 10 $\mu g\ ml^{-1}$). Stained material was filtered onto Nuclepore® filters (0.2-μm pore diameter) prestained with Irgalin Black. Slides were examined under ultraviolet light at 1,600x using a Zeiss Universal microscope with a Neofluor 100x/1.3 objective.

Statistical Analyses

For each cell in the 3 x 3 factorial experiment, I calculated the least-squares linear regression equation which best fit the relationship between the square-root transformed ash-free dry weights of tubes and animal length. Analysis of residuals ensured that the data conformed to the assumptions of parametric testing. I used a multiple linear regression with indicator variables to identify temperature and sediment treatments, to compare the regression functions for the separate cells. Preliminary experiments demonstrated that rate of tube building was a linear function of tanaid length. Thus, length was used as a covariate. The model tested was:

$$Y = b_0 + b_1L + b_2T1 + b_3T2 + b_4A + b_5B + b_6T1A + b_7T2A + b_8T1B + b_9T2B + b_{10}LT1 + b_{11}LT2 + b_{12}LA + b_{13}LB + b_{14}LT1A + b_{15}LT2A + b_{16}LT1B + b_{17}LT2B$$

where:

Y = rate of tube building ($g\ d^{-1}$)

L = tanaid length (mm)

T1 = temperature 1 (5^0C)

T2 = temperature 2 (10^0C)

A = sediment treatment A (sterile)

B = sediment treatment B (Culture I).

The indicator variables identifying the temperature and sediment treatments were created from combinations of zeros and ones. In two

cases, that of the temperature treatment "T3" (20^0C) and of the sediment treatment "C" (Culture II), the combinations were comprised entirely of zeros. Thus, terms containing either of these variables dropped out of the equation. The remaining variables were grouped by order and by type of interaction (i.e., third-order interactions, second-order interactions between length and sediment treatment, second-order interactions between length and temperature, and second-order interactions between temperature and sediment treatment) and main effects (length, temperature, and sediment treatment). I compared the full model to smaller models, derived by dropping groups of interactions in sequence, beginning with the third-order interactions (General F Testing, Weisberg 1985, p.95). Data were analyzed using Statistix II (NH Analytical Software, Roseville, MN).

I investigated selection for fine sand and coarse silt-sized particles by plotting the arcsine-transformed proportion of silt in tubes against tanaid length. Because the proportions of silt and sand available differed between the sediment treatments, the effect of the presence of microbes could not be determined by direct comparison. Thus, I recalculated the proportions of silt-sized particles in tubes as Vanderploeg and Scavia's Relativized Index of Electivity, E^* (Lechowicz 1982). The E^* index measures an individual animal's perception of the value of a particle as a function of both its abundance and the abundances of the other particles present. The index is calculated as

$$E^* = \frac{[W_i - (\frac{1}{n})]}{[W_i + (\frac{1}{n})]}$$

where:

$$W_i = \frac{(\frac{r_i}{p_i})}{[\sum (\frac{r_i}{p_i})]}$$

and:

n = number of grain size classes available

r_i = relative proportion of size class *i* in a tube

p_i = relative proportion of size class *i* in the available sediment mix.

Electivity indices were plotted against tanaid length. Although E^* is not amenable to parametric regression analysis (Lechowicz 1982), smoothed scatterplots of E^* against tanaid length were created, using the method of robust locally weighted regression (Cleveland 1979). That is, the fitted value (y_i) of a *d*th degree polynomial function is fit to the data (x_i,y_i) using a weighted least squares method. The weights (w_i) are chosen by centering each w_i at x_i and scaling the w_i to zero at the *r*th nearest neighbor of x. A different set of weights, δ_i, is then defined for each (x_i, y_i). Small residuals result in large weights and large residuals result in small weights. New fitted values are computed but with the $w_k(x_i)$ replaced by $\delta_i w_i(x_i)$. Computation of new weights and fitted values is repeated several times. The entire procedure, including the initial computation and the iterations, is known as robust locally weighted regression. The process is considered "robust" because it guards against distortion of the regression line by outliers.

An additional tube-building experiment was conducted on 10 September 1990 to verify trends in grain-size selection. Twelve tanaids, one per dish, were selected for each of the sediment treatment-tanaid size class combinations (sterile sediment/small tanaids, sterile sediment/large tanaids, precultured sediment/small tanaids, and precultured sediment/large tanaids). In this case, care

was taken that the proportions of silts and sands were the same in the sterile and precultured sediment mixtures. "Small" tanaids ranged from 0.8-1.0 mm carapace length. "Large" tanaids were 3.4-4.2 mm long. Tanaids built tubes for 24 h at 18^{0}C (photoperiod 12L:12D) before fixation with 10% formaldehyde. Tubes were collected by washing the contents of each dish on a 300 μm-mesh screen. The organic portion of each tube was oxidized by 30% hydrogen peroxide heated to 60^{0}C. Dried tube particles were spread in casting resin on microscope slides. The "projected diameters" of tube particles were measured as previously described but using JAVA, a video analysis software package by Jandell Scientific.

Field Experiment

A method was devised for determining rates of tube-building by tanaids in the field. I placed approximately 300 tanaids on sterile sand inside plastic rings cut from 50-cc syringe barrels. The light-colored foundry sand served as a marker for the length of a tube at t = 0. Tanaids built tubes overnight in this sediment in the lab (10^{0}C). The following day, the rings and their contents were transferred to the field. The contents of each ring were gently shaken into a hole from which I had removed a 1-cm deep sediment plug. I chose the locations of the plugs at random within a 1-m^2 quadrat on the sediment surface. After 24 h, I retrieved a 1-cm deep layer of sediment within a 4-cm radius of each plug. On return to the lab, I fixed the samples with 10% buffered formalin in seawater.

Fixed samples were gently washed on a 300-μm sieve. I picked 50 tubes with segments of both marker and field sediment from the samples. I removed the tanaid from each of these tubes and preserved it in 95% ethanol. I separated the field sediment portions of tubes from the foundry sand and ashed the field material in glass cuplettes for 4 h at 500^{0}C. I measured the total carapace lengths of tanaids and the projected diameters of sediment particles using the Zeiss image analyzer.

Rate of Degradation of Tubes

The data derived from the above experiments were used to model the amount of sediment bound into tubes by a population of tanaids over the course of a year. I also wanted to estimate the rate at which tubes could be degraded by macrofaunal, meiofaunal and microbial grazers. To this end, I conducted a laboratory experiment to measure the percent loss, in weight, of sediment particles from tubes over a one-month period. This experiment began on 31 August 1989. I placed a tube fragment at least 2 cm long on each of 120 55-mm dia. circles cut from 1.0 mm Nitex® mesh. Each circle had been previously rinsed, dried, weighed to the nearest 0.01 mg (tare weight), and set in the bottom of a small glass petri dish. Tanaids were removed from the tube fragments and after 5 min air-drying, gross wet weights of tubes were obtained. I then submerged the petri dishes in a laboratory water table flushed continually with unfiltered seawater (12^{0}C). Illumination was provided by a 75-W General Electric "Plant Gro-and-Sho" fluorescent bulb with photoperiod 12L:12D. At each of three time intervals: 1 wk, 2 wk, and 1 mo, I selected 30 dishes at random and removed them from the water table. I fixed the contents of each dish with buffered, 0.2-μm filtered 10% formaldehyde (± 5% final concentration). I placed the tube fragments in glass cuplettes and ashed them for 4 h at 500^{0}C. Percent loss of material from a tube at each sampling interval (t = x) was calculated as

$$\% \; LOSS_{t=x} = [AFDW_{t=0} - \frac{AFDW_{t=x}}{AFDW_{t=0}}] \; (100)$$

Thirty pieces of tube were set aside at t = 0 for the determination of net wet:ash-free dry weight. This relationship was used to estimate the initial ash-free dry weight (t = 0) of the tubes selected at each subsequent sampling interval.

Model: Rates of Tube Building by the Field Population

To facilitate the calculation of the bulk amount of sediment bound into tubes by the field population, a model was written in SAS (Statistical Institute, Inc., Carey, N.C.), Version 6.03 (Appendix A). The following variables were supplied as inputs to the model:

1. **LENGTH = Percent of the population in size class *i*.** I derived estimates of the number of tanaids in each of 19 0.2-mm size-class intervals for a minimum of three replicate cores per sampling date. Lengths were adjusted for shrinkage in preservative according to the empirically derived relationship (see Chapter II):

$$Y = 0.132 + 1.09X$$

where:

Y = fresh tanaid length (mm)

X = preserved length (mm).

For the purpose of modeling rates of tube building, tanaids smaller than 1.3 mm fresh length were not considered part of the population. Length frequencies and the total number of individuals in each sample were input to the model in the file "LEPT".

2. **DENSITY = Density of the field population (inds m^{-2}).** I sampled the field population of *Leptochelia dubia* at the study site in Yaquina Bay every two weeks from January 1986-December 1987. Three independent replicate estimates of population density were derived from samples taken on each date through early March 1987. Eight replicates were obtained per sampling date from late March through December 1987. Only individuals with fresh lengths >1.3 mm were included in estimates of population size. Details of the field sampling design are presented in Chapter II. Population densities were input to the model in the file "DENS".

3. **DATE = Dates of field sampling.** Dates of sampling, represented by date codes, were supplied to the model in the file "DATE". The model used the variable "DTCODE" to match replicate estimates of population

density with estimates of the proportion of the population in each size class interval on a given date.

Using these inputs, the model performed the following functions:

a. calculated the midpoint of each size-class interval,
b. calculated the proportion of the population in each size class interval for each replicate sample collected on a given date,
c. performed arcsine square root transformations of the size-class interval data,
d. calculated the mean and variance of the transformed values for each sampling date,
e. back-transformed the means and variances to proportions,
f. calculated the mean and variance of the replicate estimates of population density for each sampling date,
g. merged the files containing the sampling dates, the means and variances of the proportions of the population in each size-class interval for each sampling date, and the means and variances of the estimates of population density for each sampling date,
h. calculated the rate of tube building for an individual tanaid of a given size using the formula

$$TUBEWT = (LENGTH \times 0.02)^2$$

where:

TUBEWT = tube ash free dry weight (g d^{-1})

LENGTH = midpoint of a size-class interval.

This formula was constructed from the empirically derived equation for the rate of tube building described below (see Results).

i. calculated the rate of tube building by all individuals in the field population using the formula

$$CTUBEWT = TUBEWT \times DMEAN \times PMEAN$$

where:

CTUBEWT = tubes ash free dry weight (g m^{-2} d^{-1})

DMEAN = mean density of the population on a given date

PMEAN = mean proportion of the population in a given size-class interval on a given date, and

j. because the result CTUBEWT is a computed quantity, the uncertainty associated with an estimate of CTUBEWT is a composite effect of the uncertainties associated with the component variables (i.e., tanaid length, rate of tube building, population size, and the proportion of the population in a given size class) (Beers 1957). Therefore, the variance associated with each estimate of CTUBEWT was calculated from the propagation of error function described by Gore (1952):

$$S_y^2 = \left[\frac{\partial f(x_1, x_2, \ldots)}{\partial x_1}\right]^2 S_{x_1}^2 + \left[\frac{\partial f(x_1, x_2, \ldots)}{\partial x_2}\right]^2 S_{x_2}^2 + \ldots$$

where:

$$Y = f(x_1, x_2, \ldots).$$

Output from the model was in the form of a table including values for the variables DTCODE (date code), LENGTH (mid-point of a size-class interval), CTUBEWT (ash free dry weight of tubes), PROPERR (variance associated with an estimate of CTUBEWT), and COHORT (the cohort designation for each size-class interval on each date).

Output from the model was graphed as the bulk rate of tube building (g m^{-2} d^{-1}) by the tanaid population on each biweekly sampling date. The error associated with each estimate was plotted as one standard deviation from the mean. The contribution of each cohort is indicated by patterns on the bars.

RESULTS

Visual Observations of Tube-Building Behavior and Tube Structure

As described by Mendoza (1982), *Leptochelia dubia* burrow head-first, excavating sediment with their second antennae and gnathopods. Gnathopods grasp and move particles or, when closed, scrape material toward the body. The tanaid glues particles together with mucous threads extruded from pores in the dactyli of the first pair of pereopods. Scanning electron micrographs of tubes built in sterile foundry sand show that the threads capture sediment particles as though in an adhesive net (Fig. III.2). Once wrapped in mucus, material passes down the rows of pereopods until it collects in a hook formed by a ventral folding of the posterior end of the body. The tube is built from the posterior end of the animal forward. The tanaid rotates dorsoventrally completing the circumference of the tube.

In natural sediments, tube-building and feeding activities appear to be closely related. Particles are grasped initially by the gnathopods, passed to the maxillipeds, sorted, and then moved either to the mouth (food) or to the pereopods (tube material). Tube building appears to be a continuous process, permitting the animal to extend its feeding range while staying anchored to the substratum. Organic-mineral aggregates (small inorganic particles, detritus, bacteria, and microalgae), abundant in surface sediments, are woven into the structure of the tube.

Rates of Tube Building

Although each of the nine cells in the tube building experiment contained 40 tanaids at the start of the 24 h run, sample sizes were reduced by up to 50% at its conclusion. Some tanaids did not build tubes and sometimes two tanaids had been placed, accidentally, in the same dish. Data for these dishes were discarded.

Fig. III.2. Scanning electron micrograph of clean sand grains bound in a web of mucus by *Leptochelia dubia*. The mucus threads are extruded from pores in the tips of the first pereopods. Magnification is 230x. White scale bar represents 100 μm.

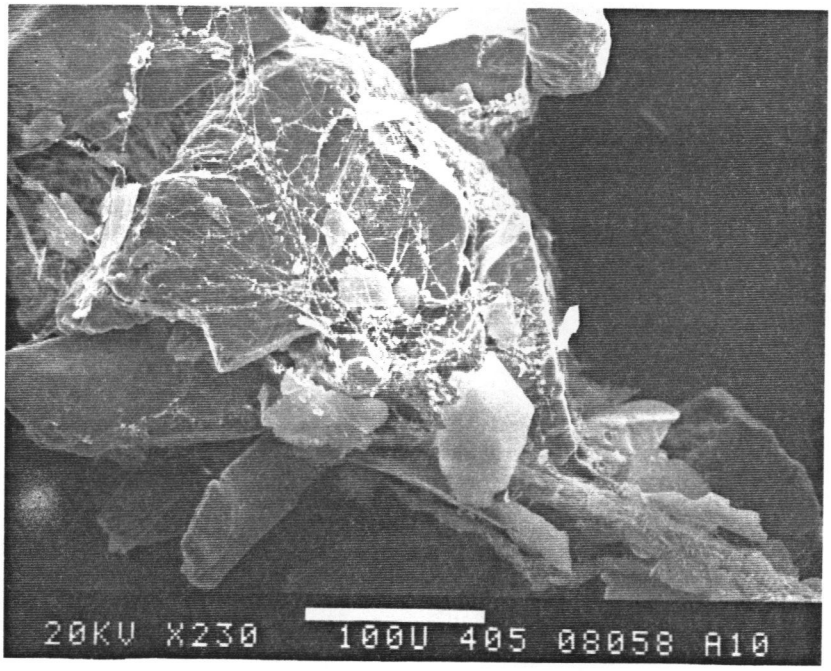


Fig. III.2

The two sediment cultures differed in that the 17^{0}C-culture (hereafter "Culture I") contained a significantly higher concentration of chlorophyll *a* but a lower number of bacterial counts than the 10^{0}C-culture ("Culture II") (Table III.2). Culture I was dominated by small pennate diatoms (*Stauroneis constricta* and *Navicula complanatula*), although cyanobacteria (*Phoridium* spp. and *Spirulina* sp.) were also abundant. The surface of Culture I was golden brown. In contrast, the surface of Culture II was bright green and the flora were more evenly divided between cyanobacteria and the diatoms *Stauroneis, Navicula,* and *Nitzschia socialis*. More importantly, the two cultures produced morphologically different types of mucus. Culture I, dominated by diatoms, produced mucus in sheets and "wads", embedded with sediment. Culture II produced mucus in strings. It was difficult to distinguish sediment particles bound by microbes in Culture II during the preincubation period from material bound by tanaids during the experiment. For this reason, the accuracy with which rates of tube-building were estimated for tanaids in sediment culture II is questionable, especially for Group C, the first examined. Particle-size selection was not analyzed for tanaids that built tubes in Culture II.

The square root-transformed rate of tube building was a positive function of tanaid length in seven out of nine cells in the experiment (Fig. III.3). Larger tanaids bound more sediment into tubes over 24 h than small tanaids, across all seven temperature and sediment treatments. In the experimental cells "5^{0}C/sediment culture II" and "10^{0}C/sterile sediment", no statistically significant relationship between tanaid size and rate of tube building could be detected. In several of the treatment cells where a linear relationship did occur (e.g., "10^{0}C/sediment culture I" and "20^{0}C/sediment culture I"), scatter around the line indicated a high degree of individual variation.

The nine regression functions were compared by multiple linear regression using dummy variables to designate temperature and

Table III.2. Estimates of microalgal and bacterial standing stocks in the sediment cultures used in the laboratory rate of tube building and particle-size selection experiment, August 1989. P-values are presented for Analysis of Variance comparisons of cultures I and II.

Culture	n	$\bar{X}$ ± SD	P
Chlorophyll *a* ($\mu g\ g^{-1}$ AFDW):			
I	30	6.1 ± 1.4	<0.001
II	30	2.7 ± 1.0	
Bacterial Abundance (x 10^7 cells g^{-1} AFDW):			
I	10	3.7 ± 1.9	<0.01
II	8	4.9 ± 1.5	

Fig. III.3. Rates of tube building as linear functions of tanaid length in the laboratory experiment. Rate of tube building is expressed in units of ash free grams dry weight m^{-2} d^{-1}. A square-root transformation of rates of tube building was used to satisfy the assumptions of parametric least squares regression testing.

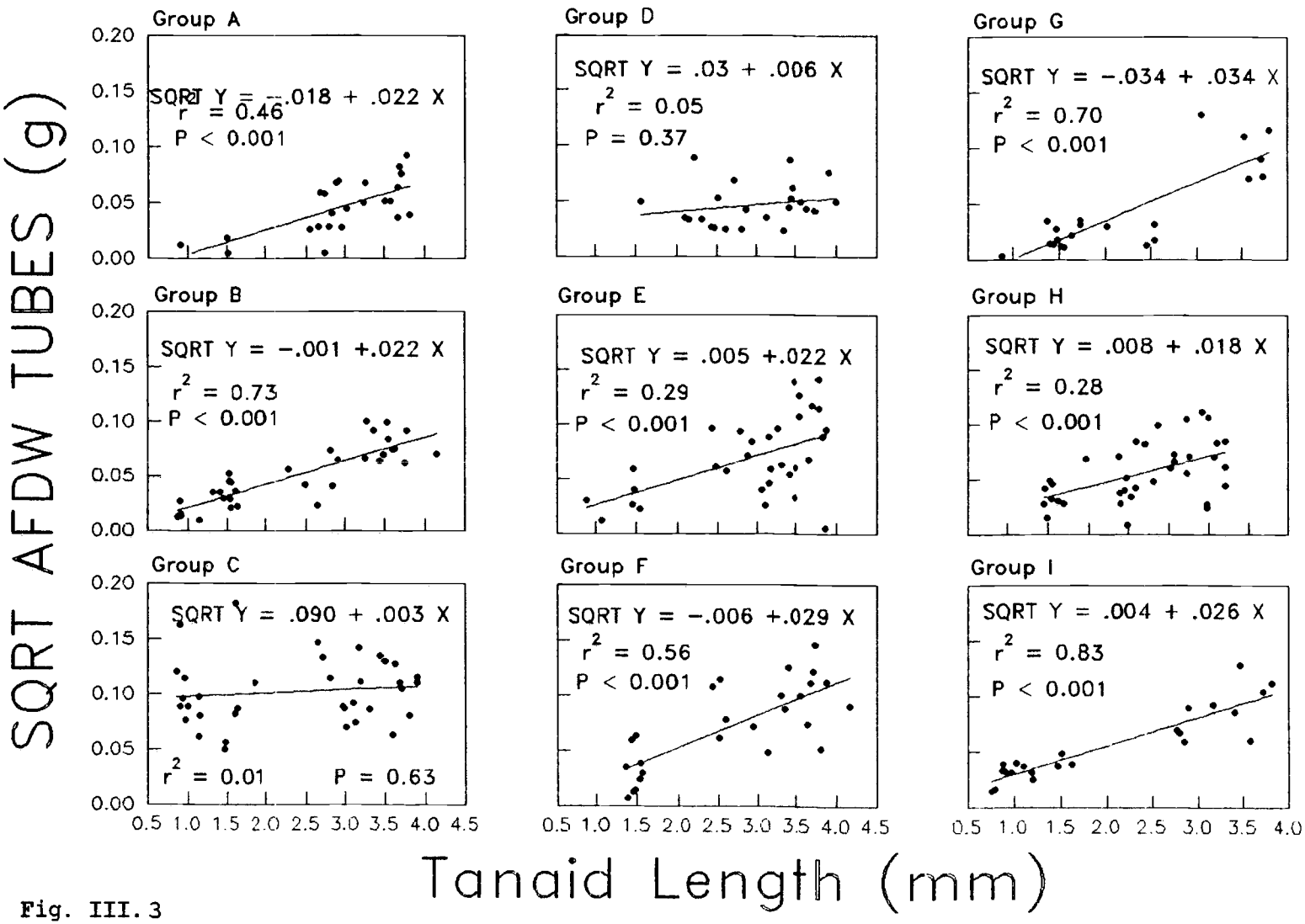

Group A
SQRT Y = -.018 + .022 X
r² = 0.46
P < 0.001
Group D
SQRT Y = .03 + .006 X
r² = 0.05
P = 0.37
Group G
SQRT Y = -.034 + .034 X
r² = 0.70
P < 0.001
Group B
SQRT Y = -.001 +.022 X
r² = 0.73
P < 0.001
Group E
SQRT Y = .005 +.022 X
r² = 0.29
P < 0.001
Group H
SQRT Y = .008 + .018 X
r² = 0.28
P < 0.001
Group C
SQRT Y = .090 + .003 X
r² = 0.01
P = 0.63
Group F
SQRT Y = -.006 +.029 X
r² = 0.56
P < 0.001
Group I
SQRT Y = .004 + .026 X
r² = 0.83
P < 0.001
0.00
0.05
0.10
0.15
0.20
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5
SQRT AFDW TUBES (g)
Tanaid Length (mm)

Fig. III.3

sediment treatments (Table III.3). The main effects could not be tested because the three-way interaction was significant. However, because there were no replicate measurements of the rate of tube building for a tanaid of a given size in a given temperature/sediment-treatment cell, the error term in the multiple regression model may have been inappropriate. As an alternative, I calculated analyses of variance for the slopes and the intercepts of the nine regression equations. In these tests, the n = 21 to 36 observations in each temperature/sediment-treatment cell provided replication. Using this approach, I detected no significant effect of temperature or sediment treatment on the slopes of the nine regression equations (Table III.4). The overall mean slope was 0.020 g mm^{-1} d^{-1} (SE = 0.003, range = 0.018 - 0.034 g mm^{-1} d^{-1}).

Before conducting the ANOVA for the nine intercepts, I adjusted each to the estimated rate of tube building for an animal of 2.8 mm, the median length of tanaids used in the experiment. Analysis of variance of the intercepts at X = 2.8 mm detected no effect of temperature although the effect of sediment treatment on the intercepts approached significance (Table III.5). Linear contrasts (Snedecor and Cochran 1980, pp. 224-225) demonstrated that the average effect of microbes in sediment on the intercepts was significant (Table III.6). In addition, the effect of Culture II was greater than that of Culture I. Both cultures were artificial so that it is difficult to interpret this latter result with respect to the field population.

To model rates of tube building by the field population, I created a new regression function. Because no significant effect of temperature or sediment treatment on the slopes of the nine regression functions could be detected, the slope of the new model was estimated from the grand mean of the slopes of the regression equations. There was a significant effect of microbial culture on the intercepts of the regression equations, however. Therefore, the intercept of the new model was estimated by the grand mean of the

Table III.3. Comparison of the nine linear regression functions for rate of tube building against tanaid length using General F Testing.

Model	df	RSS_{diff}	MS_{diff}	F	P
Temperature Intercept	2	0.070604	0.035302	64.396	<0.001
Slopes and intercepts equal	2	0.005842	0.002921	5.328	<0.005
Structure of intercepts is additive	4	0.026319	0.006580	12.003	<0.001
All slopes equal	2	0.001719	0.000860	1.568	>0.10
Differences in slopes due to sediment trmt	2	0.006627	0.003314	6.045	<0.005
Structure of slopes is non-additive	4	0.012725	0.003181	5.803	<0.001
Full model	237	0.129923	0.000548		

$$F = \frac{(RSS_{NH} - RSS_{AH}) \;/\; (df_{NH} - df_{AH})}{RSS_{AH} \;/\; df_{AH}} = \frac{MS_{diff(NH)}}{MS_{diff(AH)}}$$

where:

NH = null hypothesis (reduced model)

AH = alternate hypothesis (larger model)

Table III.4. Analysis of Variance comparison of the slopes of the regression equations derived from the laboratory rate of tube building experiment.

Source	df	SS	MS	F	P
Main Effects:					
Temperature	2	1.7180E-04	8.5876E-05	0.54	0.62
Sediment Trmt	2	3.5090E-06	1.7545E-06	0.01	0.99
Residual	4	6.3507E-04	1.5877E-04		
Total	8	8.1033E-04			

Table III.5. Analysis of Variance comparison of the intercepts at X=2.8 mm tanaid length of the regression equations derived from the laboratory rate of tube building experiment.

Source	df	SS	MS	F	P
Main Effects:					
Temperature	2	7.2676E-04	3.6338E-05	0.22	0.81
Sediment Trmt	2	1.9501E-03	9.7506E-04	5.88	0.06
Residual	4	6.6698E-04	1.6675E-04		
Total	8	2.6898E-03			

Table III.6. Linear contrasts of the intercepts at X=2.8 mm tanaid length of the regression functions derived from the laboratory rate of tube building experiment.

1. Is the effect of cultured sediments on the intercepts significantly different than that of sterile sediment?

For:

$$[\tfrac{1}{2}(\bar{a}_I + \bar{a}_{II}) - \bar{a}_{st}],$$

$$\Sigma L = (\tfrac{1}{2}) + (\tfrac{1}{2}) + (-1) = 0$$

and:

$$\hat{SE}_L = \sqrt{(\Sigma L^2)} \; x \; (s/\sqrt{n}),$$

$$t = \frac{[\tfrac{1}{2}(\bar{a}_I + \bar{a}_{II}) - 3}{\hat{SE}_L} = 4.291^{**},$$

$$t_{.005,8df} = 3.832$$

where:

$\bar{a}_{st}$ = mean of the intercepts for treatments with sterile sediment,

$\bar{a}_I$ = mean of the intercepts for treatments with sediment culture I, and

$\bar{a}_{II}$ = mean of the intercepts for treatments with sediment culture II.

Table III.6 (continued).

2. Is there a difference between the effects of cultured sediment treatments I and II on the intercepts?

For:

$$(\bar{a}_{II} - \bar{a}_{I}),$$

$$\Sigma L = (1) + (-1) = 0,$$

$$t = \frac{[\bar{a}_{II} - \bar{a}_{I}]}{\hat{SE}_{L}} = 4.078^{**},$$

$$t_{.005,8df} = 3.832.$$

intercepts (at X = 0) for the six regression functions in the cells containing microbial sediment cultures:

$$Y = 0.017 + 0.020X$$

where:

Y = square root of net AFDW of tube (g)

X = tanaid carapace length (mm).

In five of these six cases, the intercept at X = 0 was not significantly different from zero. Thus, the intercept was omitted from the equation for TUBEWT (see Methods, Model: Rates of Tube Building).

The results of the field experiment, conducted two weeks after the lab experiment, on 31 August 1989, also demonstrated a positive linear relationship between rate of tube building and tanaid length (Fig. III.4). Because the function describing rates of tube building in the laboratory was derived from the slopes and intercepts of several other functions, it cannot be compared statistically to the function derived from the field data. However, given the degree of individual variation exhibited, rates of tube building in the lab appear to reasonably approximate those observed in the field.

Particle-Size Selection

Particle-size selection was examined for tanaids in four of the nine treatment cells in the tube-building experiment, 5^0C/sterile sediment, 5^0C/sediment culture I, 20^0C/sterile sediment, and 20^0C/sediment culture I. The bulk of the particles incorporated into tubes were in the size class "very fine sand" (63-125 μm) with different patterns in the use of silt (32-63 μm) and fine sand (125-250 μm) by large and small tanaids. Medium sand (250-500 μm) comprised an average of less than 3% of the particles in tubes. Tanaids did not use grains larger than 500 μm.

To elucidate patterns in particle-size selection, I regressed the arcsine-transformed proportion of each particle size class (silt,

Fig. III.4. Rate of tube building as a linear function of tanaid length in the field experiment.

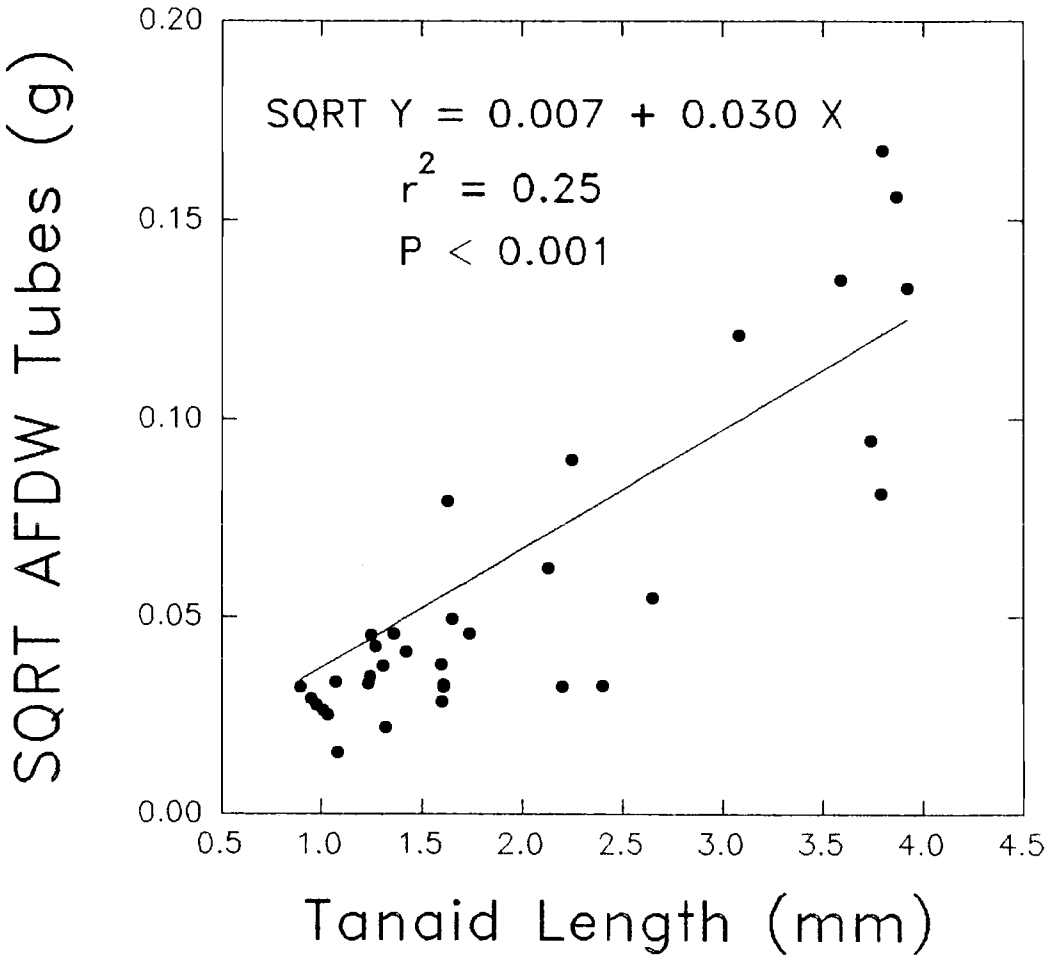

SQRT Y = 0.007 + 0.030 X
r2 = 0.25
P < 0.001
SQRT AFDW Tubes (g)
0.20
0.15
0.10
0.05
0.00
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
Tanaid Length (mm)

Fig. III.4

very fine sand, fine sand, and medium sand) in tubes against tanaid length. In general, selection for silts decreased with tanaid length whereas selection for fine sand increased (Table III.7). No consistent, significant trends were observed for very fine- or medium-sized sand. Recalling that the experiment was conducted in August, small tanaids (less than 2.0 mm) were members of the new cohort whereas large individuals were three to four months old (Chapter II). Small tanaids in both sterile sediment and sediment Culture I at 5^0C showed positive selection for silt (Fig. III.5). Results for tanaids in the treatment cell "20^0C/sterile sediment" followed this pattern but tanaids in the cell "20^0C/sediment culture I" showed no selection for any of the four particle size classes (Table III.7). In general, selection for silt by large tanaids was negative, although selection was less negative when microbes were present. However, the apparent increase in selection may have been a response to the higher availability of small particles in the precultured sediment mix. To correct for differences in particle-size distributions between the sediment treatments, I plotted Vanderploeg and Scavia's E^* against tanaid length (Fig. III.6). Small tanaids again showed positive selection ($E^*>0$) and large tanaids showed negative selection ($E^*<0$) for silt in both sterile and precultured sediments at 5^0C and in sterile sediment at 20^0C. Selection for silt by small tanaids was less positive, and by large tanaids less negative, in sediment precultured with microbes.

Both large and small tanaids showed negative selection for fine sand when building tubes in sterile sediment at both temperatures and in precultured sediment at 5°C (Fig. III.7). Large tanaids selected fine sand at a rate higher than its availability in the precultured particle mix at 5^0C. Correcting for differences in availability, plots of E^* demonstrate that, whereas selection for fine sands by small tanaids was typically less than zero, selection by large tanaids was positive (Fig. III.8). As with silts, selection for fine sands by small tanaids appeared to be more positive and by large tanaids, more negative, when tubes were built in sediments

Table III.7. Least squares linear regression functions for the abundance of each particle size class in tubes against tanaid length derived from the laboratory tube building experiment.

Sediment Treatment	Regression Fn	r^2	P
Silt (32-62 μm):			
5°C/Sterile Sediment	Y = 0.75 - 0.17X	0.71	<0.001*
5°C/Culture I	Y = 0.72 - 0.10X	0.52	<0.001*
20°C/Sterile Sediment	Y = 0.55 - 0.09X	0.39	<0.001*
20°C/Culture I	Y = 0.41 + 0.02X	0.02	0.70
Very Fine Sand (63-124 μm):			
5°C/Sterile Sediment	Y = 0.48 - 0.017X	0.00	0.9
5°C/Culture I	Y = 0.56 + 0.032X	0.12	0.1
20°C/Sterile Sediment	Y = 0.38 + 0.064X	0.17	0.05*
20°C/Culture I	Y = 0.84 - 0.003X	0.07	0.32
Fine Sand (125-249 μm):			
5°C/Sterile Sediment	Y = 0.61 + 0.071X	0.58	<0.001*
5°C/Culture I	Y = 0.52 + 0.064X	0.29	0.005*
20°C/Sterile Sediment	Y = 0.86 + 0.0034X	0.00	0.99
20°C/Culture I	Y = 0.54 + 0.02X	0.02	0.71

Table III.7 (continued).

Medium Sand (250-500):			
5°C/Sterile Sediment	Y = 0.23 - 0.014X	0.01	0.80
5°C/Culture I	Y = 0.13 - 0.002X	0.00	0.98
20°C/Sterile Sediment	Y = 0.17 - 0.010X	0.00	0.92
20°C/Culture I	Y = 0.061 + 0.001X	0.00	0.99

where:

Y = arcsin √(proportion of particle size class x in tubes)

X = tanaid length (mm)

Fig. III.5. Selection for coarse silt-sized particles for tube building by *L. dubia* in the laboratory experiment. Selection is expressed as the arcsine square root-transformed proportion of particles 32-63 μm in diameter in each tube. Dashed line represents the amount of silt-sized particles available in the sediment treatment.

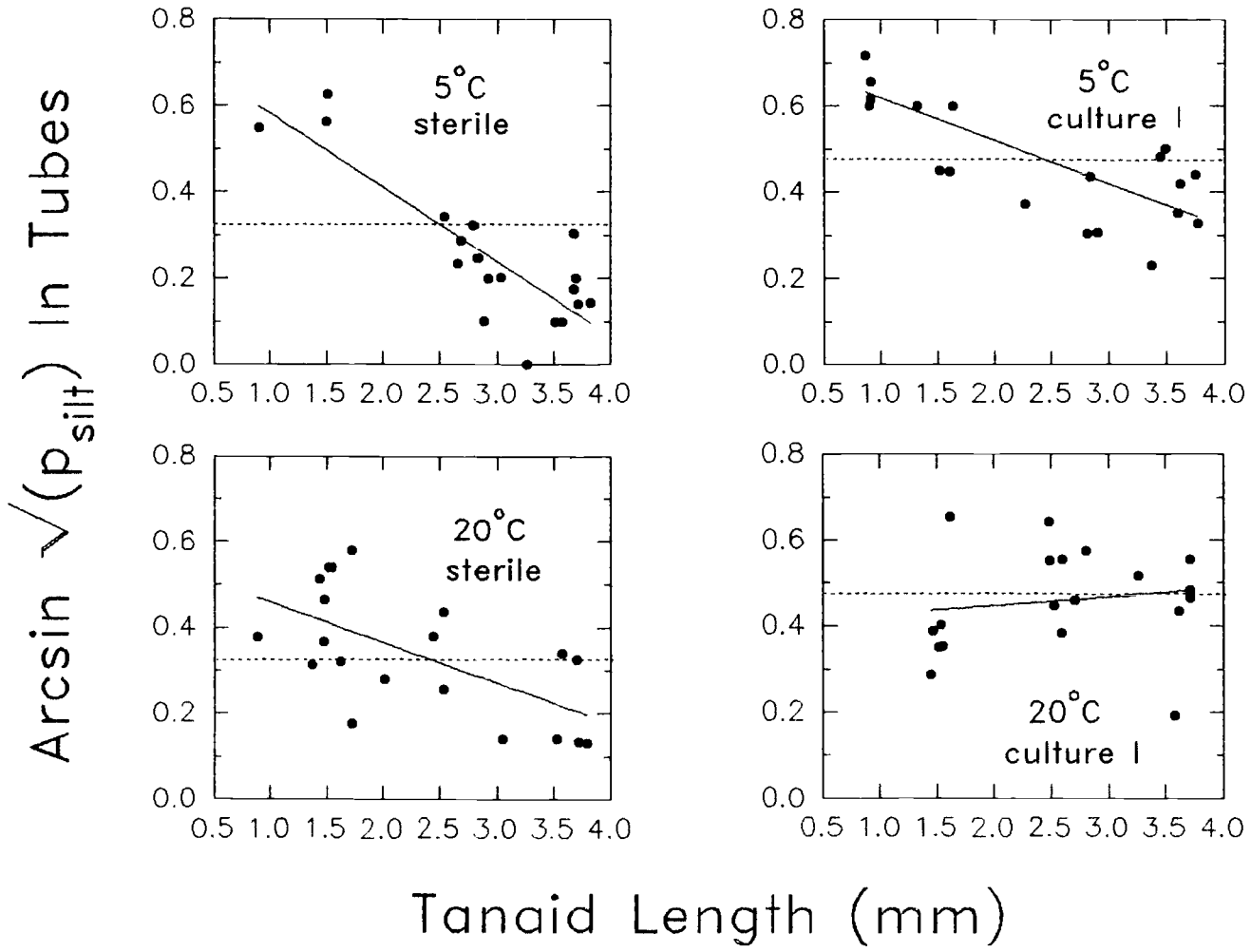

Arcsin √(p_silt) In Tubes
5°C
sterile
5°C
culture I
20°C
sterile
20°C
culture I
0.0
0.2
0.4
0.6
0.8
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
Tanaid Length (mm)

Fig. III.5

Fig. III.6. Electivity of coarse silt-sized particles for tube building by *L. dubia* in the laboratory experiment. Electivity (E^*) is expressed as Vanderploeg and Scavia's Relativized Index of Electivity. Smoothed scatterplots of E^* against tanaid length were created using robust locally weighted regression (see text).

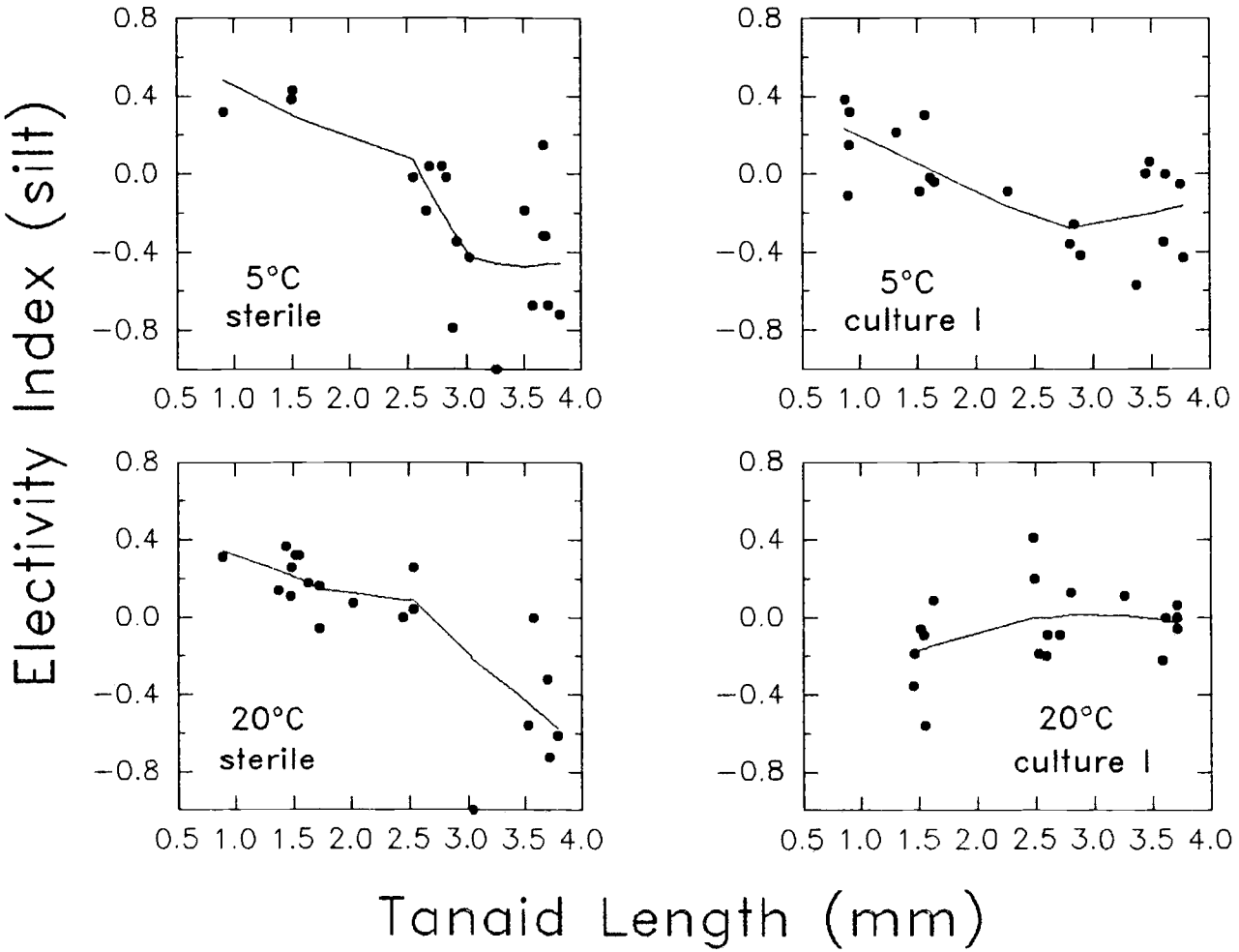

Electivity Index (silt)
0.8
0.4
0.0
−0.4
−0.8
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
5°C
sterile
5°C
culture I
20°C
sterile
20°C
culture I
Tanaid Length (mm)

Fig. III.6

Fig. III.7. Selection for fine sand-sized particles for tube building by *L. dubia* in the laboratory experiment. Selection is expressed as the arcsine square root-transformed proportion of particles 125-250 μm in diameter in each tube. Dashed line represents the amount of fine sand available in each sediment treatment.

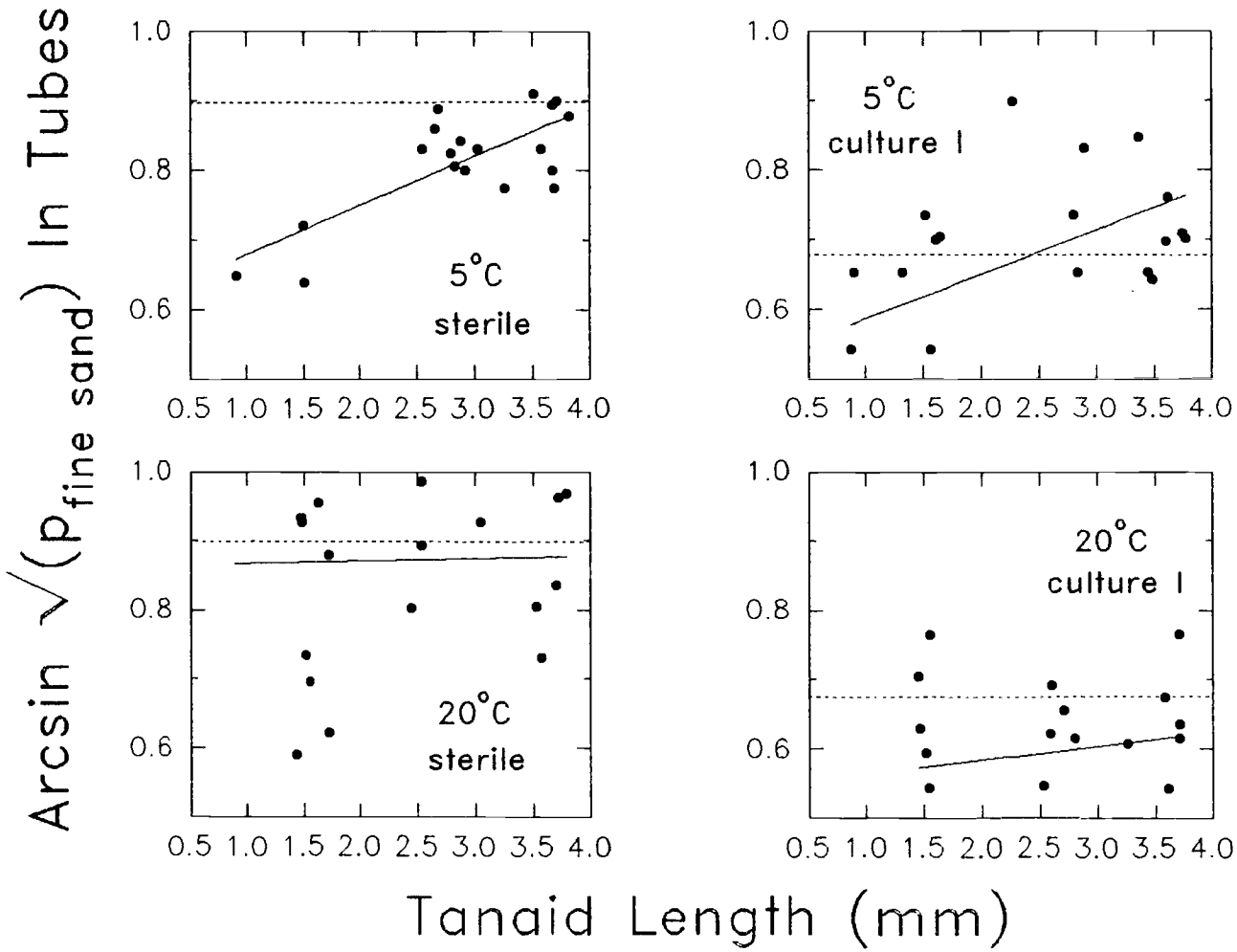

Arcsin √(p fine sand) In Tubes
1.0
0.8
0.6
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
5°C
sterile
5°C
culture I
20°C
sterile
20°C
culture I
Tanaid Length (mm)

Fig. III.7

Fig. III.8. Electivity of fine sand-sized particles for tube building by *L. dubia* in the laboratory experiment. Electivity (E') is expressed as Vanderploeg and Scavia's Relativized Index of Electivity. Smoothed scatterplots of E' against tanaid length were created using robust locally weighted regression (see text).

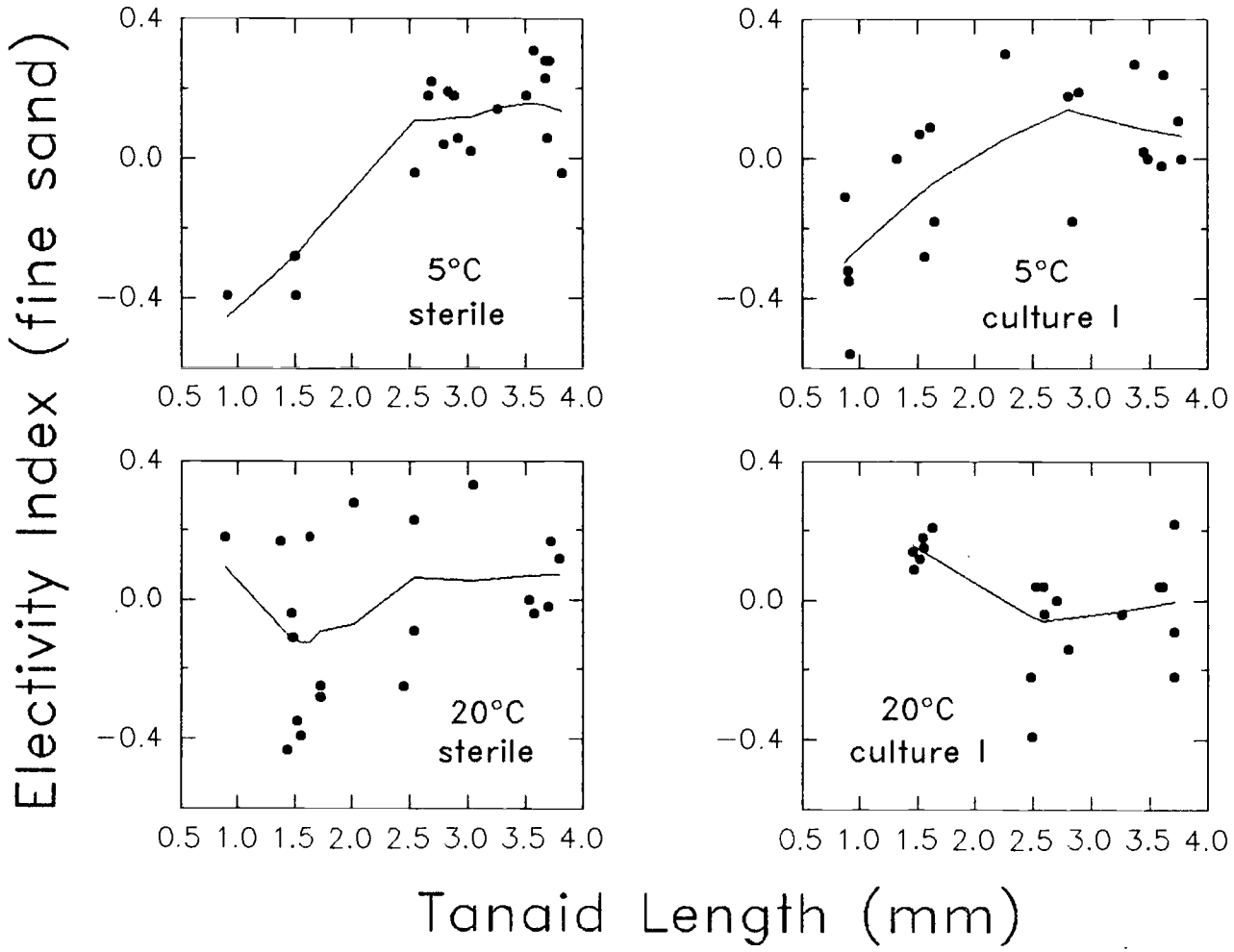

Electivity Index (fine sand)
0.4
0.0
−0.4
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
5°C
sterile
5°C
culture I
20°C
sterile
20°C
culture I
Tanaid Length (mm)

Fig. III.8

precultured with microbes.

Although E^* corrects mathematically for differences in particle availability, results may still be biased by differences in a tanaid's behavioral response. However, a second laboratory experiment conducted on 10 September 1990 corroborated the preceding results. In this experiment, there was no significant difference in the percent composition of silt-sized particles (mean = 18.2 ± 0.2% SE) between the sterile and precultured sediment mixes (Rank Sum Two Sample Test, P = 0.44, n = 4 slides, 100 grains per slide). For seven out of nine large tanaids in sterile sediment, the proportion of silt in tubes was 4% or less. In precultured sediment, the amount of silt in tubes of large tanaids varied from 5% to 23%. Results for these two sediment treatments were significantly different (Rank Sum Two Sample Test, P = 0.02, n = 9). Thus, the presence of microbes appears to increase the rate at which large tanaids incorporate silt into tubes. Silt comprised an average of 45.0% of the grains in the tubes of small tanaids in sterile sediment and 22.5 ± 7.8% in tubes built in sediment with microbes. I did not compare these means statistically because only two small tanaids built tubes in sterile sediment.

Fine sand comprised 11.8 ± 1.4% of the particles available in this latter experiment, with no significant difference in the availability of fine sand between the sterile and precultured sediment mixes (Rank Sum Two Sample Test, P = 0.25, n = 9). The overall mean percent fine sand in tubes built by large tanaids was 9.3 ± 2.0%, with no significant difference between sediment treatments. Thus, large tanaids used fine sand at a rate approximately equal to its availability. The mean percent fine sand in the tubes of small tanaids in sterile sediment was 5.0%, compared to 17.0 ± 10.9% in precultured sediment. As before, particle-size selection by small tanaids was not analyzed statistically because only two small tanaids built tubes in sterile sediment.

Neither the proportion of silt or fine sand in tubes built during the August 1989 field experiment was a function of tanaid length (Fig. III.9). This result is expected if, as observed in the laboratory experiment, electivity approaches zero as microbial densities increase. Although ambient microbial abundances were not measured during this experiment, mean epifluorescence counts of bacteria in samples from the field site varied from 1.0×10^9 to 3.6×10^9 cells g^{-1} dry wt between March 1988 and August 1989. Sediment chlorophyll *a* concentrations varied from 48 to 154 μg chl *a* g^{-1} AFDW over the same period (Figure III.10). Thus, it is likely that bacterial abundances in field sediments were two orders of magnitude higher and diatom stocks were one order of magnitude higher than those present in Culture I during the laboratory experiment.

Rate of Degradation of Tubes

The relationship between the wet weight and ash-free dry weight of tubes at t = 0 was estimated by the linear regression function

$$\text{AFD WT} = 0.00262 + 0.515\ (\text{WET WT})$$

($P < 0.001$, $r^2 = 0.98$). Within 7 d, tubes lost an average of 71.7 ± 14.4 (SD)% of their estimated initial ash-free dry weight. After 14 d, tubes appeared to be intact but disintegrated when rinsed on the sieve. Much of the organic matrix that held the mineral grains together had decomposed. After 1 mo, the tube fragments remaining in the dishes could not be distinguished from aggregates that had come in through the seawater line. The experiment was terminated at this time.

Model: Rates of Tube Building

The estimated bulk rate of tube building averaged approximately 350 g m^{-2} d^{-1} between January 1986 and December 1987 (Fig. III.11). In general, rates of tube building were higher after the fall reproductive burst than during spring, when smaller numbers of juveniles recruited into the population. The magnitude of the

Fig. III.9. Selection for coarse silt- and fine sand-sized particles for tube building by *L. dubia* in the field experiment. Selection is expressed as the arcsine square root-transformed proportion of a given particle size in each tube. Dashed lines represent the amounts of silt and fine sand available in field sediment.

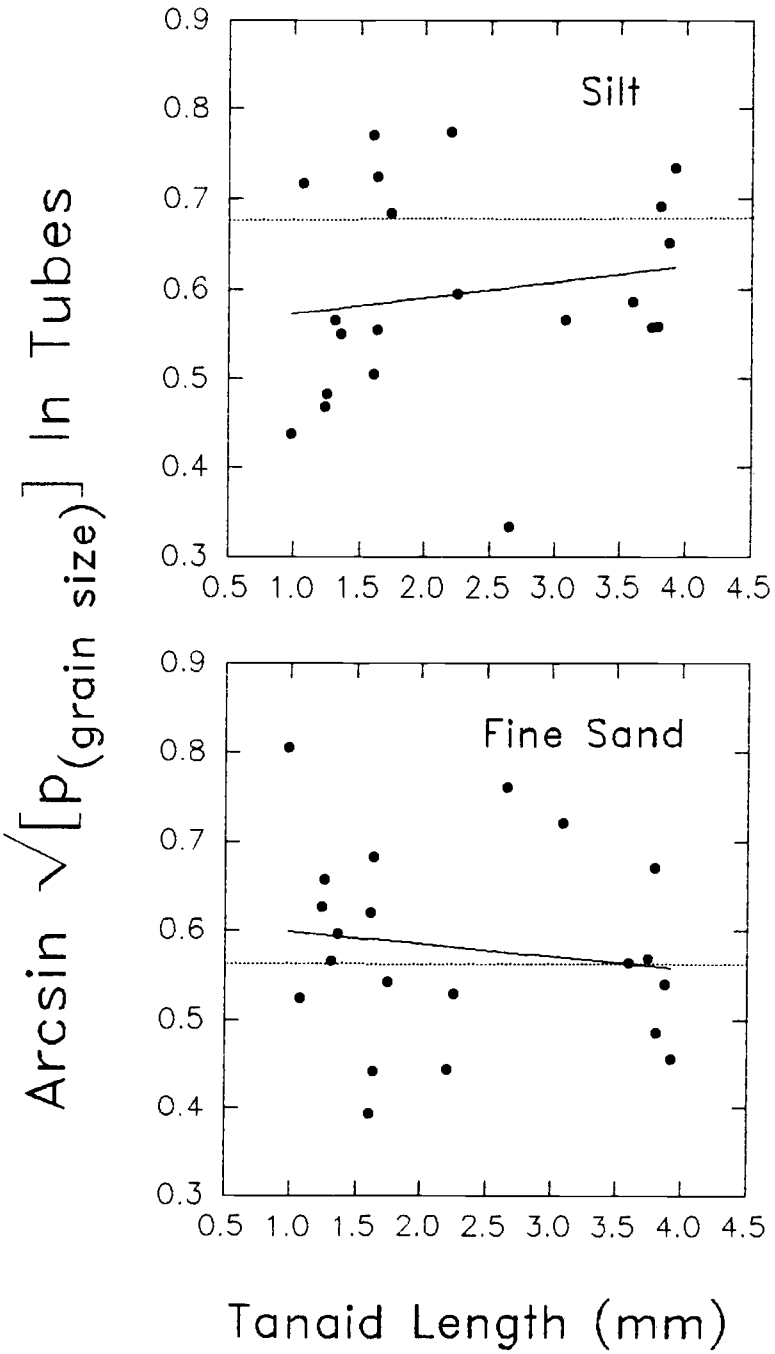

Silt
Fine Sand
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5
Arcsin √[p(grain size)] In Tubes
Tanaid Length (mm)

Fig. III.9

Fig. III.10. Mean (± 1 SE) bacterial densities (▼) and standing stocks of chlorophyll *a* (□) in sediments at the field site in Yaquina Bay, 1988-1989.

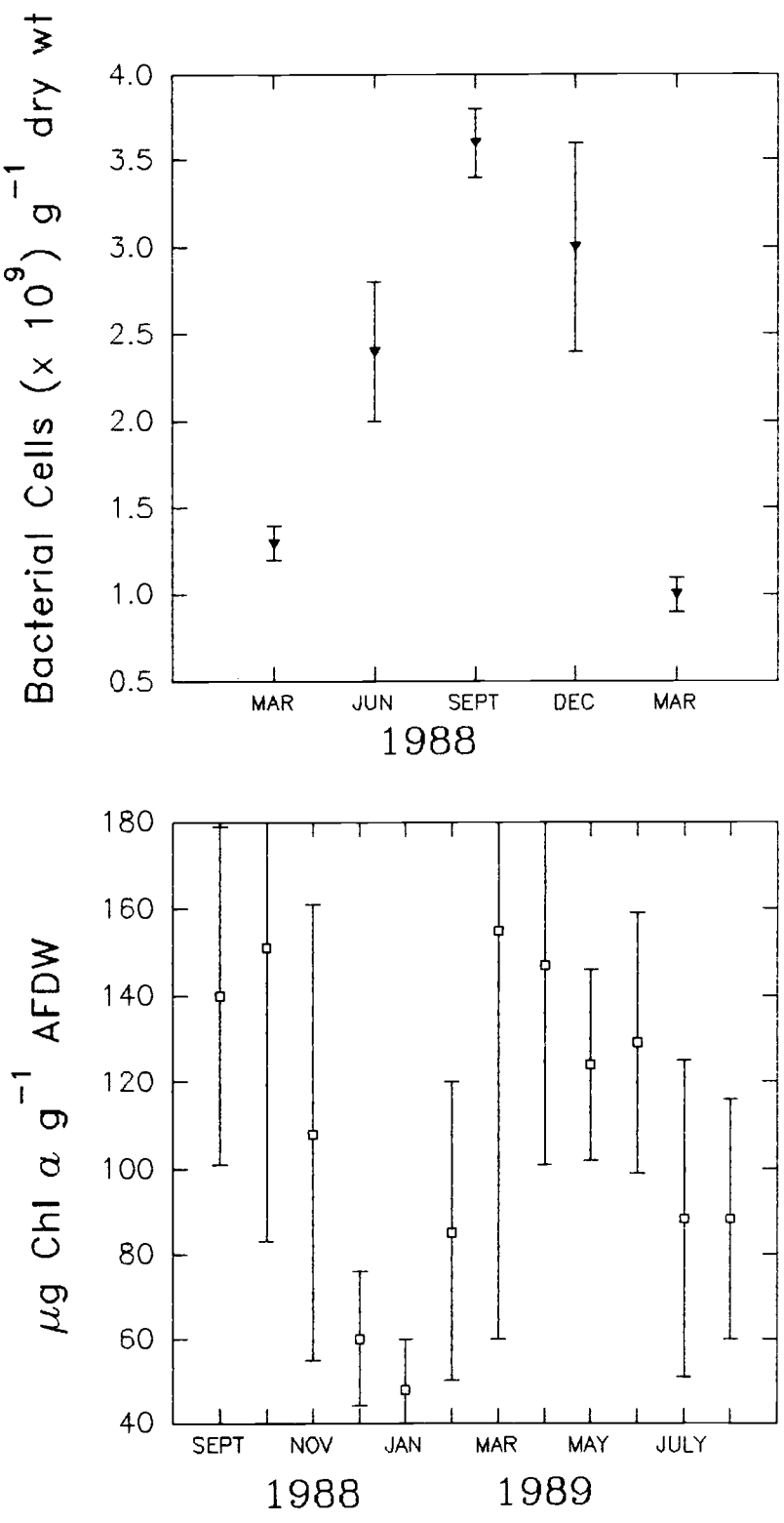

Bacterial Cells (x 10^9) g^{-1} dry wt
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
MAR
JUN
SEPT
DEC
MAR
1988
μg Chl a g^{-1} AFDW
180
160
140
120
100
80
60
40
SEPT
NOV
JAN
MAR
MAY
JULY
1988
1989

Fig. III.10

Fig. III.11. Estimated mean (± 1 SD) rates of tube building by the *Leptochelia dubia* field population at the study site in Yaquina Bay, 1986-1987. Estimates were derived using the model described in the text. The contribution of each cohort to the estimate on each date is indicated by pattern.

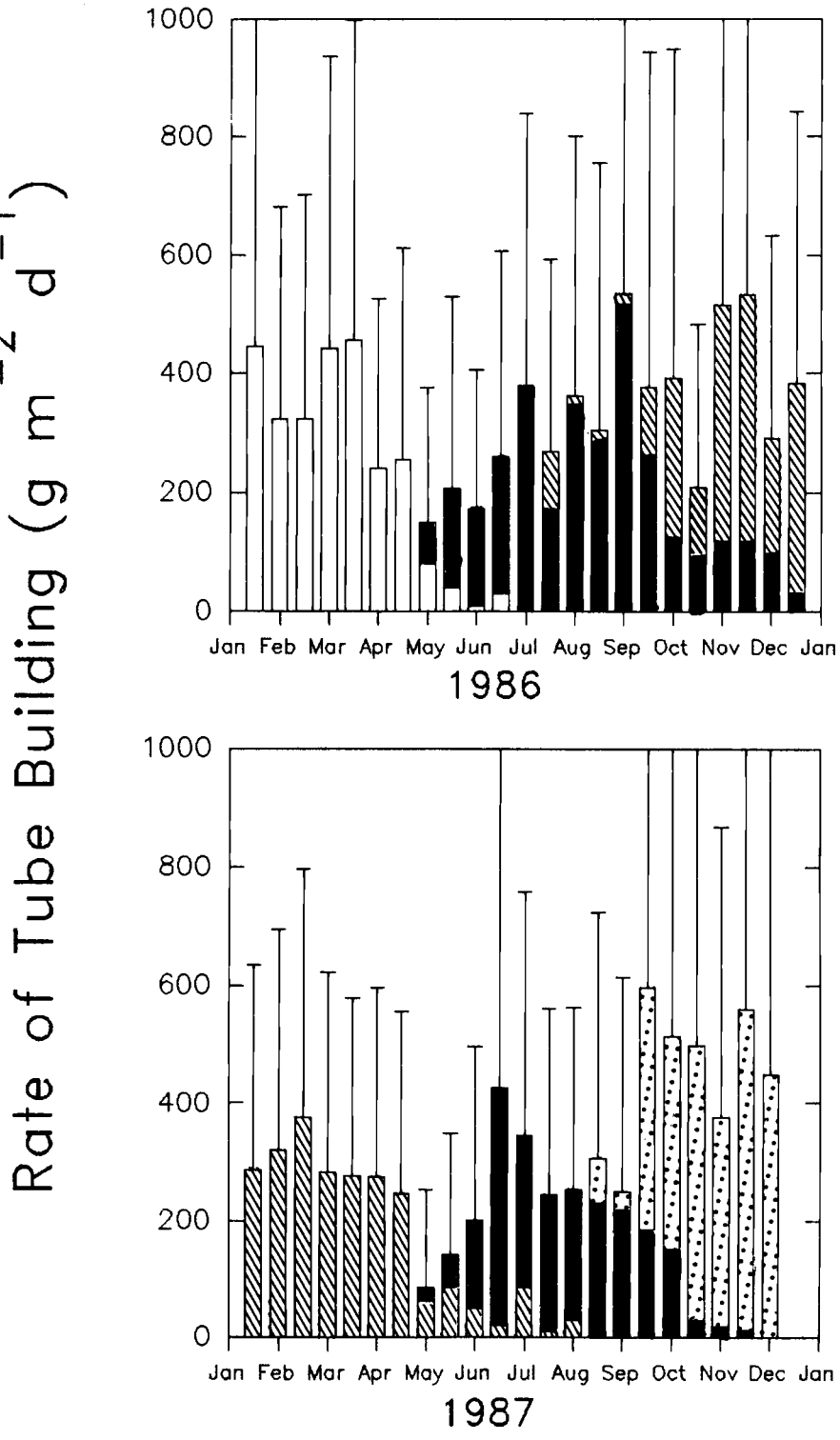

Rate of Tube Building (g m^{-2} d^{-1})
1000
800
600
400
200
0
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan
1986
1000
800
600
400
200
0
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan
1987

Fig. III.11

estimate of the standard deviation was approximately equal to that of the mean. The dominant source of variation was the variable "TANLEN" (i.e., tanaid length). A doubling of tanaid length, from 2.0 to 4.0 mm, increased the error associated with an estimate of the bulk rate of tube building by 16 times. In contrast, doubling either "PMEAN" or "DMEAN" increased the error of the estimate only four times.

The laboratory experiment on rates of degradation indicated that tubes lost an average of 71.6% of their initial ash free dry weight within seven days. In the field, the amount of tubes present at any given time is the result of the rate of production minus the rate of degradation. On average, the field population produces 2,450 g m^{-2} of tubes per week (i.e., 350 g m^{-2} d^{-1} x 7 d). If 71.6% of this production (1,754 g m^{-2}) is lost over the same period, the tanaids create a net production of 696 g AFDW m^{-2} wk^{-1}. Tanaids were observed, under the dissection microscope, to grab bits of the walls of adjacent tubes and incorporate them into their own. In this way, some tube material appears to be reinforced or protected from degradation. In the field, it appears that much of the upper 2 cm is incorporated into tubes at any one time (Fig. III.12).

Fig. III.12. *Leptochelia dubia* tubes at the edge of a tidal creek near the study site in Yaquina Bay. The pen points to the free ends of tubes, exposed as the sediment in between is winnowed away by the flow in the creek.

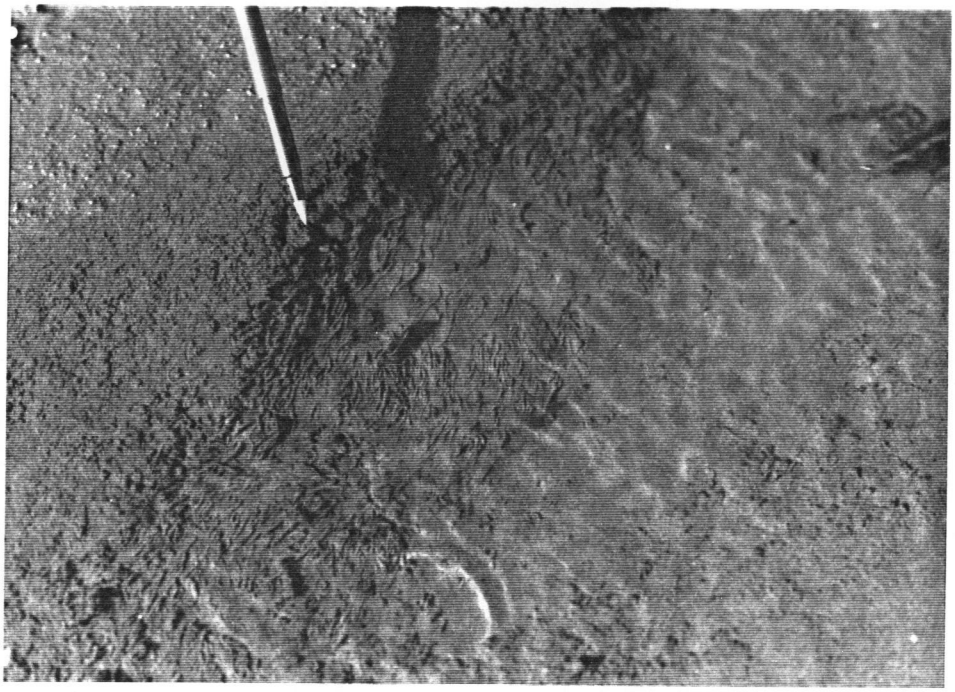


Fig. III.12

DISCUSSION

Rates of Tube Building

Although most *Leptochelia dubia* built one continuous tube, many dishes contained several fragments of tubes at the end of the 24 h incubation period. For this reason, and because I wanted to model the total weight of sediment bound by the field population, I measured tube production in units of weight, rather than length. Other authors have reported rates of tube building in units of length. Rates reported by Richards (1969) and Myers (1977) (Table III.8) were comparable to those observed in this experiment (casual observation). Mendoza's (1982) estimate, extrapolated from results obtained during the first hour of an experiment, was much higher. This disparity may indicate that the short term, initial rate of tube building is disproportionately high.

Although there are no comparable studies on rates of tube building by other chelicerate macrofauna, a number of field and laboratory studies have measured sediment-processing rates by deposit-feeding polychaetes and holothurians (Table III.9). In these cases, sediment reworking differs intrinsically from tube building by *Leptochelia*. These activities destabilize sediments by disaggregating grains whereas tube-building by tanaids stabilizes sediments against erosion. Bulk rates of sediment processing reported for polychaetes and holothurians comprise only 1 to 32% of the average rate (350 g m^{-2} d^{-1}) estimated for *L. dubia*. Thus, sediment processing by the tanaid population is a quantitatively important process.

In my experiments, rates of tube building increased with tanaid size. The error of a derived estimate of the bulk rate of tube building by the field population is also highly sensitive to tanaid size. Thus, the size-class distribution of the population is an important component of the tube building model. I also attempted to incorporate the effects of temperature and sediment-associated

Table III.8. Rates of tube building by *Leptochelia dubia* (in units of length) as reported by other authors.

Source	Particle Size-Class (μm)	Tube Len. (cm d^{-1})	Duration of Expt.
Richards (1969)	<74	4.0	3 d
	74-104	3.0	
	147-246	2.3	
	246-495	1.3	
Myers (1977)	("fine sand")	3.0	16.5 h
Mendoza (1982)	177-250	15.8	1 h

Table III.9. Rates of sediment reworking (g m^{-2} d^{-1}) by polychaetes and holothurians, as reported by other authors. "%" = Percent of bulk rate of tube building by *L. dubia*, this study.

Reference	Species	g m^{-2} d^{-1}	%
Polychaetes:			
Harkantra et al. (1989) Tomioka Bay, Japan	*Praxiella pacifica*	0.45	<1
Nichols (1974) Puget Sound, WA	*Pectinaria californiensis*	23	7
Hobson (1967) Puget Sound, WA	*Abarenicola pacifica* *A. claparedi vagabundi*	3.6 11	1 3
Rice et al. (1986) Flax Pond, ME	*Scoloplos robustus*	14-113	4-32
Holothurians:			
Hauksson (1979) Raunefjord, Norway	*Stichopus tremulus*	0.5	<1
Bakus (1973) tropics	*Holothuria atra* *H. difficilis* *H. vitens* (= *Bohadschia vitiensis*) *Stichopus moebii*	38 >2.7 5.2 37.3	11 >1 1 11

microbes into the model. Due to the significant interaction between temperature and sediment treatment in my experiment, I was unable to detect a main effect due to temperature or sediment treatment on rates of tube building. There is no clear explanation for the interaction between temperature and sediment treatment. The interaction may have been an artifact, caused by differences in the physiological condition of animals between experimental cells. Although I was careful to use only juveniles and female tanaids without oostegites or broods, there may have been other physiological or behavioral attributes of individual condition that biased activity.

The ANOVA comparisons of the slopes and intercepts of the regression equations derived from the laboratory rate of tube building experiment (Tables III.4 and III.5, respectively) indicate that the effect of temperature on rates of tube building was not significant. Two factors may explain this result. On a cloudless day, tanaids may experience a 10°C fluctuation in ambient temperature between high and low tide conditions. For example, during low tide on May 9, 1989, the temperature at the sediment surface at the study site averaged 20.1°C and that at a depth of 2 cm below the sediment surface averaged 19.7°C (n=12). The temperature of the water in the bay, measured approximately 500 m away at the R/V *Yaquina* dock, was 12.7°C (P. Henchman, Oregon State University, Hatfield Marine Science Center, Newport, OR, unpubl. data). Thus, the local population of *Leptochelia dubia* may be adapted to a wide range of temperature conditions.

Alternately, the lack of a significant effect of temperature on rates of tube building may have been due to poor control over this factor in the laboratory setup. The temperature in the culture dishes may have increased as much as 5°C when the lights were turned on (approximately 30 cm overhead) during the 12 h photoperiod. This observation was not quantified, however.

Particle-Size Selection

These experiments suggest an effect of the presence of microbes on the selection of silt-sized particles by large *Leptochelia dubia*, although the mechanisms of selection are not elucidated. My observations suggest that it is difficult for large tanaids to collect small, cohesionless particles from the substrate. The central gap in the chela of a large tanaid is wide enough that silt-sized grains easily slip through. However, when sediment is precultured with microbes, a large tanaid manipulates the organic film in which small particles are embedded. Thus, use of silts by large tanaids appears to be facilitated by the presence of microbes in the sediment mix.

Alternately, the frequency of occurence of small particles in tubes may be related to the availability of food. That is, when organic material is absent, as in sterile sediment, the tanaid may ingest small grains in "expectation" of digesting an adherent organic film. Where organic material is abundant, the tanaid may consume fewer of the small particles it encounters, incorporating a larger proportion into its tube. To further define the role of microbes, it will be necessary to determine whether *L. dubia* ingests silt-sized particles and whether the rate of ingestion of silts changes when microbes are present in the sediment mix.

This latter hypothesis implies a second active, rather than mechanical, particle-sorting capability. *Leptochelia* does appear to actively sort particles. Particles grasped by the gnathopods are passed to the maxillipeds, sorted, and then moved to the mouth (food) or to the pereopods (tube material). Miller (1984) provides a detailed description of post-capture particle sorting for amphipods of the genus *Corophium*. The first gnathopods transfer particles to the mouth where they are sorted by rapid motions of the maxillipeds and first and second maxillae and slower movements of the mandibles. Rejected particles are passed forward and brushed into the pleopodal

current or are swept posteriorly between the second gnathopods. Miller notes that post-capture sorting allows contact between sediment particles and potential chemosensory organs, permitting active selection on the basis of characteristics such as adsorbed substances and surface-attached microflora. *Corophium salmonis* have been shown to prefer glass beads coated with protein bovine serum albumin to uncoated beads (Taghon 1982).

In summary, I observed that the presence of microbes in sediments enhanced the rate of incorporation of silt-sized particles into tubes by large tanaids. I suggest that microbes influence the selection of small particles in two ways. First, adhesive films appear to enhance the tanaid's mechanical ability to collect small grains from the substrate. Second, microbes may provide textural or chemosensory cues by which tanaids actively allocate small particles to tube building versus feeding activities. In either case, the results of the present study demonstrate that microbes and tanaids can interact to enhance the stability of sediments in the field.

The significance of tube building by *Leptochelia dubia* lies, in large part, in the ubiquitous, world-wide distribution of this species and the densities it achieves in the field. Each individual binds only 1-20 mg of sediment per day but densities typically reached 100,000 individuals per square meter of sediment surface at the study site in Yaquina Bay. Smaller populations may be of less importance. At the site examined, *L. dubia*, in concert with the local microbial assemblage, may control the resuspension of particles through the benthic boundary layer. The bulk of the particles reaching the bottom appear to be bound into aggregates by microbial adhesives, woven into tubes, and stabilized against erosion (see Chapter IV).

IV. STABILIZATION OF SEDIMENTS BY SEDIMENT-ASSOCIATED MICROBES AND THE TUBICOLOUS TANAID CRUSTACEAN *LEPTOCHELIA DUBIA*

Sediment erodability is controlled by an interaction between the shear stress exerted on the bed by the overlying flow and the resistance of the particles which compose the bed to movement. Organisms can affect sediment erodability by altering the momentum of the fluid as it impinges on the bed, the exposure of particles to flow, adhesion between particles, and particle momentum (Jumars and Nowell 1984). These mechanisms are complex because the activities of macro-, meio-, and micro- fauna and flora all interact simultaneously. Some activities stabilize the bed while others lead to destabilization, with the *net* effect a greater or lesser rate of erosion (Jumars and Nowell 1984).

Historically, it has been difficult to distinguish the hydrodynamic effects of animal-produced structures from those of the ubiquitous mat-forming microbes with which they occur (Neumann et al. 1970, Yingst and Rhoads 1978, Luckenback 1986). Fager (1964) reported that subtidal sediments in La Jolla Bay were stabilized by aggregations of the tubicolous polychaete *Owenia fusiformis*, but in subsequent flume experiments by Eckman et al. (1981) sterile sediment was destabilized at all densities of *Owenia fusiformis* tubes tested. These authors suggested that, in the field, mucous binding by bacteria and filamentous algae compensates for the destabilizing effect of the tubes *per se*.

Owenia tubes are oriented vertically. Thus, their protrusion above the sediment surface provides a mechanism for entrainment of higher-velocity fluid to the bed and the creation of localized regions of enhanced shear stress (Eckman et al. 1981). Other species of macrofauna construct tubes that lie horizontally in the sediment. Little effort has been made to describe the effects of these tubes on sediment erodability, effects which are expected to be mediated by adhesion between particles rather than alteration of the near-bottom

flow regime. The ubiquitous tanaid crustacean *Leptochelia dubia* is an ideal test organism for a study of the erodability of sediments woven into a network of horizontal tubes. Laboratory and field studies of rates of tube building by *L. dubia* indicate that a field population in Yaquina Bay, OR, can bind 350 g dry sediment m^{-2} d^{-1}, securing particles with a mucous thread (Chapter III). *Leptochelia* tubes contain individual sand-sized particles and organic-mineral aggregates including silts and clays. The mucus that binds the aggregates together is thought to be derived from the extracellular secretions of bacteria and diatoms (DeFlaun and Mayer 1983, Grant et al. 1986).

In this study I compare the stabilization of sediments brought about by the tube-building activities of *L. dubia* with stabilization by components of the natural estuarine microbial flora with which the tanaid occurs. I used mass bedload transport rates, measured in a laboratory seawater flume, to compare the degree of sediment stabilization associated with several experimental treatments. I tested the behavior of sterile sediment, sediment cultured with estuarine bacteria and microalgae, and sediment cultured and then bound into tubes by *Leptochelia*. If the net effect of microbes and tanaids acting together is to stabilize sediments, the bedload transport rate of sediment precultured with microbes and bound into tubes should be lower than that of the other sediment treatments. Under the shear stress applied in these experiments, the bedload transport rate of sediment precultured with microbes was 95% less than that of sterile sediment. When tanaids were allowed to build tubes in precultured sediment, no transport could be detected.

METHODS

"Sterile" and "precultured" sediments were produced by ashing foundary sand and innoculating it with mobile, epipelic diatoms and associated bacteria, as described in Chapter III. Subsamples of the experimental sediments were spooned into 160-mm diameter glass petri dishes. Dishes containing sediments with microbes were allowed to sit under the culture lights for three days before testing in the laboratory flume. For the "cultured sediments with tanaids" treatment, 3,500 *Leptochelia dubia* were added to each petri dish, equivalent to a density of 174,000 m^{-2}, observed in sediments collected from Yaquina Bay during August 1986 (Chapter II). Dishes containing cultured sediments and tanaids were also left under the culture lights for three days so that the tanaids could build a network of tubes before the material was tested in the flume.

The flume was a straight flow-through channel, 4.4 m long, similar to that described by Muschenheim et al. (1986). Adjustable exit gates controlled flow rate and water depth. The core-box was fitted with an acrylic top that lay flush with the bed of the flume. A circular hole in the top, lined with a flexible silicon gasket, permitted emplacement and removal of a 160-mm diameter petri dish filled with the experimental sediment.

At the beginning of a run, with the exit gates open only 1.0 cm, the flume was slowly filled with seawater from Yaquina Bay. Seawater flowed from a constant head tank and was prefiltered to remove particles larger than 63 μm. When the flume was filled to a depth of approximately 13 cm, I opened the exit gates to 6.3 ± 0.2 cm. Flow depth dropped to approximately 4.7 cm over the petri dish and stayed at that level for the rest of the run. Particles transported as bedload were vacuumed up along a 15.0 cm-long line, perpendicular to the direction of flow, 2.0 cm downstream from the trailing edge of the petri dish. Vacuum sweeps were made at a rate of 35 min^{-1} along this line for 12.0 min. I collected water and

particles in a 24-l glass carboy, prewashed with 10% nitric acid and rinsed with distilled water. At the end of the collection period, the carboy was allowed to stand for 10 min so that particles ≥ 32 μm diameter settled to the bottom (Wills 1988). Water was then vacuumed back out of the carboy and through a preweighed Whatman #41 paper filter. I dried the filters to constant weight at 60°C and weighed them to the nearest 0.1 mg.

On three separate dates (29-31 August, 1990), I conducted blank runs which permitted me to correct erosion rates for particles which entered the flume through the seawater lines. During these runs, I followed the procedures described above except that particles were collected along a 15.0-cm long line 45 mm *up*stream from the petri dish containing the experimental sediment.

The bottom shear stress imposed by the flow was calculated from the formula of Henderson (1966, p.91):

$$\tau_o = \gamma R S$$

where:

τ_0 = shear stress at the solid boundary (g cm^{-1} s^{-2})

γ = specific weight of the fluid (10^3 g cm^{-2} s^{-2})

R = hydraulic mean radius = area ÷ wetted perimeter of a cross-section of the flow over the petri dish (cm)

S = longitudinal slope of the flume
= dH/dx (dimensionless)

where:

$$H = y + z + \frac{v^2}{2g}$$

H = total energy (cm)

y = change in height of the water surface over a distance (x) along the bed of the flume (cm)

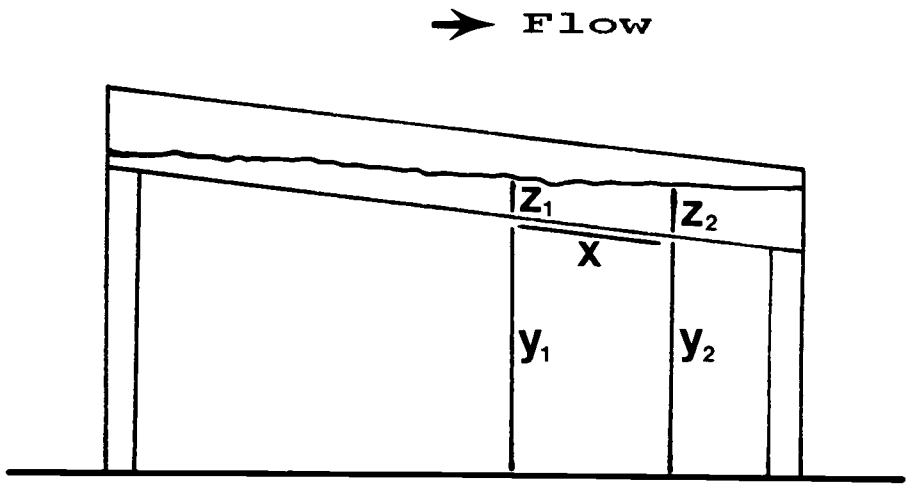
z = change in height of the bed of the flume above a datum over the distance x (cm)
v = velocity of the fluid (cm s^{-1})
g = acceleration due to gravity (cm s^{-2}).

Given the hydrodynamic conditions under which these experiments were conducted (Figure IV.1), a change in velocity of 1.4 cm s^{-1} over a distance along the bed of 150 cm would result in a 1% change in H (total energy). Although some reduction in flow velocity due to friction along the bed of the flume was expected, the loss was probably no greater than 2 cm s^{-1}. Thus, the term $v^2/2g$, was neglected and total energy was calculated as H = y + z.

Precultured sediments were subsampled for estimates of microbial standing stocks. I estimated standing stocks of both bacteria and microalgae by direct counts using epifluorescence microscopy (Fry 1988). Samples were prepared for counting following the procedure described by Montagna (1982). Very few epipelic diatoms could be seen when subsamples were examined under a dissection microscope at 400X. Diatoms from the field innoculum were probably cropped by meiofaunal grazers. In fact, several small nematodes and harpacticoid copepods were observed in the cultures. Nonetheless, the sediment was rich in biogenic adhesives as evidenced by the clumping of particles.

Fig. IV.1. Diagram (side view) of the seawater flume used in the laboratory bedload transport experiments. The dimensions x, y_1, y_2, z_1, and z_2, used in calculation of bottom shear stress (τ_0) are indicated.

SEAWATER FLUME:



e.g., if

$x = 150$ cm
$y_1 = 3.3$ cm
$y_2 = 4.4$ cm
$z_1 = 64.4$ cm
$z_2 = 63.2$ cm

then:

$$dH/dX = (-1.1 + 1.2) = 0.1$$

Fig. IV.1

RESULTS

Standing stocks of bacteria and diatoms in precultured sediments averaged $2.3 \times 10^8 \pm 1.6 \times 10^8$ (SD) g^{-1} and $2.0 \times 10^6 \pm 1.4 \times 10^6$ g^{-1} dry weight, respectively. Quarterly samples taken from a field site in Yaquina Bay between March 1988 and March 1989 (Chapter II) contained an average of $2.3 \times 10^9 \pm 1.1 \times 10^9$ bacteria g^{-1}.

Bottom shear stress, τ_0, averaged 5.0 ± 1.07 g cm^{-1} s^{-2}. Roughness Reynolds number was calculated as

$$Re_* = \frac{(u_*)\ (k_s)}{\nu}$$

where:

u_* = shear velocity = $(\tau_0/\rho)^{\frac{1}{2}}$

τ_0 = 5.0 ± 1.1 g cm s^{-2}

ρ = fluid density (1.025 g cm^{-3})

k_s = characteristic roughness length = mean particle diameter (0.090 cm)

υ = kinematic molecular viscosity (1.4×10^{-2} cm^2 s^{-1}).

According to these calculations, the roughness Reynolds number averaged 14.1, indicating transition conditions between hydraulically smooth and fully turbulent flow over the bed in the test section of the flume.

Bedload transport rate was calculated as

$$q_s = \frac{m}{At}$$

where:

q_s = bedload transport rate

m = mass of particles transported as bedload (μg)

A = area of the petri dish (201.1 cm^2)

t = collection period (12 min).

At the imposed shear stress of $u_* = 2.2$ cm s^{-1}, slightly higher than that required to erode sterile sediment, the mean bedload transport rate of sterile sediment was 84.2 μg cm^{-2} min^{-1} (Table IV.1). When sediment was precultured with microbes, bedload transport fell to 4.3 μg cm^{-2} min^{-1}. When tanaids were allowed to build tubes in sediment precultured with microbes, no bedload transport could be detected. Thus, under the hydraulic conditions imposed in the laboratory flume, tube building by *Leptochelia dubia* and the adhesive secretions of a natural estuarine microbial flora interact to stabilize sediments against erosion.

The fourth potential treatment combination, sediment containing tanaids but not precultured with microbes, was not tested. It was not feasible to clean 3,500 tanaids of all the detritus (and microbes) adhering to their legs and antennae. Thus, any treatment containing that number of tanaids also contained bacteria and microalgae. I anticipated that these microbes would have bound the tubes to the adjacent sediment during the three day period before the dish was tested in the flume. Observations of dishes containing smaller numbers of tanaids that had been cleaned of much of the adherent detritus showed that the sediment between tubes was scoured away by the flow but that the tubes remained intact.

Table IV.1. Mean (± 1 SD, n=6) bedload transport rates for experimental sediments, corrected for particles in the seawater line. All three treatments were significantly different (P = 0.05) as determined by Least Significant Difference pairwise comparisons.

Treatment	$\bar{X}$	SD
	$\mu g\ cm^{-2}\ min^{-1}$	
Tanaids + Microbes	0	-
Microbes	4.3	2.20
Sterile Sediment	84.2	73.22

DISCUSSION

The stabilization of sediments by *Leptochelia dubia* and microbes, as observed in this study, appears to be a complex process. When tanaids acted alone, tubes persisted, even under the high bottom shear stresses observed in the field. Material between the tubes was scoured away. Thus, the net effect of tubes alone depends on the extent to which the bed is incorporated into these structures. The tanaid population can bind 150-600 g dry sediment m^{-2} d^{-1} into tubes (Chapter III). This would represent the construction of a monolayer of tubes (1 mm deep) occupying 3-12% of the surface area of the flats each day or a net production equal to 15% of the surface area of the flats per week. Under the hydrodynamic conditions created in the flume (τ_0 slightly greater than τ_{crit}), microbes alone stabilized the surface of the bed. Stabilization was enhanced, albeit slightly, when tanaids and microbes acted together.

Similar processes have been described by other authors. *Corophium volutator* and *Nereis diversicolor* bind grains with thread-like secretions, 1-2 μm in diameter (Meadows et al. 1990). The mucous strands originating from bacteria, benthic diatoms, fungi, and protozoa are commonly seen in field sediments (Figure IV.2 and Drum and Webber 1966, Grant et al. 1986). As bacteria grow, cells divide within a mucopolysaccharide film, the "glycocalyx" (Costerton et al. 1985). Individual microcolonies eventually coalesce, gluing grains together. This activity increases the resistance of the bed to erosion (Grant and Gust 1987). Grant et al. (1986) describe the response of natural sediments to flow in their laboratory flume. As flow increased, organic-mineral aggregates composed of clay particles, amorphous detritus, and settled phytoplankton began to vibrate. Grains broke away, but without changing the ultrastructure of the bed. It was not until the bottom shear stress was high enough to induce mass transport that the adhesive bonds between grains were severed, leaving portions of strands behind. Thus, the combined activities of tubicolous infauna, diatoms, and bacteria can transform

Fig. IV.2. Scanning electron micrograph of organic coatings and mucus strands associated with field sediments from the intertidal study area in Yaquina Bay. Magnification is 2,000X. White scale bar represents 10 μm.

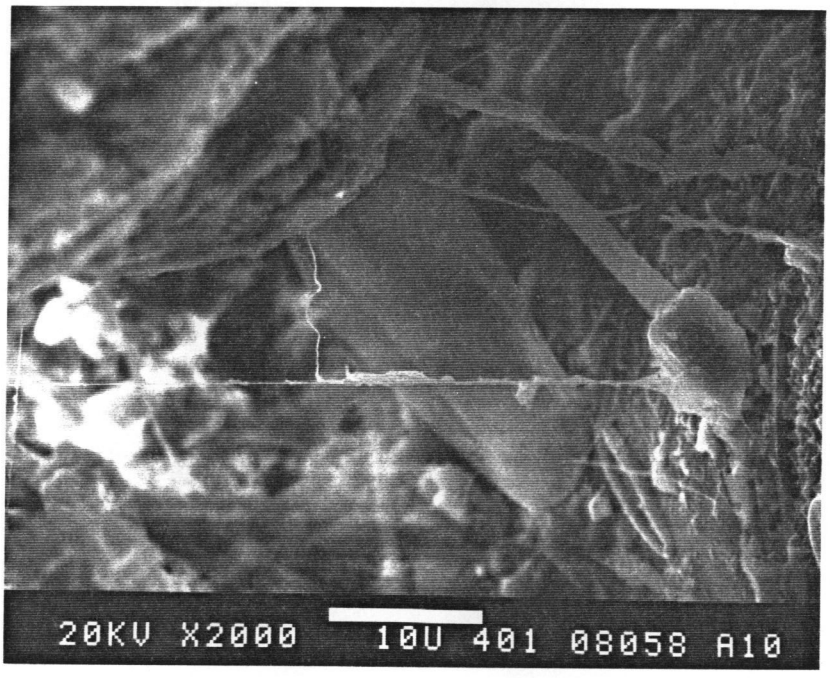


Fig. IV.2

individual particles of sediment into a fabric of great intrinsic strength.

Flume experiments in the present study used laboratory cultures, derived from field innocula, rather than natural sediments. This approach was chosen so that the adhesives in the experimental sediments could be attributed to microbes and tanaids, not to other macro- or meiofaunal organisms. It is possible that the growth forms of the microbial assemblages which developed in the laboratory may have made them more or less vulnerable to scour than those present in the field. However, lab and field studies by many authors (e.g., Neumann et al. 1970, Holland et al. 1974, Frostick and McCave 1977, Yingst and Rhoads 1978, de Boer 1981, Grant et al. 1986, Patterson 1989) indicate that the effect of microbes is likely to be in the direction of increased stabilization of sediments.

My results appear to confirm the predominant role of microbes in sediment stabilization, at least at shear stresses near τ_{crit}. In this study, tanaids further secured the mat with their own secretions. Tanaids may also contribute indirectly to sediment stabilization via effects on rates of microbial production. Not only do *Leptochelia* tubes provide a stable surface for the attachment and growth of cells, tanaid secretions and waste products are potential substrates for growth. In addition, ventilation of tubes extends the depth of the oxygenated layer deeper into the sediment. Further research should focus on the importance of these interactive mechanisms in the stabilization of sediments.

V. SUMMARY

Tube building by *Leptochelia dubia* may be an important process in the stabilization of sediments. At an intertidal site in Yaquina Bay, the tanaid population is estimated to bind an average of 350 g dry sediment m^{-2} d^{-1} into tubes. Given rates of degradation measured in the laboratory, net tube production approximates 700 g m^{-2} wk^{-1}.

Tanaid size, the size-class structure of the population, and the density of the field population were all important determinants of the bulk rate of tube building. The *Leptochelia* population in Yaquina Bay demonstrated a biannual life cycle, with one cohort in the spring and one in the fall. Densities fell as low as 30,000 m^{-2} over winter, before the release of the spring cohort, and rose to 300,00 m^{-2} after the release of the second cohort in the fall. Rates of tube building by the population were highest as large numbers of juveniles recruited from the fall cohort into the tube building population.

Rates of tube building and particle-size selection were also affected by the presence of microbes in the sediment mix. The presence of bacteria and sediment-associated microalgae significantly increased the intercept of the regression equation for the rate of tube building as a function of tanaid length. The mechanism by which this effect was mediated was not determined in these experiments.

The presence of microbes also appeared to increase the rate at which silt-sized particles were incorporated into tubes by large tanaids. An analogous effect, i.e., an increase in the incorporation of fine sand into tubes by small tanaids, was also observed but could not be confirmed by a second experiment. Microbes may influence particle selection for tube building by changing the handling characteristics of particles or by providing chemosensory clues which alter the way in which *Leptochelia* allocates particles to tube building *versus* feeding. Further research will be needed to

differentiate between these two mechanisms.

Experiments conducted in a laboratory seawater flume confirmed the dominant role of microbes in sediment stabilization. At an imposed shear stress of 5.0 g cm^{-1} s^{-2}, microbes reduced bedload transport to 5% of that observed for sterile sediments. When tanaids were permitted to build tubes in sediments precultured with microbes, no bedload transport could be detected. At higher flow rates, as observed in a tidal creek in Yaquina Bay, the role of tanaids appears to increase in importance. Material between the tubes, albeit made adhesive by microbes, is scoured away, leaving a mop-like fringe of tanaid tubes which are more resistant to erosion.

The overall importance of the tube-building activities of *Leptochelia dubia* to particle flux in Yaquina Bay has yet to be determined. Ubiquitous sediment-associated microbes clearly play an important role, both singly and in concert with the tanaid population. Other macrofauna also remove particles from the water column and sediment surface through extensive feeding activities. These species repackage sediments as larger agglomerations of particles in fecal pellets, inhibiting resuspension. However, as indicated by a review of sediment processing rates by several species of polychaetes and holothurians, tube building by *Leptochelia dubia* is, quantitatively, a more important process.

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APPENDIX

APPENDIX A

Model - Rates of Tube Building by the Field Population

```
*************************************************
RATES OF TUBE BUILDING BY LEPTOCHELIA POPULATION
          SAS, VERSION 6.03
*************************************************************;
OPTIONS PAGESIZE=200;
LIBNAME B 'A:';
FILENAME LEPT 'a:lengths.txt';
FILENAME DENS 'a:DENSITY.txt';
FILENAME DATE 'a:DATES.txt';
*************************************************
INPUTS FILE "LEPT" WITH DATE CODE, SUBSAMPLE NUMBER, TOTAL NO.
OF INDS, AND NO. OF INDS. IN EACH OF 19 SIZE-CLASS INTERVALS
*************************************************************;
DATA
JUV;
 INFILE LEPT MISSOVER;
 INPUT Dtcode SET TOTAL L1 - L19;
RUN;
*************************************************
ESTIMATES THE MIDPOINT OF EACH SIZE-CLASS INTERVAL
*************************************************************;
DATA
JU;
 SET JUV;
 ARRAY LEN{19} L1 - L19;
  DO LNT= 1 TO 19 BY 1;
   NUM=LEN{LNT};
   LENGTH= (LNT * .2) + 1.1;
   OUTPUT;
  END;
KEEP DTCODE TOTAL SET LENGTH NUM;
RUN;
*************************************************
CALCULATES THE PROPORTION OF THE TOTAL POPULATION IN EACH
SIZE-CLASS INTERVAL ON EACH SAMPLING DATE, TRANSFORMS DATA TO
ARCSINE √PROPORTION
*************************************************************;
DATA
JU;
  SET JU;
  RAWPCT=NUM/TOTAL;
  ARPCT=ARSIN((RAWPCT**.5));
 PROC SORT DATA=JU;
  BY DTCODE LENGTH;
RUN;
```

```
*****************************************************
CALCULATES THE MEANS AND VARIANCES OF THE TRANSFORMED
PROPORTIONS FOR EACH SIZE-CLASS INTERVAL ON EACH
SAMPLING DATE
*************************************************************;
PROC
MEANS DATA=JU NOPRINT;
 BY DTCODE LENGTH;
 VAR ARPCT;
 OUTPUT OUT=varPCT MEAN=PMEAN var=Pvar;
RUN;
*****************************************************
BACK-TRANSFORMS   MEANS   AND   VARIANCES   TO   PROPORTIONS
*************************************************************;
data meanpct;
  set varPCT;
  PMEAN=(SIN(PMEAN))**2;
  PVAR=(SIN(PVAR))**2;
RUN;
*****************************************************
INPUTS FILE "DENSITY" - WITH POPULATION DENSITIES ON EACH
SAMPLING DATE
*************************************************************;
 DATA
DENSIT;
 INFILE DENS MISSOVER;
 INPUT DTCODE DENSITY;
 PROC SORT DATA=DENSIT;
 BY DTCODE;
RUN;
*****************************************************
CALCULATES MEAN AND VARIANCE OF REPLICATE ESTIMATES OF
DENSITY FOR EACH SAMPLING DATE
*************************************************************;
PROC
MEANS DATA=DENSIT NOPRINT;
 BY DTCODE;
 OUTPUT OUT=DENSITY MEAN=DMEAN VAR=DVAR;
RUN;
*****************************************************
INPUTS FILE "DATE" - WITH DATES AND DATE CODES
*************************************************************;
DATA
DATE;
 INFILE DATE MISSOVER;
 INPUT DATE MMDDYY. DTCODE;
 RUN;
 PROC SORT DATA=DATE;
 BY DTCODE;
RUN;
*****************************************************
MERGES FILES CONTAINING (1.) MEANS AND VAR'S OF PROPORTIONS OF
TOTAL POP. IN EACH SIZE-CLASS INTERVAL ON EACH SAMPLING
DATE, (2.) SAMPLING DATES, AND (3.) MEANS AND VAR'S OF POP.
```

```
DENSITIES ON EACH SAMPLING DATE
************************************************************;
DATA
LEP;
 MERGE MEANPCT DATE DENSITY;
 BY DTCODE;
RUN;
*****************************************************
CALCULATES CTUBEWT FROM THE ABOVE AND THE REGRESSION FOR
RATE OF TUBE BLDG VS. TANAID LENGTH
************************************************************;
DATA
LEPTO;
 SET LEP;
 FORMAT DATE DATE8.;
 TUBEWT=((LENGTH*0.02)   )**2;
 CTUBEWT=TUBEWT*DMEAN*(PMEAN);
*****************************************************
CALCULATES AN ESTIMATE OF VARIANCE FOR EACH ESTIMATE OF
CTUBEWT
************************************************************;
 PROPERR = (((.04*(LENGTH**2)*DMEAN*PMEAN)**2)*1.02E-4)
   + (((.004*2*LENGTH*PMEAN*DMEAN)**2)*1.96E-3)
   + (((((.02*LENGTH)**2)*PMEAN)**2)*DVAR)
   + (((((.02*LENGTH)**2)*DMEAN)**2)*PVAR);
*****************************************************
IDENTIFY COHORTS (BY LENGTH) ON EACH SAMPLING DATE
************************************************************;
COHORT = 9;
LENGTH = LENGTH - 0.1;
IF (DATE <= '20APR86'D) THEN COHORT = 1;
IF ('15MAY86'D >= DATE >= '01MAY86'D) AND (LENGTH GE 2.6) THEN
     COHORT = 1;
IF ('14JUN86'D >= DATE >= '29MAY86'D) AND (LENGTH GE 2.8) THEN
     COHORT = 1;
IF (DATE = '27JUN86'D) AND (LENGTH GE 3.2) THEN COHORT = 1;
IF ('15MAY86'D >= DATE >= '01MAY86'D) AND (LENGTH LT 2.6) THEN
     COHORT = 2;
IF ('14JUN86'D >= DATE >= '29MAY86'D) AND (LENGTH LT 2.8) THEN
     COHORT = 2;
IF (DATE = '27JUN86'D) AND (LENGTH LT 3.2) THEN COHORT = 2;
IF ('07AUG86'D >= DATE >= '09JUL86'D) THEN COHORT = 2;
IF ('05SEP86'D >= DATE >= '23JUL86'D) AND (LENGTH GE 2.1) THEN
     COHORT = 2;
IF ('05SEP86'D >= DATE >= '23JUL86'D) AND (LENGTH LT 2.1) THEN
     COHORT = 3;
IF (DATE = '23SEP86'D) AND (LENGTH GE 2.4) THEN COHORT = 2;
IF (DATE = '23SEP86'D) AND (LENGTH LT 2.4) THEN COHORT = 3;
IF ('01NOV86'D >= DATE >= '15OCT86'D) AND (LENGTH GE 3.1) THEN
     COHORT = 2;
IF ('01NOV86'D >= DATE >= '15OCT86'D) AND (LENGTH LT 3.1) THEN
     COHORT = 3;
IF ('13DEC86'D >= DATE >= '13NOV86'D) AND (LENGTH GE 3.2) THEN
     COHORT = 2;
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IF ('13DEC86'D >= DATE >= '13NOV86'D) AND (LENGTH LT 3.2) THEN
     COHORT = 3;
IF ('10JAN87'D >= DATE >= '29DEC86'D) AND (LENGTH GE 4.0) THEN
     COHORT = 2;
IF ('10JAN87'D >= DATE >= '29DEC86'D) AND (LENGTH LT 4.0) THEN
     COHORT = 3;
IF ('26FEB87'D >= DATE >= '27JAN87'D) THEN COHORT = 3;
IF (DATE = '12MAR87'D) AND (LENGTH GE 1.5) THEN COHORT = 3;
IF (DATE = '12MAR87'D) AND (LENGTH LT 1.5) THEN COHORT = 4;
IF ('10APR87'D >= DATE >= '29MAR87'D) THEN COHORT = 3;
IF ('29MAY87'D >= DATE >= '13MAY87'D) AND (LENGTH GE 3.1) THEN
     COHORT = 3;
IF ('29MAY87'D >= DATE >= '13MAY87'D) AND (LENGTH LT 3.1) THEN
     COHORT = 4;
IF ('15JUL87'D >= DATE >= '11JUN87'D) AND (LENGTH GE 3.4) THEN
     COHORT = 3;
IF ('15JUL87'D >= DATE >= '11JUN87'D) AND (LENGTH LT 3.4) THEN
     COHORT = 4;
IF (DATE = '30JUL87'D) AND (LENGTH GE 4.0) THEN COHORT = 3;
IF (DATE = '30JUL87'D) AND (4.0 GT LENGTH GT 1.5) THEN COHORT
     = 4;
IF (DATE = '30JUL87'D) AND (LENGTH LT 1.5) THEN COHORT = 5;
IF ('25AUG87'D >= DATE >= '10AUG87'D) AND (LENGTH GE 4.1) THEN
     COHORT = 3;
IF ('25AUG87'D >= DATE >= '10AUG87'D) AND (4.1 GT LENGTH GT
     2.0) THEN COHORT = 4;
IF ('25AUG87'D >= DATE >= '10AUG87'D) AND (LENGTH LT 2.0) THEN
     COHORT = 5;
IF (DATE = '09SEP87'D) AND (LENGTH GE 4.5) THEN COHORT = 3;
IF (DATE = '09SEP87'D) AND (4.5 GT LENGTH GT 3.0) THEN COHORT
     = 4;
IF (DATE = '09SEP87'D) AND (LENGTH LT 3.0) THEN COHORT = 5;
IF ('21OCT87'D >= DATE >= '05OCT87'D) AND (LENGTH GE 3.5) THEN
     COHORT = 4;
IF ('21OCT87'D >= DATE >= '05OCT87'D) AND (LENGTH LT 3.5) THEN
     COHORT = 5;
IF ('18NOV87'D >= DATE >= '02NOV87'D) AND (LENGTH GE 4.1) THEN
     COHORT = 4;
IF ('18NOV87'D >= DATE >= '02NOV87'D) AND (LENGTH LT 4.1) THEN
     COHORT = 5;
IF (DATE = '12DEC87'D) AND (LENGTH GE 5.0) THEN COHORT = 4;
IF (DATE = '12DEC87'D) AND (LENGTH LT 5.0) THEN COHORT = 5;
LENGTH = LENGTH + 0.1;
RUN;
```