Northeast Gulf Science

12-1994

Influences of Larval Settlement Location and Rate on Later Growth and Mortality in a Sessile Marine Invertebrate Population (*Spirorbis spirillum*)

Joseph M. Dirnberger
University of Texas at Austin

Recommended Citation

INFLUENCES OF LARVAL SETTLEMENT LOCATION AND RATE ON LATER GROWTH AND MORTALITY IN A SESSILE MARINE INVERTEBRATE POPULATION (*Spirorbis spirillum*)

Joseph M. Dirnberger[1]
Marine Science Institute
The University of Texas at Austin
Port Aransas, TX 78373

ABSTRACT: Planktonic larvae of the tube-building polycheate *Spirorbis spirillum* (Linnaeus) settle abundantly along seagrass blades of *Thalassiaa testudinum* Banks ex Konig in bays of the northern Gulf of Mexico. Detailed demographic parameters of settled individuals were measured *in situ* by using biological stains that mark the leading margin of tubes containing living *S. spirillum* and this method yielded similar results when compared with independent estimates of settlement rate, growth, and mortality. Larvae tended to settle near the base of growing seagrass blades and subsequent survivorship and tube growth were highest for individuals nearest the base. Survivorship that is positively affected by settlement location and not negatively affected by the density of conspecifics suggests that temporal changes in settlement can have a significant influence on benthic population size over time. This was suported by a positive correlation between population size and settlement and suggests that local extinction is potentially less likely to occur because planktonic larvae may be transported distances greater than the scale of ecological processes acting on the benthic stage.

In marine sytems, the arrival of new individuals via planktonic spores and larvae often varies dramatically from place to place and time to time (e.g. Caffey 1985). It has been proposed that understanding such variation may be necessary to explain the outcome of competitive and predator-prey interactions within benthic communities (Underwood and Denley 1984). If transport processes significantly influence post-settlement population dynamics, then post-settlement distributions should be correlated with temporal and spatial settlement patterns rather than mortality patterns occurring after settlement. Vertical distribution of barnacle settlers can reflect vertical distribution of planktonic larvae in the water column (Grosberg 1979) and vertical distribution of adults can reflect distribution of settlers (Denley and Underwood 1979; Watanae 1984). In contrast, post-settlement mortality can cause spatial distributions to diverge from initial settle-

ment distribution, in bryozoans due to predation by fish (Keough and Downes 1982) and in bivalves due to undertermined sources of mortality (Luckenbach 1984; Peterson 1986).

The influence of settlement location on post-settlement population distributions should be especially strong where individuals settle at sites that enhance future growth and survival. Some larval invertebrates avoid settling at sites where future mortality is high (Grosberg 1981, Davis 1987) and future growth is low (Burshek 1988). The influence of settlement on post-settlement population distributions should be weaker where mortality is positively dependent on density, damping changes in population size caused by fluctuations in settlement rate over time. Barnacle populations exhibit density-dependent mortality at sites with high settlement rates, though not at sites with low settlement rates (Connell 1985; Gaines and Roughgarden 1985).

This study examines whether settlement location of the planktonic larvae of

[1]Present Address: Department of Biology, Kennesaw State College, Marietta, Georgia 30061

65

Spirorbis spirillum (Linnaeus) along grow-ing seagrass blades of *Thalassia testudinum* Banks ex Konig influences later growth and mortality and, if so, whether settlement sites represent better areas for growth and survivorship. A technique is described for following detailed demographic parameters (settle-ment rate, growth, and mortality) of settled individual *in situ* using biological stains that mark the leading margin of tubes containing living *S. spirillum*. In addition, the relative importance of den-sity dependent mortality versus temporal variation in settlement on changes in population size is examined.

MATERIALS AND METHODS

Study site and organism

This study was conducted off the southeast shore of Stedman Island in Redfish Bay, Texas in Spring and Fall of 1985. The seagrass bed ($\sim$100 X 75 m) runs southwest to northeast with the southeast margin facing the open bay. The site was located 9 km from the pass between Redfish Bay and the Gulf of Mexico. Salinity ranged from 20-35 ppt during the study. *Spirorbis spirillum*, a sessile, tube-building polycheate, settles abundantly (typically several hundred tubes per blade) from planktonic larvae onto blades of *T. testudinum*. Abun-dances of *S. spirillum* are greatest during these seasons (Dirnberger 1989). Experiments were set up in the center of seagrass beds (>10 m from any margin) in water 0.5–1.0 m deep. Low water levels were never observed to expose the seagrass blades. *Spirorbis spirillum* larvae, $\sim$150 μm in length, are released from adult brood chambers at midday, remain planktonic for <1 h after, and then become negatively photoactive (Dirnberger 1993). After a short search phase, larvae undergo an explosive release of mucous attaching larvae to the blade surface and initiating tube formation (Potswald 1978). The hard, white secondary tube produced by the thoracic collar is visible within 1 h of settlement (personal observation). Other epiphytes, mostly the coralline red alage *Heteroderma lejolisii* (Rasanoff) Foslie and *Dermatolithon pustulatum* (Lamouroux) Foslie are slower to colonize and dominate older, more distal blade areas (new blade tissue is produced at blade bases) (Dirnberger 1990). Blade growth is rapid with blade turnover occurring on a scale of weeks (Odum 1985).

Testing the Effectiveness of Stain to Measure Tube Growth and Mortality

Within minutes after contact, solu-tions of aniline blue stain in seawater result in discoloration along the anterior, the most recently produced tube margin of the calcium carbonate tubes contain-ing *S. spirillum*. Subsequent growth in seawater without stain results in normal deposition of white tube tissue. Such pro-perties suggest that aniline blue growth bands can be used to measure *in situ* settlement rate, growth, and mortality in ways similar to those used by Edmondson (1945) for freshwater rotifers exposed to powdered carmine and char-coal. These parameters can be measured accurately if aniline blue stains only tubes with living or recently dead in-dividuals, if aniline blue is non-toxic, and if tubes tend to remain attached to blades even after death. These conditons are examined in the following paragraphs.

To determine how long tubes con-tinue to take up aniline blue stain after death, *S. spirillum* were recovered from tubes and tubes were exposed to stain after intervals of varying lengths (0, 3, 12, 24, 48, 72 h after dissection). Blades of *T. testudinum* collected from the field were segmented and segments with a wide variety of tube sizes chosen (n = 196). From one side of blades, animals were

removed from tubes by dissection posterior to the leading margin of the tube (anterior tube sections were not disturbed). Tubes on opposite sides were left undisturbed and served as controls. Numbers of tubes on blade segments averaged 20 tubes per side. Blades were placed in aerated seawater until sampled. At each sampling time, tubes were exposed to 1g aniline blue / I seawater for 2 h and then examined under a dissecting microscope at 50X for the presence or absence of blue growth bands.

Tube staining efficiency by aniline blue biological stain of tubes containing live and dead individuals were examined by placing S. spirillum on blades in an aniline blue solution (1.0 g aniline blue / I seawater) at 22 ppt salinity, 21° C. After 2 h, blades were removed from solutions. Approximately half of all S. spirillum in each treatment were tabulated immediately after exposure and the other half were incubated for 3 d in aerated seawater (~21° C) then tabulated. The presence and absence of stained growth bands were tabulated under a dissecting microscope at 50X. Vacant tubes were scored as dead while those contained S. spirillum were scored as living. Retention of stain was also measured in this experiment by comparing percent of tubes with living individuals not stained on Day 3 with those on Day 0.

In the above experiement, mortality due to stain can be detected if frequencies of living versus dead individuals are dependent on exposure to aniline blue stain (X^2 test of independence). The individuals on 4 blades exposed to aniline (describe above) were compared to individuals on 4 blades exposed to only seawater during the same time. Decomposition is assumed to be rapid so that bodies of S. spirillum dying during staining or within a day or two after staining would not be present by Day 3. Possible toxicity effects of aniline blue on

tube growth were tested in a separate experiment. S. spirillum were allowed to settle on blade segments previously cleared of epiphytes (see Dirnberger 1990) in the field for ~4 d. These segments, bearing small, similar size individuals were returned to the laboratory and placed in two treatments (plain aerated seawater and aerated seawater with 1.0 g aniline blue / I seawater) for 6 h. All blades were then placed in aerated seawater without stain and after 2-4 d tube diameters were measured with an ocular micrometer at 50 X and compared between treatments. Experiments were run on three dates in April, July, and August (n = 5, 3, and 3 blades respectively for a total of 260 individuals tested). To increase the ability of the test to detect a difference between treatments, a 1-way ANOVA was performed on data from all dates with date representing a block.

To investigate the possibility of mortality involving complete removal of tubes from blades (which would not be detected by the staining technique), I compared in situ time-lapse photographs. Two 3 cm lengths of blade (9-12 cm from the blade base) were photographed using an underwater camera set at f/22, constant focus, Kodachrome 64® color transparency film, and electonic flash (magnification = 1.3x) every 2 d from 23 to 29 October 1985.

Field Measurements of Demographic Parameters

Rates of settlement, tube growth, and mortality were estimated in situ from stained growth bands induced by injecting stain into a field chamber during two periods in the Spring and Fall of 1985. The chamber was open to the bottom and its edges forced >1 cm into the bottom sediment. The chamber enclosed 5 l over 315 cm² of seagrass meadow. Concentrated aniline blue solution (500 ml at 10

g/l) was injected into the chamber so that the final concentration of stain within the chamber was 1 g/l. Time at this first stain addition is referred to as 't_0'. The chamber was remove after 2 h, exposing blades to ambient seawater. After several days, the chamber was placed over the same area and blades were again exposed to stain (time of second stain addition = 't_1'). After 2 h blade were harvested and dried (preventing further tube growth) for latter analysis. Settlement rates of *S. spirillum* onto blade segments cleared of epiphytes (Dirnberger 1990) were measured over the same interval (t_0 to t_1) and in Fall were measured over several consecutive 3-4 d periods from 19 September 1985 to 4 November 1985. Unmanipulated blades (n = 12 blade sides) were harvested and stained at 7 sampling times (4-27 October) to determine densities of living *S. spirillum*.

Tubes in which stain failed to produce growth bands were scored as being dead before the start of the experimental period (t_0). Tubes with a single band followed anteriorly by normal white tube deposition were score as having died some time between t_0 and t_1. Tubes with a single band on the most anterior tube tissue were scored as new recruits settling between t_0 and t_1. Mortality of new settlers could not be determined from bands (new settlers dying before t_1 would be without bands) but was approximated from numbers of tubes without bands within recently settled size classes. Tubes with both t_0 and t_1 bands present were scored as being alive during the entire period. All tubes were measured across widest dimensions (a straight line from the point of the leading edge furtherest from the spiral center to the outer edge 180° around the spiral) and this dimension is referred to as 'tube diameter'. On tubes with t_0 growth bands present,

measurements were also made across the tube from the outer point of t_0 band to the outer edge 180° around the spiral. These two parameters were used to estimate tube growth. Tube growth is considered to be proportinal to body growth because the leading edge of the tube is formed under a collar encircling the body just anterior to the thorax (Pierce and Maugel, 1987). Linear dimensions of a tube are isometric (tube spirals are logarithmic; Dirnberger 1989) so that diameter of aperture is proportional to spiral diameter.

Detailed measurements were made to both in Spring and Fall 1985 of investigate consistency of demographic trends. Procedures were changed slightly in Fall. Time between t_0 and t_1 was 2 d in Spring (17-19 April) and 4 d in Fall (23-27 October). While aniline blue stain was used at t_0 in both seasons, tubes were exposed to a different biological stain, alizarin red (producing red growth bands) at t_1 in Spring. Alizarin red was not used again in the fall because tubes without living individuals were often lightly stained by alizarin red making interpretation of mortality data more subjective. In Fall field measurements, aniline blue rather than alizarin red was used as the second stain (at t_1). Error resulting from use of the same color stain at both t_0 and t_1 would rise in very small individuals showing only a single growth band with no subsequent growth of normal white tube tissue. Such individuals could either be considered as individuals settling during the experimental period or as individuals dying during or immediately after the first staining. Low mortality in small size classes (see results) and the short time frame in which death could occur makes the latter possibility very unlikely.

RESULTS

Testing the Effectiveness of Stain to

Measure Tube Growth and Mortality

Demographic trends in *S. spirillum* can be estimated reliably using aniline blue stain. Aniline blue stain efficiently identified tubes with living or recently dead individuals. Aniline blue growth bands did not form on tubes from which animals were killed 24 h or more previous to staining (Fig. 1) indicating that the absence of staining estimates death occurring generally >24 h prior to sampling. For tubes exposed to aniline blue stain and examined after 3 d, 161 of 163 tubes with living individuals incorporated aniline blue stain and 0 of 35 tubes without individuals incorporated stain (Table 1). The percentage of stained tubes with living individuals remained similar over 3 d (99.0% on day 0 and 98.8% on day 3; Table 1), indicating tubes retained stain over 3 d (Table 1). Tubes did not stop growing and then begin again; larger individuals (greater in size than those settling between t_0 and t_1) very rarely had only $_1$ growth bands (<0.1% for all tubes measured in spring and fall). This suggests that termination of growth results in failure to produce bands and can generally be interpreted as death. Epiphytic algae and seagrass were not visibly stained by aniline blue.

Experiments failed to detect toxicity of aniline blue stain. Numbers of live and dead individuals were independent of ex-
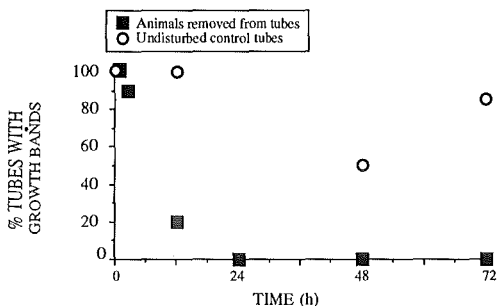
posure to aniline blue solutions ($X^2 = 0.65$, $P > 0.20$, data from Table 1 comparing total alive on Day 3 versus total dead on Day 3 in stain solution versus in seawater only.) In a similar experiment, individuals were placed in 1.0 g/l solutions of aniline blue of 18 h and again numbers of live and dead individuals were independent of exposure to aniline blue ($X^2 = 1.6$, $P > 0.20$, 680 tubes). In experiments examining possible toxicity of aniline blue on growth, no difference was detected in tube diameter between stained and un-

Table 1. Efficiency of staining and possible toxicity of aniline blue stain in the laboratory. Tubes exposed to stain solution (1 g aniline blue/ l seawater) are compared after 0 and 3 days and with tubes exposed to seawater only.

	Day 0 stain solution	Day 3 stain solution	Day 3 seawater only
A. Live, Stained	100	161	0
B. Live, No Stain	1	2	174
C. Dead, Stained	0	0	0
D. Dead, No Stain	21	35	30

stained treatments (treatment P> 0.20 F = 0.126; n = 11 blades totalling 260 individual) (mean tube diameter ± standard deviation for unstained and stained treatments respectively: for the April experiment 0.35 mm ± 0.06 and 0.36 mm ± 0.07; for July 0.37 mm ± 0.08 and 0.38 mm ± 0.07; for August 0.64 mm ± 0.19 and 0.67 mm ± 0.20).

Tube loss, determined from *in situ* photographs, was very low (0.2% of tubes observed were lost completely per day, n = 191 tube observations). Damaged tubes (30% of all tubes) remained attached between photographic sampling intervals. Tubes are difficult to remove completely, usually leaving circular 'scars' where tubes were cemented to blades (pers. obs.).

Figure 1. Precent of tubes taking up stain at various times for tubes from which individuals were removed at time 0 h (circles) and for tubes left undisturbed (squares) (n = 10-30 tubes per treatment). No controls were examined at 3 and 24 hours.

Field Measurements of Demographic Parameters

In the field, new *S. spirillum* settlers (those with t_0 bands only) settled only 0

to 9 cm from the base of blades (Fig.2) (mean blade length = 13.2 cm; n = 36).

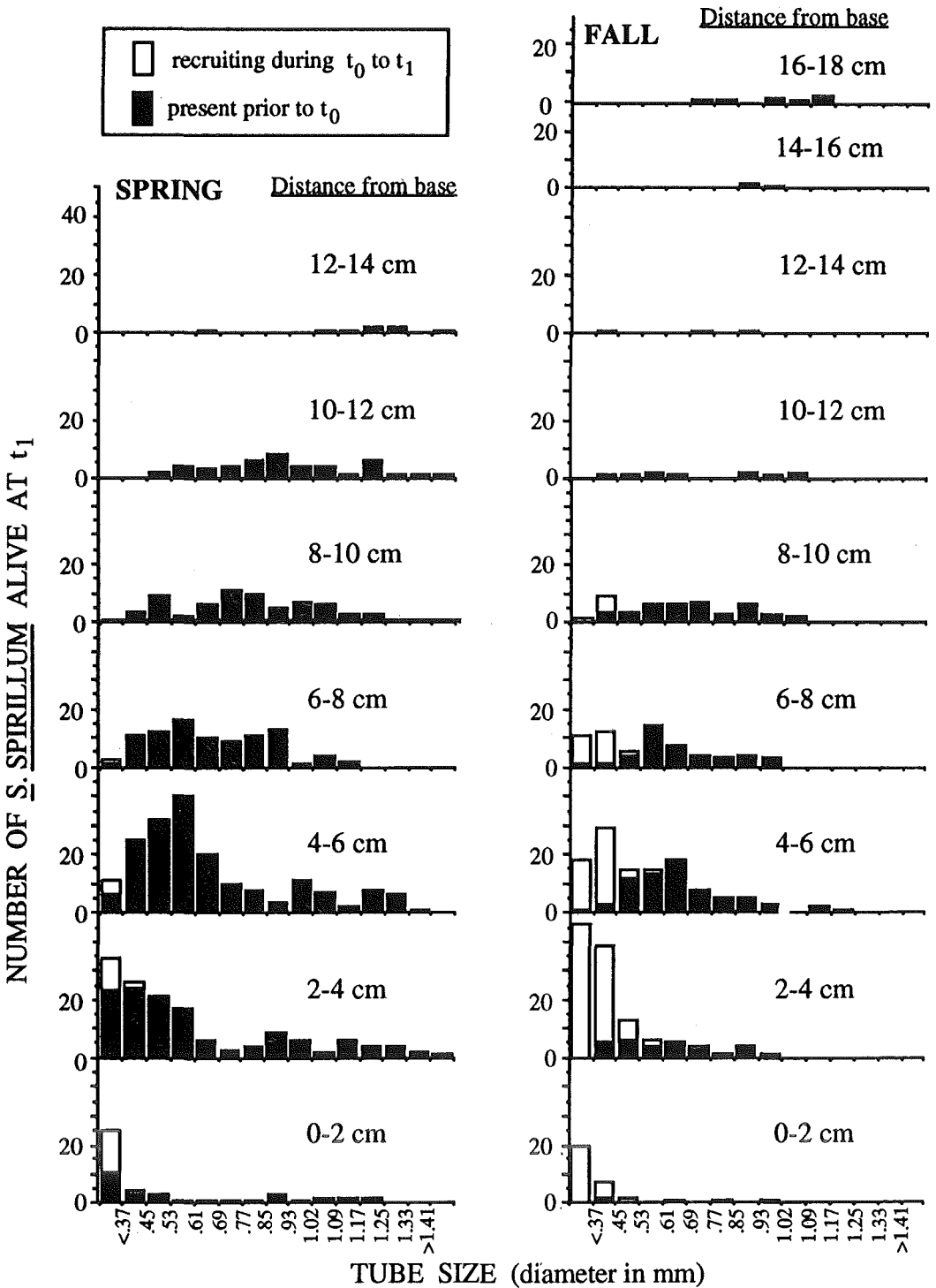As blades produce new tissue at their bases, tubes are moved further from the

Figure 2. Size frequencies of *S. spirillum* at 2 cm intervals along blades on two dates. Number of individuals in each class represents total for all blades tabulated where black bars are living individuals settling prior to first staining and white bars are individuals settling between first and second stainings.

bases over time. As a result, only larger individuals were present on distal blade areas (Fig. 2; larger individuals near the base are those on older, non-growing blades which were also included in this data set). Settlement rates estimated independently on blades cleared at t_0 (all tubes present on these blades at t_1 must be new settlers) were similar to rates estimated by the staining method (for Spring, 0.35 and 0.21 settlers/cm² leaf surface area on cleared and stained blades respectively; for Fall, 0.78 and 1.12 settlers/cm² leaf surface area). Nearly identical size distributions of settlers measured by each technique also indicate that tubes with only t_1 bands represent individuals settling during the experimental period (Fig. 3; P> 0.20, Kolmogorov-Smirnov test for goodness of fit).

Percent change in diameter over time decreased with increasing distance from the base and with increasing tube size (Fig. 4). If expressed as absolute change in diameter, growth is lower for small individuals, highest for medium sizes, and lower for large individuals. Absolute change in diameter plotted against time (calculated by subtracting mean size specific change in diameter/d from each diameter repeatedly) is linear

Figure 3. Size distribution of recent settlers onto whole, rooted blades stained at t_0 and t_1 (n = 110) and recent settlers on blade segments cleared at t_0 and placed *in situ* until 1_1 (n = 80). Frequency is plotted as a percentage so that distribution based on different sample sizes can be compared.

in the Spring and slightly sigmoidal in the Fall, though determinant growth was not achieved (Fig. 5). Individuals as small as 0.8 mm diameter were observed to be gravid and a switch to reproduction may explain the inflection in Figure 5.

Percent dying (expressed as number of tubes with t_0 bands only divided by living individuals at t_0) increased with distance from the blade base in both seasons and with size in Spring (Fig. 4). Survivorship curves were used to compare mortality occurring between t_0 and t_1 with mortality prior to t_0 (Fig. 6). Survivorship as a function of size for individuals dying between t_0 and t_1 was calculated by multiplying consecutive size-specific mortality (number dying at size x between t_0 and t_1 / number passing through size class x between t_0 and t_1) beginning at 1000 individuals. Survivorship based on deaths prior to t_0 was calculated by subtracting number of bandless individuals within consecutive size classes from the total number of bandless tubes (expressed as a proportion of 1000 individuals). Size-specific survivorship tended to be linear (resulting from increasing mortality with size) and size-specific survivorship was slightly greater in Spring than Fall.

Similarity between the shape of survivorship curves (one constructed by tabulating tubes with only t_0 bands and the other by tabulating tubes with no bands; Fig. 6) demonstrates that stained tubes reliably estimate patterns of mortality (differential ability to take up stain among size classes would inversely alter rates between the two estimates). Similarity between survivorship curves also suggests that observed trends in mortality are fairly consistent over time because animals dead at t_0 represent deaths occurring over several days prior to t_0. Survivorship based on tubes without growth bands is slightly lower initially for both seasons. This discrepancy could
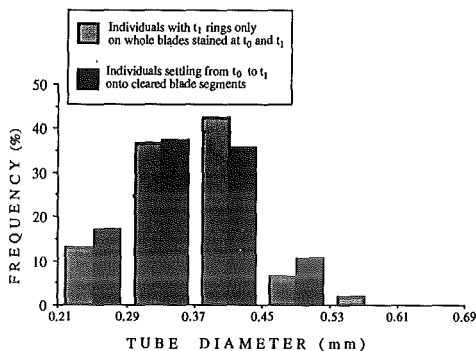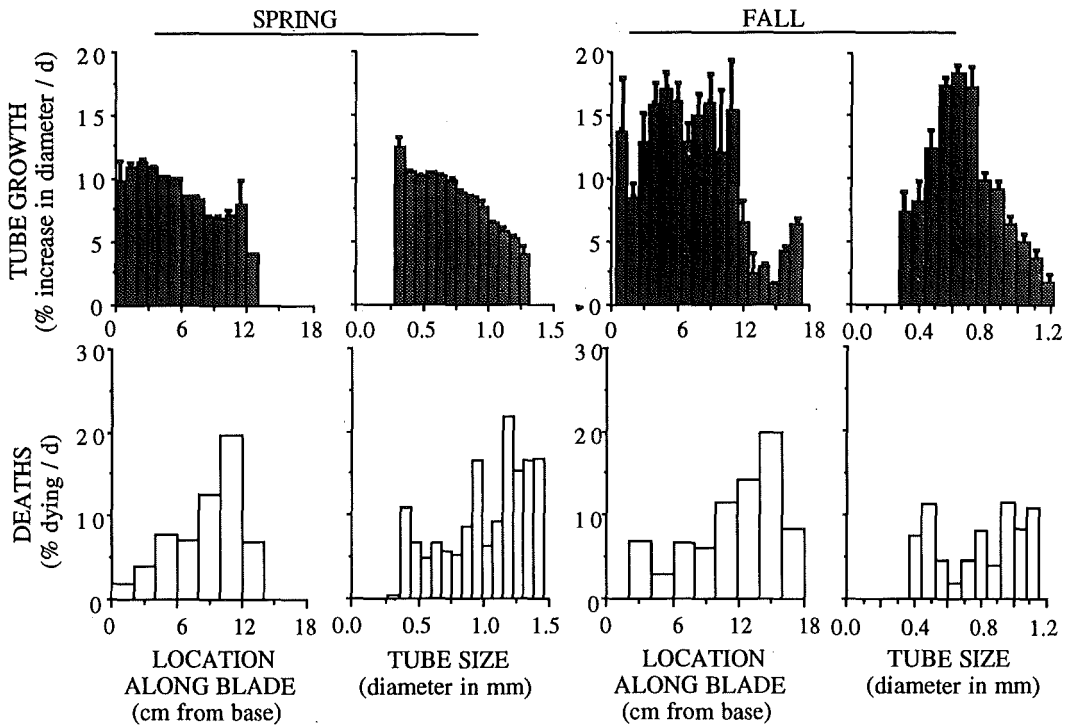
Figure 4. Tube growth and percent dying per day as functions of size and location in Spring and Fall for individuals shown in Fig. 2. Vertical bars are ±1 standard error of the mean.

result because individuals settling and dying between t_0 and t_1 would be bandless and considered as mortality occuring prior to t_0 in the estimate based on bandless tubes and not included as mortality in the estimate based on stained tubes. *In situ* photographs indicate tube removal by predators must be rare. *Spirorbis spirillum* are very rarely found in guts of small fishes foraging among seagrasses at the same site (Huh and Kitting 1985) nor was grazing of *S. spirillum* by invertebrates noted by Kitting (pers. comm.) using high resolution acoustic and photographic sampling techniques. Cages preventing fish predation failed to detect predation effects in another species of *Spirorbis* attached to rocks (Keough and Downes 1982).

Location effects on mortality may be due to position along blades at settlement. However, size increases with distance from base (Fig. 2) confounding influences of location and size on growth and mortality. Multiple regression

analysis allows the influence of location to be examined as if size has been held constant. Location and size explained about equal amounts of the variation in growth. The affects of location on growth should be interpreted with caution because size is a function of growth. While factors associated with location actually may inhibit growth, an alternative explanation is possible. If some individuals are intrinsically slower growers, these individuals would be located further from the base as the blade grows compared with younger, faster growing individuals of the same size.

Change in population size on natural blades and changes in settlement measured onto cleared blades covaried over the fall of 1985 (Fig. 7; r = 0.62). Neither growth nor mortality were negatively dependent of desnities of post-settlement conspecifics (Table 3). Density was measured both as *S. spirillum* alive at each location (1 cm of blade length) and as total tubes at each location. The
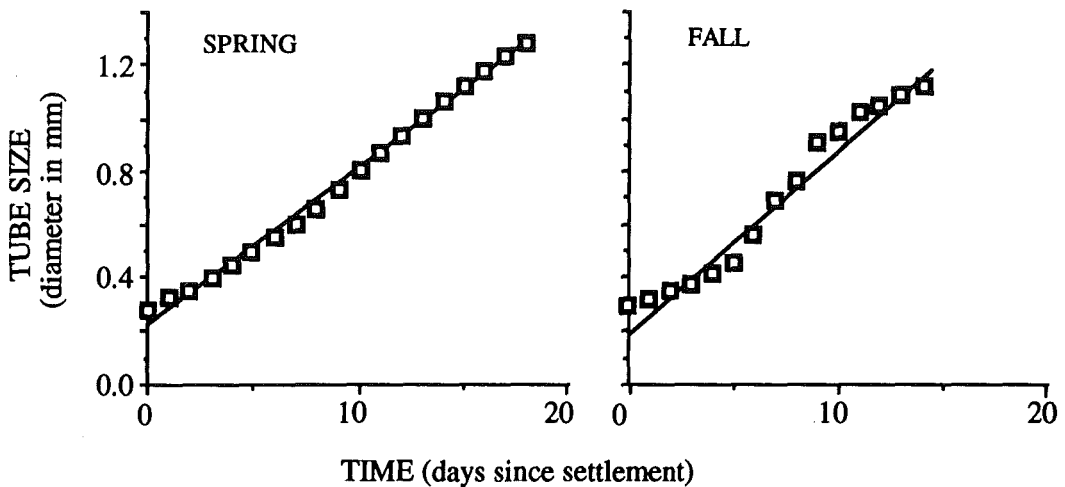
Figure 5. Estimated tube size versus time based on growth rates measured in Spring and Fall.

latter estimate investigates possible longer term effects by animals alive prior to t. In Spring, nearest epiphyte neighbors were recorded. For *S. spirillum* whose nearest neighbors were conspecifics, growth was not detectably affected by distance from neighbor (multiple regression analysis with nearest neighbor distance, location, and size as independent variables; $b'_{distance} = 0.008$, $P > 0.20$, $n = 118$).

Figure 6. Survivorship as a function of size estimated from tubes dead prior to t_0 and from individuals shown in Fig. 2 dying between t_0 and t_1.

DISCUSSION

Manipulations of blades in the field and observation of larvae in the laboratory indicate that *S. spirillum* larvae both actively avoid epiphytic cover associated with older, distal blade areas and settle deeper in the water column (Dirnberger 1990) onto newer areas near the base of growing blades where *S. spirillum* survivorship and growth are highest (Table 2). Causes of reduced survivorship and growth were not determined in this study, though tubes growing on previously cleared blade segments positioned 3 cm above the bottom were larger than tubes on blade segments positioned 23 cm above the bottom (Dirnberger 1989). Grosberg (1981) has demonstrated that several invertebrate taxa (including *Spirorbis*) avoid settling near an ascidian competitor capable of overgrowing those taxa whereas taxa that are not susceptible to overgrowth show no avoidance. Settlement near blade bases presumably maximizes number of offspring because chances of surviving to reproductive age are increased, time to first reproduction may be shortened, and larger sizes in at least one species of *Spirorbis* produce larger clutches (Daly 1978). Time to blade abscission (~40 day;
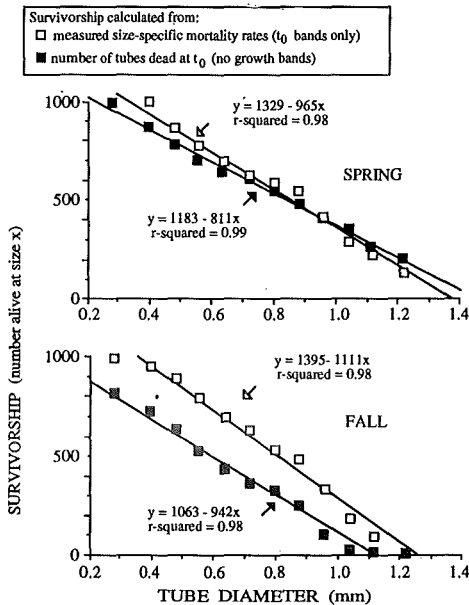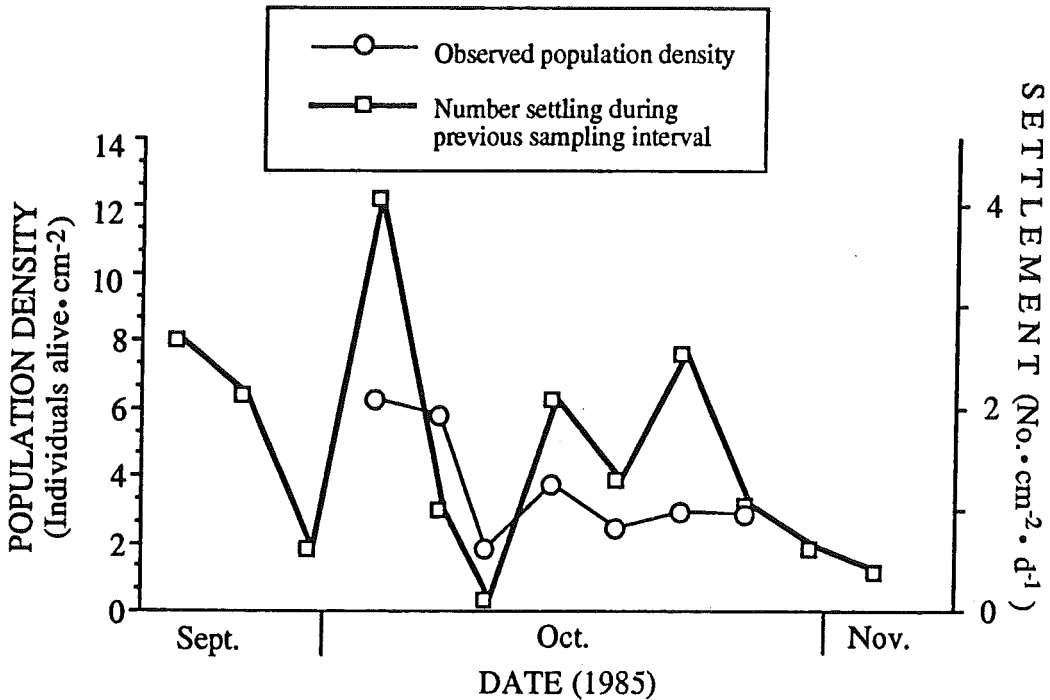
Fig. 7. Temporal variation in settlement (n = 4184 individuals) and in observed population density. (n = 3365 individuals).

Odum 1985) is often shorter than two generations making rapid growth and dispersal necessary for successful colonization of ephemeral substrata such as seagrass.

Differential settlement along the bases of growing blades, rather than differential tube growth, accounts for the absence of small individuals from distal blade area (slower growth associated with distal areas, Fig. 2, would tend to produce the opposite trend in size distribution along blades). Higher survivorship nearer to the blade base tended to enhance rather than obscure the distribution of living individuals resulting from differential settlement near blade bases. For bryozaons attached to seagrass blades, settlement, growth, and survivorship are highest on distal blade area and changes in survivorship along blades largely explain adult distributions (Keough 1986). Spatial distributions should reflect settlment location, as for barnacles on rocks (Denley and Underwood 1979, Grosberg 1979) and gastropods in kelp beds (Watanabe 1984), where survivorship is spatially homogeneous or

Table 2. Multiple regression analysis of tube growth as a function of tube size and location along the blade and of mortality as a function of size and location (r^2 = regression coefficient; n = sample size). Magnitudes of the standard partial regression coefficients (b') indicate relative contributions of each factor to variation explained by the regression line. Growth data were log transformed. For mortality, classes containing ≤3 individuals were not included in the analysis. Separate analyses were run for Spring and Fall.

	SPRING			FALL		
Y variable	r^2(n)	$b'_{location}$	b'_{size}	r^2 (n)	$b'_{location}$	b'_{size}
Growth	0.52 (95)	-0.46***	-0.51***	0.25 (158)	-0.35***	-0.23***
Mortality	0.44 (32)	0.55***	0.41**	0.39 (25)	0.87***	-0.52

* = 0.05>P> 0.01; ** = 0.01>P>0.001; *** = P <0.001

Table 3. Multiple regression analysis of tube growth as a function of tube size density and location along the blade and of mortality as a function of tube density and location (r^2 = regression coefficient; n = sample size). Growth data were log transformed. For mortality, classes containing $\leqslant 3$ individuals were not included in the analysis. Separate analyses were run for Spring and Fall and for density measured as living individuals and as all tubes.

Y variable	SPRING			FALL		
	r^2(n)	$b'_{location}$	$b'_{density}$	r^2 (n)	$b'_{location}$	$b'_{density}$
Density of tubes containing live animals:						
Growth	0.18 (131)	-0.36***	0.29***	0.30 (60)	-0.46***	0.33**
Mortality	0.24 (54)	0.48***	-0.12 ns	0.40 (24)	0.59**	-0.14 ns
Density of all tubes (occupied and vacant):						
Growth	0.14 (131)	-0.36***	0.21*	0.21 (60)	-0.44***	-0.16 ns
Mortality	0.23 (54)	0.47***	0.08 ns	043 (24)	0.61**	-0.21 ns
* = 0.05>P> 0.01; ** = 0.01>P>0.001; *** = P <0.001						

positively related to settlement as found in this study.

Survivorship that is positively affected by settlement location and not negatively affected by the density of conspecifics (Table 3) suggests that temporal changes in settlement can have a significant influence on changes in population size over time. This is supported by the positive correlation between population size and settlement (Fig. 7). Such correlations have been observed in benthic populations undergoing longer-term fluctuations in recruitment (e.g. Ebert 1981, Caputi and Brown 1986, Kendall et al. 1987). Positive phototaxis of larvae upon release from adults and current-related patterns of settlement across the seagrass bed indicate that larvae are transported up to several hundred meters by wind-driven currents (Dirnberger 1992). A likely cause of extreme fluctuations in settlement (several fold within 4 d; Fig. 7) is day to day variation in wind direction as weather fronts pass, rather than changes in amounts of space suitable for settlement (Dirnberger 1990).

Though not tested by this study, local extinction is potentially less likely to occur because larvae may be transported distances greater than the scale of ecological processes acting on the benthic stage. Dispersal events may draw recruits from several areas experiencing different mortality and reproductive rates. Some evidence for this is suggested by a 100-fold shift in *S.spirillum* population abundance among sites within a large seagrass bed over 2 months (Dirnberger 1993). The persistence of populations via migrations from patch to patch in a region where favorable conditons continually shift was proposed by Hutchinson (1951; the "fugitive species" concept) and has been modeled by Horn and MacArthur (1972), Levin (1974), Slatkin (1974) and Caswell (1978), for example. Underwood (1978) proposed that for three species of intertidal gastropods, competitive superiors can not exclude inferiors because variability in settlement from planktonic larvae prevented superior species from monopolizing limited food resources. Similarly, persistence of prey species may be explained by fluctuations in prey arriving from the plankton that either swamp predators (Dayton 1971) or prevent specialization on that prey (Connell 1970). While large-scale patterns of reproduction and mortality were not examined here, dispersal and settlement events clearly influenced the abundance and distribution of *S. spirillum* on blades in ways that potentially enhance its ability

to colonize growing seagrass blades.

REFERENCES

Burshek, D., 1988. Settlement as a major determinant of intertidal oyster and barnacle distrubtions along a horizontal gradient. J. Exp. Mar. Biol. Ecol., Vol. 122, pp. 1-18.

Caffey, H. M., 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. Ecol. Monogr., Vol. 55, pp. 313-332.

Caputi, N. and R. S. Brown, 1986. Relationship between indices of juvenile abundance and recruitment in western rock, lobster (*Panulirus cygnus*). Can. J. Fish. Aquat. Sci., Vol. 43, pp. 2131-2139.

Caswell, H., 1978. Predator-mediated coexistence: a nonequilibrium model. Amer. Nat., Vol. 112, pp. 127-154.

Connell, J. H., 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monogr. Vol. 40, pp. 49-78.

_____, 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol.,. Vol. 93, pp. 11-45.

Daly, J.M., 1978. Growth and fecundity in a Northumberland population of *Spirorbis spirorbis* (Polychaeta: Serpulidae), J. Mar. Biol. Ass. U.K., Vol. 58, pp. 177-190.

Davis, A. R., 1987. Variation in recruitment of the subtidal colonial ascidian *Podoclavella cylindrica* (Quoy & Galmard): the role of substratum choice and early survival., J. Exp. Mar. Biol. Ecol., Vol. 106, pp. 57-71.

Dayton, P. K., 1971. Competition, distrubance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr., Vol. 41, pp. 351-389.

Dirnberger, J. M., 1989. Variable settlement of planktonic larvae in a marine benthic population: *Spirorbis spirillum* (Polychaeta:: Spirorblade) settling on blades of the seagrass *Thalassia testudinum*. Austin, TX: Univ. Texas; 114 pp. Dissertation.

_____, 1990. Benthic determinants of settlement for planktonic larvae: availability of settlement sites for the tube-building polychaete *Spirorbis spirillum* (Linnaeus) settling onto seagrass blades. J. Exp. Mar. Biol. Ecol., Vol. 140, pp. 89-105.

_____, 1993. Dispersal of larvae with a short plankton phase in the polychaete *Spirorbis spirillum* (Linnaeus). Bull. Mar. Sci., Vol. 52: 898-910.

Denley, E. J. & A. J. Underwood, 1979. Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. J. Exp. Mar. Biol. Ecol., Vol. 36, pp. 269-293.

Ebert, T. A., 1981. Estimating mortality from growth parameters and size distribution when recruitment is periodic. Limnol. Oceanogr. Vol. 26, pp. 764-769.

Edmondson, W. T., 1945. Ecological studies of sessile rotatoria: Part II, dynamics of populations and social structure. Ecol. Monogr., Vol. 15, pp. 141-172.

Gaines, S. & J. Roughgarden, 1985. Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. Proc. Natl. Acad. Sci. USA, Vol. 82, pp. 3707-3711.

Grosberg, R. K., 1979. Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults. Ecology, Vol. 6, pp. 394-899.

_____, 1981. Competitive ability influences habiatat choice in marine invertebrates. Nature, Vol. 290, pp. 700-702.

Horn, H. S. & R. H. Macarthur, 1972. Competition among fugitive species in a harlequin environment. Ecology, Vol. 53, pp. 74f9-752.

Huh, S. & C. L. Kitting, 1985. Trophic relationships among concentrated populations of small fishes in seagrass meadows. J. Exp. Mar. Biol. Ecol., Vol. 92, pp. 29-42.

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

Kendall, M. A., P. Williamson, & P. R. Garwood, 1987. Annual variation in recruitment and population structure of *Monodonta lineata* and *Gibbula umbilicalis* populations at Aberaeron, Mid-Wales. Estuar. Coast. Shelf Sci., Vol. 24, pp. 499-511.

Keough, M. J., 1986. The Distributions of bryozoan on seagrass blades: Settlement, growth and mortality. Ecology, Vol. 67, pp. 846-857.

_____ & B. J. Downes, 1982. Recruitment of Marine Invertebrates: the role of active larval choices and early mortality. Oecologia, Vol. 54, pp. 348-352.

Levin, S. A., 1974. Dispersion and population interactions. Amer. Nat., Vol. 108, pp. 207-228.

Luckenbach, W. M. 1984. Settlement and early post-settlement survival in the recruitment of *Multina lateralis* (Bivalvia). Mar. Ecol. Prog. Ser., Vol. 17, pp. 245-250.

Odum, M. A., 1985. Shading effects of epiphytes on leaves of turtle grass, *Thalassia testudinum* Banks ex Konig. Austin, TX: Univ. Texas; 79 pp. Thesis.

Peterson, C. H., 1986. Enhancement of *Mercenaria mercenaria* densities in seagrass beds: Is pattern fixed during settlement season or altered by subsequent differential survival. Limnol. Oceanogr., Vol. 31, pp. 200-205.

Pierce, S. K. & T. K. Maugel. 1987. Illustrated Invertebrate Anatomy. Oxford University Press, New York, p. 154.

Postwald, H. E., 1978. Metamorphosis in *Spirorbis* (Polychaeta). In, Settlement and metamorphosis of marine invertebrate larvae, edited by F. Chia and M. E. Rice, Elsevier Science Publishers, Amsterdam, pp. 127-144.

Slatkin, M., 1974. Competition and regional coexistence. Ecology, Vol. 55, pp. 128-134.

Underwood, A. J., 1978. An experiemental evaluation of competition between three species of intertidal prosobranch gastropods. Oecologia, Vol. 33, pp. 185-202.

_____, & E. J. Denley, 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In, Ecological communities: conceptual issues and the evidence, edited by D. R. Strong, Jr., D. Simberloff, L. G. Abele, & A. B. Thistle, Princeton Univ. Press, Princeton, N. J., pp. 151-180.

Watanabe, J. M., 1984. The influence of recruitment, competition, and benthic predation on spatial distributions of three species of kelp forest gastropods

78   Dirnberger, Joseph

(Trochidae: Tegula). Ecology, Vol. 65, pp. 920-936.