THE LIFE HISTORY TRAITS AND POPULATION DYNAMICS OF THE BROODING BIVALVE, *TRANSENNELLA TANTILLA* (GOULD) IN THE SOUTH SLOUGH OF COOS BAY, OREGON

by

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A THESIS

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IS HEREBY APPROVED: Peter W. Frank
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An Abstract of the Thesis of

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In the South Slough of the Coos Bay, Oregon, *Transennella tantilla* range in size from 0.53 to 5.3 mm. Males are generally ≤ 2.7 mm in shell length and females are ≥ 2.0 mm. Male/female ratios are 56:44 for *T. tantilla* inhabiting the Portside mudflat and 63:37 for animals located on the Metcalf mudflat. The sex ratios at the two locations do not vary significantly from month to month. Females produce, brood and release young throughout the year. Both brood size and embryonic developmental rates are seasonably variable. Fecundity is positively correlated with female size. Growth rates for juveniles and adult *T. tantilla* were estimated from size-frequency distribution data and were found to be fairly constant and continuous throughout the year.

Densities of *T. tantilla* normally range between 500-6,000/m^2. Densities decreased at all study sites during the late spring and summer. It was determined that predation by juvenile Dungeness crabs, *Cancer magister* was responsible for the decline in numbers of *T. tantilla*. Foraging behavior by juvenile by *C. magister* was observed in the laboratory and is described in detail.

The life history traits described in this study are compared with those reported for the species in False Bay on San Juan Island, Washington and Tomales Bay, California. The role of biological and physical factors in contributing to the observed differences in size and reproductive traits at the three geographic sites is considered. Finally, the life history strategy of *T. tantilla* is discussed in light of theoretical predictions for optimal life histories in disturbed environments.

ERRATA

Please attach to Master's Thesis: The Life History Traits and Population Dynamics of the Brooding Bivalve, *Transennella tantilla* (Gould) in the South Slough of Coos Bay, Oregon; by Mary Ann Asson-Batres, September, 1982

Page 14, line 19, "Size-class # 1 included cleaving eggs..." should read

> "Size-class # 1 included cleaving eggs (from approximately 0.250 mm in diameter) and embryos less than or equal to 0.400 mm; size-class # 2 included embryos greater than 0.400 mm to size at time of release (approximately 0.550 mm)."

Page 15, line 16, "... 4.4 *cm* ..." should read "... 4.4 *mm* ..."

Page 19, line 1, cross out "...for..." at end of line.

Page 24, Figure legend should read:

		WINTER	SUMMER
SIZE-CLASS I	EGGS AND EMBRYOS < 0.4 mm	○——○	●——●
SIZE-CLASS II	YOUNG > 0.4 mm	○- - -○	●- - -●

Page 27, substitute attached Table 2.

Page 33, line 13, "...sample size for *May* ..." should read "...sample size for *Apr* .

Page 40, line 17, "...mudflat from December, 1980 to *May*, 1981. *Four* test trays, MS, MR,..." should read "...mudflat from December, 1980 to *June*, 1981. *Five* test trays, MS, MR, *MT*,..."

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Table 2. Monthly sex determinations of Transennella tantilla by site.

	MAR	APR	MAY	JUL	AUG	OCT	DEC
Site: PA							
Number Males	20	16	39	16	61	55	50
Number Females	10	17	21	16	28	60	56
Number ?	-	-	3	-	-	-	-
Total Dissected	30	33	63	32	89	115	106
N ≥ 1.85 mm	57	94	63	32	89	115	106
Number Sub-Samples Used	2	1	3	3	3	3	3
Site: PB							
Number Males	43	93	22	7	7	23	25
Number Females	25	57	20	2	1	38	28
Number ?	-	-	6	1	-	2	-
Total Dissected	68	150	48	10	8	63	53
N ≥ 1.85 mm	81	469	48	14	8	63	53
Number Sub-Samples Used	2	1	3	2	3	3	3
Site: MP							
Number Males	65	59	99	-	36	73	81
Number Females	42	44	74	-	31	26	36
Number ?	-	12	4	-	-	-	-
Total Dissected	107	115	177	-*	67	99	117
N ≥ 1.85 mm	345	224	263	116	67	149	361
Number Sub-Samples Used	1	1	2	-	3	2	1
Site: MS							
Number Males	58	-	34	44	26	70	73
Number Females	23	-	20	31	41	38	31
Number ?	-	-	3	-	-	4	3
Total Dissected	81	-**	57	75	67	112	107
N ≥ 1.85 mm	81	62	57	215	67	112	151
Number Sub-Samples	3	-	3	1	3	3	2

*Clams were not dissected due to sampling problems

**Clams were not dissected due to poor preservation of tissues

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INTRODUCTION

Transennella tantilla (Gould) is an abundant member of intertidal soft-sediment communities ranging from Alaska to Lower California (Keen, 1937). These small venerid bivalves are ovoviviparous and are found with young in their gills throughout the year. Embryonic development is direct and juveniles are expelled through the excurrent siphon onto the mudflat. Hansen (1953) carried out a histological examination of *T. tantilla* collected at False Bay on San Juan Island, Washington and determined the organisms to be protandrous hermaphrodites.

In spite of its abundance and the interesting characteristics of its reproductive strategy, *T. tantilla* has received little attention from investigators. Only two references include information on the population ecology of this species. As part of a larger study of the community metabolism and productivity of an intertidal mudflat, Pamatmat (1966) presented data on the monthly size-frequencies, estimated growth rates,and fecundity of *T. tantilla* found in False Bay, Washington. Obrebski (1968) provided information on the patchy distribution; reproductive state and fecundity of clams of various size-classes; the amount and seasonality of parasitic infestation; and the monthly size-frequencies of *Transennella* sampled on Lawson's Flat in Tomales Bay, California.

The paucity of specific ecological information on *Transennella tantilla*, in particular, the absence of predation studies, and the absence of any formal attempt to compare field data collected in distinct geographic areas, indicates a need for further study of this organism. The life history traits of *T. tantilla* make it a particularly interesting and important species to consider in testing predictions of optimal life history strategies under various environmental conditions.

The purpose of this study is to:

(1) describe aspects of the life history of *T. tantilla* in Coos Bay

(2) describe predation on *T. tantilla* by the juvenile Dungeness crab, *Cancer magister*

(3) discuss and compare data from this study with data in the literature on the life history characteristics of *T. tantilla* in other geographic locations.

(4) examine the life history strategy of *T. tantilla* in light of predictions of current life-history theory

(5) consider the role of predation in contributing to the locally-observed differences in size, density, shell color polymorphism, distribution, and reproductive traits of *T. tantilla* in the three geographic sites where studies have been done.

BIOLOGY OF TRANSENNELLA TANTILLA

Transennella tantilla were first described on the Eastern Pacific Coast by Gould (1852). They inhabit the upper 0-4 cm of sediment in mid-intertidal to sub-tidal zones of bays and sounds. Their location in the top layer of the sediment probably results from their feeding mode - they are suspension feeders with very short siphons.

In Coos Bay, densities of T. tantilla commonly range between 500-6,000/m^2. I have sampled areas with as many as 13,000/m^2. In South Slough, T. tantilla exhibit a variety of shell coloration patterns from a cream white shell with tan or purple markings on the posterior edge to a completely purple shell. Other color patterns exist between these extremes. T. tantilla attain sizes up to 5.3 mm in this area. Although fairly abundant, both shell coloration and size of the clam make the species relatively inconspicuous in Coos Bay.

T. tantilla are very mobile and will quickly burrow into the sediment if disturbed. They secrete a byssal thread (Narchi, 1970) which is attached to grains of sediment, thereby granting them some protection from dislocation. Large waves or tidal surges do dislodge Transennella and carry them to new sites. This partially accounts for the high concentration of T. tantilla in troughs where wave and surf action tend to deposit the animals (Pamatmat, 1966).

In a recent study, Gray (1978) has shown that there are two distinct, sympatric, morphological variants of the genus *Transennella* which have previously been considered as one species, *Transennella tantilla*. In addition to anatomical differences, there are external shell shape and pigmentation differences which can be used to distinguish the two morphs. One morph has a purple streak on the posterior end of the shell and is subtrigonal with the length longer than the height. The other is unpigmented and is more ovate with the length almost equal to the height. Pending actual names for each species, Gray has coined the names, *Transennella* sp., purple morph and *Transennella* sp., white morph. Gray (personal communication) found specimens of the white morph in *Zostera* beds on the Portside mudflat in South Slough. The animals considered in this study were identified with Gray's distinctions in mind. Only *Transennella* sp., purple morph were used in the data analyses. Where the names, *Transennella tantilla*, *T. tantilla*, or *Transennella* appear in this thesis, they refer to the purple morph described by Gray.

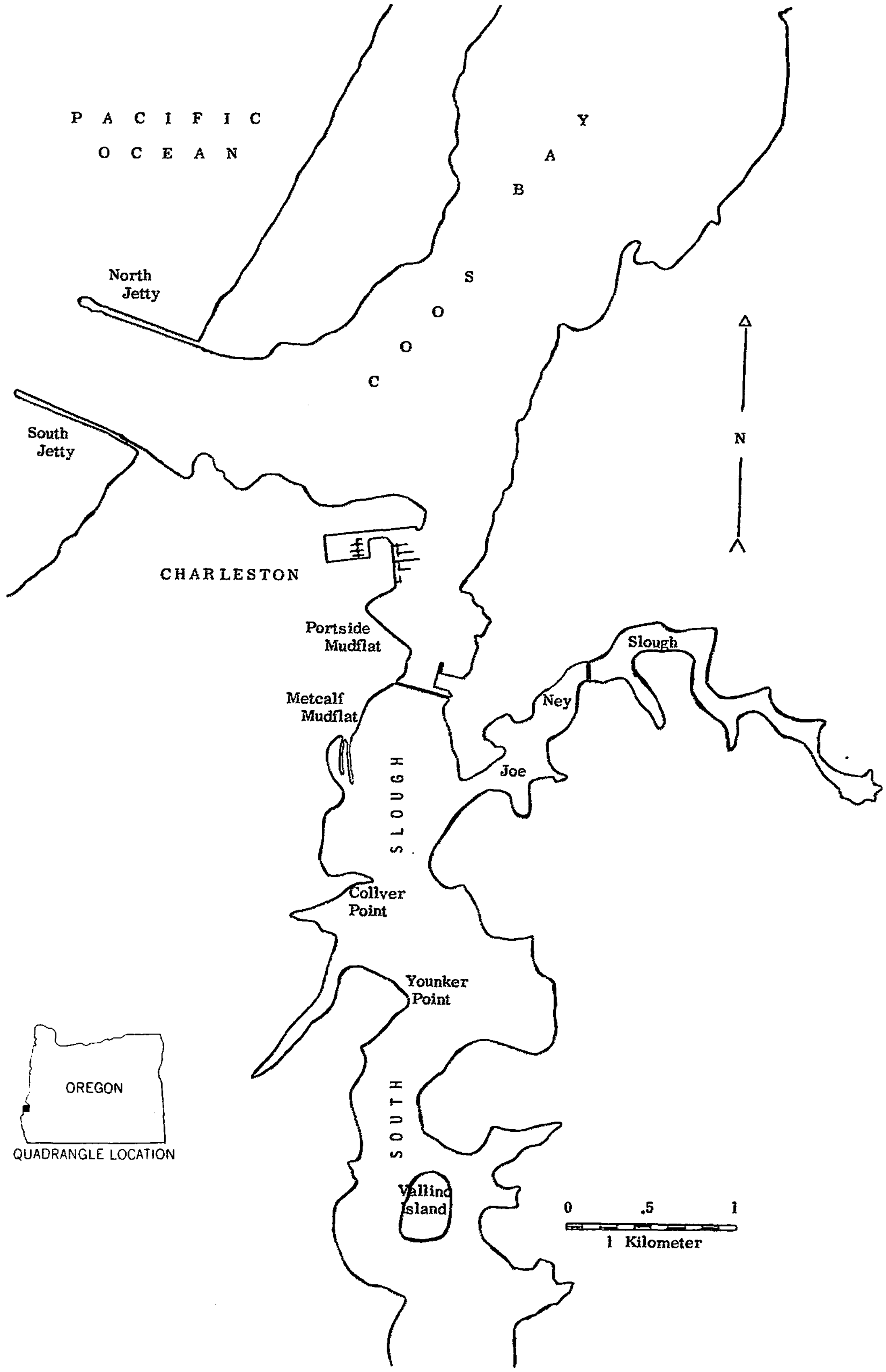
DESCRIPTION OF STUDY SITES

Field studies were carried out on the west bank of the South Slough of the Coos Bay estuary in Charleston, Oregon. The Coos Bay is 320 km south of the Columbia River and 760 km north of San Francisco Bay at 43.8^{o}N latitude. The South Slough empties into the main channel of the Coos Bay, approximately 1.3 km from the mouth of the bay. Three permanent study sites were established on the Portside mudflat and two were located on the Metcalf mudflat (see Figure 1).

Site PA

Site PA was located on a sandbar close to the center of the Portside mudflat. The tidal elevation of the site was about +0.57 m. Tidal elevation was determined by reading the tide guage at the Charleston Boat Basin at the time that the site was first covered by the incoming tide. A stake was driven into the sediment to mark the area. Sampling studies were conducted within a 11 m X 11 m area about the stake. The substrate at this site was characterized by an upper layer of sticky, fine-grained, muddy sediment, grey in color, variable in depth from 0.5 to 2 cm, overlying a layer of firm, medium-grained sand. The upper layer was deposited in ripples about 0.5 to 1 cm from peak to trough. This substrate pattern was uniform throughout the immediate vicinity of the site. Very little, if any, sediment transport was noted within this site throughout the year, and

Figure 1. Map of a portion of the Coos Bay Estuary, Oregon, depicting the location of the Portside and Metcalf mudflats on the west bank of the South Slough.


PACIFIC OCEAN
COOS BAY
North Jetty
South Jetty
CHARLESTON
Portside Mudflat
Metcalf Mudflat
Joe
Ney
Slough
SOUTH SLOUGH
Collver Point
Younker Point
Vallino Island
N
0
.5
1
1 Kilometer
OREGON
QUADRANGLE LOCATION

the composition and conformation of the substrate remained constant, as described above.

Site PB

Site PB was located 144 m south of site PA and was marked by a single, unattached piling. The tidal elevation was about +0.33 m. Sampling was carried out in a 7 m X 11 m area about the piling. The substrate in one-half of the site was similar to that at site PA, the other half was medium to coarse-grained sand. The sandy area was firm at certain times of the year and unstable at others. From November to June, sediment was transported into the site, adding a vertical layer of 10 to 30 cm of sand; during the summer months, this sediment was transported out of the area.

Site PC

Site PC was located at the far south end of the Portside mudflat, 65 m southwest of site PB. Although the tidal elevation was about +0.72 m, the substrate was very wet throughout the low tide cycle. The surface layer of sediment was 1 to 3 cm thick, sticky, fine-grained and muddy. This upper layer overlay a layer of firm, medium-grained sand. Shallow salt water streams meandered throughout the site. An area 25 m X 32 m within this site was used for sampling during the field study period.

Site MP

Site MP was located on the Metcalf mudflat approximately 640 m south of site PA on the Portside mudflat. The tidal elevation was about +0.75 m. This site was characterized by a series of standing salt water pools that remained filled with water throughout the low tide cycle. All through the site, the substrate was composed of firm, medium-grained sand. About the pools, the sand was deposited in a rippled pattern about 1 to 2 cm from peak to trough. Sediment transport probably occurred, but was not measured. Obvious differences in substrate composition or profile were not observed during the year. A definite sampling zone was not staked out within this site since the area was so consistently uniform and distinct from neighboring mudflat areas.

Site MS

Site MS was located 45 m west of site MP at a tidal elevation of about +1.11 m. The site was on a gentle downward slope 50 m below (east of) a bed of *Salicornia* and *Distichlis*. The upper layer of sediment was wet and silty, of variable depth from 1 to 3 cm. Firm, medium-grained sand underlay this "ooze" layer. Sediment was transported in and out of the site during the year. Sampling was carried out in a 9 m X 5 m area immediately adjacent to stakes set out for "caging" experiments.

In May, a black, odoriferous, anoxic layer moved up to just below the surface at site PC. The layer was present everywhere in the site, penetrating the substrate to the underlying sandy zone. This black layer persisted at the site until August. By September, the layer had broken up into patches of blackened sediment and the sulfide odor was gone. By November, blackened sediment could only be found 4 cm or more below the surface of the substrate. A sulfide layer was apparent at site PA in August and September, at site MS in August, and at site PB in June.

Both mudflats are popular clam-digging spots, but during the year and a half I carried out field studies, I noted very little digging activity within or about sites PA, PB, PC or MS. There was a moderate amount of activity at site MP. Cages left on the mudflat from month to month were not disturbed by dogs or passersby.

The infauna associated with *Transennella tantilla* was fairly similar from site to site, and included polychaetes, amphipods, nemerteans, nematodes, large numbers of cumaceans and the tanaid, *Leptochelia dubii*, and low densities of 8 to 10 species of small or juvenile bivalves. Algae, such as *Ulva*, *Enteromorpha* and *Vaucheria*, were present at sites MS and MP from April to October, becoming very dense by August. Algae were also present at site PB, but only on hard surfaces such as the piling, experimental test trays and plastic stakes.

According to a study carried out by Harris, et al (1979), the South Slough is a well-mixed system that exhibits quick flushing so that the effect of fresh water runoff directly into South Slough is minor. Salinity conditions are reflective then, of those in the main channel of the Coos Bay at the entrance to the slough. Salinity at the sites can be assumed to be oceanic except during periods of heavy freshwater flow into Coos Bay.

MATERIALS AND METHODS

Sampling and Analytical Methods for Size-Frequency Distribution Studies

Each of the five sites was sampled monthly from February to December, 1981. Before sampling, each site was searched at random to spot-check for the presence and abundance of *Transennella tantilla*. Since the clams are patchy in distribution, such a check was necessary to prevent sampling an area with few or no clams. A depauperate sample would provide little information about the monthly size-frequency distributions of individuals within a sampled area and could lead to false interpretations about population trends within a site.

If obvious within-site population abundance differences existed, the spot within the area found to have the greatest *T. tantilla* abundance was chosen for sampling. A circular sampler (diameter = 35.7 cm, area = 0.1 m^2) was tossed onto the substrate. A second check for presence of *T. tantilla* was made next to the sampler to eliminate the chance of sampling a patch with low numbers or no clams within this pre-selected zone. Thus, samples from each site are representative of patch areas observed to have the greatest abundance of *T. tantilla* within the site for any particular month.

Once the sampler was positioned, the 0.1 m^2 area was divided into three equal sub-samples. A coring device, made of a metal can calibrated with 2 and 4 cm divisions, was used to remove sediment 4 cm deep from each sub-sample. Sediment from each sub-sample was either sieved fresh in the field or returned to the lab in a plastic bag. Unsieved samples which were brought back to the lab were stored in out-of door, running sea water aquaria and sieved within 24-36 hours. All samples were sieved live through a 500_u mesh. Sieved samples were fixed in 70% isopropyl alcohol and stored in plastic sealed culture dishes.

A dissection microscope was used to separate preserved *T. tantilla* from the sediment. Sorted clams were transferred to plastic 35 mm film canisters containing 70% isopropyl alcohol.

For size-frequency studies, the antero-posterior dimension (length) of the shell was used as an indicator of clam size. All clams were measured with an ocular micrometer (at a magnification of 100 X, 1 division = 0.074 mm). A total of 2009 preserved *T. tantilla* from the samples collected at sites PA, PB, MP, and MS during the months of March, April, May, July, August, October, and December were dissected to determine male/female size (length) ranges and sex ratios. Sex was determined by examining gonads if brooded embryos were not present. Testes in preserved specimens appear as white, translucent, finger-like, branching structures. Preserved ovaries from non-brooding, mature females can be identified by the presence of irregularly-shaped, opaque eggs which appear white or light yellow. In a few cases, owing to the small size of the gonads of the particular specimen, the identification of sex was questionable. In larger specimens, it was difficult to determine whether the organism was a large male or a female with parasitized gonads. The questionable identifications were recorded, but were not included in subsequent data analyses. I examined individuals greater than or equal to 1.85 mm in shell length because of the difficulty of dissecting smaller specimens. Clams from samples collected at site PC were not included in the male/female analysis because there were less than 25 animals longer than or equal to 1.85 mm in the entire 0.1 m^2 sample for five of the seven months considered.

Sampling and Analytical Methods for Brood Size Studies

Transennella tantilla were collected monthly from the Portside and Metcalf mudflats for the purpose of following seasonal brood size and within-brood embryo size-frequency distributions in females of varying sizes. Since access to a running sea water table was not available, the organisms were retained in glass culture dishes filled with fresh, unfiltered sea water and maintained under refrigeration at 4^oC. Food was not provided. *T. tantilla* was found to survive for over two weeks with no apparent ill effects under these conditions.

Living clams were measured and dissected within one week from the date of collection. Under 200 X magnification (1 division = 0.037 mm), brooded embryos were removed from the gills, separated into two size classes and enumerated. Size-class # I included cleaving eggs (from approximately 0.0250 mm in diameter) and embryos less than or equal to 0.400 mm to size at time of release (approximately 0.550 mm).

Specimens collected during the months of February, March and August were preserved in 70% isopropyl alcohol before dissection. Of the 97 T. tantilla examined from the April 1981 collection, 64 were examined while still living and 33 were examined after preservation in 70% isopropyl alcohol.

If present, the type and degree of parasitism was noted for all dissected clams. Clams infected by parasites invading the gonads were not included in the data analysis for brood size or within-brood embryo size-frequency distributions.

Cage Studies

A cage experiment was designed to monitor individual clam growth and release of juveniles on a month-to-month basis. The cages were made of empty 35 mm film containers with either end removed and fitted with fabric that had an approximate mesh size of 0.350 mm, a mesh size that is about the height of the smallest released juvenile. Each film container was half-filled with clean bay sand and one measured clam was added. Individual clams within a test tray ranged from 1 to 4.4 cm in length. Twenty-eight cages were held in place in an array of drilled holes in a piece of polyurethane-coated exterior plywood, constituting one test tray. The test trays were tethered to stakes on the mudflat and brought into the lab for examination either once monthly or once every two months. Three test trays were maintained at site PB and five at site MS.

When the cages were brought into the lab for examination, the sand was removed and examined under a dissection microscope. The size (length) and condition of the "caged" clam was recorded and the number and condition of any juveniles released during the month was noted. Records were kept only for "caged" clams that were still alive after the exposure period on the mudflat; all juveniles, dead or alive, were enumerated, however, in cages where the "caged" mother was living. Juveniles were discarded and the "caged" clam, if still living, was returned to its cage. Fresh bay sand was added to each cage. Dead clams were discarded and replaced with a measured individual collected from the mudflat. Test trays were kept in out-of-door, running sea water aquaria and returned to the field within 24 hours of retrieval.

Laboratory Studies of Crab Predation

In July, 1981, I set up five out-of-door sea water aquaria to test the hypothesis that crab predation was responsible for the drastic reduction in the abundance of living *Transennella tantilla* and the concomitant appearance of large numbers of half-shells and shell fragments on the substrate surface, in particular, at site PC. Tanks # 1 and 2 were 61 X 31.5 X 42 m. Tanks # 3, 4, and 5 were 23 X 17 X 16 m. Clean bay sand was added to cover the bottoms of each tank to a depth of 10 cm. Fresh, unfiltered sea water flowed continuously through the tanks. *T. tantilla*, large juvenile *Cancer magister*, and an unidentified hermit crab were collected from the Portside and Metcalf mudflats. The small juvenile crabs were collected from the Portside docks. The tanks were set up as outlined in Table 1. All tanks were examined one month later. Condition and size of crabs was noted, and numbers and condition of clams was recorded.

TABLE 1. Experimental Design for Test of Possible Predator-Prey Interactions Between Juvenile *Cancer magister* and *Transennella tantilla*

TANK #	CONDITION	NUMBER OF *TRANSENNELLA TANTILLA*	SHELL LENGTH	NUMBER AND IDENTIFICATION OF CRABS	CARAPACE WIDTH
1	Experimental	150	Variable	5 *C. magister*	2.1, 2.2, 2.3, 3.1, 3.4 cm
2	Control	150	Variable	______________	_________
3	Experimental	50	Variable	1 *C. magister* 1 *C. antennarius* 3 Unidentified sp.	All Less Than 1 cm
4	Experimental	50	Variable	1 Hermit Crab	_________
5	Control	50	Variable	______________	_________

RESULTS

Reproduction and Sex Ratios

Broods removed from the gills of females collected on the Portside and Metcalf mudflats contained uncleaved eggs, embryos without shells, and embryos with shells. Uncleaved eggs and the smallest embryos were tightly held together in packets in the gills; older embryos were more loosely connected to the rest of the brood. Asynchronous embryonic development occurred year-around. Eggs were nearly spherical, ranging in size from 0.212 to 0.259 mm in diameter. The largest embryos observed in the brood were 0.530 to 0.550 mm in shell length. The largest embryos were white with a purple/brown mark on the posterior edge of the shell. Females are found with broods every season of the year from maturity until death. The only exceptions to this rule are females with parasitized gonads.

It is assumed that males spawn and females take up sperm through the incurrent siphon, but specific details of the fertilization process are unknown. On one occasion, I observed active sperm inside packets of eggs dissected from the broods of two females. This observation may indicate that fertilization occurs in the gills.

From Figure 2, which gives the best fit regression line for data obtained from monthly clam dissections, it can be seen that fecundity is positively correlated with adult size (measured as length). The correlation coefficients for the regression lines range from a high

Figure 2. Each line is the best fit regression line for for data obtained from monthly clam dissections. An average of 36 ± 13 broods were counted each month. Regression lines extend beyond the length of the longest clam dissected for all months except October, 1980.

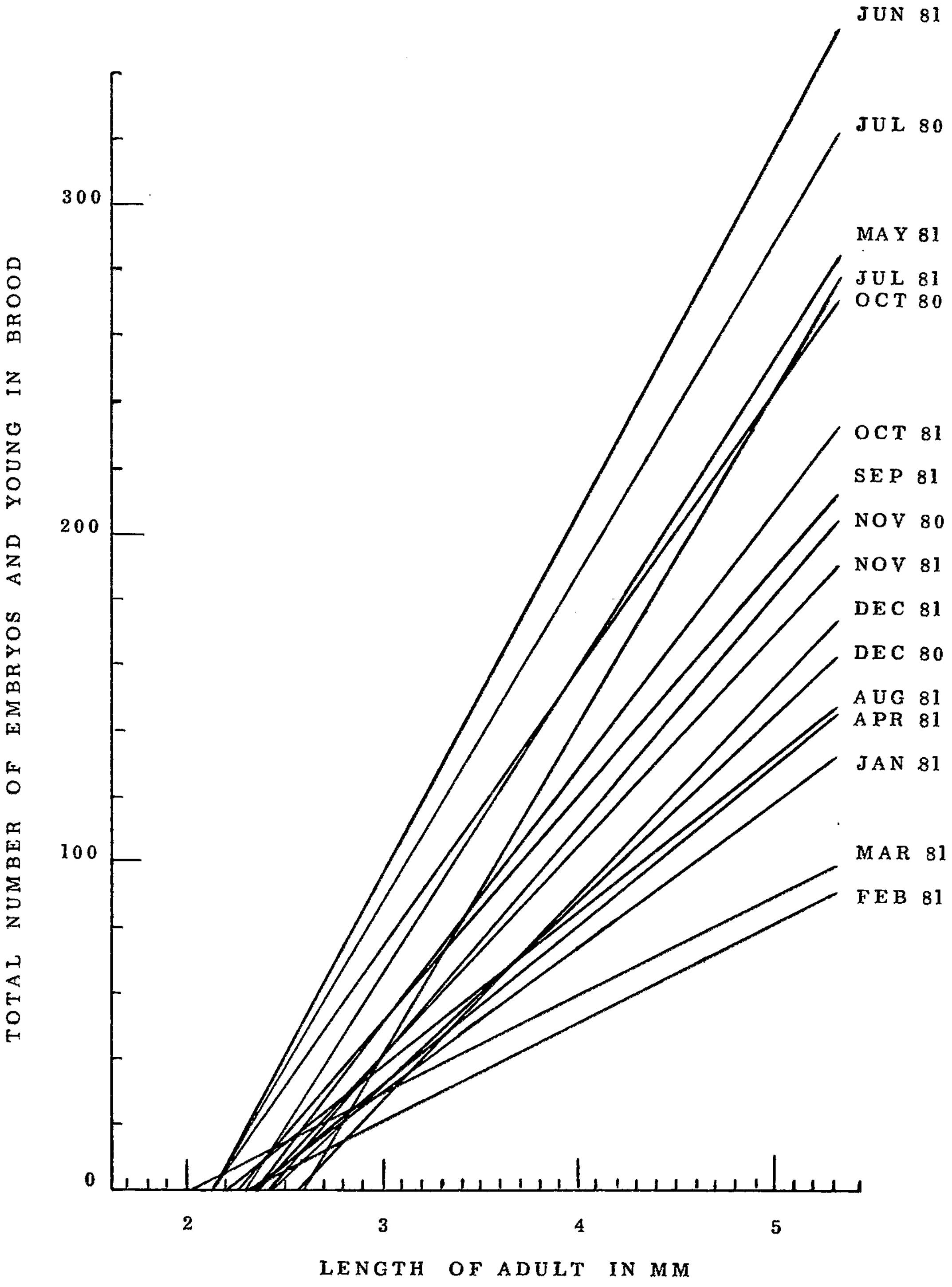


FIGURE 2. Seasonal Change in Fecundity-Size Relationship in Adult *Transennella tantilla*.

of 0.97 (December, 1980 and June, 1981) to a low of 0.76 (August, 1981). The smallest specimen dissected which contained a brood was 1.9 mm, the largest was 5.3 mm. Broods ranged in size from one egg in each of three clams, 2.1, 2.3, and 2.4 mm in length, to 327 embryos in a specimen 5.1 mm in length. An average of 36 ± 13 broods were counted monthly (range, N = 15 to N = 56).

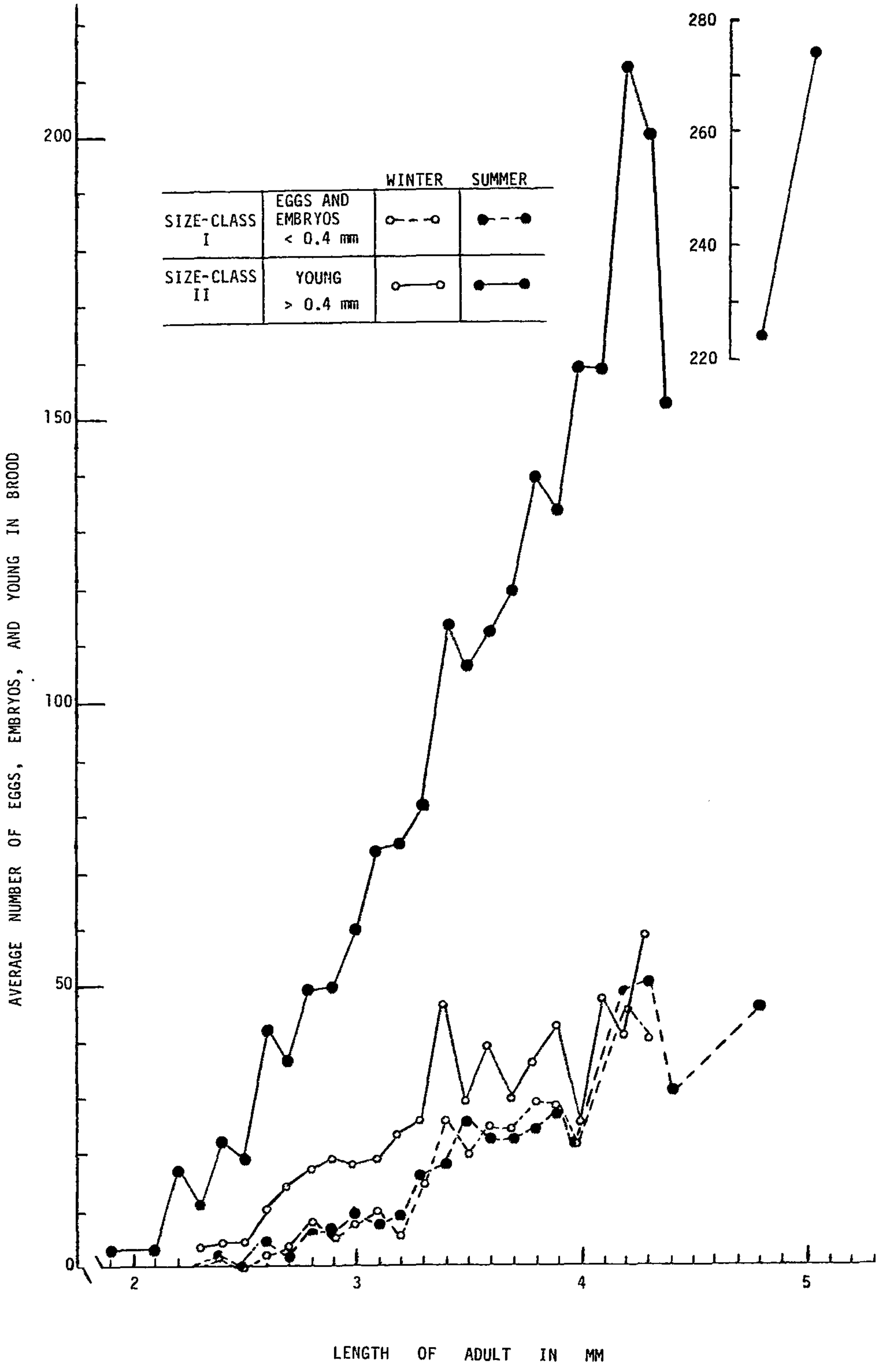
In every sample except those taken October, 1980 and December, 1981, trematode sporozoites containing cercaria were found attached to the gonadal tissue in 2 to 15% of the dissected specimens. In all cases of gonadal infection, brood size was notably depressed. For this reason, only clams without gonad parasites were used for statistical analyses. Trematode metacercaria were also found living in pits in the shells of dissected clams. Since the shell parasites had no detectable effect on brood size (except possibly during the month of August, 1981; see below), these animals were included in the data analyses. The trematodes were not keyed out, but were most likely _Telolecithus_ _pugetensis_ (DeMartini and Pratt, 1964) and/or _Parvatrema_ sp. (see Obrebski, 1968 for further clarification).

It is also apparent from Figure 2 that fecundity changes with season. Females are more productive during summer months than during winter and early spring months, and broods are intermediate in size during the fall of the year. As can be noted from regression lines for the months of July, October, November and December, this trend is maintained from one year to the next. The brood sizes of females sampled in August, 1981, were smaller than one would have predicted from the trends observed during other months. The reason for this is unclear. There was high degree of shell parasitism during this particular month (70% of those dissected had one or more metacercaria).

The time period for embryonic development is not known. The rate of development does vary with season, however, as can be seen in Figure 3. In this figure, the solid lines represent size-class I (eggs and embryos < 0.4 mm in length), and dotted lines represent size-class II (young >0.4 mm to birth size). The points for the winter data were obtained by averaging the number of size-class I and size-class II embryos found in broods of females sampled in December, 1980, January and February, 1981. Likewise, the summer data points are averages of numbers of embryos in the two size-classes found in animals sampled May, June, and July, 1981.

During summer and winter there are more size-class I eggs and embryos represented in the brood, indicating that females are producing ova throughout the year. The average number of size-class II young making up the brood shows little variation with season, while the abundance of size-class I eggs and embryos is considerably higher in the summer. That the ratios of size-class I to size-class II embryos are different implies that developmental rates are seasonably variable. If one assumes that upon entrance into the gill chamber, an ovum undergoes immediate cleavage and fairly constant growth throughout development, it becomes apparent from the data depicted in Figure 3, that eggs, embryos and young are developing and leaving the mother more quickly during the summer months. The fact that

Figure 3. Seasonal Comparison of Brood Size-Class Structure.


WINTER
SUMMER
SIZE-CLASS I
EGGS AND EMBRYOS < 0.4 mm
SIZE-CLASS II
YOUNG > 0.4 mm
0
50
100
150
200
220
240
260
280
2
3
4
5
AVERAGE NUMBER OF EGGS, EMBRYOS, AND YOUNG IN BROOD
LENGTH OF ADULT IN MM

juveniles are released during every month of the year (as will be verified in a later section) makes the assumptions plausible.

Transennella tantilla range in size from 0.550 to 5.3 mm in shell length in the populations studied on the South Slough mudflats. Males are generally ≤ 2.7 mm in shell length; the largest male found during the study period was 3.5 mm (dissected live, January, 1981). Females are larger than males, for the most part, ≥ 2.0 mm in shell length. The smallest female found in sample collections was 1.7 mm long (dissected live, July, 1981; this specimen was not brooding, but had ripe ovaries.)

Sex determinations of dissected T. tantilla sampled at the Portside and Metcalf sites are presented in Table 2. As indicated previously, only clams ≥ 1.85 mm were selected for sexual identification. The values reported as N ≥ 1.85 mm indicate the total number of sexually mature individuals available in all three sub-samples collected at each site for any particular month. In half of the samples, all clams meeting the defined dimension were dissected and sexed. In cases where the total dissected is less than the total available, all the clams within one or two sub-samples were examined, so the results are representative of the whole sample. There were so many clams present in the April collection at site PB, that only the first 123 clams ≥ 1.85 mm encountered in one sub-sample were dissected.

It was possible to make a positive sexual determination with confidence for over 98% of the clams observed. Clams listed as

Table. 2. Sex Determinations of *T. tantilla* Sampled at the Portside and Metcalf Sites.

	MAR	APR	MAY	JUL	AUG	OCT	DEC
SITE: PA							
N ≥ 1.85 mm*	57	94	63	32	89	115	106
No. Males	20	16	39	16	61	55	50
No. Females	10	17	21	16	28	60	56
No. ?	-	-	3	-	-	-	-
No. Sub-Samples Used	2	1	3	3	3	3	3
SITE: PB							
N ≥ 1.85 mm*	81	469	48	14	8	63	53
No. Males	43	84	22	7	7	23	25
No. Females	25	39	20	2	1	38	28
No. ?	-	-	6	1	-	2	-
No. Sub-Samples Used	2	< 1	3	2	3	3	3
SITE: MP							
N ≥ 1.85 mm*	345	224	263	116	67	149	361
No. Males	65	59	99	Did	36	73	81
No. Females	42	44	74	Not	31	26	36
No. ?	-	12	4	Dis-	-	-	-
No. Sub-Samples Used	1	1	2	sect @	3	2	1
SITE: MS							
N ≥ 1.85 mm*	81	62	57	215	67	112	151
No. Males	58	Did	34	59	26	70	73
No. Females	23	Not	20	41	41	38	31
No. ?	-	Dis-	3	-	-	4	3
No. Sub-Samples Used	3	sect †	3	1 + Part of Another	3	3	2

*Total Number Clams ≥ 1.85 mm/Sample.

@Clams Were Not Dissected Due To Sampling Problems.

†Clams Were Not Dissected Due To Poor Preservation of Tissues.

"question marks" either had gonads which were too small to sex or gonads which were infected by trematodes. Questionable clams are not included in the analysis which follows.

When sex ratios for all sites were compared, a significant difference was found (G-statistic = 12.33, X_3^2 (0.01) = 11.34). Further analysis of partitioned data did not reveal significant differences in sex ratios between sites located on the same mudflat. Highly significant differences were detected, however, when data collected from PB + PA were combined and compared with results from MP + MS (G = 11.12, X_1^2 (0.001) = 10.83). Significant month to month differences in sex ratios were not found.

Combined data for the Portside sites yield a male/female ratio of 56:44; combined data from the Metcalf sites produce a ratio of 63:37. It must be kept in mind that many animals $\leq$ 1.85 mm in length are most likely viable males, so, if anything, these calculated proportions of males to females are too low.

Table 3 shows the size ranges in which male and female T. tantilla overlap. Since sex ratios were different for populations sampled at sites on the Metcalf and Portside mudflats, male/female percentage data by size-class were compared. The results show that area to area differences in the size at which sex reversal occurs are slight.

Size-Frequency Data

Size-frequency data were collected at each site over a period of eleven months, although results for only nine are available for

TABLE 3. Size Range in Which Male and Female *Transennella tantilla* Overlap at Sites on the Metcalf Mudflat (MP + MS), Sites on the Portside Mudflat (PA + PB), and at All Sites Combined.

	MP + MS		PA + PB		COMBINED SITES	
SIZE CLASS	% Male	% Female	% Male	% Female	% Male	% Female
1.85 - 2.07 mm	93	7	85	15	90	10
2.15 - 2.37 mm	67	33	70	30	68	32
2.44 - 2.66 mm	35	65	41	59	38	62
2.74 - 2.96 mm	16	84	13	87	14	86
> 2.96 mm	0	100	0	100	0	100

analysis. Tables 4 and 5 are compilations of this data converted by size-class to percent of the total number of clams in the sample (N) for purposes of between-site and between-month comparisons. Since *T. tantilla* is patchy in distribution, direct comparison of raw data is difficult and can lead to erroneous interpretations.

The shaded areas in Tables 4 and 5 encompass size-classes showing an increase in frequency over the preceding month. Where shaded areas in three or more subsequent months overlap, the trend has been combined into a single, continuous, shaded zone. The clams making up such a block of data are considered to be part of a cohort exhibiting synchronous growth. A solid line underscores the largest size-class occurring within each monthly sample. For any given site, three pieces of information can be discerned from the table: (1), reproduction trends; (2), growth trends; and (3), seasonal changes in population structure.

When samples were sieved through the 500_u mesh, newly-released juveniles, whose smallest dimension is about 0.350 mm, were not retained. A lag of about one month probably exists between the actual time of reproduction and the time when clams of the smallest size-classes were retained for analysis. Thus, for example, the majority of the clams making up the cohort traced at site PA were most likely released during February.

Reproduction was moderate to high at sites MP and MS for all months considered. Release of juveniles peaked at these sites during spring and late summer, making it possible to follow two cohorts

TABLE 4. Size-Frequency Distributions of *T. tantilla* Collected at Sites on the Portside Mudflat. Numbers Represent Percent of Total Number of Clams in the Sample. Shaded Areas Indicate Cohorts of Clams Exhibiting Synchronous Growth. A Solid Line Underscores the Largest Size-Class Occurring Within Each Monthly Sample.

	SITE PA									SITE PB									SITE PC								
SIZE CLASS (mm)	FEB	MAR	APR	MAY	JUL	AUG	SEP	OCT	DEC	FEB	MAR	APR	MAY	JUL	AUG	SEP	OCT	DEC	FEB	MAR	APR	MAY	JUL	AUG	SEP	OCT	DEC
.592-.740		2	1	1	0	0.5	0.4	0.7	0.6	0	0	0.2	0	0	1	0	0	1	0	0	0.4	1		0	0	0	3
.814-1.04		51	48	23	21	12	5	4	20	7	9	3	4	26	12	6	10	23	9	7	8	54		4	0	5	13
1.11-1.33		29	25	44	23	23	11	4	8	9	10	5	9	25	40	9	11	24	13	14	11	34		11	0	0	3
1.41-1.63		8	11	22	37	26	19	7	2	15	17	9	12	30	28	13	9	10	17	15	15	7		48	5	5	0
1.70-1.92		4	6	7	17	27	26	19	6	19	13	16	16	13	15	23	3	11	17	15	17	2		30	22	9	0
2.00-2.22		2	3	2	3	11	23	30	13	26	21	20	20	5	2	22	15	4	18	17	18	2		7	27	27	3
2.29-2.52		2	3	1	0	1	14	20	19	14	14	18	4	2	1	9	16	6	13	15	13	0		0	22	5	16
2.59-2.81		0.8	1	0.4	0	0	1	11	13	6	7	14	12	0	0	10	15	4	6	9	7	0		0	16	9	23
2.89-3.11		0.2	1	0.3	0	0	0	4	14	5	3	8	13	0	0	6	8	4	4	5	5	0		0	5	32	13
3.18-3.40		0.5	0.3	0.4	0	0	0	0.7	4	0	1	5	10	0	0	2	9	5	2	2	4	0		0	3	5	16
3.48-3.70		0.3	0	0	0	0	0	0	0.6	0	1	3	0	0	0	0	2	5	0.9	0.4	0.7	0		0	0	5	3
3.77-4.00		0.3	0.1	0.1	0	0	0	0	0	0	1	0.3	0	0	0	0	2	1	0.5	0.2	0	0		0	0	0	3
4.07-4.29		0.2	0.1	0	0	0	0	0	0	0	0.7	0.3	0	0	0	0	0	0.6	0	0.2	0.6	0		0	0	0	3
4.37-4.59		0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0		0	0	0	0
4.66-4.88		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0
4.96-5.18		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0		0	0	0	0
N		593	1172*	1018	344	376	203	152	158	86	145	612*	69	101	136	82	92	158	577	467	550	161		56	37	22	31

*PA - Approximation Based on Two Sub-Samples (2/3 X 0.1 m^2)

*PB - One Sub-Sample Taken in Trough Close to Pier; Two Sub-Samples Taken on Level Substrate Away from Pier

TABLE 5. Size-Frequency Distributions of _T. tantilla_ Collected at Sites on the Metcalf Mudflat. See Table 4 For Explanation.

	SITE MP									SITE MS								
SIZE CLASS (mm)	FEB	MAR	APR	MAY	JUL	AUG	SEP	OCT	DEC	FEB	MAR	APR	MAY	JUL	AUG	SEP	OCT	DEC
.592-.740	0.2	0	4	2	6	6	1	0.5	0.2	2	0	2	2	1	4	2	0.8	0
.814-1.04	27	11	43	35	32	62	43	13	14	29	55	61	42	20	35	33	23	20
1.11-1.33	18	10	16	30	27	15	35	22	19	15	15	18	33	17	12	35	19	17
1.41-1.63	19	14	9	10	20	7	13	26	22	11	8	7	11	18	11	14	18	12
1.70-1.92	11	17	9	6	10	5	5	21	20	15	6	4	5	17	9	5	16	13
2.00-2.22	12	24	8	6	3	3	2	9	13	9	6	2	2	13	9	3	9	18
2.29-2.52	6	14	6	5	1	1	1	4	5	7	4	3	2	6	12	4	5	8
2.59-2.81	4	5	3	2	1	0.5	0.6	2	3	2	2	0.9	0.8	3	2	2	2	5
2.89-3.11	1	2	1	2	0.6	0.2	0	1	0.8	3	0.7	0.6	0.9	2	2	2	2	3
3.18-3.40	0.2	0.7	0.7	1	0.3	0	0	0.3	0.7	3	0.2	0.5	0.9	1	0.9	0	3	2
3.48-3.70	0.8	0.7	0.1	0.4	0	0	0	0	0.3	3	0.4	0	0.2	1	0.5	0	3	2
3.77-4.00	0.2	0.7	0	0	0	0.1	0	0	0.1	0.7	0.7	0.3	0	0.3	0.5	0.2	0	0
4.07-4.29	0	0	0	0.2	0	0	0	0	0	0	0.9	0	0	0.2	0	0	0	0
4.37-4.59	0	0	0	0.1	0	0	0	0	0	0.7	0	0	0.2	0.2	0	0	0	0
4.66-4.88	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0
4.96-5.18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N	479	606	1418*	1355	1163	929	1038	663	1147	136	450	644	635	625	212	550	386	350

*MP - Approximation Based on Two Sub-Samples (2/3 X 0.1 m^2)

over several months. At site PA, the period of greatest reproduction was from February to April. A small spurt in reproduction also occurred sometime between November and December. One major cohort is discernible at this site. The results at sites PB and PC are not as straightforward as at the other three sites. Reproduction occurs at a very low level during most months, and growth from one size-class to the next is not as easy to follow. There appears to be a cohort born in late spring at each site which can be followed into the late fall. Reproduction peaks a second time in both areas during November and December.

Densities of _T. tantilla_ are high at sites MP, MS, and PA all year. Numbers of clams at site PB are low, but fairly constant. The sample size for May at site PB is spurious because it includes animals collected from the slope of the pier where wave action deposits _T. tantilla_ in higher than normal numbers. Site PC exhibits a notable decline in the density of _Transennella_ between April and December. The site was throroughly searched for specimens during June and July of 1981, but finding none, samples were not collected during these months. A year later (June, 1982), another search made it clear that the site had not recovered from the population crash. After numerous (> 10) samples were sieved in the field (500_u mesh), only one living _T. tantilla_ was found. The half-shells and shell fragments that were so abundant in 1981 were not present either. Examination of the underscored portions of Table 4 reveals that larger clams are missing at the Portside sites during May through August. Sites

MP and MS (Table 5) do not show this trend.

When site mean densities of _Transennella tantilla_, obtained by averaging sub-sample densities, were plotted against time (see Figure 4), it was apparent that there was a decrease in the population sizes of clams at all sites during the late spring and summer months. The decrease was most noticable at sites PA, PB, and PC. There appears to be a one month lag in the response of the Metcalf sites, but nonetheless, the trends are comparable to those observed at the Portside sites. The results of a two-factor analysis of variance are presented in Table 6. Between-site and between-month differences were found to be highly significant.

Growth Rates

By determining the monthly mean length of those size-classes making up the cohorts found in each site (Tables 4 and 5), it is possible to estimate the growth rate of _T. tantilla_ in the two mudflat locations. Table 7 summarizes this data by month and by site. The values in parentheses represent a monthly change in length calculated by dividing the observed change in length by the number of intervening months. Stars (***) separate the estimated growth rate of one cohort from any others within the same site.

Despite sketchy data, growth rates are similar from month to month within each site and between sites, except during August through October when increases in clam growth rates are evident at all sites. According to these data, the average growth per month

Figure 4. Mean Density of _Transennella tantilla_ by Site v.s. Time by Month and Day, 1981.

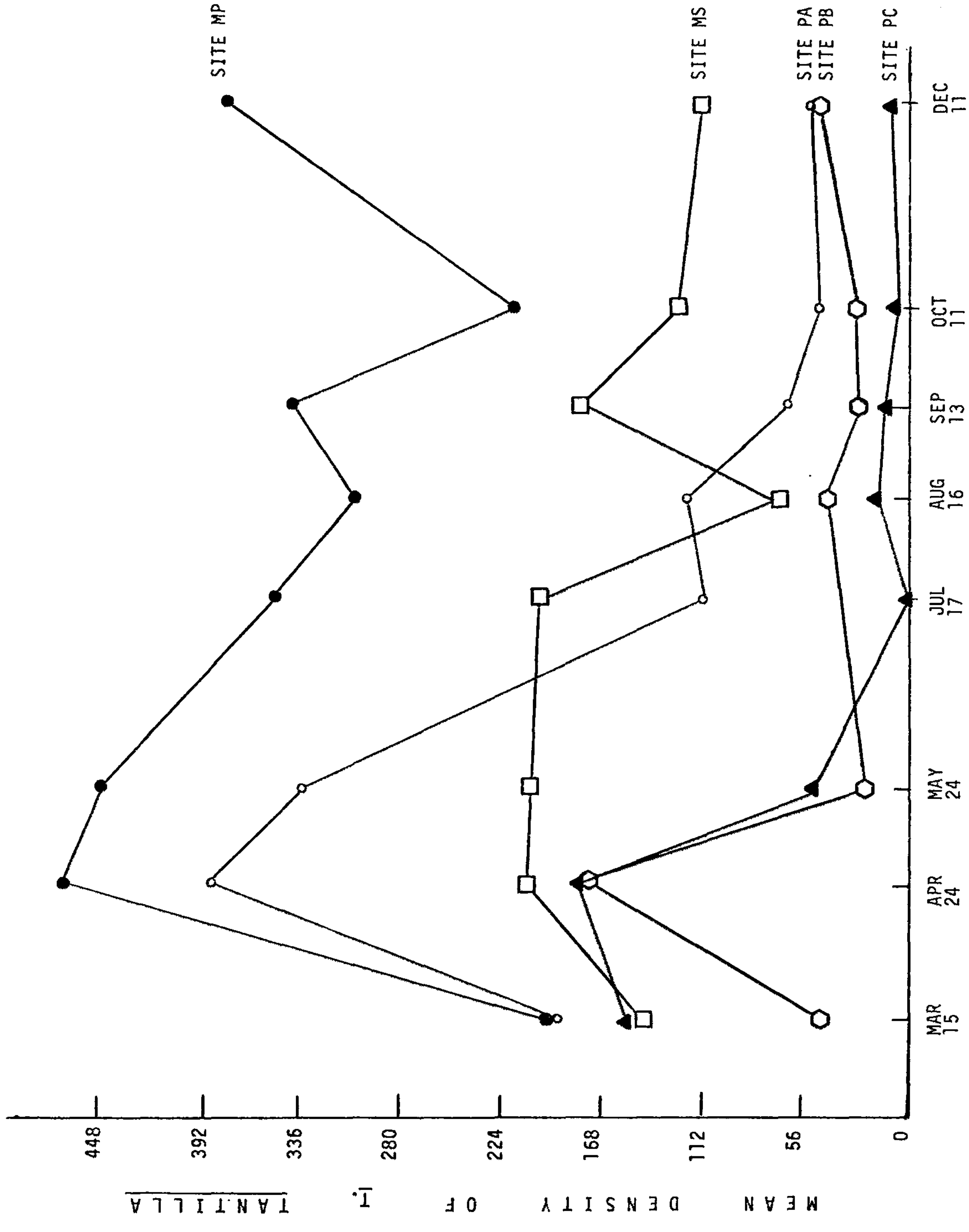

MEAN DENSITY OF T. TANTILLA
0
56
112
168
224
280
336
392
448
MAR 15
APR 24
MAY 24
JUL 17
AUG 16
SEP 13
OCT 11
DEC 11
SITE MP
SITE MS
SITE PA
SITE PB
SITE PC

TABLE 6. Analysis of Variance of Mean Densities of *Transennella tantilla* by Month and by Site.

Source of Variation	Sum of Squares	DF	Mean Square	F	p.
Factor 1 (Sites)	1,224,838	4	306,209	300.3	(.001)
Factor 2 (Months)	353,915	7	50,559	49.6	(.001)
Interaction	382,427	28	13,658	13.4	(.001)
Error	78,523	77	1,019		
Total	2,039,703	116			

Table 7. Monthly Growth Rate of *Transennella tantilla* at Sites on the Portside and Metcalf Mudflats.

	SITE PA		SITE PB		SITE PC		SITE MP		SITE MS	
MONTH	ML[1] (mm)	Δ L/mo (mm)	ML (mm)	Δ L/mo (mm)	ML (mm)	Δ L/mo (mm)	ML (mm)	Δ L/mo (mm)	ML (mm)	Δ L/mo (mm)
MAR	0.95									
		0.26								
APR	1.21						1.00		0.98	
		0.15						0.30		0.37
MAY	1.36				1.04		1.30		1.35	
		(0.14)[2]				(0.21)		(0.16)		(0.29)
JUN										
		(0.14)				(0.21)		(0.16)		(0.29)
JUL	1.64		1.23				1.62		1.93	
		0.25		0.20		(0.21)	**************		**************	
AUG	1.89		1.43		1.67		0.92		0.92	
		0.33		0.81		0.77		0.38		0.39
SEP	2.22		2.24		2.44		1.30		1.31	
		0.14		0.60		0.66		0.47		0.51
OCT	2.36		2.84		3.10		1.77		1.82	
		(0.20)				(0.20)		(0.25)		(0.26)
NOV										
		(0.20)				(0.20)		(0.25)		(0.26)
DEC	2.75				3.50		2.26		2.34	
AVG GROWTH PER MONTH:	0.20 mm		-------		0.35 mm		0.28 mm		0.34 mm	

[1] ML = Mean Length of Clams of a Given Cohort

[2] Values Within Parentheses Are Estimates of Monthly Growth Obtained by Dividing Observed Change in Length by the Number of Intervening Months

ranges from 0.20 mm/month to 0.35 mm/month. At these rates, a newly-released clam, 0.550 mm in length, could grow to between 3.0 and 4.8 mm in one year's time. _T. tantilla_ probably has a life span of 1-1½ years, and these predicted growth rates seem appropriate given the actual shell lengths recorded for clams occurring in the largest size-classes.

Cage Studies

The field "caging" experiment was set up in an attempt to provide information on the seasonal growth and reproductive habits of individual _T. tantilla_. As it was not possible to design adequate controls to test for "cage" effects, results from these experiments are indicative of potential trends, rather than absolute determinations of growth and reproduction rates. The cage data and the field sampling data can be compared and used to confirm or reject implications of one or the other data source.

Three test trays, PB, PC, and PD, were followed on the Portside mudflat from December, 1980 to May, 1981. Four test trays, MS, MR, MU, and MA, were followed on the Metcalf mudflat from December, 1980 to December, 1981. Table 8 provides the schedule of examination times and conditions of cages left in the field. Some cages were examined monthly, others bimonthly.

Shifting sediment covered the test trays and most likely affected current flow within the individual cage cells. Although sediment burial was a continuing problem throughout the year at both locations,

TABLE 8. Schedule of Examination Times and Conditions of Cages Followed at the Portside and Metcalf Mudflats from December, 1980 to December, 1981. Table Is Continued on Page 43.

CAGE	DEC 80	JAN	FEB	MAR	APR	MAY
PB	Begin	X	-	X	-	X
COMMENTS:						Sulfide Layer Next to Board; Covered With 2-3 cm Sediment and Algae
PC	Begin	X	X	X	X	X
COMMENTS:			Covered With 6 cm Sediment	*Enteromorpha* Growing on Side of Board	Covered With Fine Layer of Sediment and Algae	Same as PB
PD	-	Begin	X	X	X	X
COMMENTS:			Same As PC		Covered With 2-4 cm Sediment, Algae and Barnacles	Same as PB
MS	Begin	-	X	-	X	-
COMMENTS:			Clean Board		Covered With Fine Layer Sediment and Algae	
MR	Begin	X	-	X	-	X
COMMENTS:				Clean Board		Covered With Fine Layer of Sediment and Algae
MT	Begin	X	X	-	X	-
COMMENTS:			Clean Board; One End Under 2 cm Sediment		Covered With 2 cm Sediment; Sulfide Layer in Cages	
MU	Begin	-	-	X	X	X
COMMENTS:					Clean Board	Covered With Fine Layer Sediment and Algae
MA	-	-	-	-	-	-
COMMENTS						

Table 8 Continued.

JUN	JUL	AUG	SEP	OCT	NOV	DEC 81
X Sulfide Layer in Cages; Covered With 15-25 cm Sediment; Clams All Dead	-	-	-	-	-	-
X Same as PB	-	-	-	-	-	-
X Same as PB	-	-	-	-	-	-
X Sulfide Layer in Cages; Covered With Fine Layer of Sediment and Algae; Clams All Dead	-	-	-	-	-	-
-	X Covered With 1 cm Sediment and Algae	-	-	-	-	-
X Sulfide Layer in Cages; Covered With Heavy Layer Sediment and Algae	X Sulfide Layer in Cages; Covered With 1 cm Sediment and Algae	X Covered With ½ to 1 cm Sediment and Algae	X Covered With Fine Layer Sediment	X Covered With Algae	X Covered With 1 to 2 cm Sediment	X Board Half Covered With 2 to 4 cm Sediment
X Covered With Fine Layer Sediment and Algae	X Sulfide Layer in Cages; Covered With 1 cm Sediment and Algae	X Covered With ½ to 1 cm Sediment and Algae	X Sulfide Layer in Cages; Fine Layer Sediment	X Sulfide Layer in Cages; Clams Dead	X Fine Layer Sediment	X Board Half Covered With 2 to 4 cm Sediment
Begin	X Covered With Fine Layer Sediment	-	-	-	-	-

at least until June, the problem seemed worse at the Portside. For this reason, cages were discontinued at this site.

Ulva, Enteromorpha, Vaucheria, and barnacles settled and grew on the plywood, but not on the fabric mesh of the cage. The algae, in some cases, were very large and dense and the individual cage cells were covered over with a mat of plant blades. A diatomaceous film was visible on the cage fabric, but it did not prevent water flow. Experimental determination of the effects of sedimentary or algal cover on nutrient availability to caged clams was not carried out.

The sediment in some cages, particularly those which had been covered by a heavy load of sediment or algae, was anoxic. As a result, clams present in these cages suffered high mortality rates. Dead clams had blackened shells that were still articulated. The few survivors were found tightly closed lying on the surface of the sediment. When placed in fresh sea water, they would immediately extend their siphons and begin filtering.

The test trays did not deteriorate during the course of the field study. The fabric held up very well; only 32 of the 983 cages examined were found with holes in the top mesh. Of these 32, 18 were caused by an adult C. magister which occupied the lab storage tank where the trays were kept during monthly observations. It was not immediately known that the crab was present or that it would attack the cages. Dactyl prints were found on the plastic film containers leaving evidence that they had been crushed by the crab's chelipeds.

Clean supra-tidal bay sand was added to all cages each time they were readied for return to the field. By the next examination, those cages which were sulfide-free mimicked the surrounding field community with amphipods, cumaceans, tanaids, polychaetes, nemerteans, and nematodes established in the sandy "cage" environment. When living *T. tantilla* were removed from these cages, they were immediately responsive and mobile. From time to time, various species of snails and juvenile bivalves were observed in the cages. A white sea urchin with red spots (test diameter = 1.11 mm), which had metamorphosed only recently, was removed alive from one of the cages of test tray MR on May 22, 1981 and a juvenile crab, of undetermined size, was found in a cage in test tray PC on March 15, 1981. The fabric in both of these cages was intact and there were no small holes in the mesh.

Cage results from test trays examined after the same amount of field exposure (one month or two months) were combined for data analysis. Comparisons between cages left at the Portside and Metcalf mudflats were not made due to the lack of adequate overlapping observations. Between-site comparisons would be important if the experiment had proper controls and had been designed to provide absolute answers, but as discussed previously, this is not the case. Test trays with 100% mortality in the cages were not included in the data compilations. Dead clams were not measured and the cage sediment was not checked for the presence of offspring.

Tables 9 and 10 present survival and growth information for caged

TABLE 9. Growth Record of *Transennella tantilla* Retained in Cages on the Portside and Metcalf Mudflats, 1981*.

Condition of "Caged" Clam	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Alive	54	27	48	65	66	17	34	25	33	4	46	45@
Dead	9	22	4	14	11	11	39	30	19	15	4	10
Missing	16	7	4	5	7	0	4	1	4	9	6	1
Δ Length (mm)												
0.000	14	26	14	29	37	7	12	5	6	0	8	33
0.074	25	1	23	14	17	4	11	10	17	1	11	6
0.148	8	0	8	11	3	4	2	5	9	2	10	0
0.222	5	0	2	7	2	0	2	4	1	0	13	0
0.296	1	0	1	2	1	0	1	0	0	0	2	0
0.370	0	0	0	1	1	0	3	0	0	0	1	0
0.518	0	0	0	0	0	0	1	0	0	0	0	0
Δ L < 0.000 (error)	1	0	1	5	2	2	2	1	0	1	1	3
Per Cent of Clams Exhibiting Growth	72	4	71	54	36	47	59	76	82	75	80	14

*Data Combined From All Cages Examined Once Per Month

@Three living clams were not measured this month

TABLE 10. Growth Record of <u>Transennella tantilla</u> Retained in Cages on the Portside and Metcalf Mudflats, 1981@.

Condition of "Caged" Clam	DEC-FEB	JAN-MAR	FEB-APR	MAR-MAY	APR-JUN	MAY-JUL
Alive	30	22	26	27	5	11
Dead	12	26	30	17	22	16
Missing	1	8	0	12	1	1
Δ Length (mm)						
0.000	9	7	1	8	1	3
0.074	10	7	8	4	2	2
0.148	7	4	7	2	0	1
0.222	3	3	7	4	1	0
0.296	0	0	0	2	0	4
0.370	0	0	0	2	0	0
0.518	0	0	1	0	1	0
0.888	0	0	0	1	0	0
Δ L < 0.000 (error)	1	1	2	4	0	1
Per Cent of Clams Exhibiting Growth	67	64	88	56	80	64

[@] Data Combined From All Cages Examined Once Every Two Months

T. tantilla. Table 9 contains data from cages observed after one month of field exposure and Table 10 contains data obtained after an interval of two months. The row headings "Alive" and "Dead" and their monthly values indicate the condition and number of clams found after field exposure. The category "Missing Clams" is made up of very small (< 1 mm in shell length) caged clams which were not found again, clams which were missing from cages with holes in the mesh, and clams which were accidentally dropped or lost. The "Error" row includes clams whose shell length decreased from one month to the next.

Survival of clams was > 50% for 8 of the 12 months considered in Table 9. In February, the heavy sediment cover was probably responsible for the low survivorship and interrupted growth. The presence of sulfide adversely affected clam survivorship, particularly during July and August. Growth of living clams during these months does not appear to have been affected. The reasons for the low survivorship of clams during October and the low level of growth in December are not clear.

Survivorship was close to 40% or better in the two month cages for all but the Apr-Jun time interval. Sulfide was the probably cause of clam mortalities during this period.

Growth of caged clams ranged from 0.074 to 0.888 mm. More than 50% of the clams observed in 14 of the 18 time intervals considered showed an increase in size from one examination time to the next. While the growth rates are probably not representative of field conditions, given the sediment transport, algal attachment and sulfide problems besetting the cages, an interesting growth phenomenon is apparent: T. tantilla is capable of growing every season of the year. This result confirms observations reported previously in the section describing field sampling results. That some clams grew ≥ 0.222 mm during most months also lends credence to the growth rate estimates given earlier.

Table 11 is divided into two parts, each of which provides information on the number of offspring released in cages during the stated time intervals. It should be noted that there is insufficient data for a meaningful interpretation to be made for October in Part A. Since females cannot be identified externally, only the sediment in cages of individuals larger than 2.67 mm was examined microscopically for the presence of offspring. The number of offspring found in any one cage ranged from 0 to 65 (Table 11).

The most important information resulting from this part of the caging experiment is that T. tantilla releases young at all times of the year. Contrary to the field data discussed in a previous section, females appear to release more young between November and April than during the summer months. This result could be misleading, however, considering the presence of sulfide in the cages during the summer and fall of the year.

Crab Predation Studies

The results of the laboratory experiment which was conducted

TABLE 11. Number of Offspring Released By Living *Transennella tantilla* Retained in Cages on the Portside and Metcalf Mudflats.

PART A: DATA OBTAINED FROM CAGES EXAMINED AT ONE-MONTH INTERVALS

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Number of Adult *T. tantilla* ≥ 2.67 mm	24	8	21	42	37	9	16	11	14	2	26	29
Mean Number of Offspring	2.6	1.5	0.5	1.1	0.6	0.2	2.3	1.2	0.1	0	0.2	0.1
±												
Standard Deviation	4.0	2.7	1.0	1.6	1.1	0.7	3.2	1.8	0.5	0	0.4	0.3
Per Cent of Adult Females With Offspring	58	50	29	45	32	11	50	36	7	-	15	10

PART B: DATA OBTAINED FROM CAGES EXAMINED AT TWO-MONTH INTERVALS

	NOV-JAN	DEC-FEB	JAN-MAR	FEB-APR	MAR-MAY	APR-JUN	MAY-JUL
Number of Adult *T. tantilla* ≥ 2.67 mm	5	26	10	12	14	4	7
Mean Number of Offspring	6.2	10.2	3.0	2.2	0.7	1.0	0.7
±							
Standard Deviation	7.9	14.8	2.9	4.4	1.1	1.4	1.0
Per Cent of Adult Females With OffSpring	100	58	80	33	43	50	43

to determine whether C. magister juveniles and other crab species use T. tantilla as a food source are presented in Table 12. In addition to proving that juvenile crabs do prey on T. tantilla, Table 12 provides information on the eating habits of those crabs tested. The hermit crab destroys the shell when it eats the clams, while the other crabs leave half-shells and fragments behind.

When the tanks were examined, four of the five C. magister which were added to tank # 1 at the beginning of the experiment were still alive. They showed an average increase in carapace width of 0.8 cm. Only the C. antennarius was alive in tank # 3. Carapace pieces of the other 4 crabs were present in the tank. The hermit crab in tank # 4 was found alive.

Juvenile C. magister were observed searching for, handling, and consuming T. tantilla in laboratory aquaria. During rest periods, the crabs sat quietly, half-buried in the bay sand which covered the bottoms of the tanks. When a clam was added to the tank in the vicinity of a crab, it responded by increasing antennular flicking. Rhythmic beating of the maxillipedal flagellae also began. The crab rose from its resting position with its chelipeds extended forward and above the surface of the sand. It began moving slowly, first to one side of the aquarium, and then to the other. As the crab moved from side to side, the dactyls were used to sift the sediment in a circular motion that was directed toward the mouthparts. The crab searched an entire area by moving back and forth in a non-random pattern. From time to time during the search, the crab would stop

TABLE 12. Results of Laboratory Test of Possible Predator-Prey Interactions Between Juvenile *Cancer magister* and *Transennella tantilla*

TANK #	NUMBER OF *T. TANTILLA* AT BEGINNING	NUMBER AND SPECIES OF CRABS AT BEGINNING	NUMBER OF *T. TANTILLA* AT END	NUMBER OF DEAD *T. TANTILLA*		
				NUMBER OF ARTICULATED SHELLS	NUMBER OF HALF-SHELLS	NUMBER OF SHELL FRAGMENTS
1	150	5 *C. magister*	0	1	103	Many
2	150	____________	118	29	0	2
3	50	1 *C. magister* 1 *C. antennarius* 3 Unidentified sp.	0	0	38	Many
4	50	1 Hermit Crab	10	1	1	Many
5	50	____________	35	14	0	1

and reorient the antennules.

When a clam was encountered, the dactyls quickly and adeptly picked it up and brought it to the mouthparts. The chelipeds positioned the clam between the maxillipeds and the maxillae in such a way that the valves were parallel with the right and left side of the crab. The mouthparts rotated the clam round and round while one cheliped helped keep the clam in position and the other probed between the tightly closed valves. This "clam-spinning" and "dactyl-probing" activity continued until the crab successfully separated the valves. The time spent in opening a clam varied from 15 seconds to several minutes. If the crab dropped a clam during the spinning and probing process, it would pick it up and resume the activity. Sometimes the crab would reverse the direction of the spin, slow down the spinning movements, or make more forceful probing attempts with the dactyl. In several instances, crabs gave up trying to pry open the valves of a clam. After the unsuccessful attempt, the clam was dropped and searching behavior began again.

In the process of penetrating and opening the valves, the crab crushed one half-shell and left the other half-shell intact. Sometimes the hinge would remain attached to one of the pieces. The crab used its chelipeds and dactyls to manipulate and clean out all the clam tissue in the half-shell and shell pieces. The dactyls were used like cocktail forks to scoop out clam meat and direct it to the maxillipeds and mandibles. The shells were also directed into the mouthparts where they were completely cleaned and subsequently ejected onto the substrate. When the crab finished with one clam, if not satiated, it would repeat the entire foraging process. There was little variation in the foraging behavior exhibited by one crab or between one crab and another.

Agonistic behavior was observed between crabs when one crab had located a clam and the other was still searching. Crabs were very adept at holding a clam next to the body with one cheliped (somewhat akin to a football player tucking a ball) and using the other to fend off an intruder (with a forward and outward-directed waving action of the cheliped). Sometimes the crab would move sideways toward the agressor, while at others it would move away. I never saw a crab lose possession of its clam during a confrontation with another crab.

DISCUSSION

In Coos Bay, _T_. _tantilla_ produce, brood and release young every season of the year. Production of offspring is lower and embryonic growth rates are slower during the winter. Fecundity is positively correlated with adult size throughout the year. Juveniles are released at a shell length of 0.53-0.55 mm. The clam grows year-around and there is no apparent seasonality in growth rate. An overall estimate of the growth rate was determined from size-frequency data and found to be 0.20-0.35 mm/month. At these rates, males would be sexually mature 4 to 6 months after birth (males may actually mature sooner than this if organisms < 1.85 mm produce viable sperm; see results section for clarification) and females would begin producing broods 4 to 7 months after birth. Females continue to produce offspring until death. Individuals probably live for 1-2 years.

In False Bay, on San Juan Island, Washington, _T_. _tantilla_ is a conspicuous, numerically-dominant member of the mudflat community. It is not uncommon to find densities ranging between 6,000-12,000/m^2 (Brenchley, 1981; personal observation). Wilson (personal communication) reported seeing densities up to 20,000/m^2. The organism can attain a shell length of 6.6 mm (personal observation). In this area, the coloration of _Transennella_ _tantilla_ fit the characteristic description: cream white shell with a purple/brown stripe on the posterior edge. The only observed variation is in the width of the stripe (personal observation). This shell marking stands out against the light grey sandy sediment background. The size, density and shell coloration of T. tantilla in False Bay make them very easy to spot in pools on the mudflat at low tide where they lie about fully exposed or partially buried.

T. tantilla brood and release young year-around in False Bay (Mottet, personal communication). Hansen (1953) and Pamatmat (1966) claimed that the organism only released young in the spring and summer; this oversight probably resulted from their sampling techniques. I have found fecundity to be seasonally variable and positively correlated with adult size. In addition, females collected from False Bay had smaller broods than females collected in Coos Bay (personal, unpublished). Males range in size from 1.5-4.6 mm (Hansen, 1953) and females begin brooding at 2.8 mm (personal, unpublished). Juveniles are released when approximately 0.65 mm in shell length.

Pamatmat (1966) estimated growth rates of T. tantilla in False Bay from size-frequency distribution data. He found the growth rate to vary with size and with season. Juveniles grow faster than adults (juveniles grow 0.40-0.88 mm/month and adults grow 0.27-0.55/month), and adults grow more during the summer than during the winter (approximately 0.28 mm/month, Jan-Mar; 0.35 mm/month, Mar-May; 0.42 mm/month, May-Jul; 0.53 mm/month, Jul-Sep). Pamatmat did not collect samples from October to December, so it is not known if growth occurs throughout the year in False Bay.

Although there is less information available on the life history traits and population characteristics of Transennella tantilla from Tomales Bay, what is known is included here because there are important geographic differences worth noting. According to Gray (1978), the purple morph of T. tantilla is released in Tomales Bay at a similar size as clams in Coos Bay (0.52 mm) but it attains shell lengths somewhat longer than those observed in False Bay (7.0 mm). According to Obrebski (1968), the release size of T. tantilla in Tomales Bay is comparable to that of juveniles in False Bay (0.65 mm) and adults attain considerably larger sizes in Tomales Bay (8.1 mm) than they do in False Bay. Gray indicates that the white morph of T. tantilla ranges between 0.59-8.0 mm in Tomales Bay. If Obrebski combined data from purple morphs and white morphs, this would explain his reported upper size range difference for T. tantilla in Tomales Bay, but the difference in the lower value remains unexplained.

Obrebski and Gray both state that T. tantilla can be found brooding young throughout the year. DeMartini in a personal communication to Pamatmat (1966) indicated that Transennella exhibits seasonal release of young in Tomales Bay Obrebski observed as many as 500 embryos in one brood. His data show a tendency for brood size to increase with adult size. Although not clearcut, the data also suggest that brood sizes are larger in the summer than during the rest of the year. The smallest size of mature males is not recorded, but Obrebski includes data on dissected males ranging in size from 2.25 to 4.75 mm. Females begin brooding at 3.2 mm in Tomales Bay (Obrebski, 1966).

As is evident in Table 13, a compilation of the life history data for *T. tantilla* in False Bay, Coos Bay, and Tomales Bay, geographic variation in size and reproductive traits cannot be attributed to the effects of a latitudinal gradient. Several points stand out in the data:

(1) Egg diameter is approximately the same at all locations.

(2) False Bay females appear to be brooding fewer, larger young than females in other locations.

(3) Local pressures in Coos Bay seem to be selecting for smaller individuals which mature at a smaller size and brood larger numbers of smaller young.

(4) As discussed above (data not included in Table 13), the sizes, shell coloration patterns, and densities of *T. tantilla* contribute to making them conspicuous in False Bay and cryptic in Coos Bay.

There are many possible explanations which could account for the apparent differences between populations of *T. tantilla* in the three locations. However, with some speculation, it may be possible to narrow the field of choices to a few testable predictions. The range of possible explanations fall into three main categories - physical stress, competition for resources, and predation. These will be discussed in order, below.

Physical Stress

A suspension-feeding organism, such as *T. tantilla*, which lives close to the sediment surface is faced with temporal fluctuations in surface-sediment temperature and salinity; a gradient of oxygen concen-

TABLE 13. Life History Traits of *Transennella tantilla* from Three Geographic Locations on the West Coast of North America.

LOCATION TRAIT	FALSE BAY WASHINGTON	COOS BAY OREGON	TOMALES BAY CALIFORNIA
Body Size	0.65-6.6 mm	0.55-5.3 mm	0.52-7.0 mm (Gray, 1978) 0.65-8.1 mm (Obrebski, 1968)
Brood Size (maximum observed)	293	327	500 (Obrebski)
Diameter of Uncleaved Egg in Gill	0.250 mm	0.212-0.259 mm	0.250 mm (Gray, Obrebski)
Release Size of Juveniles	0.650 mm	0.530-0.550 mm	0.520 mm (Gray) 0.650 mm (Obrebski)
Age Distribution of Reproductive Effort	Brooding and Release of Embryos and Juveniles Continuous after Maturity (Mottet)	Brooding and Release of Embryos and Juveniles Continuous after Maturity	Brooding Continuous (Gray, Obrebski) Seasonal Release (DeMartini)
Male Size	1.5-4.6 mm (Hansen, 1953)	?-1.85-3.5 mm	?-2.25-4.75 mm
Female Size (Brooding)	≥ 2.8 mm	≥ 1.9 mm	≥ 3.2 mm (Obrebski)
Growth Rate of Individuals	Variable with Size and with Season (Pamatmat, 1966)	Slow, Constant, Continuous	?
Life Span	1-2 years (Hansen)	1-2 years	1-2 years (Obrebski)

trations ranging from saturation to anoxic; and sediment transport processes which subject the organism to removal or burial or the presence of harmful concentrations of fine-grained particulate matter. These environmental stresses are similar at the three geographic locations under consideration. The salinity of overlying water at high tide is close to oceanic at all sites (Harris, 1979; Obrebski, 1968; Woodin, 1972). Woodin's (1972) measurements of the salinity of surface-sediment water in False Bay during tidal exposure ranged 28-36 ^{0}/oo. I suspect similar fluctuations occur in Coos Bay and Tomales Bay. The surface water temperature in the Strait of Juan de Fuca varies from 8^{0} C in the winter to 12^{0} C in the summer (Pamatmat, 1966). In Coos Bay, surface water temperatures recorded from January to March, 1980 and 1981, varied from $8\text{-}13^{0}$ C (Rowell, 1981). In False Bay, Woodin recorded sediment-surface temperatures during tidal exposure of $15\text{-}28^{0}$ C. Obrebski reports that sediment-surface temperatures in Tomales Bay fluctuated between $15\text{-}28^{0}$ C. Anoxic conditions occur at all sites within the sediment layer occupied by _T. tantilla_ (Gray, 1978; Woodin, 1972, personal observation). Sediment transport occurs at all sites, but differences in magnitude exist. Pamatmat (1966) reported seeing slight erosion of sand bars at the mouth of False Bay during rough weather, but indicated that sand bars within the bay were relatively stable. In South Slough, substantial sediment transport occurs on a seasonal basis in some parts of the mudflat and rarely occurs, if at all, in other parts. Obrebski (1968) states that in Lawson's Flat, tidal currents up to

1.8 m/sec in 0.9 m of water create extensive rippled areas on the surface. Maurer (1967a, 1967b) concluded from laboratory studies of _T. tantilla_ that their high filtering efficiency and the low mortality rate and absence of clogging in short-term burial experiments make them well adapted to live in a variety of sediment types and to survive short periods of turbidity in the water column. _T. tantilla_ can shut down water flow into the mantle cavity for a period of time (Gray, 1978; Maurer, 1967b) which would also improve their chances of survival in an environment characterized by fluctuating temperature, salinity and oxygen regimes.

Although specific local variations in physical parameters exist, the overall impact to the organism is similar in all three locations, and considered alone, could not account for the observed differences in size and reproductive traits of _T. tantilla_.

Competition for Resources

Woodin (1976) describes three distinct types of dense infaunal assemblages occurring in intertidal soft-sediment environments: infaunal deposit feeders, infaunal suspension feeders, and infaunal tube builders of varying trophic types. She predicts that epifaunal bivalves such as _T. tantilla_, which brood their young, will reach their highest densities among the tube builders. According to this hypothesis, _T. tantilla_ will be less successful in suspension-feeding groups because the smallest individuals can be eaten; in deposit-feeding assemblages, _T. tantilla_ would be subject to continual sedimentary disturbance which could have negative effects.

Brenchley (1981) found that organisms which disrupt the sediment by burrowing through it or by processing it through their digestive system (bioturbators), cause a decrease in the density of tube-builders and sedentary suspension feeders. Densities of mobile organisms and burrowers were not affected by bioturbation. Brenchley cites reduced filtration rates, lower growth rates and high larval mortality rates as typical responses of sedentary suspension-feeding bivalves to increased levels of suspended particles. *T. tantilla* did not show these responses in her study, most likely because of their ability to escape burial or clogging by moving to a different location or by shutting down water flow into the mantle cavity, as discussed above.

T. tantilla is probably adapted to a variety of sediment conditions and to coexistence with a number of species occupying the marine soft substrata. Rather than being limited by competition for space due to interspecific adult-adult interactions, *T. tantilla* may be responding to local variations in food availability and to competition with other suspension-feeders for this resource. Menge's study of two intertidal starfish (1972) is an example of small size resulting from interspecific competition for food.

Predation

Predation on *Transennella tantilla* has not been studied. Obrebski (1968) states that gut contents of birds collected at Bodega Bay, California contained *Transennella* and that bird droppings on Lawson's Flat in Tomales Bay contained *Transennella* valves. In a personal comment to Gray (1978), Obrebski indicated that crabs also feed on *Transennella*. Obrebski was not concerned with the possible role of predators in causing the observed exponential decline in *T. tantilla* in his monthly samples; rather, he considered the coincidence of high levels of trematode infestation in *T. tantilla* at the time of the population decline to be highly suggestive. Dead *Transennella* half-shells occur throughout the habitat range of living *T. tantilla* in False Bay and Tomales Bay. They accumulate in channels and troughs where they are carried and deposited by wave action. In Coos Bay, the presence of dead half-shells is not as obvious throughout most of the year, so that when large numbers of single valves suddenly appeared in one area of the mudflat, the activity of a predator was suspected.

As shown in this study, the juvenile Dungeness crab, *Cancer magister* is an important predator on *T. tantilla* in Coos Bay. Crabs caused a substantial reduction in the density of *T. tantilla* at site PC on the Portside mudflat. Before arrival of the crabs, there were approximately 500 clams/0.1 m^2 in this area. After the crabs visited the site between April and May of 1981, the population density was down to < 50 clams/0.1 m^2. The population had still not recovered a year later (June, 1982). It is known that crabs were responsible for the clam mortality because of the sudden appearance and condition of shells in the site. Juvenile *C. magister* observed in the laboratory predictably pry *T. tantilla* valves open and pick out the meat. As a result of their foraging, half-shells and shell fragments, some with the hinge still attached, are left behind as evidence. While clam shells may be present in bird and fish droppings, it is unlikely that they would all be deposited in the same location as was the case at site PC. The elevation of the sulfide layer in this area does not account for the increased mortality of *T. tantilla* since clams which succumb to anoxia, die with their shells still articulated.

Crab predation occurred at the other four sites as well, but to a lesser extent than at site PC. It is notable that the largest size-classes disappeared from sites on the Portside mudflat during the summer months, reappearing again in the fall. It is possible that crabs have a preference for the largest size-classes of *Transennella*.

The implication of predation by juvenile *C. magister* in particular, arises from the fact that this species is present in greatest abundance from spring, when the megalopae settle and metamorphose, to late fall, when Dungeness crabs migrate offshore. The period of crab presence in the bay coincides with the time when *T. tantilla* exhibits a decline in abundance in South Slough. *Hemigrapsis oregonensis* have also been observed eating *T. tantilla* in the laboratory (personal observation). It is possible that *H. oregonensis* prey on small numbers of *T. tantilla* throughout the year, but that with the arrival of *C. magister* juveniles, there is an additive effect which causes an increased reduction in numbers of *T. tantilla*.

The results of two independent studies on the effect of predation among the infauna of mudflat communities were published in 1977. One study was carried out in Königshafen, Germany (Reise) and the other, in York River, Virginia (Virnstein). Both investigators reached the same conclusions: (1) species populations in the community did not appear to be resource limited and (2) predation pressure influenced the community structure and dynamics. Virnstein found that the blue crab, *Callinectes sapidus*, and a bottom-feeding fish, *Leiostomus xanthurus*, reduced densities of infauna. Reise determined that the most important predators in the Königshafen system were shrimp, *Crangon crangon*, shore crab juveniles, *Carcinus maenus*, and gobiid fish, *Pomatoschistus microps*. These predators were all present on the mudflat from July to September and the results indicate that infaunal densities declined to their lowest level during this time period.

Certainly, then, there is precedence for believing that predation has a controlling influence on the dynamics of some species in mudflat communities. A comparative study of predation in False Bay, Coos Bay, and Tomales Bay on *T. tantilla* may come closest to pinpointing reasons for the differences in size, density, shell coloration, and reproductive traits that are present.

Hughes (1980) indicates that predators may affect communities in two ways: one is to reduce prey densities, and by doing so, to influence species richness and community stability; the other, is to induce evolutionary changes in the physiology, behavior, and life history of both predators and prey. The first effect has been examined with predator exclusion experiments, but the second has barely been explored. Hughes suggests that attention should be directed at testing theoretical predictions of optimal diets, optimal foraging behavior and optimal patch use. The predator-prey interaction described in this study is one that is begging for the type of experimental manipulation that Hughes suggests. Both juvenile *C. magister* and *T. tantilla* exhibit complex behaviors which may provide interesting information on predator-prey dynamics if they were better understood. One example which raises questions concerning patch selection by predators and predator-induced extinction of prey in local patches, is the concentration of *T. tantilla* in patches (such as at site PC in this study) and the focused predation of *C. magister* in such patches.

Some preliminary work has been done on the feeding behavior of *C. magister*. *C. magister* uses chemosensory and tactile cues to locate prey (Pearson, et al, 1979). The crab keys in on an area with an aggregate of clams, and as the chemosensory threshold increases, the crab begins to search for buried prey. The foraging behavior of juvenile *C. magister* observed in this study was similar to that of adults observed in Pearson's study, with one major difference. The juveniles use a different method to open clams.

Pearson, et al reported that adult Dungeness crabs crush live mussels (*Mytilus californiensis*) between the dactyls; the chelipeds hold the broken shell pieces while the maxillipeds and mandibles clean off the tissue. Pearson and Olla (1977) report that blue crabs (*Callinectes sapidus*) crack mussel shells with the cheliped and "...pry open the valves with both chelae as one would open a book". *C. magister* juveniles use the chelipeds to bring the whole clam up to the mouthparts where it is rotated by the maxillipeds and maxillae until the dactyls are able to penetrate the opening between the valves and pry open the shell. A juvenile may lack the necessary strength or dactyl size to grip and crush clam shells.

T. tantilla live in a hostile environment. They are subject to wide fluctuations in temperature, salinity and oxygen concentration. Sediment transported by water currents or destabilized by bioturbators can bury them for indefinite periods of time, and strong tidal surges can displace them. Predators, such as juvenile *C. magister*, effectively reduce their densities. The species seems well adapted to the physical disturbances which it encounters, but its responses, if any, to competitors or predators have not been elucidated. r and K selection theory (MacArthur and Wilson, 1967; Pianka, 1970; Stearns, 1976) predicts that the optimal life history traits for a species living in a disturbed environment should be a short life; a large reproductive effort that results in the production of many, small young; semelparity; rapid development; and early maturity. Contrasted to this strategy is the bet-hedging model (Murphy, 1968; Schaffer, 1974) which predicts that in unstable environments, long life, late maturity, iteroparity, and the production of few, large offspring are favored traits. A reexamination of the life history traits of _T_. _tantilla_ in Table 13 indicates that this organism does not fit the predictions of either model. It may be that there is no one particular set of traits that defines an optimal strategy to suit a particular environment, but that for any given environment, there is an array of combinations of traits which can be matched successfully to optimize fitness. There is a need for a more dynamic explanation of life history strategies that allows for organisms to "experiment" with combinations of traits within the same environment. There are, after all, a range of life histories exhibited by coexisting species. Current theoretical predictions are not adequate to explain apparent diversity or relative success of life history strategies present in the same community (Wilbur, Tinkle, and Collins, 1974; Menge, 1975; Strathmann and Strathmann, 1982; Stearns, 1977).

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