

Factors Affecting the Distribution of *Tylos punctatus* (Isopoda, Oniscoidea) on Beaches in Southern California and Northern Mexico¹

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ABSTRACT: Populations of the isopod *Tylos punctatus* were studied at five widely separated beaches between Los Angeles, California, and Punta Banda, Baja California (Mexico). Population densities at these sites were 10^3 – 10^5 animals per meter of beach frontage; smaller populations were not located, although more than 30 intermediate sites were sampled.

Cross-beach distribution appears to be related to sand moisture content rather than sand coarseness. Longshore distribution on a given beach is patchy, but the causative factors for this were not determined.

Studies of the isopods' population dynamics on two beaches indicated that the populations were increasing, with doubling times of 2–12 years. If these are minimum values, it is hypothesized that the discontinuous distribution of the animals on this coast can represent a balance between catastrophic beach erosion and the natural ability of the populations to regenerate and disperse.

Tylos punctatus Holmes & Gay is a dominant member of the fauna on a number of marine sand beaches in southern California and northern Baja California (Mexico). On this coast, it is the only species of its genus that has been collected, although a somewhat different form, possibly an undescribed species or subspecies, is present in the Gulf of California (Dr. Milton Miller, personal communication). Other species, such as *T. niveus* Budde-Lund and *T. latreillei* Audouin (a Mediterranean form), are definitely known from the Caribbean area, where *T. punctatus* does not occur. Schultz (1970) discussed the various species that have been recorded from North and South America.

Where it occurs, *T. punctatus* can build up enormous populations. Hamner, Smyth, and Mulford (1969) reported concentrations of up to 64,000 individuals per meter of beach frontage (a 1-meter-wide strip of beach from the upper beach margin to the water line) at Estero de Punta Banda, near Ensenada, Baja California. I have measured nearly 90,000/m beach frontage there, and more than 30,000/m

beach frontage at some southern California beaches (Hayes 1969). Since the animals are detritivores, concentrations such as these will have decided effects on the local patterns of beach energy flow, which are generally based on detrital kelp. Hayes (1974) investigated this problem. The isopods are nocturnal, emerging from the sand at night after high tide to feed on kelp, primarily *Macrocystis pyrifera* (L.) Agardh, which washes up on the lower beach face. They rebury about dawn, near the high-tide mark, and are not seen during the day. During the winter (October–April), the animals appear to hibernate and do not emerge to feed.

The present paper is concerned with the distribution pattern of *T. punctatus* on various scales of measurement in that portion of its range which has been well sampled. An attempt will be made to relate the rather peculiar distribution of this species to environmental factors and to its probable evolution.

GEOGRAPHICAL DISTRIBUTION

Tylos species tend to be warm-temperate to tropical in their distribution throughout the

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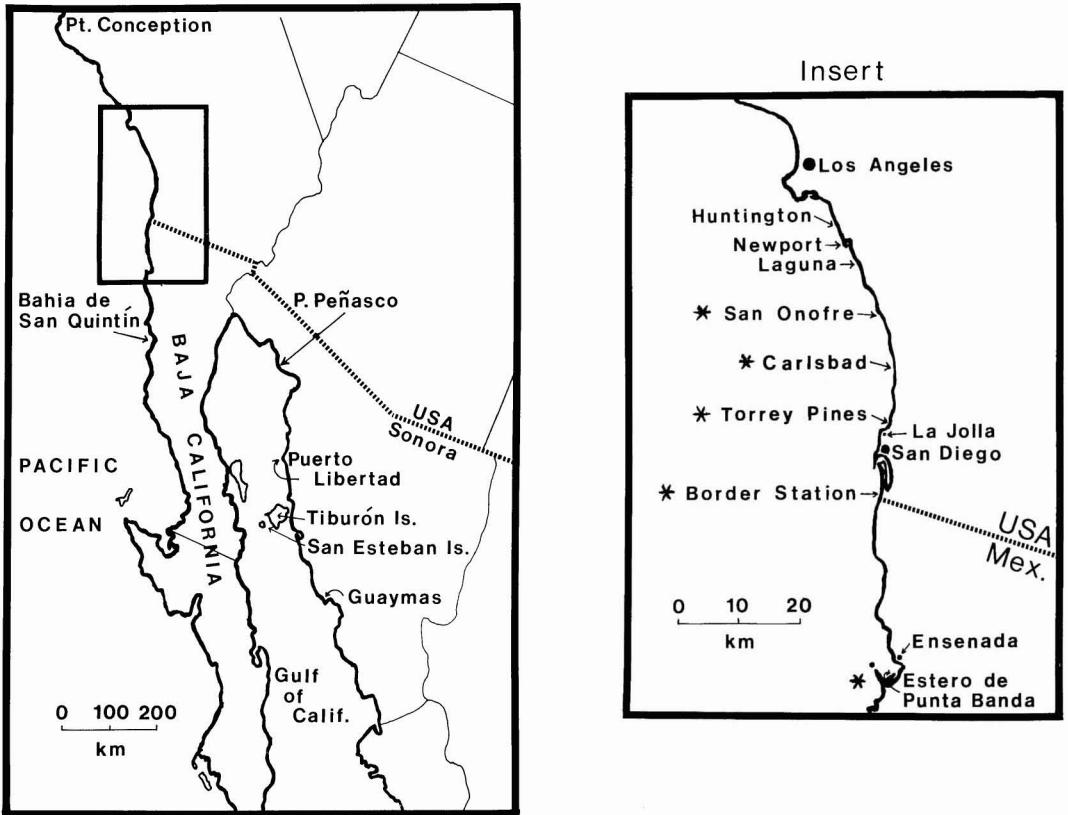


FIGURE 1. Pacific coast of California and Mexico where *Tylos punctatus* is known to occur. Insert shows the region where sampling was done for the present study. Starred (*) beaches are the only ones at which *T. punctatus* was located.

world (Vandel 1945), so it is perhaps not surprising that *T. punctatus* has never been recorded from Canada, Washington, Oregon, or northern California. The northern limit of its range is probably somewhere around Point Conception (see Figure 1), although there is one unverified report from Tomales Bay, near San Francisco (Johnson and Juskevics 1965), and the organism has been included in a well-known manual of "central California" invertebrates (Light 1954). Dr. Darl Bowers, who has made extensive collections of amphipods from central California beaches, noted in a personal communication that he had never encountered *T. punctatus*, although he had sampled as far south as Venice (near Los Angeles).

South of Los Angeles, the literature gives

records for the organism at Laguna Beach (Stafford 1913) and in a plankton tow taken near the beach at Newport Bay (Menzies 1952). However, I have sampled the beaches around both of these localities without encountering any of the isopods. The type locality (Holmes and Gay 1909) is given as "San Diego," a somewhat vague reference since the city limits include a long coastline with a variety of beach habitats.

In Mexico, Hamner, Smyth, and Mulford (1969) studied the large population of *T. punctatus* at Estero de Punta Banda near Ensenada, Baja California. Mulaik (1960) recorded "*T. latreillei*" from Bahía de San Quintín, but Schultz (1970) felt that this is actually *T. punctatus*. The same is true of Mulaik's records of the species from Tiburón

Island, Punta Peñasco, San Esteban Island, and Punta Zascosa, all in the Gulf of California or on the Sonoran coast. Schultz also noted records from Guaymas, Puerto Libertad, and Bahía de Cholla, Sonora. The southern extent of the range is not known, since many of the beaches in southern Mexico and Central America have not been sampled. There is no record of the species from the western coast of South America, below the equator.

AREAS INVESTIGATED

In an effort to clarify the distribution patterns of the isopods in the northern part of their range, I took samples at 35 different beaches, from Huntington Beach on the north to Estero de Punta Banda on the south. These samples consisted of 20–30 shovelfuls of sand (about 100 liters total) taken from the surface 30 cm of the beach. This sampling was concentrated in the region near the previous night's high tide mark, where the isopods bury themselves during the day. The sand was sifted through a screen with a 3-mm mesh, which retains the large- and medium-sized animals. A number of sites along each beach were checked. Isopods were found at only a few of these locations (see Figure 1), but were quite numerous where they did occur. Later quantitative sampling indicated that the lowest concentrations thus encountered were in excess of 1000 animals/m beach frontage. The survey sampling was quite capable of detecting lower concentrations of animals, since isopods such as *Alloniscus perconvexus* Dana were found on many beaches and were an order of magnitude less abundant than the lowest concentrations of *Tylos*. Apparently *T. punctatus* either is present in rather high concentrations or is absent.

Three beaches were selected for further study:

1. Estero de Punta Banda, about 10 km south of Ensenada, Baja California. The beach was flat (2° – 4°), without a pronounced berm crest, and was partially protected by the Punta Banda peninsula to the south.

It was bordered to the east by a large salt marsh. There was some camping in the area, but the beach was receiving little public use at the time of the study. Although it contained the largest isopod population of any of the beaches surveyed, it was the most difficult to reach for sampling.

2. Torrey Pines State Beach (southern end), between La Jolla and Del Mar, California. The beach had a slightly elevated berm crest with face slopes below the crest of 2° – 3° . It was backed by cliffs, 30 m or more in height, and was relatively unprotected from wave action. Although the beach was in a densely populated area, it received only moderate public use since it was about 2 km from the nearest public road. The isopod population there was among the lowest encountered.
3. Carlsbad State Beach, near Carlsbad, California. This beach had a face angle of 3° – 4° , sloping almost continuously seaward from the low (3–10 m) cliffs at the upper margin. There was a rocky reef offshore, exposed during minus tides, which reduced wave action somewhat. This was a public recreation area; campsites lined the cliff margins overlooking the beach and large wooden stairways descended to the sand at intervals of 300 m or so. According to the park supervisor, kelp was usually scraped off the beach face by tractors at least once a year—at the start of the season in May and at intervals thereafter if kelp deposition warranted it. The isopod population was, however, second in size only to Estero de Punta Banda. The bulk of the sampling work was done at this beach.

SAMPLING PROCEDURES

To locate the regions where isopods could be found, I performed survey sampling, as described above, on all of the beaches in the summer of 1965. The animals were concentrated into zones 1–3 km long on these beaches. On each of the study beaches, I located a permanent reference stake within

the isopod zone, using a method based on random numbers. The stakes were sunk at the upper beach margins, and transects were made seaward from them for quantitative sampling.

During 1966, various quantitative sampling methods were tested. Large sand cores, 16 cm in diameter and 30 cm deep, provided animals in adequate numbers for analysis; however, I found such cores difficult to take and to sieve. They also gave no information about the depth distribution of the isopods, and they missed that fraction of the population that buried deeper than 30 cm.

The fastest and most repeatable method proved to be an auger-and-casing technique. A cylindrical casing, 7.3 cm in diameter and 25 cm in length, was driven vertically into the sand until completely buried. An auger of slightly smaller diameter was then used to remove cores of sand from the casing. Coring could be done in approximately 10-cm increments of depth, providing stratified samples, and could be continued below the bottom end of the casing to a depth of 100 cm or more. The sand below 25 cm was damp enough to prevent the hole from collapsing. The method produced an unbiased sample and did not mutilate specimens, but sometimes it did not produce enough animals for a good analysis.

I normally stretched a transect line seaward from the reference stake and located the core holes at random within 1-meter intervals along the line. About 10–15 such holes were usually sufficient to traverse the zone where the isopods were buried. After this method was developed, samples of this sort were taken monthly at Carlsbad during the isopods' active season in 1966. Some sample runs were also made at the other two beaches.

In 1967, I changed sampling emphasis to pitfall trapping in order to collect more animals. Although trapping could produce many thousands of animals in a night, the method was later shown to yield biased samples (Hayes 1970). Therefore, the population dynamics calculations were restricted to the core samples. In addition, however, Dr. William Hamner, who had sampled extensively on the Punta Banda beach, kindly

provided raw data from that site which I used for comparison with my own samples.

Two other beaches (one near the San Onofre nuclear power plant and one at the United States Navy Border Field Station near the California-Mexico border) also had isopod populations, but the populations were too small for analysis from core samples. They were not sampled regularly, although measurements were made of beach erosion at these sites (see below).

RESULTS

Small-Scale Distribution Patterns

The isopods were not distributed evenly along the beach but appeared to be concentrated in large patches, as suggested by Figure 2. Since the beaches were relatively flat and even, without cusps or other obvious variations, I had difficulty relating these patches to any environmental features. It was usually not possible to locate the patches by eye in the daytime, since the isopods did not leave conspicuous open burrows in the sand as the beach amphipods (e.g., *Orchestoidea* spp.) did. Since the isopods moved around considerable distances on the beach at night, their regions of maximum concentration could shift with time. Thus, a series of samples taken along a transect would not necessarily contain the same number of animals as a similar series taken at a later date. This could lead to confusion in the interpretation of changes in population size (see "Population Mortality" below).

Patch location may have been related to kelp deposition on the beaches. It was generally possible to find more isopods buried beneath or near piles of stranded kelp than in regions where such piles were absent, although the isopods will not consume decayed kelp (Hayes 1969). Broken kelp exudes fucoidin, a mucuslike carbohydrate, and it is possible that patchiness along the beach was related to the presence or absence of this material in the sand. No field experiments were conducted to examine this problem, however.

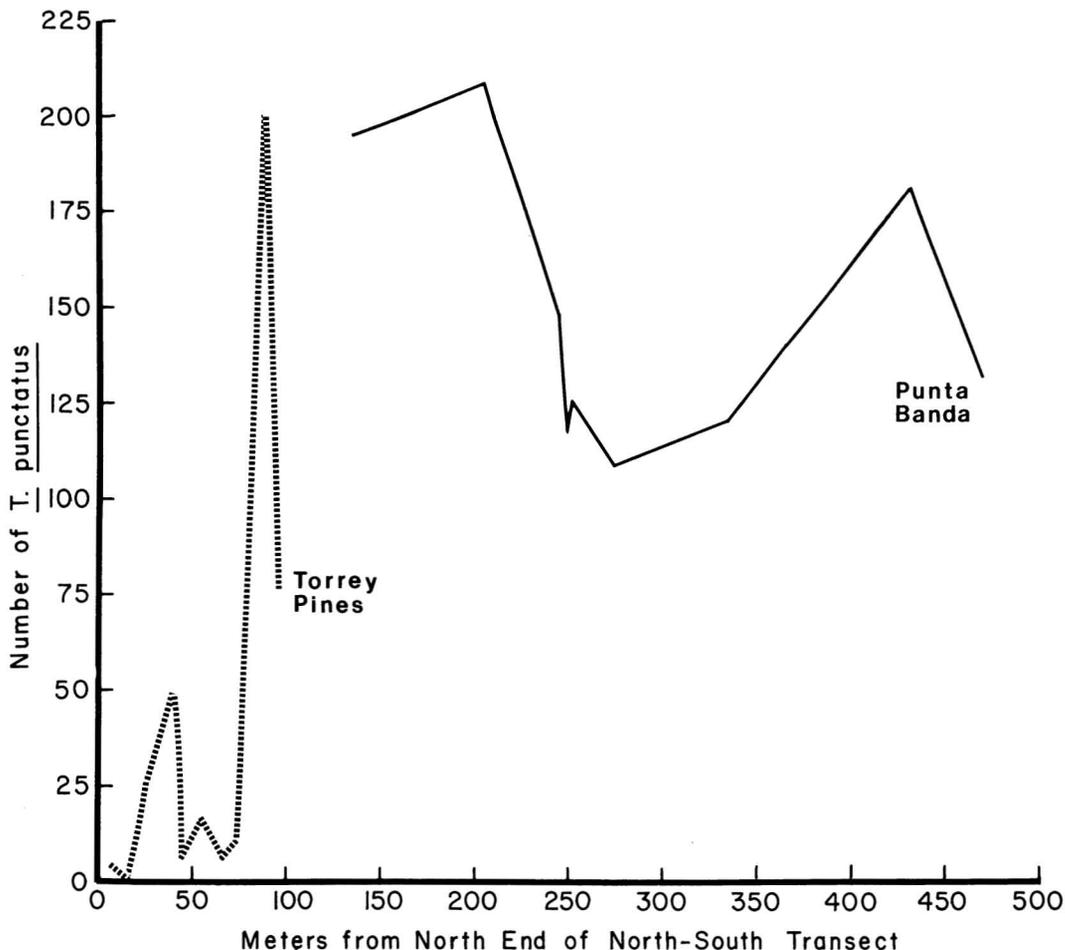


FIGURE 2. Longshore distributions of *Tylos punctatus* on sections of two beaches. Counts represent animals screened from sand cores of approximately 4 liters volume, located at randomly selected sites along 100 m (Torrey Pines) and 500 m (Punta Banda) transects parallel to the waterline. Punta Banda data supplied by Dr. Monte Lloyd.

EFFECTS OF SAND MOISTURE: Sampling at Carlsbad and Punta Banda confirmed Hamner's, Smyth's, and Mulford's (1969) results in regard to the restriction of the isopods to a high-beach zone. At both beaches, they were normally found in a strip of beach somewhere near the previous night's high-tide mark, although this band was never as well defined at Carlsbad as at Punta Banda. Hamner, Smyth, and Mulford noted that the band usually became narrower after several nights of tides of nearly equal height; apparently this condition creates a sharp demarcation between wet and dry sand.

The animals can definitely react to small differences in sand moisture. Hamner, Smyth, and Mulford (1968) noted that moisture, or lack of it, can reverse the orientation of *T. punctatus* on shallow slopes. The isopods' high-beach distribution suggests that they may bury themselves at a point which is at least partly determined by the degree of surface dryness of the sand.

Figure 3 shows the relationship between isopod numbers and sand moisture in a series of surface cores (5 cm diameter, 20 cm deep) from Carlsbad and Punta Banda. The mean sand moistures preferred by the two popu-

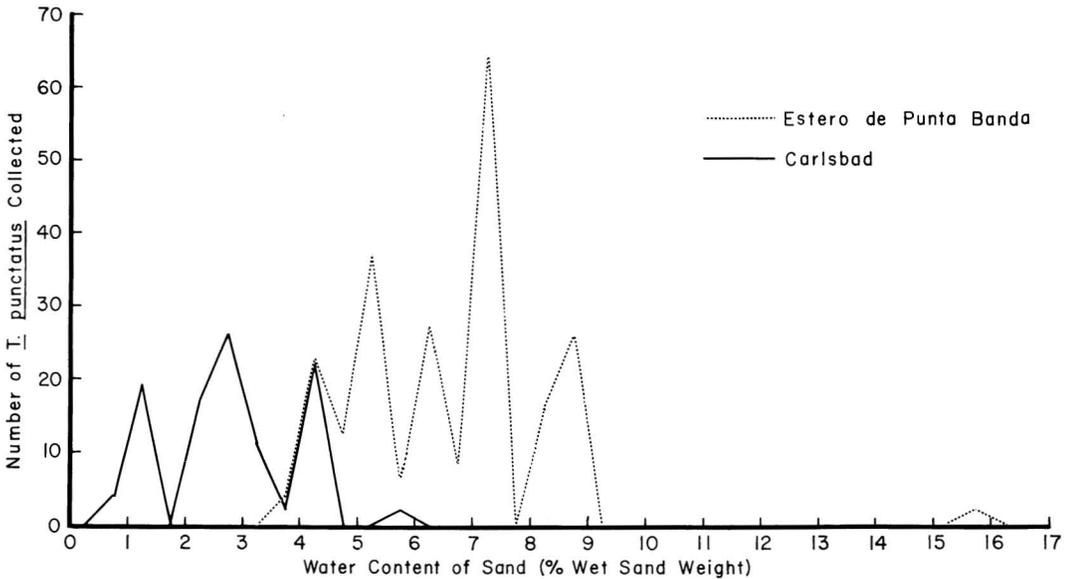


FIGURE 3. Distribution of *Tylos punctatus* at two beaches in relation to the water content of the sand cores.

TABLE 1

DEPTH DISTRIBUTION OF *Tylos punctatus* IN SAND-FILLED TUBES DURING THREE LABORATORY EXPERIMENTS

DEPTH (cm)	DISTRIBUTION AFTER 48 HOURS (EXP. 1)	DISTRIBUTION AFTER 120 HOURS (EXP. 2)	DISTRIBUTION AFTER 120 HOURS WITH DRY SAND IN 10-20 CM ZONE (EXP. 3)
0-10	52	55	72
10-20	29	19	27
20-30	11	14	1
30-40	6	5	0
40-50	1	5	0
50-60	1	2	0
> 60	0	0	0

lations differed significantly ($P \ll .001$) according to a t -test, a fact which cannot be accounted for by physical differences between the two beaches; that is, sand grain size and distribution showed no significant differences between the two beaches, and, in the general high-beach region, sand was present which was both drier and wetter than that in which the isopods burrowed. This suggests that the isopods on a beach may have rather specific preferences as to sand moisture, but that these preferences can be different on different beaches.

The distribution of the animals indicates

that they will not burrow in dry sand even if there is damp sand underneath. I verified this observation in the laboratory by obtaining a 6.35-cm-diameter Lucite cylinder, 90 cm long, and cutting it into 10-cm sections. The top of each section was fitted with a collar so that it could be fitted snugly over the bottom of an adjacent section. The tube was reassembled in an upright position, filled with moist sand, and stocked with 100 freshly collected isopods at the top. After 48 hours, I removed the sections sequentially and screened out the animals to determine their depth distribution. The experiment was then repeated (with fresh

animals and sand), except that the apparatus was left for 120 hours before disassembly. The distribution of the animals in these two tests is shown in Table 1; a Kolmogorov-Smirnov test for cumulative percentage differences (Tate and Clelland 1957) showed no significant difference between the depth distributions in the two runs ($P > .20$). The tube was then set up again, except that the second section from the top (10–20 cm below the surface) was filled with oven-dried sand. One hundred animals were introduced as before, and their distribution noted after 120 hours. The results are also shown in Table 1. Run 3 differed from the other two runs with $P < .02$, indicating that the dry sand acted as a barrier to the animals burrowing downward. Only one animal passed the barrier; most of the others found in the 10–20 cm section were clustered near the top, where the dry sand picked up some moisture from the overlying damp sand in the upper section.

EFFECTS OF SAND GRAIN SIZE: The importance of grain size to the animals on a beach lies not so much with the grain size itself as with the various physical properties of the beach that are related to grain size. The beach profile, surface firmness, resistance to penetration, oxygen content, moisture permeability, capillarity, and resistance to erosion are all factors that may be important in this respect.

Other things being equal, the isopods can burrow more easily in coarse sand than in fine. Three short "burrowing tubes," consisting of three 10-cm sections each, were assembled as described above. One tube was filled with sand of .09–.18 mm grain diameter, one with sand of .25–.50 mm grain diameter, and one with sand of .70–1.4 mm grain diameter. The tubes all contained equal quantities of moisture. Fifty isopods were introduced into each of the three tubes and their depth distributions checked after 24 hours. The results, shown in Table 2, indicate a greater average depth of burrowing in the coarser sand. One might expect to find animals buried more deeply on a beach with coarser sand, although such a beach will be

TABLE 2

DEPTH DISTRIBUTION OF *Tylos punctatus* IN 30-CM TUBES FILLED WITH SAND OF VARYING COARSENESS

SAND GRAIN SIZE (mm)	DEPTH (cm)		
	0–10	10–20	20–30
0.7–1.4	20	13	17
0.25–0.50	20	22	8
0.09–0.18	31	19	0

NOTE: Experiment lasted 24 hours.

eroded more easily than one with fine, hard-packed sand.

Sand-grain size distributions were determined for all of the beaches where populations of *T. punctatus* occurred (see Figure 1). There was little variation either in mean grain size (which ranged from 0.1 to 0.5 mm) or in the shape of the size-frequency plots for the sand on these beaches. Although *T. punctatus* was never collected on a beach with really coarse sand, many beaches with grain sizes in the 0.1–0.5 mm range also had no isopods. It appears, therefore, that grain size in itself is not a major factor in determining the distribution of the isopods. This supports the conclusions of Kensley (1972) regarding the distribution of *T. granulatus* in South Africa, but contradicts Giordani-Soika's (1954) findings on the separation of *T. latreillei* subspecies on Mediterranean beaches.

EFFECTS OF BEACH EROSION: Most beaches are subject to seasonal building-and-wasting cycles, due to changes in the height, period, and direction of waves from summer to winter (Shepard 1963). Naturally, these effects are most noticeable on the lower beach, but severe storms can also have striking effects on the high beach.

A series of monthly beach-height surveys was taken during 1968–1969 at the four California beaches where populations of *T. punctatus* were noted; these are summarized in Figure 4. The heights are relative to the height of the permanent reference stake at the upper margin of each of the beaches. Sand heights at the stakes (which were above the isopod zone on the beach) varied only a few

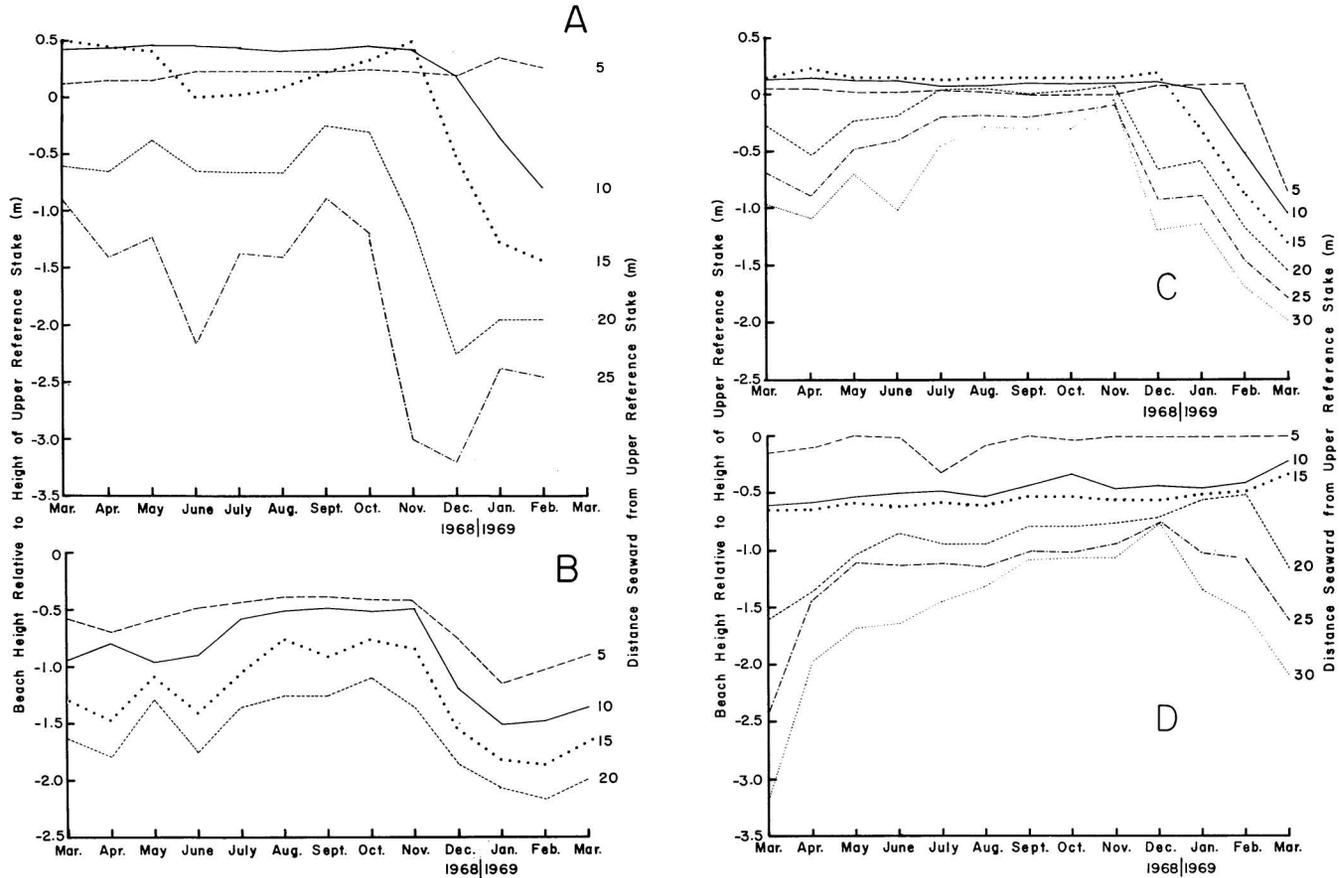


FIGURE 4. Changes in beach height during 1968–1969 at the four California beaches where *Tylos punctatus* was found. A, San Onofre; B, Carlsbad; C, Torrey Pines; D, United States Navy Border Field Station. Heights are relative to a permanent reference stake at the upper beach margin and are accurate to ± 2 cm.

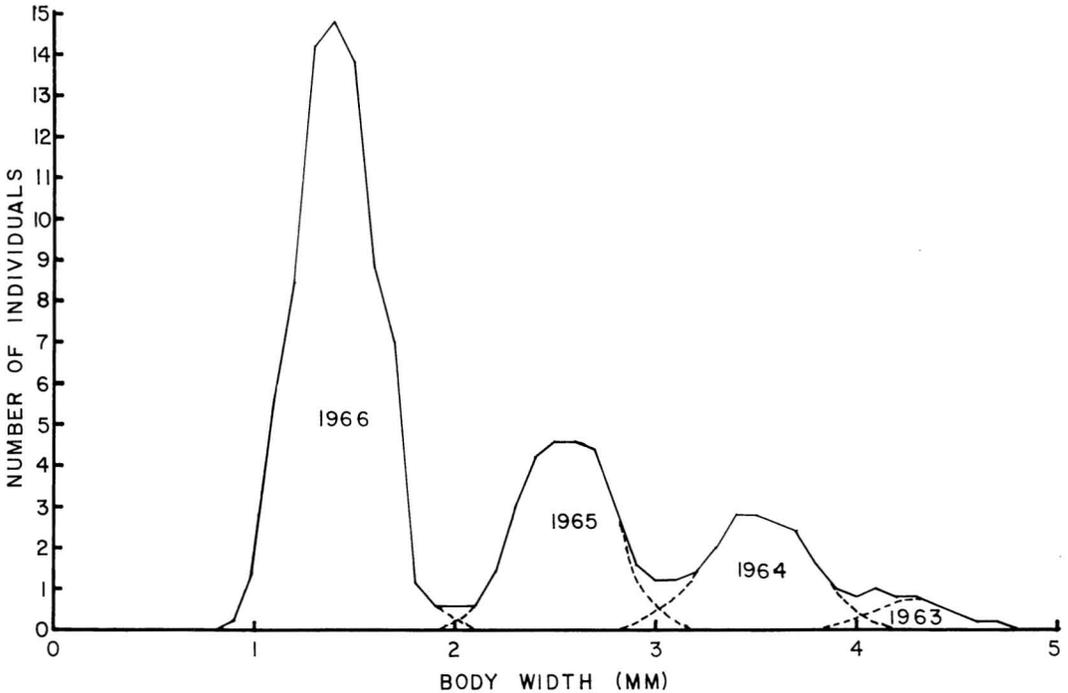


FIGURE 5. Size-frequency distribution for *Tylos punctatus* collected at Punta Banda, September 1966. Curve smoothed with a moving average over five successive 0.1-mm width increments. Approximate outlines of the component year-class curves (fitted by eye) are indicated.

centimeters during the year due to wind movement of the dry sand. The isopod population tended to be located in a band 5–15 m seaward from the stakes.

The seasonal cycle was apparent in all of the plots, although it varied in magnitude. The beaches tended to be at their highest in the fall (September to October) and at their lowest from January to March. Note that changes of .5 meter are not uncommon from one month to another at a particular spot and that some monthly variations exceed 1 meter.

Because storm conditions vary considerably from year to year, one should not assume that these plots necessarily represent a “typical” year for any of the beaches. In fact, casual observations over a 4–5 year period indicate that the winter of 1968–1969 was somewhat more severe than average in terms of beach erosion. The plots should be considered more as a comprehensive picture of how the various beaches reacted to approximately similar weather conditions.

Population Dynamics

I needed to study the isopods’ population dynamics to assess the growth potential of the populations. The calculations were carried out on core samples taken at Carlsbad and Punta Banda during 1966–1967 and were checked against the data of Hamner, Smyth, and Mulford (1969) from their Punta Banda collections of 1965–1966.

The calculations for birth rate and mortality rate were made after analysis of the size-frequency distributions of the isopods in the cores. When organisms produce young only at a certain breeding season and live for several years, their distributions contain several separable peaks, corresponding to age-classes. If the size overlap between adjacent year-classes is small, then the classes can be separated easily by eye; this occasionally happened with *T. punctatus* (Figure 5). It was more common to have considerable overlap, and I then had to employ analytical proce-

TABLE 3
EGGS PER GRAVID FEMALE AND MEAN GRAVID FEMALE SIZE FOR *Tylos punctatus* ON DIFFERENT BEACHES IN DIFFERENT YEARS

BEACH	YEAR	SAMPLING TECHNIQUE	NUMBER OF GRAVID FEMALES	\bar{X} EGGS OR EMBRYOS PER GRAVID FEMALE*	\bar{X} WIDTH (mm)*
Punta Banda	1965	pipe cores	55	13.76 (12.8–14.7)	3.74 (3.7–3.8)
	1966	auger cores	14	12.43 (11.2–13.7)	3.83 (3.7–4.0)
Carlsbad	1966	auger cores	31	13.61 (12.9–14.3)	3.89 (3.8–4.0)
	1967	surface cores and traps	88	12.17 (11.6–12.7)	3.56 (3.5–3.6)
Torrey Pines	1967	traps	4	13.50 (12.6–14.4)	3.82 (3.6–4.1)

NOTE: Nineteen sixty-five Punta Banda data recalculated from Hamner, Smyth, and Mulford (1969).

*95-percent confidence limits of mean in parentheses.

dures to determine the average size (mean position) and number of individuals (area) for each of the year-class components.

I extracted the component curves from the size-frequency plot, using a set of techniques described at length in the appendix to Hayes (1969). In general, this consisted of the sequential removal of Gaussian component curves that were not highly overlapped (Taylor 1965), followed by the separation of the highly overlapped residuals on a specialized analog computer (Müller 1966). Such activities must be tempered by biological common sense; any "noisy" curve can be fitted increasingly well through the addition of more hypothetical component curves. This is the basis of such techniques as Fourier analysis. However, if one knows something of the biology of the organisms being studied (breeding pattern, approximate growth rate and size limits, hibernation period, etc.), then the degrees of freedom are reduced. The number of component curves and their approximate position will generally be known. Under these circumstances, the analog approach is quite powerful and usually gives an unambiguous separation of the frequency curve components.

The analysis has two basic assumptions. First, there must be no systematic sampling bias in favor of a particular size-class; that is, any sample must be an unbiased sample of the entire population. Trap samples violate this assumption (Hayes 1970) and, therefore, were not used in these analyses. The second assumption is that the component cohort

curves are Gaussian distributions with negligible skewness and/or kurtosis, i.e., the linear dimensions of animals of a given year-class are distributed normally about the mean for that class. In some distributions, such as that in Figure 5, the separation between age-classes is good enough so that the components can be detached by eye and tested against normal distributions with the same mean, variance, and area. In all the cases where such tests could be made, the component curves indeed proved to be Gaussian. For the distributions where such testing was not possible, normality of the components was assumed.

EGG COUNTS AND EGG MORTALITY: Table 3 compares values for eggs per gravid female and for mean gravid female size at three beaches during 3 years. Size is given in terms of maximum body width; because of the animals' tendency to curl up, body length measurements are somewhat dependent on the amount of pressure applied to the animal to straighten it out.

The 95-percent confidence limits for the mean values in Table 3 show considerable overlap. This indicates that the variability is not statistically significant, except between years at Carlsbad. The 1967 Carlsbad value includes animals collected both by trap and core. This is permissible since, although the traps undersampled the gravid females (Hayes 1970), those that were trapped were representative of the total gravid female population in terms of size and egg count. A plot

gravid females were collected in the entire study, and these were apportioned in small numbers over samples taken from various beaches at various times. No other single core series contained enough gravid females for an accurate birthrate analysis.

Figure 7 gives the size-frequency distributions for the males, gravid females, and nongravid females in the 14 June Carlsbad series. Each of these three curves was analyzed separately by the technique of component curve extraction discussed above, and the total population curve (all males and females) was similarly analyzed; component values for the total curve are given at the bottom of Figure 7. The discrepancies between the total curve components and the sums of the partial curve components are small and appear to be no more than rounding errors. N_1 in all cases represents the crop of animals released in the summer of 1966. For convenience, they may be called 1-year-olds, although their actual age at the time of sampling was 10–11 months. N_2 represents the 1965 cohort (2-year-olds), etc.

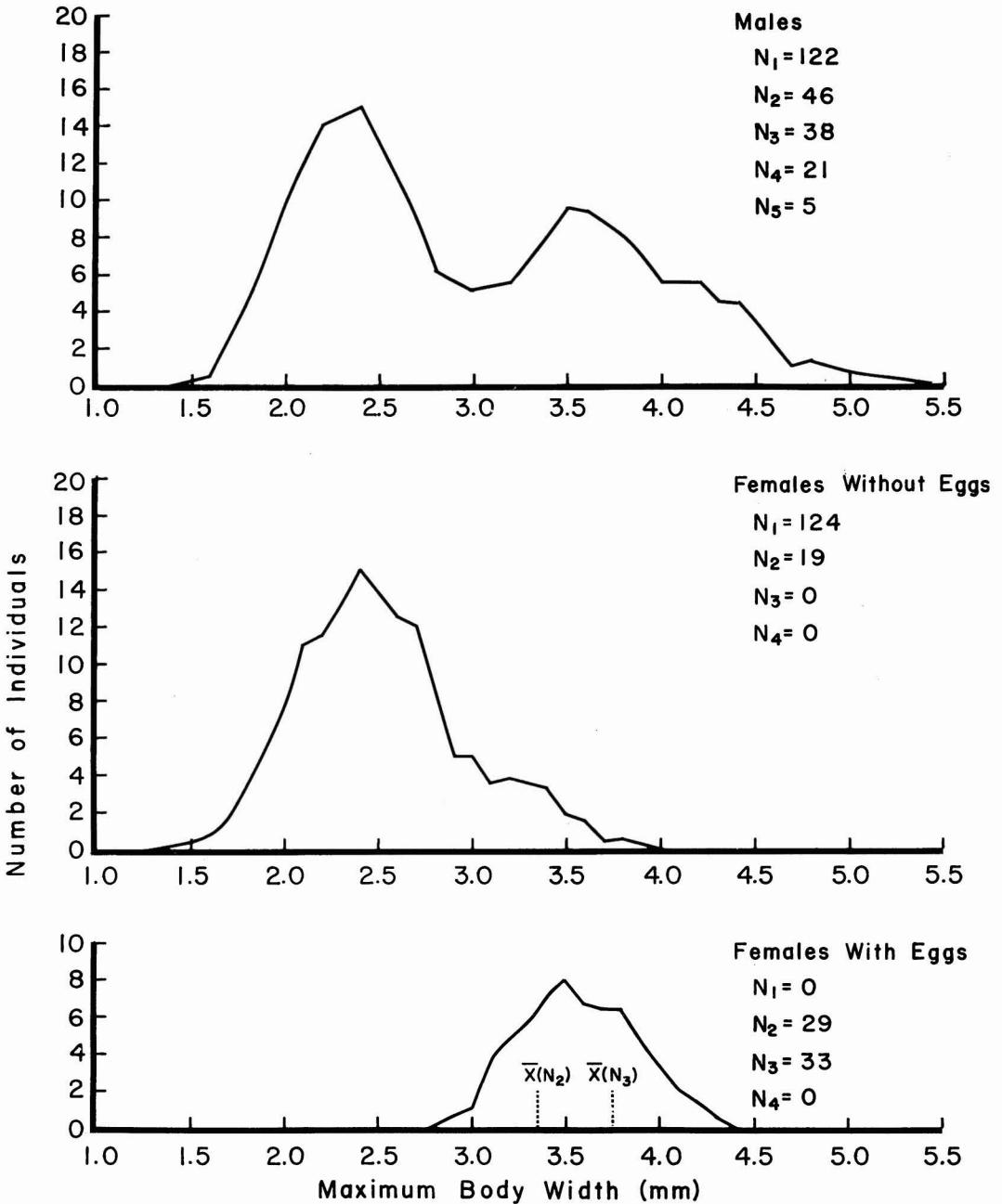
In the case of the gravid females, it is necessary to decide whether the frequency curve represents a single component (2- or 3-year-olds) or a combination of two components (both 2- and 3-year-olds). A much better fit is obtained on the analog curve resolver for the latter alternative, but, of course, two components will almost always give a better fit than one. The fact that the gravid female frequency curve is relatively symmetrical but decidedly platykurtic argues in favor of two components; curve components that can be isolated by eye (such as those in Figure 5) have negligible kurtosis. Moreover, the mean size for the 62 gravid females taken together is intermediate between the expected mean sizes for 2- and 3-year-olds at that time of year, indicating that both components are probably present. The best-fit situation for two components suggests that both the 2- and 3-year-old females are reproducing in the population in approximately equal numbers. Hamner, Smythe, and Mulford (1969) also thought that both 2- and 3-year-old females could breed, but felt that the contribution of the

2-year-olds was much smaller than that indicated here.

The nongravid females must also be considered. This sample represents a single moment in time. If the females in the fraction without eggs in these samples were to breed later in the season, the birthrate calculations would be in error. Observations of the breeding patterns of the isopods suggest that this was not the case. Hamner observed the first gravid females at Estero de Punta Banda in May (1965), with the first manca (juvenile isopods that have not yet molted) being released from the females' brood pouches in August. This indicates an incubation period of around 3 months and does not leave time for a second brood before the animals' hibernation period begins, usually in October. My observations on the California beaches confirm this pattern; I have not collected gravid females on any beach later than early August, and these were females almost ready to release their broods. Thus, it is probably safe to take the gravid : nongravid ratio in the 14 June Carlsbad samples (29:48) as a reasonable estimate of the fraction of the 2-year-old females that are breeding.

Apparently all of the 3-year-old females breed, since the analysis of the frequency curve for nongravid females shows none older than the 2nd year. Of course, these proportions may differ for isopod populations farther south. *Tylos punctatus* is near the northern limit of its range at these beaches, and more tropical locations could well have a more extended breeding season.

The individual natality rate can be calculated from the data in Figures 6 and 7. From the curve analysis, I determined that the mean size of the 2-year-old gravid females was 3.35 mm (width), while that of the 3-year-olds was 3.75 mm. The regression line in Figure 6 then gives the best estimate of mean eggs/gravid female as 11.45 and 13.60, respectively. The 1.87-percent egg mortality rate lowers these values to 11.24 and 13.35. To put this in terms of viable eggs per female in the population, rather than eggs per gravid female, the factor for 2-year-olds must be multiplied by 29/48, the fraction of females that are breeding. The value for 3-year-olds



For Total Distribution Curve (All Animals):

$N_1 = 247$

$N_2 = 94$

$N_3 = 68$

$N_4 = 28$

Total = 437

FIGURE 7. Size-frequency diagram for males, non gravid females, and gravid females of *Tylos punctatus* collected at Carlsbad, California, 14 June 1967. The curves are smoothed with a moving average over five successive 0.1-mm width increments. N_1 , N_2 , N_3 , and N_4 represent the number of animals in the 1966, 1965, 1964, and 1963 age-classes. Component curves extracted by methods discussed in the text.

TABLE 4
NATALITY SCHEDULE FOR *Tylos punctatus*

AGE IN YEARS*	b_x †	b_x ♀‡
0.5	0	0
1.5	6.79	3.395
2.5	13.60	6.800
> 2.5	0	0

NOTE: Data are based on a 1 : 1 sex ratio (Hayes 1969).

*Midpoints of Intervals.

†Viable young per female.

‡Viable female young per female.

does not change, since all of them are breeding. There seem to be no breeding females older than age 3. Therefore, the b_x schedule is as given in Table 4.

MORTALITY RATE: Population mortality is a difficult parameter to measure. Classically, it is measured either (1) by determining the age at death of a large random sample of individuals (e.g., Murie 1944); (2) by determining the age at death of the individual members of a cohort (e.g., Hatton 1938); or (3) by determining the age-structure of a large random sample of individuals and calculating survivorship from the relative numbers in the various age-classes. The latter method is the one most broadly applicable to most populations and the one most often used, although it makes the greatest number of assumptions about the populations.

When the component year-class curves are extracted from the size-frequency distributions for the isopods, several sorts of calculations can be made. The changes in the mean position of a component along the x -axis over time represent growth; this factor was discussed by Hayes (1974). It is the changes in the areas of the component curves (i.e., the numbers of individuals in them) that can be used in mortality calculations. Method (3) above assumes that one has only a single size- (age-) frequency curve, and that one is comparing the sizes of successive component curves within it. This assumes constant year-to-year natality and may be referred to as a "steady-state" analysis. In the present study, size-frequency curves were available for sam-

ples collected over a series of months. The steady-state assumption can then be avoided, since each age group, regardless of its initial size, is compared only with itself at a later time in the sampling program. Of course, such an analysis requires that immigration to and emigration from the study area be in approximate balance. This did not prove to be the case at Carlsbad, as will be shown below.

The operation of the method is demonstrated by using Hamner's, Smythe's, and Mulford's (1969) size-frequency data for the Punta Banda isopod population in 1965, combined with my own collections there in 1966. Note that the cohort-extraction methods employed in the present study are not the same as those used by Hamner, Smyth, and Mulford. Table 5 gives the number of individuals in each of the component year-class curves, obtained from the curve analysis methods discussed above.

In theory, one can calculate age-specific mortality directly from Table 5 by determining the slope of a regression line of number of individuals (in a particular year-class) versus time. In practice, however, such an approach is not possible. The "noise" in this time series (sampling and counting errors, variability of sampling effort, errors in curve extraction, stochastic factors, etc.) covers up the mortality trends almost completely.

A rather crude correction procedure is necessary. The 1961-1964 age-classes are present throughout most of the sampling period and, since there can be no further input to these cohorts, their total numbers should decline with time. Figure 8 shows this decrease. Although there is considerable scatter, the regression line represents the best estimate of overall 1961-1964 survivorship during the 1965-1966 sampling period. It is about 39 percent per year.

This value is a mean for four year-classes. To obtain the survivorships for each one, and for the 1965 and 1966 classes, each of the points in Figure 8 has been corrected back to the regression line. The resulting numbers are given in Table 6 as "1961-1964 corrected sample sizes," along with the uncorrected

TABLE 5

ABSOLUTE SIZES OF YEAR-CLASSES IN SAMPLES OF *Tylos punctatus* FROM PUNTA BANDA IN 1965–1966

COLLECTION DATE	AGE CLASS						TOTAL
	1961	1962	1963	1964	1965	1966	
Jan 1965	53	82	109	127			371
Mar 1965	68	150	151	177			546
May 1965	23	40	101	87			251
Jul 1965	18	32	21	41			112
Aug 1965	35	62	220	191	32		540
Sep 1965	35	78	86	190	317		706
Nov 1965	53	173	121	142	293		782
Jan 1966	27	88	74	59	61		309
Aug 1966		23	90	53	262	931	1359
Sep 1966			5	18	28	77	128

NOTE: Nineteen sixty-five data recalculated from Hamner, Smyth, and Mulford (1969). Loss of the 1961–1962 classes in the 1966 samples is caused by the decreases in numbers of these cohorts to the point where they could not be distinguished from the next larger curves.

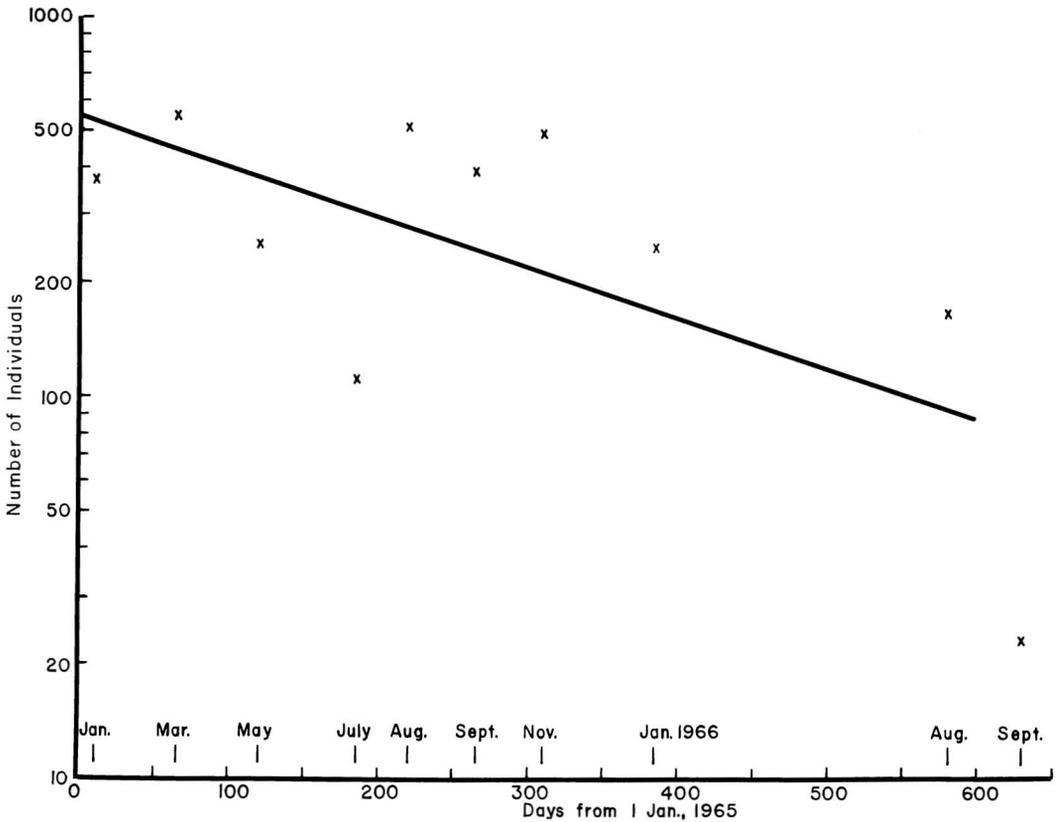


FIGURE 8. Least-squares regression of the summed sizes of the 1961–1964 cohorts of *Tylos punctatus* at Punta Banda during 1965. Calculations were made from raw data supplied by Dr. William Hamner; see text for method.

TABLE 6
CORRECTED COHORT SIZES FOR *Tylos punctatus* AT PUNTA BANDA, 1965-1966

COLLECTION DATE	AGE CLASS						1961-1964 (UNCORRECTED SAMPLE SIZES)	1961-1964 (CORRECTED SAMPLE SIZES)
	1961	1962	1963	1964	1965	1966		
Jan 1965	77	120	159	186			371	542
Mar 1965	57	125	126	147			546	454
May 1965	35	61	154	132			251	382
Jul 1965	50	89	58	114			112	312
Aug 1965	19	34	122	106	18		508	281
Sep 1965	22	49	54	118	198		389	243
Nov 1965	23	75	53	62	128		489	213
Jan 1966	18	60	50	40	42		248	169
Aug 1966		13	49	29	144	513	165	91
Sep 1966			17	62	96	264	23	79

NOTE: See text for correction procedure applied. The totals may differ slightly from the sums of the individual cohorts since all numbers have been rounded to integers.

values (the sums of the 1961-1964 year-classes in Table 5). Corrected cohort sizes are then obtained by substitution, as follows:

$$\frac{\text{uncorrected cohort size/uncorrected 1961-1964 sample size}}{\text{corrected cohort size/corrected 1961-1964 sample size}}$$

These values are also given in Table 6. For example, the 9/65 sample, after curve analysis, produced 78 individuals in the 1962 year-class (Table 5). The uncorrected 1961-1964 total was $35 + 78 + 86 + 190 = 389$ (Table 6). When this number was corrected back to the regression line in Figure 8, a corrected 1961-1964 sample size of 243 was obtained (Table 6). Therefore, the corrected 1962 cohort size for the 9/65 sample is $(78)(243)/389$ or 49 (Table 6). Although the 1965 and 1966 cohorts were not included in the summation (including them produces discontinuities in the average mortality curve when the new crop of juveniles is introduced into the population), their numbers can be related to the 1961-1964 totals in exactly the same way. Their corrected cohort sizes are also included in Table 6. Regression lines can now be plotted for each of the year-class component sizes versus time. This is done in Figure 9. The slopes of these lines are the best estimates for the survivorships of the

various cohorts during 1965-1966; the mortality rates are shown, with their 95-percent confidence limits, in Table 7.

This method of determining survivorships was tested on a series of artificial age-classes (with built-in random variations) constructed by Dr. E. W. Fager. When the calculated survivorships were compared with the true ones, the maximum discrepancy was found to be 7 percent, with most of the survivorships agreeing to within 1 percent. There is no tendency, as one might first suspect, for the method to "force" the individual year-class survivorships to fall near the total survivorship (39 percent, above); this is analogous to one's saying that fixing the mean of a distribution does not affect the variability within that distribution.

There is considerable similarity in the individual 1961-1964 survivorships, and the 95-percent confidence limits for all of them overlap. The 1965 value is not as trustworthy because of the large degree of variability in the data points. It is interesting, however, to note the similarity between the slopes of the first two 1965 points (dotted line on Figure 9) and the two 1966 ones. These are the newly hatched animals, and apparently they are subject to heavy mortality shortly after their release; survivorship in 1966 was 48 percent per month for the young and in 1965

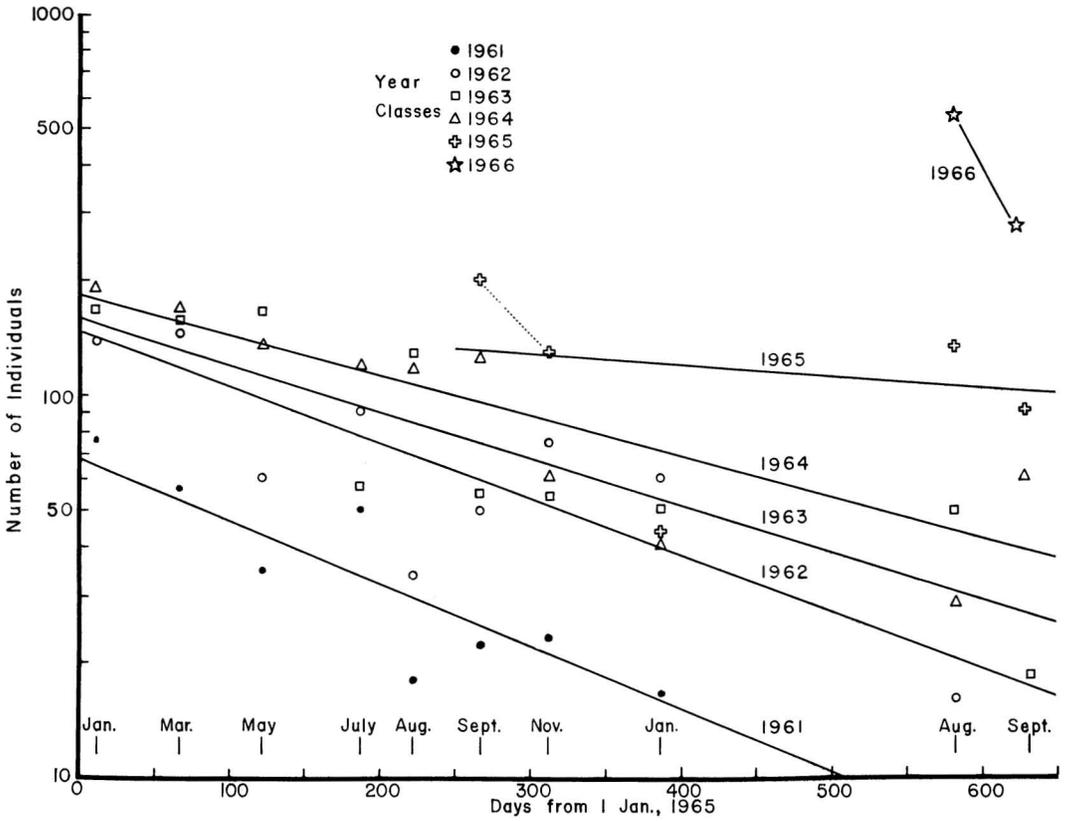


FIGURE 9. Survivorships of the individual cohorts of *Tylos punctatus* at Punta Banda (1965–1966). Nineteen sixty-five data points recalculated from raw data of Hamner, Smyth, and Mulford (1969). Nineteen sixty-five cohort value for September 1965 is questionable and has not been included in the regression line calculations.

TABLE 7

SURVIVORSHIPS OF *Tylos punctatus* OF THE YEAR-CLASSES IN THE 1965–1966 SAMPLES FROM PUNTA BANDA

YEAR-CLASS	SURVIVORSHIP (%/year)	95% CONFIDENCE LIMITS
1961	25	13– 48
1962	30	15– 60
1963	34	22– 53
1964	40	27– 59
1965	82	10–100
1966 (1st 2 months)	0.55	—

NOTE: Values are the slopes of the regression lines in Figure 9 converted to percentages, with the 95-percent confidence limits for the slopes.

it was 35 percent per month. The August 1965 point for juveniles has not been plotted, since that sample apparently was taken before the new hatch was fully released. These data do not support the supposition that mortality

beyond the juvenile stage varies significantly with the age of the animal.

For comparison, I calculated mortality rates using a steady-state model (Robson and Chapman 1961). This model does not

distinguish between survivorships of the various age-classes but does give an average population survival rate on the assumption that such survival is constant with time. It is frequently used in fisheries studies. An average of the results from all the monthly samples gives an estimated annual survival rate of 51.8 percent, with 95-percent confidence limits from 44.8 to 58.8 percent. This figure is not really comparable with those obtained from the age-class analysis, since different things are being measured. The steady-state model is estimating the history of mortality on the beach over a 5-year period with an unknown inaccuracy due to fluctuations in year-class size. The age-class analysis, based on extraction of component curves from the size-frequency distributions, is measuring the rate at which the various age-classes were declining during the period when samples were being taken. Thus, while the latter model is more assumption-free on a limited time scale, its applicability as a predictive model depends on whether the sampling period was typical of longer term beach conditions.

Age-class analysis was also applied to the samples from Carlsbad. It was found, however, that the total sample sizes showed a dramatic decrease throughout the sampling period, corresponding to a population survivorship of 0.6 percent per year. Since trap samples on a nearby part of the beach showed no such decrease, I conclude that this was an artifact caused by a change in the long-shore distribution of the population. Figure 2 shows that high concentrations of isopods alternated along the beach with areas where the animals were less abundant. If the fixed sampling transect passed through a patch which later shifted its position, an apparent population decrease resulted.

It was still possible to do steady-state calculations on the Carlsbad samples, since such calculations are dependent only on the relative numbers of animals in the various year-classes and not their absolute size. The Robson and Chapman (1961) model gave a population survivorship at Carlsbad of 50.24 percent per year, with 95-percent confidence limits of 45.5 to 55.0 percent. This is very

close to the values obtained by this method for the Punta Banda population (51.8 percent, with 95-percent confidence limits of 44.8 to 58.8 percent).

LIFE TABLE CALCULATIONS: The dynamics of the isopod populations are conveniently summarized in a life table, although this requires some simplifying assumptions about what constitutes "average" conditions for the populations. Such a table may or may not be valid on a long-term basis; it depends on how typical the natality:mortality conditions were over the period of study.

Since the best natality data come from Carlsbad and the best mortality data come from Punta Banda, one has a choice of two types of errors in constructing the table. One can either (1) use steady-state mortality estimates for Carlsbad (assuming similar conditions from year to year), or (2) use the best estimates of natality and mortality (which combine data from two beaches and assume identical conditions on both). Life tables for both of these sets of conditions were constructed and are given in Tables 8 and 9.

For case (1), the survivorships were calculated directly from Table 7. One obtains the l_x schedule in case (1) for the 1st year by comparing the number of viable eggs and embryos in the population from Figure 7 (750) with the number of individuals in the first year-class (246), thereby making the dubious assumption of equal natality for these 2 years. Beyond year 1, the Robson-Chapman steady-state mortality measure is used. The b_x schedule is obtained from Table 4 in both cases. As is customary, the life table considers only females. There will be a number of males surviving to greater ages than those indicated, but, since they can add nothing to the population's intrinsic rate of increase, they are not included.

If the steady-state assumption is correct, the net reproductive rate (R_0) should be 1.0. Both cases deviate somewhat from that figure, indicating that a steady-state assumption is not wholly justified. Using the methods given in Birch (1948) for calculating the intrinsic rate of increase of the population

TABLE 8

LIFE TABLE FOR *Tylos punctatus* IF STEADY-STATE MORTALITY OCCURS AT CARLSBAD AFTER SPECIES' FIRST YEAR

AGE-CLASS MIDPOINTS IN YEARS (x)	SURVIVORSHIP	l_x	b_x	$l_x b_x$
0.5	.328	.328	0	0
1.5	.502	.165	3.395	0.560
2.5	.502	.083	6.800	0.564
3.5	.502	.042	0	0
				$R_0 = 1.124$

NOTE: $r = 0.06$; $\lambda = 1.06$; doubling time, 11.6 years.

TABLE 9

LIFE TABLE FOR *Tylos punctatus* IF CONDITIONS OF MORTALITY AND NATALITY ARE EQUIVALENT AT PUNTA BANDA AND CARLSBAD

AGE-CLASS MIDPOINTS IN YEARS (x)	SURVIVORSHIP	l_x	b_x	$l_x b_x$
0.5	.82	.820	0	0
1.5	.40	.328	3.395	1.114
2.5	.34	.112	6.800	0.759
3.5	.30	.033	0	0
				$R_0 = 1.873$

NOTE: Survivorship figures are from Table 7. $r = 0.34$; $\lambda = 1.405$; doubling time, 2.04 years.

(r), I obtained a value of 0.06 for case (1) and a value of 0.34 for case (2). Population doubling times are, therefore, 11.6 or 2.04 years, respectively. Since the respective errors associated with these two values cannot be estimated, there is no reason to choose one over the other.

DISCUSSION

Tylos punctatus was found only at five locations in the 200 km or so of coastline surveyed (see Figure 1), but it was present in rather large numbers at these locations. The isopod was not found either at Newport Bay or Laguna Beach, where it had been collected by earlier investigators. The beaches where large isopod populations occurred were separated by 20–200 km, and many intermediate beaches appeared to be equally suitable for the animals in terms of physical conditions, food supply, and the composition of the beach communities. It seems unlikely that the isopods were being excluded from all of

these areas by unfavorable environmental factors.

If the animals are present only on a few of the habitable beaches, zoogeographical theory could suggest several possible histories for the species:

1. Such a distribution might arise if the present populations are relicts of a distribution that was once more widespread. The absence of animals at Laguna Beach makes this at least a plausible hypothesis, but it is not supported by the physical evidence. Relict populations would remain separate only if the intermediate areas were unsuitable for colonization, and there is no evidence that this is so. *Tylos punctatus*, because of its habits, is a very motile animal; individuals moving on the surface of the beach at night are often washed about by high waves, and many are undoubtedly carried out to sea. If a handful of live isopods is dropped into water, however, about half of them will curl around air bubbles and float, this

fraction being increased if the water is aerated with bubbled air (like the front edge of a wave). Isopods survived more than a week while floating in an aerated aquarium in this fashion. It is hard to believe, therefore, that the animals would lack the means to be spread from their high-population areas to adjacent beaches.

2. The observed distribution would be noted if the animals were new arrivals and were expanding their populations for the first time from several epicenters. This seems much more unlikely. Vandel (1945) commented on the similarities between the *Tylos* species in the Americas and those in Europe; the European species *T. latreillei* (found in the Caribbean) is very similar to *T. punctatus* in appearance. This supports Vandel's feeling that Europe represents a dispersion center for the Tylidae. Certainly the East Tropical Pacific Barrier would effectively prevent colonization of North American shores from the Indo-Pacific region.

Assuming the present means of dispersal, *T. punctatus* could not have been in direct contact with the Caribbean populations, at least since the Pliocene, when there was a water connection across Central America. If the species has evolved since that time, then it has had plenty of time to move into all suitable habitats. A sudden eruption of five new population epicenters, at about the same time, would not be likely.

3. A third hypothesis, which I find the most reasonable, is based on the unstable character of the beach environment. Beaches are in a constant state of flux, on a time scale of hours to years. Besides the seasonal erosion cycles mentioned above, there are usually longer term changes that can influence the severity of erosion. For instance, Shepard (1963) noted that the beach around the Scripps Institution of Oceanography (La Jolla, California) at one time was scoured down to gravel and cobbles every winter, then was built back up again in the summer. Since 1951, however, the sand has not been removed at all. The reasons for this change are

not understood. It is hardly surprising that *T. punctatus* was never found on this beach while it was a seasonal one, but there seems to be no reason why it should not become established there now, since there are substantial numbers of the animals on a beach only 2–3 km away. However, if the population should establish itself, and then the old seasonal erosion cycle should return, the new population would be destroyed.

The random occurrence of catastrophic beach erosion due to unusually severe storms could be an even more important factor. King (1959) reported instances of beach erosion in southern California of two vertical meters or more in a day. Although such instances are historically unusual, they probably have occurred many times, at any given spot on the coast, over the evolutionary history of the isopod species, i.e., several million years. On a lesser scale, beach erosion by waves in the study areas was noted at all locations (see Figure 4). The scarp at Torrey Pines beach was displaced nearly up to the upper reference stake during a 2-day period of active wave-cutting in February 1969. This approximates a sand removal rate over the whole beach of about 20 vertical centimeters per day.

Since the isopods are buried in the sand, in hibernation, during the winter when most of the erosion occurs, there is little that they can do to escape it. Many of them (particularly the juveniles, who cannot bury themselves as deeply as the adults) are undoubtedly washed out to sea each winter, and this factor must be reflected in the mortality rates calculated above (*T. punctatus* has few natural predators [Hayes 1969]). A really severe storm, of the sort that might only occur once each century or so, could probably remove the entire population by washing away most of the top meter of sand. It is a virtual certainty that, given enough time, such a storm will occur at practically any given beach. It is also likely that long stretches of coastline would be extensively reworked by a storm of this magnitude.

The fate of an isopod washed out to sea is

problematical. Most of them will drown, but some will curl around air bubbles and float. If they escape predation by fish or birds, the floating isopods will probably be redeposited on the shore again, such being the fate of most small, floating objects in nearshore waters (Shepard and Inman 1950). They could be carried some distance by longshore currents before this happens, however. A longshore drift of 0.5 knots (almost 1 km/hour) is not unusual, and the isopods can survive in oxygen-saturated water for several days.

An observation by Menzies (1952) makes this contention plausible. He collected a male and a female *T. punctatus* of breeding size in a surface plankton tow made late in the afternoon off Newport Beach, California (July 1951). Since this is a month when the isopods are active, it is likely that these animals were washed out to sea while feeding, perhaps during the previous night. They were described as "quite lively," so apparently an immersion of at least 10–12 hours duration did not bother them.

The distribution of isopod populations along the coast, when subjected to density-independent population control measures of this sort, will depend on the rate of recovery of the populations. The life tables for the animals (Table 8) give approximate population doubling times of 2–12 years. If the doubling time is 2 years, and exponential population growth is assumed, a single gravid female isopod stranded on a beach could produce a population density similar to that observed at Punta Banda in 55–60 years. A 12-year doubling time, on the other hand, would require 330–340 years to produce the same numbers. The more rapid rate of increase would seem to permit the population to escape density-independent control and to reach levels where it would be controlled by density-dependent factors such as food supply. The expected result in this case would be a more-or-less continuous distribution of isopods along the coast, concentrated in areas where food supply is greatest (e.g., those beaches having offshore kelp beds). Gaps in the distribution caused by storm erosion would be filled up in a few

years from the populations in adjacent areas.

If, however, the true doubling time of the population is on the order of 12 years (or more), the final distribution might well be similar to the observed one. Small "seed" populations would grow slowly and would reach large numbers only if they escaped severe storm erosion for several centuries. Throughout its growth, the population would supply isopods to other beaches (in the direction of the longshore drift) from individuals that were washed out to sea while feeding in the summer or eroded out of the beach by normal winter storms. A severe storm could wipe out much of the parent population along several kilometers of beach, leaving the outlying populations, on the storm fringe areas, to begin the growth process again. Repetition of this pattern over many thousands of years would produce scattered populations of the animals separated by long intermediate zones which were suitable for isopods but which had been scoured clean at some time in the past and had not yet been recolonized. The populations would not necessarily be concentrated near kelp beds, since they would be unlikely to grow to a size in which competition for food was a significant factor. The actual number of discrete populations would represent a balance between severe storm mortality and the populations' intrinsic rate of growth.

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