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Proximate Causes of Mortality Determining the Distribution and Abundance of the Barnacle *Balanus improvisus* Darwin in Chesapeake Bay[1]

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ABSTRACT: The effects of predation and competition on survival of the barnacle, *Balanus improvisus* Darwin, in the upper Chesapeake Bay varied from location to location in 1972 and probably vary from year to year. The flatworm, *Stylochus ellipticus* Girard, was the predominant predator on barnacles, and the bryozoan, *Victorella pavida* Kent, was the major spatial competitor. Those intertidal barnacles not killed by the flatworms or bryozoans died from exposure to a combination of high winds (25 knots) and low air temperature (−9° C) in the winter. Subtidal barnacle populations were not eliminated by biotic or physical factors and may be the source of those larvae recolonizing the intertidal zone every spring.

Introduction

Balanus improvisus Darwin is the dominant barnacle in the intertidal zone of the upper Chesapeake Bay. This work describes proximate causes of seasonal fluctuations in abundance of this species. Preliminary observations revealed that pilings encrusted with barnacles in densities approaching 30–40 per cm^2 in the summer months are covered only by the dead shells by the following winter. This raises the following questions. Do biological or physical factors have relatively more influence on individuals' survival? What are the predators and spatial competitors, and which are most effective at limiting barnacle survival? Are there temporal or spatial refuges by which barnacles escape some of the causes of mortality? Is there an extensive subtidal population of barnacles which might repopulate the intertidal zone of the Bay?

Most studies of mortality in intertidal barnacles have been conducted along more open coasts (Connell 1961a, 1961b, 1970; Paine 1966; Dayton 1971). These populations are exposed to physical and biological factors quite different from those experienced by an estuarine population. This study provides a comparison of the ecology of the Chesapeake Bay barnacles with that of the coastal intertidal populations.

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Study Areas

Intertidal barnacle populations were studied in detail at two sites in Chesapeake Bay. The northern site was a pier in Rhode River (Fig. 1) maintained by the Chesapeake Bay Center for Environmental Studies. The Rhode River is a small estuary without rapid current flow and with almost no wave action. The intertidal zone is quite narrow (mean tidal range = 46 cm), and the tidal cycle is irregular, being determined in part by the direction and velocity of the wind and by barometric pressure. During this study, salinity varied between 2.1 ppt and 13.7 ppt and water temperature ranged from 0.5° C to 32.6° C (Cory et al. 1975).

The southern site was a pier located at the Chesapeake Biological Laboratory in Solomons, Maryland, near the mouth of the Patuxent River. There is considerably more wave action and a more rapid current flow than at the northern site. The tidal range is 51 cm. Although a strong wind can influence tidal level, barnacles in the high intertidal are usually exposed twice a day. In 1972-73, salinity ranged from 2.5 ppt to 15.0 ppt and water temperature ranged from 3.0° C to 29.0° C.

Observations were also made on subtidal populations to determine possible differences in species and numbers from those noted in the intertidal at the study sites. Samples were taken in October 1972 on both sides of the Bay from Baltimore to the Potomac River (Fig. 1). In March 1973, both shores of the bay were again sampled, the northernmost station being Rhode River, the southernmost being Solomons.

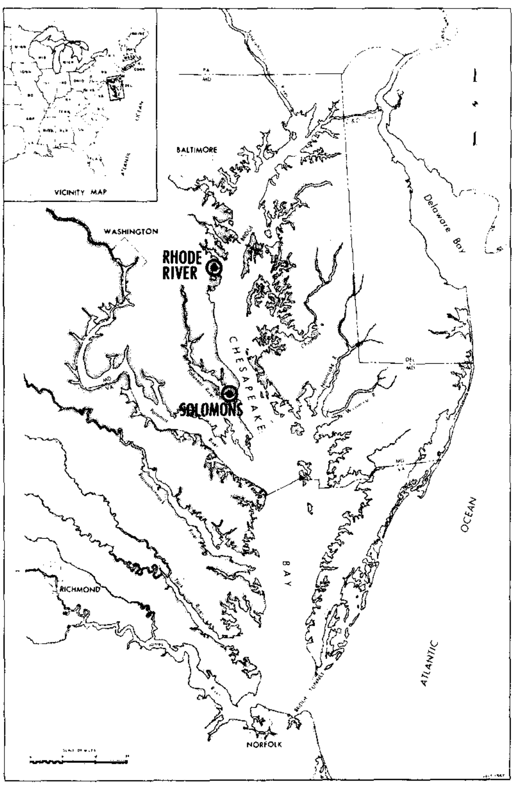

Fig. 1. Map of the Chesapeake Bay; R and S indicate the study sites at Rhode River and Solomons.

Materials and Methods

At each site, four 15 cm × 30 cm wooden settling panels were suspended at each of 3 levels. The highest panels (H) were barely submerged at mean high tide; middle panels (M) were 30 cm below panel H, and the lowest panels (L), 60 cm below panel H, were rarely exposed. With a wax pencil, I marked off two areas of 144 cm^2 (12 cm × 12 cm) on each panel. One area was protected from large predators such as fish or crabs by a cage of 1/4-inch mesh hardware cloth. The other area was left unprotected.

All panels were in place by mid-April 1972, and each site was checked on an average every 2 to 3 weeks for a year. Initially, I counted and measured live barnacles in subquadrats and from the data calculated percent cover of live barnacles and mean increase in the rostrocarina diameter for each observation. Percent cover was determined by dividing the sum of the areas of the individuals by 144 cm^2. Later, acquisition of a camera enabled me to keep a permanent record of cohort survival on each panel. Use of photographs permitted an increase in subquadrat size and accuracy of measurements.

Data for the graphs were taken from three H and three M panels at each site, and averaged. Data were not presented as graphs for L panels because they differed little from M panels. Diameter measurements are based on the whole population present at a given time and include the few individuals which settled after June. The probabilities for comparison of barnacle diameters are based on the Mann-Whitney U-test.

Observations on the predatory behavior of *Stylochus ellipticus* Girard were made in the laboratory. Flatworms were released on a partially submerged panel upon which barnacles were attached, and their behavior observed through a dissecting microscope.

Although the quantitative study ended after a year in March 1973, qualitative observations were continued an additional year through occasional visits to the two sites.

Results

Growth Rates

In 1972, the only barnacle species to settle at Solomons and Rhode River was *B. improvisus*. This settlement began in June at Rhode River. Individuals on panels M and L attained a diameter of 11–12 mm by late August. At this time, panel H individuals, averaging 9.3 mm, were significantly smaller (.001 < P < .01) (Figs. 2 and 3). by December, barnacles on panel H were nearly full size (13 to 14 mm diameter) and were not significantly smaller than the panel M or L barnacles (.5 < P < .9). One group of individuals (N = 33), which settled at L level in August, attained an average diameter of 10.0 mm in 30 days.

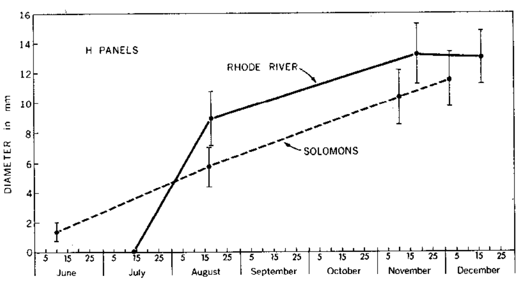

Fig. 2. Six-month change in mean diameter for barnacles on H panels at Rhode River and Solomons.

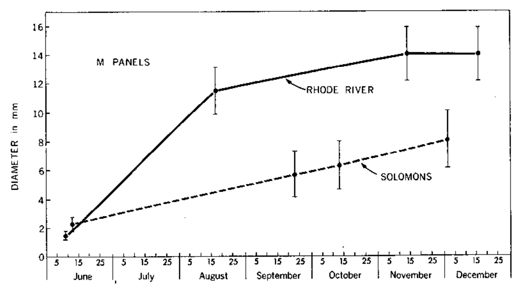

Fig. 3. Six-month change in mean diameter for barnacles on M panels at Rhode River and Solomons.

Balanus improvisus began settling at Solomons on panels M and L by mid-May and on panel H two weeks later. Barnacles at all three depths were roughly the same size (.4 < P < .5) in August (Figs. 2 and 3), but by December, panel H individuals were significantly greater in diameter than those at lower depths (P < .001). Those barnacles at the lower depths may have had a slightly greater volume, however, due to their average height being 2 to 3 mm greater.

Effects of Biotic Factors

After an initial heavy settlement of cyprid larvae in June at both Solomons and Rhode River, colonization of the panels by barnacles was relatively light for the rest of the season. Consequently an increase in percent cover reflects survival and growth of the June set, and not the settlement of new barnacles.

Percent cover generally increased on the panels at Rhode River until December (Figs. 4 and 5). No marked mortality due to predation occurred on any of the panels. A heavy set in June by the bryozoan, *Victorella pavida* Kent, on panels M and L, however, resulted in the smothering of many barnacles at these levels. It was difficult to make more than a qualitative estimate of density of the bryozoans; however, the colonies frequently formed mats of 3 to 4 cm in thickness. Barnacles completely covered by these bryozoan mats were found dead but not physically damaged as by a predator. The shells and panel surface were black from hydrogen sulfide stains, and even bryozoan zooids at the bottom of the mats were dead. Many of these colonies sloughed off by August, and the fall in barnacle survival on the lower two panels was reversed.

The other macrofauna asociated with *B. improvisus* on the panels at Rhode River include: amphipods, *Corophium lacustre* Vanhoffen; polychaetes, *Nereis succinea* Frey and Leuckart, *Polydora ligni* Webster; crabs,

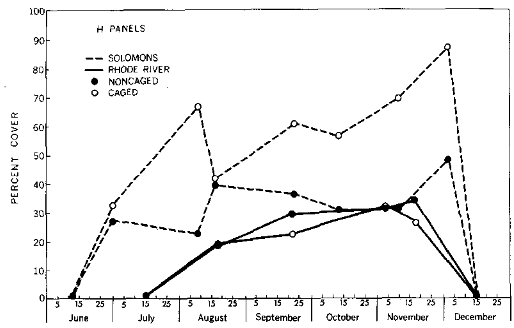

Fig. 4. Percent cover by live barnacles on H panels at Rhode River and Solomons, from June to December 1972.

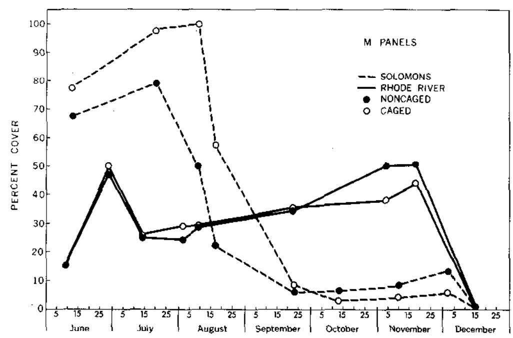

Fig. 5. Percent cover by live barnacles on M panels at Rhode River and Solomons, from June to December 1972.

Callinectes sapidus Rathbun, *Rhithropanopeus harrisii* Gould; grass shrimp, *Palaemonetes pugio* Holthuis. Apparently none of these were significant predators on *Balanus improvisus.*

Victorella pavida settled on panels at Solomons but the set was not as heavy as at Rhode River. The colonies could be described as a light, scattered covering occasionally approaching 1 to 2 cm in thickness. Barnacle mortality due to smothering was not indicated on these panels. Except for the flatworm, *Stylochus ellipticus*, and 2 species of calcareous bryozoans, the macrofauna appearing at Solomons also appeared at Rhode River.

As a result of predation, barnacle populations on panels M and L at Solomons began to experience mortality in late June. By August, mortality was very high as indicated by the drop in percent cover (Fig. 5). This motality was due to predation by the flatworm, *Stylochus ellipticus*. Flatworms, which first appeared on the panels in late June, reached densities of 30 or more large (> 5 mm) worms per panel by August. The number of smaller flatworms could have been in the thousands.

Survival on caged panels was no higher than that for uncaged panels. Physical damage to shells was rare. Frequently even the opercular valves on dead barnacles were intact; however, opening the shells usually revealed a flatworm hiding within.

Panel H barnacles in Solomons were not attacked by *S. ellipticus*. Flatworms were never found on these panels, and survival of barnacles at this level was high (Fig. 4) until December. The difference in cover between caged and non-caged panels is not due to mortality. Rather, it indicates the variation in settlement of cyprid larvae at this level of the intertidal zone.

Laboratory observations revealed the following behavior by *Stylochus ellipticus* when preying on *B. improvisus*. The flatworm crawls over barnacles, stopping at the opercular valves and apparently feeling the edges of the valves with its pharynx. Normally a barnacle so approached closes. If the worm is able to insert its pharynx, it retreats from the valves and flattens itself on the shell plates. The pharynx remains inserted either between the valves or between one of the valves and one of the shell plates. Fluids were observed being pumped into the barnacle and masses of tissue being pumped out in turn. Usually a second fold of the pharynx is then inserted into the barnacle. In as little as 90 minutes, the barnacle gapes and the worm enters the shell. Frequently four or five tiny flatworms were seen entering the barnacle after the larger worm had killed it.

During one observation the water level was lowered experimentally while a flatworm was attacking a barnacle. Rather than abandon its prey, the worm edged down with the water level to the panel surface leaving its pharynx within the barnacle. The film of water on the panel was sufficient to keep the animal moist throughout the rest of the attack.

Effects of Physical Factors

Tropical Storm Agnes caused an unusually high freshwater run-off in June which lowered salinities in the bay for 1972. This apparently had no direct effect on *Balanus improvisus*

TABLE 1. Physical data for days of lowest air temperature during the winters of 1972–73 and 1973–4.

	Solomons			
Date	12-17-72	12-18-73	1-3-74	1-13-74
Min. air temp. °C	−8.9	−6.7	−5.6	−5.0
Min. water temp. °C	7.0	5.0	3.3	3.0
Wind speed knots	25	0–10	0–10	10–15
Tide height: cm below mean low tide	54.3	15.3	1.8	9.8
	Rhode River			
Date	12-17-72	12-18-73	1-3-74	1-13-74
Min. air temp. °C	−7.2	−8.3	−1.7	−6.7
Min. water temp. °C	1.5	1.0	3.0	1.6
Wind speed knots	25	0–10	0–10	10–15
Tide height: cm below mean low tide	70	21	9	20

which is very tolerant of low salinities. Since both *Stylochus ellipticus* and *Victorella pavida* were observed to settle at about the same time in 1974 and 1975 as in 1972 it is also unlikely that these species were strongly affected by the lowered salinity.

Physical factors did not affect survival until mid-December. On December 17, 1972 the air temperature dropped below the previous low for that autumn of −3° C to −9° C at Solomons and −7° C at Rhode River (see Table 1). Tides were extremely low at both sites due to high winds from the west which blew water from the Rhode and Patuxent River estuaries.

Prolonged exposure to the low air temperature and high winds resulted in extensive mortality in barnacles due to freezing at both Solomons and Rhode River (Figs. 4 and 5). All barnacles on panels H and M were killed during this period. Only those individuals on the lowest portions of L panels, which were still submerged, escaped freezing.

Survival was monitored at both sites during the winter months of the following year (1973-74). While there was no survival on panel H, individuals were alive on M and L panels. Although air temperatures dropped as low as they were the year before, there were no extraordinarily low tides to subject the panel M individuals to a prolonged exposure (Table 1).

Subtidal Barnacles

In October 1972, sampling of oyster shells on the bay bottom revealed a patchy subtidal distribution of *B. improvisus*. Densities varied among stations with oyster shells from 0 to 20 per cm². *S. ellipticus* was occasionally found on the oyster shells with the barnacles and within some barnacle shells. However, flatworms did not occur in large numbers and frequently were not found at all.

In March 1973, many subtidal barnacles were still alive and contained developing eggs. Probably most of these survived to release larvae in the spring. Evidently there is an extensive subtidal population of barnacles that does not die off every winter.

Discussion

Although experimental verification is lacking, observations indicated that under certain conditions bryozoans are capable of overgrowing and smothering barnacles. This is in agreement with reports by Cory (1967), McDougall (1943), Bousfield (1954), and Weiss (1948). Conditions beneath the colonies of zooids were definitely stagnant as indicated by the presence of hydrogen sulfide, and the barnacles would have been unable to extend their cirri for respiration. Moreover, had they been killed by a predator, it is unlikely they would have been left to decay in their shells. Hence death was probably due to overgrowth by the bryozoans.

Cory (1967) suggested that *Stylochus ellipticus* might be responsible for up to 90% of the barnacle mortality in the Patuxent River, but he had no observations of predation. Based on laboratory observations reported here, there can be no doubt that the flatworm is capable of preying on barnacles, and field evidence suggests that predation by *S. ellip-*

ticus is a significant biotic factor in reducing barnacle survival.

The similar mortality for the caged and non-caged barnacles on the lower panels at Solomons is readily explained by the ability of the flatworm to penetrate the cages. High mortality did not occur until after flatworms appeared on the panels, and was noted only on the lower panels which were accessible to the worms. The H panels were not subject to flatworm predation. This was probably due to the frequent exposure of these panels by the tides and the inability of *S. ellipticus* to withstand desiccation. Observations at Rhode River and on subtidal barnacles indicated that whenever there were few or no flatworms present, barnacle mortality was relatively low. Were larger animals such as blue crabs or fish preying on the barnacles, the non-caged populations would have experienced a higher mortality. Moreover the dead shells would have been crushed or scraped from the panels. Obviously, a controlled experiment, in which the predator is excluded from its prey, would provide stronger evidence (see Addendum); but barnacle survival did not vary with the presence or absence of species of macrofauna other than *S. ellipticus*. For this reason, it is probable that the flatworm was the primary predator on the barnacle populations at Solomons.

It was shown in Connell's (1970) study of *Balanus glandula* that the lower limit of the barnacle zone is often determined by the presence of predators. These predators, the commonest being three species of the snail *Thais*, are capable of killing virtually every accessible barnacle. In areas where the predators occur, *B. glandula* survives only in the high intertidal; but the *B. glandula* zone extends into the subtidal where predators are scarce or excluded.

Connell emphasized the importance of some refuge in time or space for the escape of a prey from its predator. In Chesapeake Bay, *Balanus improvisus* is in need of a refuge because theoretically *S. ellipticus* is capable of killing most of those barnacles accessible to it. In the intertidal zone, there are about 30 barnacles per cm^2 in June and settling rates are low in succeeding months. There are about 30 large flatworms per panel (144 cm^2). If the flatworms killed one barnacle per day, all barnacles would be killed between June 1 and October 30. This ignores any mortality due to small flatworms.

The upper 15 cm of the intertidal zone provides a refuge from predation. The flatworms appear unable to endure the exposure occurring here. The subtidal barnacles are also surviving in a refuge zone, for on many of the oyster bars examined, barnacle densities were high while flatworm densities were very low. It is not clear why there should be a refuge here. From my observations and those of Webster and Medford (1959) flatworm distribution in the Chesapeake Bay is patchy. Whatever produces this patchiness may have caused the absence of *S. ellipticus* on some oyster bars and in small estuaries such as Rhode River. It is also possible that since *S. ellipticus* is a major predator of oysters (Webster and Medford 1959; Provenzano 1959) and may prefer them to barnacles (Landers and Rhodes 1970), the flatworms ignored the subtidal barnacles, attacking oysters instead.

Other macrofauna associated with the barnacles are not probable predators on *B. improvisus*. As competitors for space or food their actual interference would be physical, and only *Victorella pavida* occurs in the numbers sufficient to effect such a physical interference.

Bousfield (1954) noted that *B. improvisus* located in the intertidal zone of the Miramichi estuary is killed every year by freezing. In the present study, it is obvious from the data from both years that *B. improvisus* was not killed by low air temperature alone. Rather it was the combination of a prolonged exposure to high winds and a low temperature which proved lethal. Barnacles at panel H level are particularly susceptible for they frequently experience exposure for periods of 24 hours or more. Panel M individuals are more likely to survive the winter months since, under normal conditions, their period of exposure is usually limited to six hours. However, the strong winds to which they were exposed for at least 24 hours in December 1972, produced a wind chill factor that proved lethal. Winter winds may not kill all intertidal barnacles on both sides of the bay at the same time; however, it is possible that some years this may occur in the upper bay.

This estuarine population of barnacles does differ from coastal intertidal populations of the temperate zone. The entire intertidal population can be destroyed by physical stresses which are frequent but unpredictable. Were it not for the subtidal populations which persist year after year, it is possible that *B. improvisus* would not survive in the upper bay. However, other proximate causes of variation in distribution and abundance are similar to those described for intertidal barnacles on open coasts. Both predation and interspecific competition for space appear to be important causes of mortality at Rhode River and at Solomons, although competition is less effective than predation in this study because the bryozoans were sloughed off when the barnacles died.

ADDENDUM

During the summer of 1975 another attempt was made to control predation by *Stylochus ellipticus* on *Balanus improvisus*. Most of the experimental work was carried out by Joanne Jones of the Chesapeake Biological Laboratory and to her I am grateful for her enthusiasm and help in the tedious work involved.

Eight bricks (20 cm × 5.8 cm × 5.8 cm) were suspended separately on April 15 at a depth where they would not be exposed. By May 29 a set of *Balanus improvisus* had covered all the bricks at densities approaching 25 per cm². To reduce the number of individuals to be counted and to permit less crowded growth, some barnacles on the sides of the bricks to be studied were removed. An even distribution of barnacles was left. By July 10 *S. ellipticus* had settled on the bricks. At this time bricks 1–4 were soaked in a 15% salt solution for 10 minutes to kill the flatworms; bricks 5–8, the controls, were not

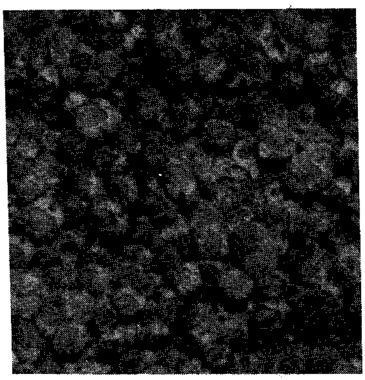

Fig. 6. Brick #1 shows density of *Balanus improvisus* typical of all bricks before the experimental period began. The enclosed area is 2 cm × 2 cm.

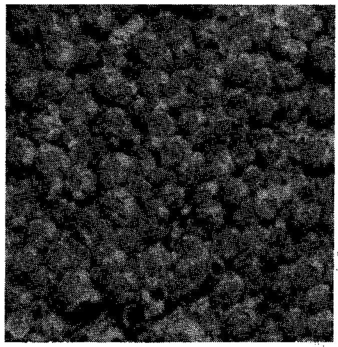

Fig. 7. Brick #8 before predation on barnacles by *Stylochus ellipticus*. The enclosed area is 2 cm × 2 cm.

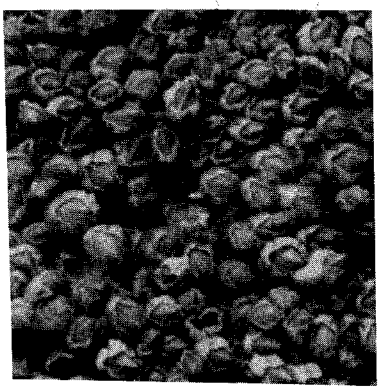

Fig. 8. Brick #1 after three weeks; the salt treatments reduced barnacle mortality.

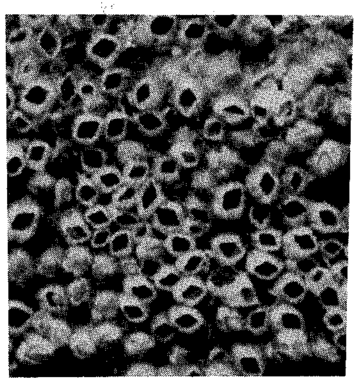

Fig. 9. Brick #8 after three weeks; barnacle mortality due to predation was extremely heavy.

TABLE 2. Survival of *Balanus improvisus* on each of seven bricks. Bricks 1–4 were immersed daily in a 15% solution of salt water; bricks 5–8 were not treated.

Treated bricks			Untreated bricks		
	Barnacles alive July 10	Barnacles alive July 29		Barnacles alive July 10	Barnacles alive July 29
#1	119	105	#5	116	83
#2	103	96	#6	150	106
#3	Lost		#7	125	81
#4	141	124	#8	130	41
	Percent survival: 89.5%			Percent survival: 59.7%	

treated. Photographs were taken of all eight bricks.

Brick #3 was lost, but the other three test bricks were soaked in 15% salt water on a daily schedule. On July 29 the seven bricks were photographed again. Figs. 6 and 7 show bricks #1 and #8 with barnacle densities typical of all seven bricks on July 10. Figs. 8 and 9 show the same bricks on July 29. The enclosed areas are 4 cm^2.

In an area (2 cm × 2 cm) at the center of each brick, all barnacles which had died during the experiment were counted. The results are given in Table 2. The data were tested in a Chi squared contingency table ($P < .005$) and the conclusion is that barnacle mortality was not independent of the salt treatment. Clearly, reducing the number of flatworms had reduced barnacle mortality.

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