

Burrowing Limitations in Pelecypoda

BY

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(4 Text figures)

INTRODUCTION

STUDENTS OF LAMELLIBRANCHS have given attention to their several modes of locomotion.

Some clams creep or crawl through sand and mud (*Trachycardium quadragenarium* CONRAD, 1837); others swim (*Pecten irradians* CONRAD, 1837); most burrow downward (*Tresus nuttalli* (CONRAD, 1837) or *Panope generosa* GOULD, 1850), leaving only the tip of the siphon to protrude above the surface. Observations on the burrowing of clams have been made by MACGINITIE & MACGINITIE (1949, pp. 80-81, 329, 352), GUTSELL (1930, pp. 569-625), BORRADAILE *et al.* (1961, pp. 622-635), RICKETTS & CALVIN (1952, pp. 196-197, 268-305), and BUCHSBAUM (1955, pp. 188-198). However, no one has established the existence of a mechanism whereby clams, once in position and covered with sand, could elevate themselves back toward the surface. This I intend to do in this paper.

As one attempts to understand how lamellibranchs might maintain themselves at certain depths in the medium in which they are buried, certain hypotheses may be drawn regarding beneath-the-sand locomotion: (1) there is no movement in the burrow but rather adjustment to water-sand level through action of the siphon alone; (2) upward movement of the clam in the burrow may be achieved by such means as (a) rapid extension of the foot "downward," resulting in an "upward" pushing movement, (b) continual digging in an arc, thus placing the clam near the surface or (c) shell action, perhaps coordinated with foot action, involving filling the mantle cavity then ejecting water forcibly, resulting in elevation; and (3) the clam may elevate through the effect of buoyancy, the clam being less dense than the medium in which it lives. These hypotheses are based upon illustrations, references, and discussions of clam locomotion and under-the-sand position found in the

above listed references plus those of Pohlo (1963, pp. 98-103) (1964, pp. 321-330), FITCH (1950, pp. 285-311), LIGHT *et al.* (1954 pp. 219-238), FRASER & SMITH (1928, pp. 249-268), FRASER (1930, pp. 569-626), WEYMOUTH (1920, pp. 29-63) and observations of the writer.

MATERIAL AND OBSERVATIONS

Ten species of clams were selected for this study, and results are based upon observations of these. The species studied were (1) *Macoma nasuta* (CONRAD, 1837), (2) *Macoma secta* (CONRAD, 1860), (3) *Protothaca staminea* (CONRAD, 1837), (4) *Saxidomus nuttalli* CONRAD, 1837, (5) *Mya arenaria* LINNAEUS, 1758, (6) *Tresus nuttalli* (CONRAD, 1837), all studied in field experiments at Drakes Estero, Marin County, and Bodega Bay, Sonoma County, California, (7) *Tivela stultorum* (MAWE, 1823), Pismo Beach, California, (8) *Panope generosa* GOULD, 1850, Puget Sound, Washington, (9) *Siliqua patula* (DIXON, 1788), Copalis Beach, Washington, and (10) *Chione californiensis* (BRODERIP, 1835), two specimens of which were obtained alive from Baja California but were not observed under field conditions. All clams did not respond identically.

To test the hypotheses outlined above, clams were dug up and then reburied in aquaria, five gallon cans, or in the sand in open clam beds.

It was soon evident that the conditions inside an aquarium or can are quite different from those in the open clam bed with natural wave action. Temperature, water action, water oxygenation, and the proportion of solid media suspended in water are all factors which are very difficult to duplicate when trying to reconstruct the natural environment for the clam inside the aquaria or cans. No clams planted in aquaria or five gallon cans showed any ability to elevate.

All clams in this study extended their siphon tip to or very near to the surface of the sand for exchange of water (LIGHT *et al.* 1954, p. 232). In normal posture the posterior end bearing the siphon is nearer the surface; the

¹ This study was part of a thesis for the Master of Arts Degree in Biology at San Francisco State College.

ventro-anterior end with the extensible foot points downward. The clams used appeared to be in normal posture when near a 90° vertical angle, regardless of the depth or age of the clam; *Macoma* was a partial exception, being inclined nearly $30-60^\circ$ with the incurrent siphon making a soft bend to reach the surface. All clams studied have an extensible downward-pointing foot. It serves as a probe, anchor, and contractor during digging.

In downward digging, generally speaking, the clam extends the foot and simultaneously changes the foot shape into a thin, blade-like projection, the tip inserting into the sand if digging from on top the sand, or probing deeper into the sand if already buried. The sinuses fill with blood, the body of the foot enlarges and may exceed the shell diameter, and then the foot contracts, drawing the shell into or through the sand. Under the sand this movement is accompanied by spurts of water through the excurrent siphon.

Digging action below the sand can be seen in part by using aquaria, and in all clams so examined the over-all foot action was similar, but degree of extension, frequency of contractions, and intensity of contraction differed markedly in different species. In no case was any action seen or felt which might suggest the clam could reverse this mechanism and push upwardly.

EXPERIMENTS AND RESULTS

Replanting and Depth Experiments: To check a clam's ability to move upward or show directional movement other than downward, clams were dug and replanted in a series of planting experiments at various depths in open clam beds, in aquaria, and in five-gallon cans. The aquaria and cans were then planted at different depths in the clam bed. Controls of two types were used in all cases: (1) clams of about the same size were marked in the bed and left untouched; (2) other clams were dug up, reburied at the same depth and marked. This allowed size, age, and natural depth comparisons between experimental clams and controls. Stakes were used for marking in all cases.

Of the species used in this study, 25 were planted at depths less than extended siphon length plus two to four inches, all 25 clams lived and within one week each established its burrow. In all experiments where the clam was planted in excess of extended siphon length plus about seven inches, they all perished within seven days.

Of 25 *Protothaca staminea* planted in excess of three to four inches deep, 18 were dead within a week and the seven remaining were dead at one month. Twenty-five planted at extended siphon length plus two inches remained alive. Critical depth for this species is about two inches. *Tivela stultorum*, when planted at approximately

18 inches, reestablished at normal depth within 48 hours if planted within bounds of active surf. Normal depth for *Tivela* is 2-6 inches, fully extended siphon approximately 4-6 inches. Plantings on the beach above the region of wave action showed the clams did not change position. Using 20 *Siliqua patula*, a similar experiment showed the clam regaining normal depth by the next low tide from an 18 to 24 inch burial. Normal depth for *Siliqua* is 2-10 inches, with fully extended siphons 6-9 inches. The above measurements are of mature clams with shell length of approximately 6 inches. As in the experiments with *Tivela*, *Siliqua* also failed to show any movement when planted in moist sand above the level of wave action.

A single *Panope generosa* was planted at six inches below extended siphon depth, and when checked in one month was found alive. It had created a six-inch-deep conical depression in the surface layer of sand, and the siphon tip emerged from the lowest point. The clam had not elevated.

Additional Cover Experiments: Using *Tresus nuttalli* and *Protothaca staminea*, a variation of the planting experiment was devised. Four-sided wooden frames with sides from four to twelve inches high were built (see diagram, figure 1). These were then placed around undisturbed clams in various regions of the beds. The frames were anchored in place and filled with sand. Sixteen *T. nuttalli* covered with approximately four inches or more of sand were all dead at the end of three weeks, while 16 covered with approximately two to three inches of sand

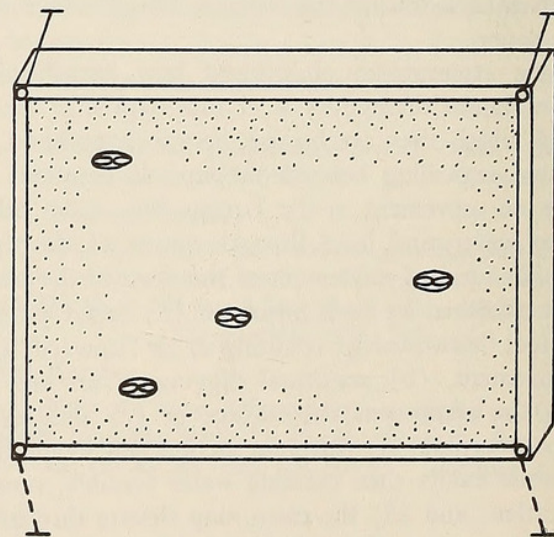


Figure 1: Wooden frame in position for adding environmental sand to clams, where siphons are at surface level.

(Surface view looking down onto the clam bed)

[the size of the frames varied, depending upon the species involved; for *Protothaca staminea* the frames were 4 feet by 4 feet, while for *Tresus nuttalli* they were 6 feet by 8 feet]

were alive at the end of three weeks. Ten *P. staminea* covered with one inch of sand remained alive while 14 having three inches of additional cover had perished in the same length of time.

As a final check to determine a clam's ability to move upward, *Tresus nuttalli* with enlarged concave burrow openings were selected. Ten selected burrows were measured and marked; the depressions were then filled gently with sand. The ten clams occupying burrows with depressions about two inches deep were alive with the burrow depressions partly reformed at the end of two weeks. Ten clams in depressions four or more inches deep were dead (see diagram, figure 2).

In any of these cases one might conclude that if the clam could have elevated rather than perish, it would have done so.

Clams used for the experiments with reburial, additional cover, and burrow depression filling appeared unable to move upward and adjust to these modifications of the environment. They did show some ability in siphon extension of about one to four inches and thereby remained alive.

Posture and Reorientation Experiments: In order to determine directional movement other than downward, a series of posture experiments was devised and executed using 15 *Tresus nuttalli*, 10 *Protothaca staminea*, 10 *Tivela stultorum*, and 25 *Siliqua patula* in each experiment. The clams were immediately replanted at the depths at which they were located. Posture variations in the experiments involved (1) a 180° reversal of the clam, siphon straight down, foot up; (2) a 135° inclination, siphon down; (3) 90° inclination of three types: (a) mantle edge up, (b) mantle edge down, and (c) mantle edge to the side; and (4) a 45° inclination with the siphons up (see diagram, figure 3). Results of these experiments show that two species, *Tresus nuttalli* and *P. staminea*, could not reorient and survive in any position except the 45° inclination. Twelve *Tivela stultorum* and 24 *S. patula* repostured in the 45° inclination within 24 hours. In no case could the species used reestablish themselves from a complete reversal (all 51 specimens died); 90° inclination (all 50 specimens died); mantle edge up (all 50 specimens died); or 135° inclination, siphon down (all 50 specimens died).

Relative Density and Water Action: The clams studied have no known method of self-elevation by voluntary means, yet some elevate in the field. It is therefore strongly suggested that they may be elevated by water action. Ten species of clams were subjected to quantitative analysis in their individual densities in relation to the density of their immediate environment. The data from this work show that each clam is less dense than its environment (see Table No. 1: Table of Comparative

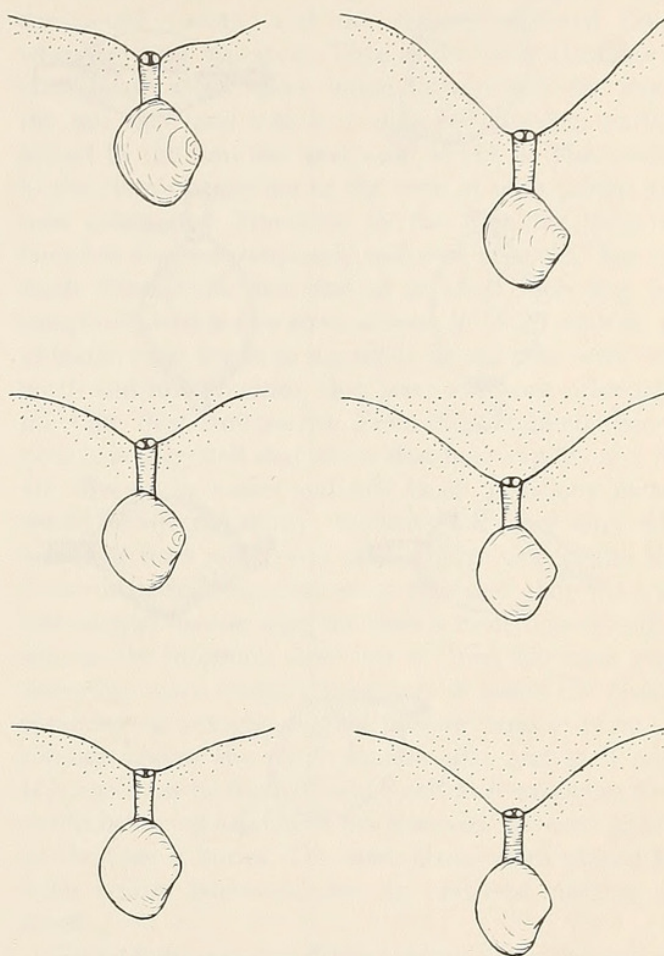


Figure 2: Addition of sand covering to concave burrows. Natural burrow depressions are marked and filled flush with sand. The depth of these burrows ranged from about one to six inches and the diameter from about two to ten inches.

Natural burrow depressions

Covered

After three weeks

Density). This evidence led to the hypothesis that relative density resulting in a positive buoyancy will, under prescribed conditions, elevate a clam in its burrow. This suggests that clams must dig down to establish themselves within the sand at depths appropriate to their anatomy, that depth in general is dictated by the siphon length, and that clam buoyancy causes any elevation that occurs. In either case the problem of the clam is to dig downward only. My experiments show that they cannot actively,

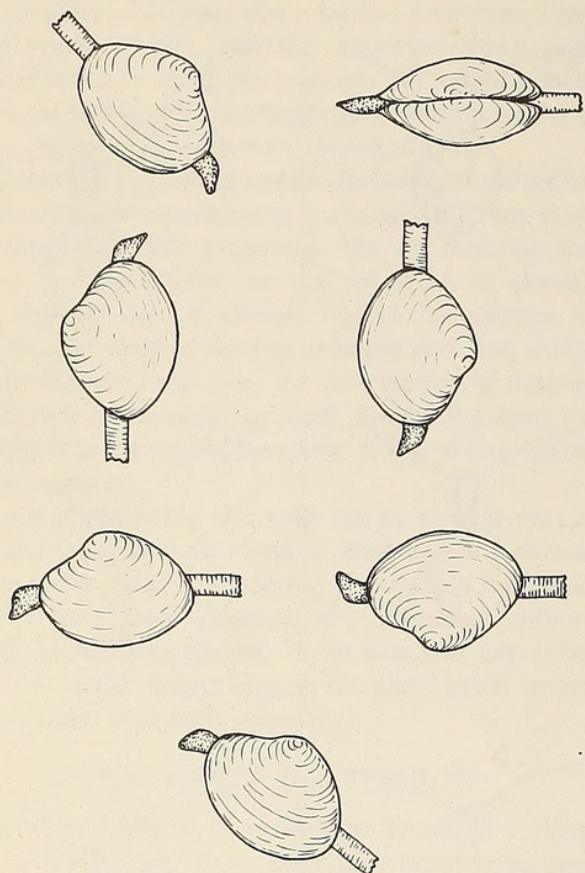


Figure 3: Diagram of posture studies

(illustrating the general procedure used in this study)

- a - 45° inclination b - 90°, flat c - 180°, reversed
 d - control(s), natural depth and posture for each species used
 e - 90° inclination, mantle edge down f - 90°, mantle edge up
 g - 135° (reverse) inclination

voluntarily elevate even when not to do so causes them to perish.

Effect of Water Action on Clam Buoyancy Inside an Aquarium: To check the effect of density on the buoyancy and digging of clams, the following experiment was conducted. Clams of different species and sizes were placed at the bottom of an aquarium (see diagram, figure 4). The aquarium was placed on a log and filled with water. Varying amounts of sand were added and the aquarium

Table 1

Table of Comparative Density
 of
 Clams and Sand

Base Reference = Density of sand at 3.00 gm/cc as an average of ten observations.

<i>Panope generosa</i>	1.38
<i>Mya arenaria</i>	1.31
<i>Tivela stultorum</i>	1.83
<i>Tresus nuttalli</i>	1.27
<i>Saxidomus nuttalli</i>	1.47
<i>Siliqua patula</i>	1.14
<i>Chione californiensis</i>	1.71
<i>Macoma nasuta</i>	1.21
<i>Macoma secta</i>	1.24
<i>Protothaca staminea</i>	2.04

was then rocked. If the difference in buoyancy between clam and medium were similar to that in nature, and the buoyancy hypothesis correct, the clams would be buoyed up. In all cases this did occur.

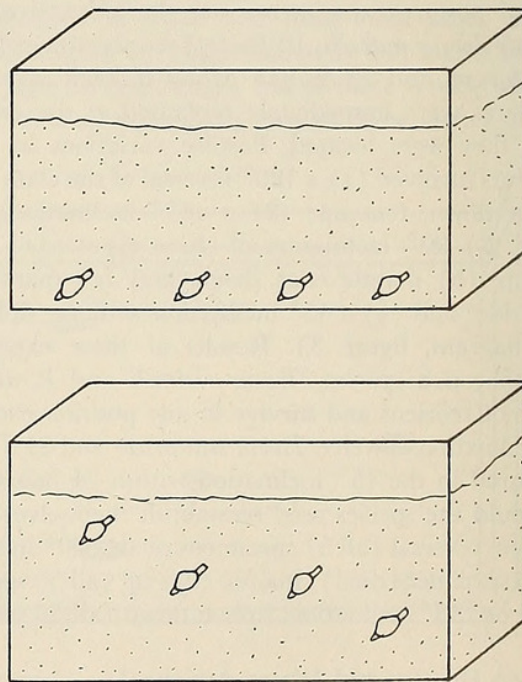


Figure 4: Demonstration of effect of buoyancy under controlled experimental conditions.

[figures indicate density in gm/cc]

- a - living clams, sand, water and aquarium at start of experiment
 b - same aquarium after rocking 30 tilts per minute for 10 minutes
 1 — *Macoma secta* 2 — *Protothaca staminea*
 3 — *Tresus nuttalli* 4 — *Tivela stultorum*

The density of the clam as compared to the environment determines the relative buoyancy and appears to be the basis for variation in the clam's digging ability and related activity. For example, *Tivela* and *Siliqua* represent clams which can move upward in the field. They live in an environment of rapid, severe, and forceful interaction of water, sand and clam. They are constantly affected by the difference in relative density which serves to buoy them upward through the sand. They maintain correct depth and position by digging downward. Conversely, *Tresus* and *Panope* live in areas of calm, slow-moving waters and are not affected by such an interaction of water, sand and self. Burrow construction, depth, burrowing ability and anatomical differences of species used clearly demonstrate adaptation to sand-buoyancy.

Burrowing and Geographical Orientation: General observations on a clam's position in the sand, which I found interesting but which were not resolved in this study, concern the geographical direction of some clams. It has been noted (WEYMOUTH, 1920) that certain clams, e.g. *Siliqua patula* and *Tivela stultorum*, are always found in a given position or direction relative to the wave front. This fact was confirmed during this study. The apparent reason for such directional orientation is the action of the wave front on the clam. It is suggested that regardless of the geographical direction of the wave front these types of clams would show this definite orientation on the beach, and East and West are used for convenience in these remarks, because both *T. stultorum* and *S. patula* were so oriented in the beaches studied. Those two species of clams are found with the hinge and excurrent siphon facing the ocean (west), and the mantle edge and incurrent siphon facing the land (east). In rechecking these observations (WEYMOUTH, 1923), 50 *T. stultorum* were carefully dug at Oceana, California, and in each case they were in the sand as indicated above. Ten individual *T. stultorum* were placed in an aquarium and observed as they dug into the sand. East-west orientation was not observed as they covered themselves. The orientations of well over 200 *S. patula* were observed (FRASER, 1930). In this case one needs only to walk along the ocean side of a sand spit in about one to two inches of water and observe the exposed siphon tips to see the position. In every case each clam of over 200 observed was in an east-west orientation. Twenty-four *S. patula*, with shell lengths of two to four inches, were placed in about six inches of water in a lagoon adjacent to the spit and observed as they dug back in. No directional orientation was noted. Ten clams of similar size were then placed on the ocean side of the same spit so that they were partially covered by wave action. The waves did not move or dislodge the clam and hit the clams when each wave was almost completely spent, resulting in a gentle flushing action over the clam. The

clams buried in from 20 to 60 seconds, the smallest burying the most rapidly. It appeared that those clams most severely affected by wave action would be positioned by the action of the in-coming wave so that the foot was oceanward (west), and the siphon landward (east), when the wave was spent. Then as the wave withdrew the clam made a few quick initial thrusts with the foot in the soft sand and was in a diagonal position, partially buried by the time the next wave struck it. This resulted in the clam's beginning to dig back in with partial east-west orientation. However, by the time the clam was buried it was not completely east-west oriented. Two very small clams with shell size of one-half inch dug back completely within two wave actions, in 15-20 seconds, and although each began to dig while on the side, with hinge north and mantle south, they were east-west oriented by the time they had buried. From these limited observations it is suggested that clams that bury rapidly and that are affected by waves and surf (such as *Siliqua patula*) would be affected thusly: the wave has more force when incoming than retreating; as the hinge side of the clam is narrowed and offers less water resistance than the wider and rougher mantle edge, the clam is turned like a weather vane as the incoming wave hits it. Then the more gentle retreating wave flushing back over it assists the clam in obtaining an upright digging posture because of the resistance against the rough mantle edge and shell edges. It is again hit by the next wave and as it continues to dig would be swung around to the observed east-west position by the time it buries. The same clams when placed in a quiet lagoon burrowed, but no east-west position was noted.

Tivela stultorum and *Siliqua patula* were the only two species of clams in this study living in heavy surf beaches, subjected to intense wave action during each tidal change. It is my opinion that wave action is the reason for their east-west orientation. Fifty *Panope generosa* and 50 *Tresus nuttalli* were observed in Puget Sound, near Olympia, Washington, and no orientation was evident. The clams appeared to be buried completely at random even though they were affected by gentle water action because of incoming and outgoing tides. The method of observation of these two species at the site was merely to walk along, observe the siphon tips and note the direction of each. In this area the species can be distinguished without digging because, when adult (four to six years), *Tresus nuttalli* frequently has barnacles on the cornified part of the siphon tip, while *Panope* was never observed with them. The reason for this was not apparent and I have not found an explanation in the literature.

Well over 500 *Tresus nuttalli* have been observed in Limatur Inlet, adjacent to Drakes Estero, Marin County, and only random positions have been noted. Two hundred

Saxidomus nuttalli were observed in Bolinas Bay. The clams checked did not show any pattern in position, including those closest to the channel. Of 200 burrows checked, in six cases two clams shared the same burrow. The clams of this species are found at about 14 to 18 inches in depth, and, because the burrows are large enough at this site, one can determine orientation by reaching into the burrows.

Judging only from these limited observations it is most probable that wave action coupled with the anatomical differences in the two edges of the clam account for an east-west orientation while the species living in more quiet waters bury in a random pattern.

SUMMARY

Experiments with ten species of clams revealed that they did not voluntarily elevate in their burrows or show directional movement other than rotational and downward.

(1) Clams replanted four to seven inches or more in excess of extended siphon length died, unless they were affected by heavy surf. If clams normally found in the beds are covered by additional sand they will perish unless they can extend the siphon through the new cover to the surface, or form a sand-free cone-shaped depression by which they have access to the surface. If the clams studied have their burrows destroyed, but the clam itself is not moved, a new burrow will be formed, provided the clam is completely covered by water for a period of time following burrow destruction.

(2) Clams living in beds subject to severe surf action can regain normal posture if they are placed in abnormal positions involving something less than a complete reversal with siphons down, a position from which no clam in this study recovered. Clams living in very calm waters cannot regain normal posture, although some do continue to live by bending their siphons to reach the surface.

(3) All clams used in this study were found to be less dense than the medium in which each species lives. If placed in aquaria and agitated along with sand and water all were buoyed upward.

This study suggests that those clams which dig downward, and continue digging downward as environmental conditions may dictate, cannot move upward without the buoyancy produced by differences in relative density and the action of the water.

Tivela stultorum and *Siliqua patula* showed definite orientation, with the hinge seaward and mantle edge

shoreward. The other species studied showed no directional position in the sand. Limited observation suggests that this is due to the active and forceful effect of water in the form of waves and surf on the former two species of clams.

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