

## Predators on *Olivella biplicata*, Including a Species-Specific Predator Avoidance Response

BY

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(Plate 51; 1 Text figure)

IN THE COURSE OF MORE GENERAL STUDIES of *Olivella biplicata* (SOWERBY, 1825) (EDWARDS, 1965, 1968) it has been possible to assemble for the first time a list of its predators with some observations on their feeding. The predators include *Octopus* sp., *Conus californicus* HINDS, 1844, *Polinices reclusianus* (DESHAYES, 1839), *Pisaster brevispinus* (STIMPSON, 1857), *Astropecten armatus* GRAY, 1840, one or more species of crabs, shore birds, and man. *Olivella* was also found to exhibit a specific, vigorous escape response to *Pisaster brevispinus*, but not to *P. ochraceus* (BRANDT, 1835) or *Astropecten armatus*. The new information on predators extends food lists and will aid community energetics studies; it should also facilitate further studies of the ecology of *O. biplicata* and could form the basis of a thorough investigation of the effect of predation on this long-lived (see below), abundant, intertidal gastropod. The demonstration of a species-specific avoidance response to a predator adds to the growing literature on this ecologically important form of chemical communication.

Field work was done from Newport, Oregon, to Ensenada, Baja California. Most observations were made at low tide when the animals were exposed or shallowly immersed; snorkeling was also used at most sites. Laboratory studies were done at the Oregon Institute of Marine Biology, Charleston, Oregon, and at Scripps Institution of Oceanography, La Jolla, California.

### PREDATORS

The most diverse and possibly the chief predators on adult *Olivella biplicata* are other mollusks. Numerous laboratory and field observations by R. T. Paine (personal communication), N. Fotheringham (personal communication), and myself show *O. biplicata* of all sizes (8.5 to 26.1 mm)

are eaten by small *Octopus bimaculoides* PICKFORD & McCONNAUGHEY, 1949, or *O. bimaculatus* VERRILL, 1883, or both, in southern California. (*Olivella* size data hereinafter are shell lengths from siphonal canal to apex.) The octopuses emerge from beneath rocks on sand flats, seize *Olivella*, drill a very small hole (ca. 0.5 mm maximum external diameter) near the shell apex (edge of body whorl or on whorl above; Plate 51, Figure 1), and apparently inject a paralyzing venom (see PILSON & TAYLOR, 1961). The effect of *Octopus* predation on natural *Olivella* populations, however, appears small: very few empty *Olivella* shells bear *Octopus* bore holes (see below), and the proportion remains small even when shells are collected near a regularly occupied *Octopus* burrow.

Several gastropods eat *Olivella*. In the San Diego, California, area *Conus californicus* eats *O. biplicata* both in aquaria and in the field (SAUNDERS & WOLFSON, 1961); and, of 56 known observations of prey taken by this predator in nature, more (10) were of *O. biplicata* than any other species (KOHN, 1966). *Conus* swallows its prey whole and may prefer small *Olivella*: two large *C. californicus* (> 25 mm) kept in an aquarium provided with running sea water, a sand substrate, and 20 medium to large *O. biplicata* (20 - 28 mm) for three weeks ate no *Olivella*.

Another carnivorous prosobranch, *Polinices reclusianus*, widely co-occurs with *Olivella biplicata* in California and Baja California, and a small percentage of empty *O. biplicata* shells from the field regularly bears the characteristic countersunk bore hole of this predator (Plate 51, Figure 2). *Polinices*, which is rarely abundant, feeds primarily on bivalves; it also accepts gastropods as alternative food, but probably takes few olives in nature (see below). The maximum rate of predation on *O. biplicata*, were no other prey available, was determined, using three *Polinices* of similar size (means and standard errors:  $33.43 \pm 1.05$  mm shell height  $\times$   $29.50 \pm 1.15$  mm shell width;  $1531 \pm 234$  mgm shell-free dry weight). The predators were first acclimated to eating *Olivella* in cap-

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tivity and then placed in an aquarium provided with running sea water, a sand substrate, and ca. 20 prey ranging in size from 18.3 to 28.4 mm. The three *Polinices* (4593 mgm total shell-free dry weight) ate 13 *O. biplicata* (4198 mgm total shell-free dry weight) in 15 days (3 - 18 November 1965); thus, the *Polinices* consumed 6% of their own dry weight per day. This feeding rate, while exceeding the 1.2 to 4.6% rate of some species of *Conus* in the tropics (KOHN, 1959, and in press), falls far short of the 15 - 25% of body weight per day rates given for other predatory gastropods, including *Polinices duplicatus* (SAY, 1822) and other *Conus* (THORSON, 1958; KOHN, in press). Possibly the non-preferred prey status of *Olivella* and the season of observations - many predaceous gastropods feed little, if at all, in winter - or both affected the feeding rate of *P. reclusianus*.

The feeding behavior of *Polinices reclusianus* is like that described for other naticids (GONOR, 1965; FRETTER & GRAHAM, 1962). Prey are seized with the propodium, drawn under the predator, and wrapped up in the concave ventral surface of the mesopodium. Under attack, *Olivella* moves with strong forward lurches and often forces its way under or around the enclosing mesopodium; escapes then continue their lurching progression for 8 - 10 cm. *Polinices reclusianus* may carry captured prey around in the mesopodium before burrowing into the sand and drilling them. Through apparently stereotyped behavior in the handling of prey, *P. reclusianus* always bores *O. biplicata* on the body whorl near the posterior end of the aperture (Plate 51, Figure 2). Boring the shell seems an extremely inefficient way to attack *Olivella*, whose operculum is a thin corneous scale. In fact, of 21 *O. biplicata* eaten in aquarium trials, only 4 were completely bored, 14 were incompletely bored, and 3 were unbored. Incompletely bored, empty *Olivella* shells are also taken in the field. Although *Polinices* may occasionally force its prey's operculum, the incomplete bore holes suggest another explanation, viz., that *O. biplicata* suffocates while wrapped in the predator's foot and relaxes. Since *Olivella* suffers no harm from being deeply withdrawn into its shell for 10 hours or more in response to osmotic stress (EDWARDS, 1965), this answer requires the snails be deprived of oxygen for lengthy periods. Moribund, but unbored, *O. biplicata* can be recovered from *P. reclusianus*. Since partially drilled, live snails also occur, escape is still possible after drilling begins. Probably the length of time the prey is enveloped in the predator's foot determines the mode of death.

Although *Olivella biplicata* often frees itself from *Polinices*' grasp, both the largest (28.4 mm) and smallest (17.0 mm) individuals available in feeding trials were eaten by the medium-sized *P. reclusianus*: neither was there any statistically significant difference between the

sizes of *Olivella* taken and those surviving, though sample sizes were inadequate (13 vs. 9 respectively). Other field and laboratory observations by N. Fotheringham (personal communication) and myself show olives of all sizes (10.4 - 28.4 mm) fall prey to *P. reclusianus*. Occasionally *O. biplicata* exhibits strong escape responses upon coming in contact with *Polinices* (see below).

Other gastropods may prey on *Olivella*. Larger olivids, though absent from the area under study, feed on *Olivella* species in Latin America (OLSSON, 1956). In the laboratory small *O. biplicata* are drilled (Plate 51, Figure 3) and eaten by *Acanthina spirata* (BLAINVILLE, 1832) (FOTHERINGHAM, 1966). These two species do not normally occur together in the field, *A. spirata* preferring rocky shores; but at more exposed sites *Olivella* are most abundant on sand near rocks and pilings where predators from solid substrates could attack them. *Jaton festivus* (HINDS, 1844), *Nassarius fossatus* (GOULD, 1849), and the opisthobranch *Navanax inermis* (COOPER, 1862) co-occur with *O. biplicata* and may eat it. No *Jaton* bore holes have been found in *Olivella* shells, however, and *Nassarius* is mainly a scavenger. *Navanax* proved unresponsive to *Olivella* in the field (Edwards) and in the laboratory (PAINE, 1963), and *O. biplicata* is not found in *Navanax* fecal pellets (PAINE, *op. cit.*).

FOTHERINGHAM (1966) has noted a distinctive bore hole on the columella of *Olivella* (Plate 51, Figure 4) and other gastropod shells. These shells were occupied by hermit crabs and were collected from rocky intertidal sites in the San Diego area. I have not found this marking on the shells of living *Olivella* or on hermit crab shells collected from subtidal sand bottom. The bore hole resembles those of gastropods, but may be made by a barnacle (TOMLINSON, 1953) or a flatworm (WOELKE, 1961). The much higher incidence of the bore holes in worn, encrusted "old" shells than in clean, "new" shells, though, suggests a non-predatory agent (Fotheringham, personal communication).

Asteroids commonly prey upon gastropods, and at least two eat *Olivella biplicata*. *Pisaster brevispinus* was occasionally observed taking these snails on the northern California and Oregon coasts. At Duxbury Reef (37°54' N Latitude), the only site where the two species co-occurred abundantly at low tide, ca. 40 seastars were examined; only one was feeding, taking an *Olivella* (22.7 mm) whose shell lip was damaged, possibly by a crab. These two species also live together near extreme low tide at Monterey Harbor and subtidally off North Spit at Coos Bay. *Olivella biplicata* shows a species-specific avoidance response to this seastar (see below).

The second asteroid predator on *Olivella biplicata*, *Astropecten armatus*, is more specialized for sand bottom life. The two species are commonly taken together in

southern California and Baja California, usually subtidally (Scripps Pier) but occasionally intertidally (Estero de Punta Banda, below Ensenada, Baja California). The feeding sequence was observed in an aquarium provided with fresh sand and running seawater. The seastar, apparently using distance chemoreception, quickly "runs" to and over an *O. biplicata* placed nearby and begins forcing its arms into the sand around the prey. While burying its arms, the seastar may shift laterally in the direction the snail was moving, or it may appear to carry or push the prey for a distance. *Astropecten* does not extrude its stomach but swallows prey whole. Even the largest *O. biplicata* do not gain safety through their size or strength: a 29.0 mm snail was readily taken and completely ingested in just over 2 minutes. During ingestion the predator's central disc may swell aborally and prey *Olivella* shells can be felt inside. Intraoral digestion may be an adjustment to life in sand or to the loss of suckers on the podia, or both; in any case, external examinations in the field will fail to reveal the foods of *Astropecten*. Although the shell of the 29.0 mm *Olivella* was still inside the seastar 23 hours after ingestion, in several aquarium trials an initially unfed *Astropecten* regularly ate > 1 adult snail per day over 4 - 5 days; and MACGINITIE & MACGINITIE (1949) report 3 or 4 snails (species unspecified) may be found at one time in an *Astropecten*. Clearly *Astropecten armatus*, to which *O. biplicata* shows no definite escape response (see below), could be an important predator upon *O. biplicata*.

Various crabs eat snails, either by cracking them open or by pulling them from their shells (see SHOUP, 1968, for references). Small *Cancer magister* DANA, 1852, which co-occurred with *Olivella biplicata* on several beaches in Oregon, ate live, though possibly moribund, *O. biplicata* in the laboratory. The crab held the snail with the legs of one side of its body, while reaching deeply into the shell aperture with the opposite cheliped. Considerable indirect field evidence - shells broken into many pieces (sometimes with all the fragments lying within a few square centimeters), empty shells with the body whorl alone broken away (Plate 51, Figure 5), occupied and empty shells with the lip broken back, and rare moribund snails with both the shell lip broken away and the foot torn raggedly - indicates crab predation on *O. biplicata*. Suspects include adult *Portunus xantusii* (STIMPSON, 1862), *Cancer antennarius* STIMPSON, 1856, and *Cancer magister*, all of which have been taken with *O. biplicata*. EBLING *et al.* (1964) found *Carcinus maenas* LINNAEUS, 1758, *Portunus puber* (LINNAEUS, 1767) and *Cancer pagurus* LINNAEUS, 1758, when kept in cages in the field with *Nucella lapillus* (LINNAEUS, 1758) (similar size range as *Olivella*), smashed and ate the snails as well as

removed others from their shells. Further, *Portunus puber* observed in the laboratory, used its master chelae to break away the body whorl of *Nucella*, producing shell damage like that observed in *Olivella* shells (Plate 51, Figure 5). Similarly, КОHN (1959) found xanthid crabs attacked *Conus* in the laboratory, breaking the outer lip of the snail's shells. These crabs never killed snails, though, probably because the latter could retreat into older, thicker portions of the shell. Clearly, then, crabs can and do produce the type of shell damage observed in *Olivella* shells.

Among vertebrates, gulls and other shore birds regularly forage in the sand at low tide, taking snails and other forms. *Olivella* is eaten by shore birds in northern Peru (КОЕРСКЕ & КОЕРСКЕ, 1952), and Stohler (personal communication) and I have observed gulls taking *O. biplicata* in California and Oregon, respectively. The gulls, probing irregularities in the sand, sometimes throw the snails out on the surface, and then overlook their find. All along the Pacific coast small *Olivella* shells can occasionally be found in the droppings of shore birds\*. With the rising tide, on the other hand, fish, which are major predators on snails in some areas, move in large numbers over *Olivella*-rich sand flats and may well prey upon the snails, but this has not been observed. Purple dye substances irritating to fish are known for some olive shells (ABBOTT, 1954).

Probably the most important depredator on *Olivella biplicata* in accessible localities is man. Humans do not eat olive snails on our Pacific Coast, though they do in Brazil, where one species is locally called "vitela" (veal) or "vaquinho" (little cow) (MARCUS & MARCUS, 1959), and in Peru (OLSSON, 1956). *Olivella biplicata* shells were extensively traded by the American Indians, who used them as jewelry and money (STEARNS, 1889; HENDERSON, 1930; BAILY, 1935; GIFFORD & GIFFORD, 1942; and ABBOTT, 1954). Today the animals are collected in great numbers simply for the beauty of their shells. Shell dealers take them for sale at tourist stands across the country; some shells are made into earrings. A few West Coast residents also use *Olivella* to "decorate" furniture and to construct "artistic" shell mosaics. The protective shell has caused heavy losses for *O. biplicata*.

Thus, at low tide, *Olivella biplicata* are attacked by shore birds, especially gulls, and man; and, as the tide rises, they are preyed upon by seastars, octopuses, at least two species of gastropods, and probably by crabs and fish as well.

\* REEDER (1951) also found *Olivella* in the stomach of a Marbled Godwit, *Limosa fedoa*, in southern California.

### SPECIES-SPECIFIC PREDATOR AVOIDANCE RESPONSE

Various marine gastropods show specific escape reactions to predatory seastars and gastropods. The literature has been reviewed regularly (BULLOCK, 1953; PASSANO, 1957; KOHN, 1961; FEDER, 1963, 1967; MARGOLIN, 1964a; FEDER & CHRISTENSEN, 1966). Further work is available on herbivorous gastropods responding at a distance to carnivorous ones (see KOHN & WATERS, 1966, and references therein). The escape responses generally consist of rapid movement ("running," "galloping") away from the predator, sometimes with the shell being violently swung about, and occasionally accomplished by means of curious "leaping"; some naticids, *Haliotis rufescens* SWAINSON, 1822, and *Diodora aspera* (ESCHSCHOLTZ, 1833) extend a fold of the foot or mantle over their shells, preventing seastar tube foot adhesion (MARGOLIN, 1964a; MONTGOMERY, 1967). The stimulus is chemical and apparently emanates from the external epithelium of the predator, especially from the epidermis of tube feet (FEDER & LASKER, 1964). Contact with a single tube foot elicits vigorous escape reactions. Effective stimulation also occurs through distance chemoreception of whole animals and extracts.

Tests of escape responses in *Olivella biplicata* consisted of touching the snail's foot (propodium and parapodia) with isolated and intact tube feet from the seastars *Pisaster ochraceus*, *P. brevispinus*, and *Astropecten armatus*, as well as observing outcomes of contacts between whole animals. Controls consisted of similarly touching snails with a blunt probe or a glass rod. *Olivella biplicata* exhibited a vigorous avoidance response to contacts with *P. brevispinus* tube feet, but no greater reaction to *P. ochraceus* and *A. armatus* than to control treatments. The snails failed to give strong responses to contacts with the aboral surfaces of any of the three seastar species.

The minimum escape reaction of *Olivella biplicata* consists of a sharp turning away from the point of contact with *Pisaster brevispinus* or one of its tube feet, followed by top-speed crawling. More often upon contact *O. biplicata* rears up on the hind portion of its foot, withdrawing the propodium and throwing the parapodia forward; this response frequently flips the snails over backwards in a reverse half-somersault. In the extreme form of the response the animal, after throwing itself on its back, pumps the expanded metapodium up-and-down violently, lifting the snail from the substrate and carrying it away some 5 - 10 cm in a form of upside-down swimming. This metapodial swimming response is qualitatively distinct from any previously reported gastropod escape behavior. It is effected by holding the parapodia close to the sides

of the shell, especially at the anterior end, so the vigorous down beats of the large, horizontally extended metapodium force water down and back, lifting the gastropod and propelling it forward. After each of the more energetic responses the snails quickly right themselves and rapidly crawl a short way (ca. 8 - 12 cm) before resuming a normal pace. Escape movements, while carrying the animals away from the point of first contact with a whole seastar, may carry them up against another ray of the predator; in this case the avoidance reaction is repeated.

Initially *Olivella biplicata* gave no noticeable response to *Polinices reclusianus* in feeding trials, even crawling over the predator's propodia without reaction. Later in the trials, however, *Olivella* occasionally gave violent avoidance responses to contacts with *Polinices*, including the "swimming" response. Whether experience with the predator accounts for the appearance of the sporadic escape behavior is not known. *Olivella* also forces its way from the grasp of *Polinices* as described above.

*Pisaster ochraceus* is abundant on rocks and pilings projecting from beaches, but only occasionally ventures onto the sand; whereas, *P. brevispinus*, the species *Olivella biplicata* avoids, is a natural neighbor of and predator on *Olivella* (see above). Thus, the escape reaction is only elicited by the species of *Pisaster* that *O. biplicata* is likely to meet in the field, and the response appears to have direct survival value in carrying the snail away from a known predator. *Astropecten armatus*, on the other hand, lives with and eats *O. biplicata*, but elicits no definite avoidance response from it. Qualitative observations indicate *Astropecten* moves so quickly over sand that escape efforts by *O. biplicata*, including the "swimming" response with its slow start, would be futile and could not be selected for. Several *Astropecten* species can crawl 10 mm/sec (FEDER & CHRISTENSEN, 1966), which exceeds all but the fastest escape responses of gastropods (KOHN & WATERS, 1966).

Animals exhibiting avoidance responses show varying abilities to discriminate between possible predators. Two highly specific responses are pertinent to the case of *Olivella*. Appropriately for its rocky intertidal habitat and vulnerabilities, *Acmaea pelta* ESCHSCHOLTZ, 1833, shows a "running" escape response to *Pisaster ochraceus*, but not to *P. brevispinus* (MARGOLIN, 1964b) - the opposite reactions from those of *O. biplicata*. In contrast, *Dendroaster excentricus* ESCHSCHOLTZ, 1831, responds like *Olivella*, avoiding the predatory *P. brevispinus* by burrowing into the sand, while ignoring *Astropecten armatus* (MACGINITIE & MACGINITIE, 1949), even though the latter commonly feeds on sand dollars (E. W. Fager, personal communication). These differing responses could be used as bioassays in isolating the specific chemicals eliciting

avoidance reactions. Whether animals of the various taxa respond to the same or different chemicals is a question of particular interest; representatives of different phyla do respond to certain seastar extracts (FEDER & ARVIDSSON, 1967), and the substances in extracts of different seastars show chemical similarities (MACKIE *et al.*, 1968).

GONOR (1966), from a consideration of the escape responses of various prosobranchs, suggests these behavior patterns were not evolved *de novo*, but developed from pre-existing locomotory and righting mechanisms. In the case of *Olivella biplicata* the minimum avoidance response of rapid crawling does, but the more vigorous responses do not, appear to agree with this view. The "rearing" and "swimming" escape behavior has, however, other uses than predator avoidance: it is seen when, under conditions of crowding, one olive is bitten by another, or when a snail is placed in an alien environment, e. g., a plastic bag. The truly striking thing about *Olivella* is the dexterity and versatility with which it uses its foot — in locomotion, burrowing, handling of live prey, and in reproductive behavior. Perhaps a more intriguing, and resolvable, aspect of the development of avoidance responses concerns not the movements themselves but the acquisition of, and sensory mechanisms used in, the discrimination of substances from predators.

Various investigators have seen gastropod avoidance behavior succeed in permitting at least some individuals to escape predators (see FEDER, 1967; MARGOLIN, 1964a). FEDER (1963) found that snails exhibiting escape responses to *Pisaster ochraceus* were not fed upon in proportion to their abundance and availability, whereas mussels and barnacles were; the non-responding *Acmaea scabra* (GOULD, 1846), on the other hand, ranks high on the seastar's food list even though few live within the latter's range. The apparent rarity of captures of *Olivella biplicata* by *Pisaster brevispinus*, despite the abundance of both, was noted earlier. Defensive escape reactions, even if effective in only a limited percentage of predator contacts, would be of selective advantage to gastropods. Indeed, that these behavior patterns have evolved demonstrates both their adaptive value and, in turn, the effectiveness of asteroids as predators.

## POPULATIONAL EFFECTS OF PREDATION

The significance of predation for *Olivella biplicata* populations can only be speculatively evaluated since available information is fragmentary. Probably larvae and newly metamorphosed young, vulnerable to a wider and different array of predators than adults and to fluctuations in physical factors as well, suffer heavy losses, though the evidence is circumstantial. Size frequency distributions obtained through quantitative sampling of natural populations at Coos Bay, Oregon, Yaquina Bay, Oregon, and Duxbury Reef, California (EDWARDS, unpubl.) show that, while new young are occasionally abundant, proportionally few reach reproductive size (over 16 mm). *Olivella* populations are often primarily composed of larger, slow-growing animals, which may live 10 years or more (P. W. Frank and D. C. Edwards, unpubl.; STOHLER, 1962, and personal communication). Yet, despite a potentially lengthy reproductive life during which increasing numbers of progeny are likely produced each year, even a medium-sized *Olivella* female (20.6 mm) produced 4 236 eggs in a single spawning period (EDWARDS, 1968). Also the species reproduces year-round (EDWARDS, *op. cit.*). Thus many young are spawned for even the low, though continuous, population turnover indicated. Numerous suspension feeders and small predators could, of course, take heavy tolls on the bottom-swimming larvae (EDWARDS, *op. cit.*) and newly settled young. In some species the escape responses of smaller animals to seastars are less successful than those of larger individuals (FEDER, 1967). Gulls and *Conus* also take small, immature *Olivella* (see above).

Although a variety of predators has been shown to attack adult *Olivella biplicata*, several factors mitigate their populational effects. First, the snails may evade predators. A species-specific avoidance response to *Pisaster brevispinus* was detailed above, and escape reactions to *Polinices reclusianus* were noted. In addition, larger *Olivella*, which live higher on the shore, tend to remain buried during bright light conditions (EDWARDS, 1965); and this behavior may aid in the avoidance of visual pred-

### Explanation of Plate 51

Figure 1: *Olivella biplicata* shell (11 mm) bored by *Octopus* sp. (photograph by Ron Lam)

Figure 2: *Olivella biplicata* shell (22 mm) bored by *Polinices reclusianus* (photograph by Ron Lam)

Figure 5: *Olivella biplicata* shells (ca. 25 mm) with the body whorl broken back, possibly by crabs (photograph by John W. Evans)

Figure 3: *Olivella biplicata* shell (8 mm) bored by *Acanthina spirata* (photograph by Ron Lam)

Figure 4: *Olivella biplicata* shell (15 mm) with bore hole of unknown origin (photograph by Ron Lam)

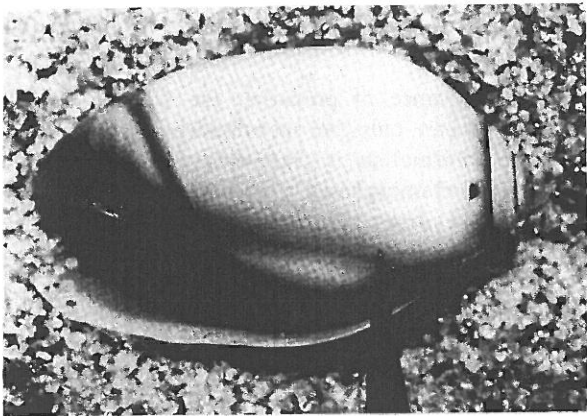


Figure 1

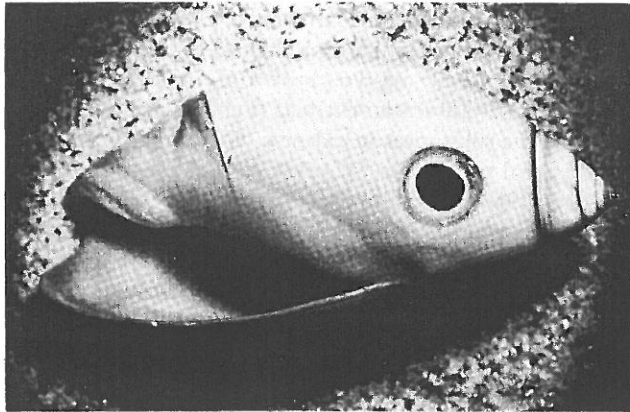


Figure 2

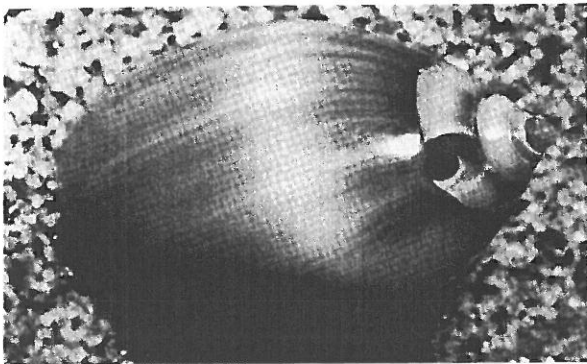


Figure 3

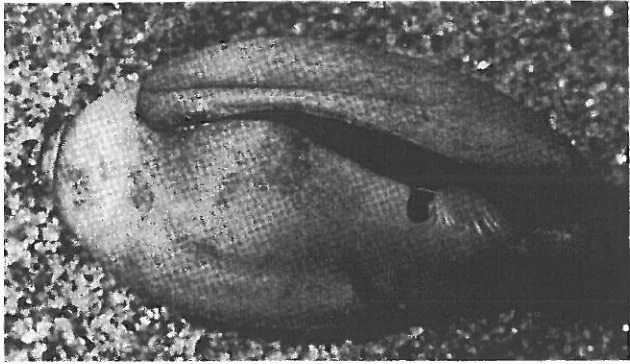


Figure 4



Figure 5

ators. Second, not all the predators attack *O. biplicata* in any given locality, e. g., *Conus californicus* and *Astropecten armatus* occur only in southern California, whereas *Cancer magister* and *Pisaster brevispinus* are more northerly species. Further, in the temperate latitudes under consideration predator food choices may vary seasonally and feeding may cease altogether in winter. But likely the main factor reducing predation on adults is their size: they have simply grown too large to be taken by small carnivores, e. g., various worms. Indeed the larger snails themselves prey on polychaetes (Edwards, unpubl.). Nonetheless, *Polinices*, *Astropecten*, and *Octopus* eat even the largest *Olivella*.

Since empty *Olivella* shells of different sizes probably do not disintegrate at very different rates, an unbiased collection of such shells would provide information on both size specific mortality rates and predation rates for predators that leave distinctive marks. Empty shells are always rare on *Olivella* beaches, so hermit crabs, *Holopagurus pilosus* HOLMES, 1900, were employed as collectors. (A difficulty here is that bored shells, which should afford less protection, may be selected against by the crabs.) E. W. Fager kindly provided me with an arbitrary sample of 130 *O. biplicata* shells from a large hermit crab aggregation in 18 feet of water at Scripps Pier. The size-frequency distribution of the shells (Text figure 1) shows a sharp decline in the abundance of larger ones: only 12 shells (9%) were of adult size (>16 mm). Although the size structure of the La Jolla population is not known, the shell data suggest relatively high mortality among immature snails, but very low mortality among adults. Only 10 (7.7%) of the 130 *Olivella* shells gave

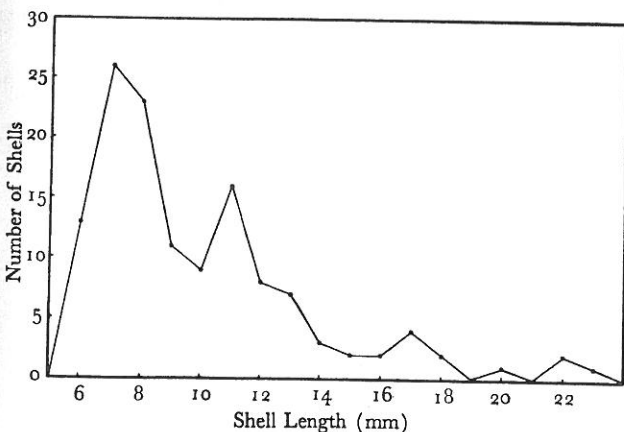


Figure 1

Size-frequency distribution of 130 *Olivella biplicata* shells from a *Holopagurus pilosus* aggregation at Scripps Pier

evidences of particular predators: 4 had *Polinices* bore holes, 4 had broken shell lips indicative of crab attacks, and 2 bore possible *Octopus* drill holes. Possibly *Polinices* and *Octopus* prefer larger prey, as half their marks fell among the few adult shells.

With the possible exception of man's destruction of snails in some localities, predation on adults is apparently not important in the regulation of *Olivella biplicata* populations, though losses among the more vulnerable young may well be crucial. In nearly 3 years of observations that included diving, only a few scattered cases of predation were observed. Neither is food availability likely limiting in this gregarious, omnivorous species (Edwards, unpubl.), at least not until great densities (> 130 per m<sup>2</sup> on bay beaches, over 700 per m<sup>2</sup> in lagoons) are attained, and here again the stress falls primarily on the very young (EDWARDS, 1965). *Olivella biplicata* populations are often heavily infected with parasitic trematodes (STEINMETZ, 1951; DUERR, 1965; EDWARDS, 1968; Ivan Pratt, personal communication), and well over 50% of adults may be unsexed by the infections (EDWARDS, 1968). Parasitic disease definitely reduces natality and could limit population sizes. Sporadic "disasters" may also kill many *Olivella*. Exceptional fresh water flooding and silting took heavy tolls in the San Diego Flood Control Channel in November, 1965; and similar threats arise periodically on the northern coast. Storms and winter sea turbulence – also tidal waves like that from the 1964 Alaska earthquake – produce shifts of beach sand, posing dangers of deep burial and transport out of suitable habitat. Whole beaches may be carried away in winter, and one storm (October, 1963) deposited 1-2 m of new sand on a Coos Bay, Oregon, beach, markedly reducing *O. biplicata* densities (EDWARDS, 1965). These erratic upsets eliminate snails, but probably occur too rarely and unpredictably to regulate densities or to account for the regular size-frequency structure of most *Olivella* populations. The size ( $\approx$  age) structure in *Olivella* populations, characterized by a preponderance of adults, probably results from high mortality among juveniles (and possibly reduced adult fecundities in parasitized populations) and excellent survivorship and individual longevity among adults; turnover of the breeding population is likely limited.

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