On the structure of a population of *Oliva oliva* (L., 1758) in Papua New Guinea (Studies on Olividae. 22)

Bernard TURSCH (°), Jean-Marc OUIN (°°) and Jean BOUILLON (°°)

(°) Laboratoire de Bio-Ecologie, (°°) Laboratoire de Zoologie, Fac. Sciences, Université Libre de Bruxelles, 50 av. F.D. Roosevelt, B-1050 Brussels, Belgium.

KEYWORDS: Mollusca, Gastropoda, Olividae, *Oliva oliva*, size, colour.

SUMMARY. Monthly samplings of the population of *O. oliva* on the black sand beach of Sisimangum (Hansa Bay, Papua New Guinea) were effected during 8 months. The very sharp size frequency distribution did not vary appreciably and suggests a high mortality at about half of the maximum size. No significant change was observed in the distribution of shell colour classes. Predation pressure is high: counts of the presence of scars on the shell show that most of the specimens have survived an unsuccesful attack. The distribution of scars suggests that the responsible predator(s) form a "search image" adjusted to the most abundant class of prey (16-20 mm black shells). Such apostatic selection could stabilise the balanced colour polymorphism observed in the population. Abrupt changes in shell colour were experimentally induced by maintaining black specimens on white sand. These induced colour shifts allow an estimation of the growth rate, which averages 4.0 mm/year (for shells in the 13-22 mm range).

RESUME. Des prélèvements mensuels de la population d' *O. oliva* vivant sur la plage de sable noir de Sisimangum (Hansa Bay, Papouasie Nouvelle-Guinée) ont été effectués pendant huit mois. La distribution très pointue des fréquences de taille n'a pas varié appréciablement et suggère une mortalité élevée à environ la moitié de la taille maximale. Aucun changement significatif n'a été observé dans la distribution de la couleur des coquilles. La pression de prédation est forte: le comptage de la présence de cicatrices sur les coquilles montre que la plupart des spécimens a survécu à une attaque infructueuse. La distribution des cicatrices suggère que le(s) prédateur(s) responsable(s) forme(nt) une "image de chasse" centrée sur la classe de proies la plus abondante (coquilles noires de 16-20 mm). Une telle selection apostatique pourrait stabiliser le polymorphisme de couleurs observe dans la population. Des changements abrupts de la coloration de la coquille ont été induits expérimentalement en maintenant des spécimens noirs sur du sable blanc. Ces changements de couleur induits permettent d'estimer la vitesse de croissance à une moyenne de 4.0 mm/an (pour des coquilles de 13 à 22 mm).

1. INTRODUCTION

No data whatsoever are available on the basic biological parameters (growth, reproduction, longevity, etc ...) of any *Oliva* species, in spite of the abundance of these animals in the tropical Indo-Pacific region. This paper presents the results of a survey of a population of the type species of the genus, *Oliva oliva* (Linnaeus, 1758), in Hansa Bay (Papua New Guinea). It reports some unexpected observations, but yet raises more questions than it gives answers.

In Hansa Bay, *O. oliva* is restricted to the low water level on soft, sandy beaches directly exposed to frequent surf. In twenty years of survey it has never been found in any other biotope (with the exception of a few juveniles collected around a World War II wreck, 6 m).

This narrow niche might explain why *O. oliva* appears to be (at least in our hands) much more difficult to keep in aquaria for prolonged periods of time than many other *Oliva* species.

Oliva oliva is polytopic and cryptic (see VAN OSSELAER et al., 1994). The matching of shell colour to background colour strongly suggests cryptic adaptation to counter diurnal predation by hunters endowed with good vision. During previous experiments in aquaria, a mixed group of black and white olives were given a choice between black and white sand. Only 52.9 % of the black *Oliva* preferred black sand (non significant) while 63.5 % of the white *Oliva* actually preferred black sand

----

(significant at 0.05). The observed matching of shell colour with sediment colour is therefore not likely to be the result of a choice by the *Oliva* but most probably results from selective predation (VAN OSSELAER, BOUILLON & TURSCH, 1993). In another series of aquarium experiments, reported in the same paper, *O. oliva* was shown to be much more mobile during the night than during the day, like its rather distant relative *Olivella biplicata* (see PHILLIPS, 1977). Only 14-27% of the small *O. oliva* and none of the large specimens do move during daytime. Mobility is not affected by the colour of the substrate and is not correlated to the colour of the shell. Olives are carnivorous, eating small bivalves, small gastropods, dead flesh, etc. that they could obtain equally well by daytime. This suggests that their nocturnal activity could also be a counter-adaptation to diurnal predation (VAN OSSELAER, BOUILLON & TURSCH, 1993).

Two colonies of *O. oliva* are present in Hansa Bay (specimens of both are illustrated in TURSCH, 1994). One small population lives on white, coarse coral sand at Boro Beach, where heavy swell is generally prevalent. Specimens from Boro reach a moderate size (H_{max} 33.15 mm). All 42 specimens collected are "white" (see § 2.2) and have an elongated spire. The aperture is short and consistently reddish brown.

Another population (this one very large) extends all the way from the northern tip of the bay to the mouth of the Sakula River, on fine, dark volcanic sand, with occasional, moderate swell. Specimens from Sisimangum reach a larger size (H_{max} 42.31 mm). On nearly one thousand specimens collected, 72.1 % are "black", 17.3 % are "white" and 10.6 % do not fit into these categories (see § 3.1.4). The spire is short, the aperture long and mostly dark purple. Most shells of this population very closely match the two syntypes of *O. longispira* Bridgman, 1906 (British Museum, Natural History : 1906.7.4.9-10).

These two very distinct populations actually come within 1.5 km of each other, separated by a rocky point and the mouth of the small Sakula River. Their characters have been stable for more than 20 years (see TURSCH, 1994) and we have never observed any intergrading specimen. Such isolation would in theory simplify studies on populations dynamics, since one could presumably neglect the influence of immigration and emigration.

At Sisimangum Beach, *O. oliva* is by very far the dominant species of *Oliva*. A total sample of about one thousand specimens collected over eight months contained less than 10 specimens of other species. At the turn of the low tide, it crawls in great numbers on the lower stretches of the beach, offering a good opportunity for the comparing sizeable monthly collections without depleting the population.

2. MATERIAL and METHODS
2.1. Collection.

Monthly collections of *O. oliva* were made from February to September 1992 on the beach at Sisimangum, at the turn of a strong low tide. This period encompasses both the rainy and the dry season. The dates of collections are: February 2, March 9, April 10, May 12, June 6, July 10 and September 11.

All specimens seen were collected until the desired number of animals (approx. 100) was obtained, and preserved in 40% alcohol. It is important to stress that, for nearly all captures, the collector sees only a track in the sand, at the extremity of which the animal lies buried under a little protuberance of sand. In these conditions, neither the colour nor the size of the animal can be known *a priori*. The samples are presumably without bias, excepted for very small shells (< 10 mm?) that will tend to be overlooked.

2.2. Observations on preserved specimens.

Shell length (H) was measured to 0.01 mm with a digital display calliper, from the apex to the distal part of the aperture (see TURSCH & GERMAIN, 1985). The expression "adult shells" refers to large shells with a thickened lip.

The shells were sorted into three rough, arbitrary colour classes ("black", "white" and "others"). The spire of *O. oliva* shows that there is often a progressive darkening of the background colour in the very early whorls. This could cause some confusion between "white" and "others" for very small specimens (< 10 mm).

Each specimen was examined under magnification to detect the presence of scars on the shell. Errors on the frequency of scars would necessarily be underestimations. As the animals live on a large stretch of smooth sand, collisions with hard objects are most improbable, so all scars are deemed to result from attacks by predators.

2.3. Observations on live specimens.

All experiments were carried out at King Leopold III Biological Station, at Laing Island, Hansa Bay. White painted (epoxy) marine plywood aquaria, equipped with an open circulation of natural sea-water flowing slowly from a storage tank, were placed under an open corrugated iron shelter shaded with curtains of fishing net. Specimens were fed once a week with meat morsels. Two different sediments (one black, terrigeneous fine sand of volcanic origin collected at Sisimangum Beach, and one white, coarse coral sand collected on the East coast of Laing Island) were used for substrate effect experiments. Analysis of both substrates has been given in VAN OSSELAER *et al.* (1994).

3. RESULTS and INTERPRETATION
3.1. Analysis of monthly samples.

3.1.1. Size frequency distribution. This study started by the casual observation that a sample of 109 *O. oliva* collected at Sisimangum Beach on February, 2, 1992 had a very sharp, quite unexpected distribution of sizes, given in Fig. 1. This contrasted with the much flatter distributions generally observed for other molluscs (see for instance JONES, FERRELL & SALE, 1990). It was also at sharp variance with the observation that "*Olivella* populations are often primarily composed of large, slow-growing animals" (EDWARDS, 1969, referring to several size frequency distributions, from different localities). This is also the impression given by other common shoreline *Oliva* populations in Hansa Bay (*O. elegans*, *O. caerulea*, etc.) in which "adults" are much more numerous than young shells (unpublished results).
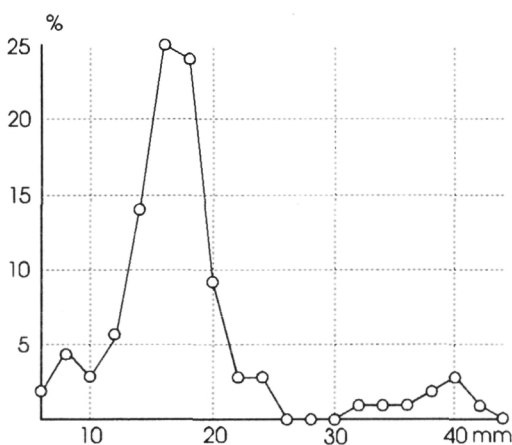

Fig. 1. Distribution of sizes, in percentage of total. Sample: February 1992 (N=109).

"Adult" *O. oliva* shells reach a length of over 40 mm in this locality. The sharp peak at 16-18 mm, well separated from a small peak of "adult" shells, was first interpreted as corresponding to an age cohort (siblings from a same clutch of eggs or class resulting from synchronous reproduction). If this was the case, we would have a tool to estimate the growth rate of *Oliva oliva* in natural conditions. All we had to do was to repeat collecting samples at regular intervals of time, measure the expected shift of the distribution peak towards larger sizes and calculate the rate of growth (for examples of this technique, see LOREAU & BALUKU, 1987 and BALUKU & LOREAU, 1989). Monthly collections were therefore effected from February to September 1992.

3.1.2. Contrary to such expectations, a very similar distribution of sizes was observed month after month (see Fig. 2). The distribution of sizes for all the shells caught during the eight months period is depicted in Fig. 3. It is strikingly similar to that of Fig. 2 (although "adult" shells appear to be even rarer than presumed earlier).
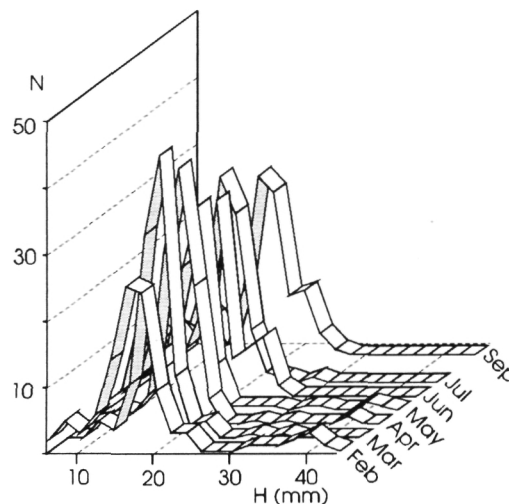

Fig. 2. Distribution of sizes. Total of all samples: February to September 1992. (N=991).

From Fig. 3 we can see that young individuals between 14 and 22 mm constitute over 75% of the population, and those between 16 and 20 mm amount to 55%. The chances for a specimen of *O. oliva* to reach "adult size" are very dim: only about 1% of the population reaches 38-42 mm. The small irregularity at the left of the peak (towards small sizes) will not be interpreted, as it could result from non-random collection of very small specimens

(their traces in the sand are not easy to detect).
There should be no such problem for shells of
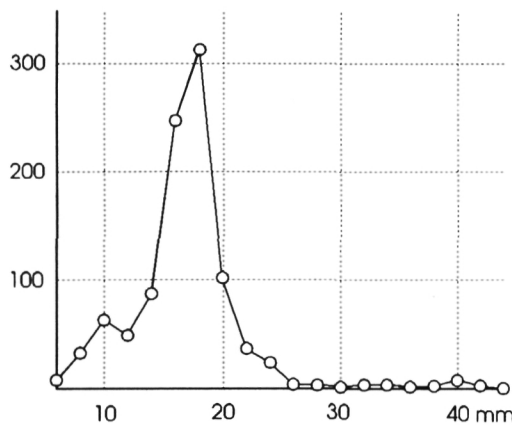12 mm and above.

Fig. 3. Distribution of sizes. Total of all
samples: February to September, 1992.
(N= 991).

4	N	mean	median	mode
Feb.	109	18.65	17.5	19.0
March	160	18.31	18.3	18.3
April	182	18.85	18.8	18.6
May	167	17.00	17.6	18.3
June	122	17.37	18.1	18.1
July	128	16.53	17.3	19.2
Sept.	123	17.38	17.8	17.6

Table 1. Means, medians and modes of
monthly collections.

3.1.3. The mean, the median and the
mode of all monthly collections are compared
in Table 1. There is no indication whatsoever
of an increase in size. The hypothesis of the
age cohort should be abandoned, unless one is
willing to accept that the growth of *O. oliva* is
so extremely slow that it cannot even be de-
tected within eight months.

It is much more likely (see Discussion, §
4.1) that the observed distribution results from
a dynamic equilibrium between growth and
massive mortality (starting at a size around
16-18 mm). As the size frequency distribution
(Fig. 2 and Table 1) is very stable, it follows
that this mortality must vary little throughout
the year.

3.1.4. Colour classes frequency. On
nearly one thousand specimens of *O. oliva*
collected from February to September 1992,
72.3 % were "black", 17.9 % "white" and

9.8% "others". The relative proportions of
these colour classes did not change much
during the eight months of observations (see
Fig. 4). The relative proportions of "black"
shells in February and in September is the
same (72.5%), indicating that the observed
fluctuations are probably due to sampling.

This observation indicates the relative ob-
jectivity of our arbitrary colour classes: should
the colour composition of the sample have
changed, it is unlikely that, on seven occa-
sions, our error would have been just the val-
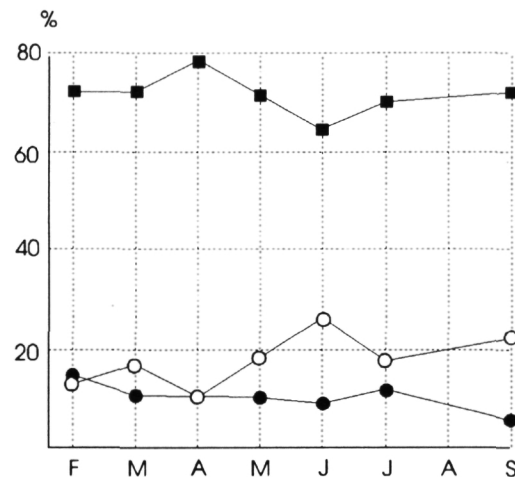ues required to offset the variation.

Fig. 4. Colour composistion of all samples
(February to September 1992), in percent-
age of monthly total. Black squares:
"black" shells. White circles: "white" shells.
Black circles: "others".

3.1.5. Frequency of scars. To acquire
some indirect information on predation, the
presence of scars was counted on all shells,
without distinction of the type or the size of
scar. For correlation studies, to deal with sig-
nificant samples, the shells were ordered into
six arbitrary size intervals (selected so that the
classes are of comparable size, N>86 for each
class). All observations are summarised in
Table 2.

3.1.6. At least one scar on the body whorl
was observed on 42.5 % of all shells. As all
the shells have several whorls, one can con-
clude that the vast majority of *O. oliva* living
at Sisimangum) have survived at least one
unsuccessful attack from a predator. This high
frequency of surviors also means that the
characteristics of the shell are effective in
protecting the gastropod against fatal breakage
(VERMEIJ, 1982).

| size (mm) | "black" | | | "white" | | | "others" | | | Total |
	no scar	with scar	Total	no scar	with scar	Total	no scar	with scar	Total	1
< 12	46	11	57	27	3	30	12	7	19	106
12 to 15.99	50	42	92	13	12	25	10	10	20	137
16 to 17.99	85	94	179	26	16	42	21	5	26	247
18 to 19.99	118	134	252	22	16	38	15	7	22	312
20 to 21.99	36	38	74	13	5	18	6	4	10	102
> 22	49	12	61	14	4	18	6	2	8	87
total	384	331	715	115	56	171	70	35	105	991

Table 2. Distribution of scars per shell size and colour.

The percentage of scar-bearing shells is correlated to shell colour. On the total sample (N=991), scars were found on 46.3 % of the "black" shells, 32.7 % of the "white" shells and 33.3 % of the "others". The sample being large, the difference between the frequencies of scar-bearing "black" and "white" shells is highly significant (at the 0.01 level, two-tailed Student's t-test, t=3.177). For "black" *vs.* "others", the difference is significant (at the 0.05 level, t=2.233. For "white" *vs.* "others", the difference is not significant.

That "black" specimens suffer more attacks was a rather unexpected observation. The population of *O. oliva* under study lives on black sand, where one would expect "black" shells to be attacked less often than "white" ones.

The percentage of scar-bearing shells is correlated not only to shell colour but also to shell size: it is over 46 % for shells between 12 and 22 mm, but only about 20 % for smaller or larger specimens. For shells between 16 and 22 mm (66.7 % of the population), scars are observed on 53 % of the "black" shells (51 % of total population) but only on 34 % of all others ("white"+ "others", 15.7 % of total population).

Based upon the frequency of scar-bearing shells, maximum predation corresponds to the most abundant category: "black" shells between 16 and 22 mm.

3.2. Induction of colour changes.

3.2.1. As on many other molluscs, colour shifts are occasionally observed on *Oliva* shells. A generally abrupt change in background coloration occurs along a growth line and the mollusc often continues building its shell with a distinct, new background colour. Sometimes the mollusc reverts to its original colour and the event results in a more or less wide longitudinal stripe. In some rare instances the phenomenon is repeated, resulting in several parallel stripes.

As crypsis (matching shell colour with the colour of the substrate) appears quite general amongst *Oliva* species (VAN OSSELAER, BOUILLON & TURSCH, 1993), it was tempting to check if shifts in shell colour could be experimentally induced by changes of substrate. That such colour changes could be induced by external events had already been proposed by GREIFENEDER (1981b), who observed apparently synchronous colour shifts on the shell of populations of the East African *O. bulbosa* and suggested that such changes could be used as a "chronicle of the habitat".

3.2.2. Induced colour shifts would be easier to observe is growth rate is rapid. One had therefore to experiment on young individuals, the growth of which being well known to be faster. 23 black specimens (mean size: 15.63 mm, average deviation 2.39), were collected on the black sand of Sisimangum beach and placed in an aquarium containing white sand (see Methods, § 2.3). The experiment started on April 9, 1993, and ended on November 21, 1993. Observations are summarised in Table 3. *O. oliva* is not the easiest *Oliva* to keep in aquarium (see Introduction), and a number of specimens (accounted for in the Table) died before that date.

Colour changes were induced in 19 (82.5 %) of 23 tested specimens. The induced colour shifts are very clearly marked, as seen on Fig. 5. No such colour change could be detected in a control group of black specimens kept in the

same conditions, but on their original black substrate.

Simultaneously with the above experiments, a group of 22 white specimens (mean size: 15.38 mm, average deviation 3.51), collected together with the previous lot, were kept on their original black sand, in the same conditions. None of the 22 specimens exhibited any colour shift.

Experimental induction of colour shifts also allows an estimation of the growth rate of *O. oliva* (at least in the size range H=13 to 22 mm). One can easily measure the number of postnuclear whorls before and after the colour transition, as this occurs rapidly and quite abruptly.

On the twenty specimens in which a colour change was observed a mean angular growth of 0.38 volution/year was found (max: 0.65; min: 0.25). The plot of shell length (H) *vs.* the number of postnuclear whorls (pnw) is given in Fig. 6 for the 20 specimens under consideration here. For a rough approximation, we can consider that the relation is linear, (the size interval being of only a few millimetres). From this graph one can estimate the mean linear growth as being roughly 4.0 mm/year (max: 7.5; min: 3.0). From the observed growth rate, a large (40 mm) *O. oliva* would be about 10 years old. This is certainly an underestimation, because growth rates are well known to decrease with size.

date		colour change	no colour change	elapsed time (days)
June 29	2 dead	1	1	81
Oct. 24	2 dead	2	0	198
Nov. 7	2 dead	2	0	212
Nov. 16	3 dead	3	0	221
Nov. 20	3 dead	2	1	225
Nov. 21	end exper.	9	2	226
	total	19	4	

Table 3. Induction of colour shifts. 23 "black" specimens originating from black sand and kept on white sand.
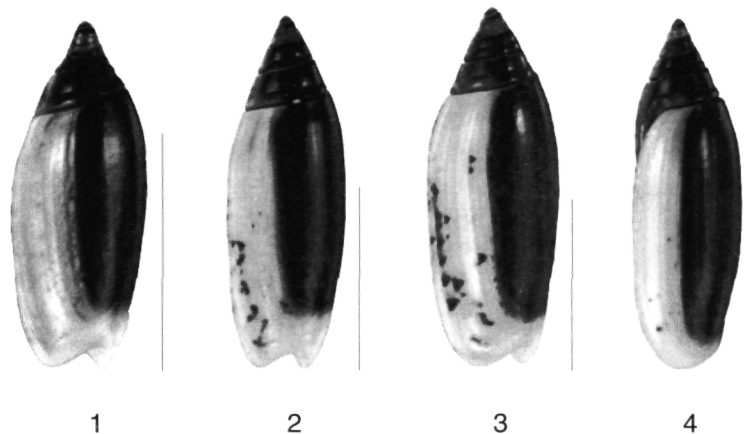

1   2   3   4

Fig 5. Experimental induction of colour changes in the shell of O. oliva. 1-4: "black" specimens collected at Sisimangum Beach (black sand) and kept in aquarium for 226 days on white sand. Scale bars: 10 mm.
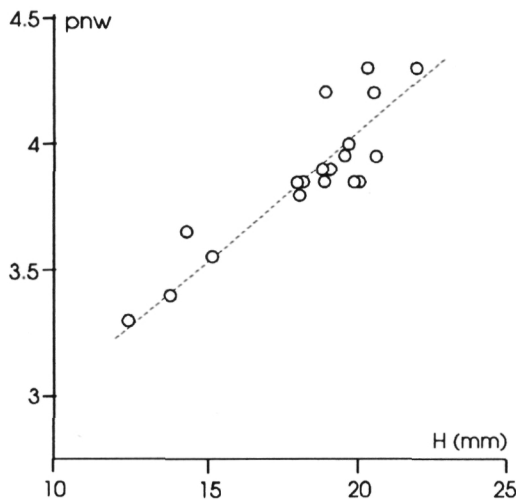
Fig. 6. Shell length (H) *vs.* number of postnuclear whorls (pnw). 19 specimens with induced colour change (see text § 3.2.2).

4. DISCUSSION

4.1. Size frequency distribution.

The sharpness of the size distribution peak was first interpreted as indicating an age cohort. This hypothesis raises serious difficulties. First, where are the other age cohorts?

Their absence could be explained if there was a segregation of habitats according to age classes. Indeed, GREIFENEDER (1981) called attention upon the fact that juveniles of some Olividae species (*Olivella biplicata, Olivancillaria auriculata*) are mostly found in deeper water. This is the contrary of what happens here: predominance of young shells in the intertidal zone. In the particular case of the very abundant *O. oliva* population of Sisimangum Beach, the hypothesis of habitat segregation seems untenable. Over the last 20 years, the beach has been carefully combed on many occasions over large distances, the area has been frequently dredged (from the shore to beyond -35 m), and nearly one hundred dives effected in the vicinity, without any indication of age-related habitat segregation. Not a single specimen of *O. oliva* was found during recent series of quantitative quadrats effected at -3, -5, -10 and -15 m off Sisimangum (VAN OSSELAER, 1992).

A second, admittedly far-fetched explanation would be that reproduction of *O. oliva* occurs synchronously, and at such large intervals of time (ten years or more) that a second peak would not have the time to appear. This hypothesis seems most improbable: we are not

aware of the existence of such a long reproductive cycle in any gastropod. Furthermore, the several *Oliva* species we have kept in aquaria seem to lay eggs all year round (this is also the case for *Olivella biplicata*, see STOHLER, 1969).

In any case, the stability of the peak in time (no increase of size could be detected, see Table 1) makes very unlikely that it represents an age cohort.

But then, why such a sharp peak? By far the most probable explanation is that our stable size frequency distribution curve reflects an equilibrium between steady growth and a steady mortality. The sharp increase in size frequencies (left side of the peak) is understandable: for all animals, growth is expected to be much faster at very small sizes. Rapid transit of young specimens through the small size classes would produce exactly the observed result. It is the sharp decline of the distribution curve that requires an explanation. One would expect a much flatter, regular decrease of the curve unless shells above a given size undergo a specially high mortality. By proper adjustment of parameters, computer simulations (not given here because a simulation does not prove anything in this case) do yield quite comparable distribution curves. The data at hand suggest massive mortality, especially at a size around 16-18 mm. As the size frequency distribution (Fig. 2) is very stable in time, it must follow that this mortality varies little during the year.

The observed phenomenon is possibly not unique to Hansa Bay: Dr. Dietmar Greifeneder (personal communication) has observed a very similar size distribution on a large (probably unbiased) lot of *O. reticulata* collected at Kesuma Sari (Bali) by the late Renate Wittig-Skinner (WITTIG-SKINNER, 1981). The sample, sorted into 2.5 mm size classes (from 10-12.5 mm to 42.5-45 mm) has a very sharp size frequency peak at 20-22.5 mm.

4.2. Predation.

What could cause such a massive mortality? We know practically nothing about diseases and parasites of Olividae, excepted for the mention that over 50% of adult *Olivella biplicata* are infested (and unsexed) by trematodes (EDWARDS, 1968), reducing their natality but not necessarily killing their hosts.

In contrast, we have many indications that other animals feed on Olividae (see GREIFENEDER, 1981). Generalised crypsis, nocturnal behaviour, occasional chemical defences and aposematism, (see VAN

OSSELAER *et al.*, 1993) as well as thick shells, tight coiling and short spires (see VERMEIJ, 1978: 35) all suggest that macropredators are by far the most likely candidates to explain massive mortality. In the case of the *O. oliva* population under study, this is furthermore supported by striking individual colour pattern variations. These have been linked in *Olivella* and *Donax* (SMITH, 1975) to protection against predation by oxypodid ghost crabs, abundant on Sisimangum Beach.

We cannot yet point to the most important predators, Hansa Bay harbouring a great variety of fish, starfish, crustaceans and other molluscs (predatory Gastropods and Cephalopods) liable to feed on *Oliva oliva*. The diversity of scar types observed on the shells suggests however that different predators are at work. The generally turbulent, sand-laded shallow waters of Sisimangum beach allow no direct study of predation on *O. oliva* at high tide. Predation by crabs has been occasionally noted on the beach at low tide, and successful attack by a stomatopod was observed in aquarium. Marks of drilling molluscs (Naticidae and Muricidae) or the characteristic bite of *Octopus* were observed on dead, but not on live shells, suggesting that attacks by these predators are generally successful. The impact of shorebirds (rather uncommon on Sisimangum Beach) and of man (possibly the most effective predator on *Olivella biplicata,* see STOHLER, 1969) is probably negligible here.

Most macro-predators fall roughly into two handy categories (for a more refined classification see VERMEIJ, 1978). *"Crunchers"* (for instance many crustaceans) aim at the shell and, if unsuccessful, often do leave traces of their attack (scars). By contrast, *"gulpers"* (for instance many species of fish) swallow their prey whole or reduce it to unrecognisable fragments, leaving neither corpse nor smoking gun to tell the story.

High pressure from "crunchers" has been evidenced (see § 3.1.6). On a black sand substrate one would expect "black" shells to be more protected than "white" shells. The distribution of scars amongst *O. oliva* shells shows exactly the contrary. This might appear surprising and deserves some comment. Similar situations have been studied (SMITH, 1975; VERMEIJ, 1978): the preferences of ocypodid ghost crabs and other predators for *Donax* and *Olivella* species. It has been shown that the crabs appear to form "search images", for either the most common or the most conspicuous prey, depending on prey density. In the present case, the "crunchers" favour the most

abundant category of prey: "black" olives between 16 and 22 mm. It is known that such apostatic selection is effective in maintaining variability (see ALLEN, 1972). In this case it probably stabilises the balanced colour polymorphism observed in the *O. oliva* population at Sisimangum Beach.

Here again, the observed phenomenon is possibly not unique to Hansa Bay: a rather similar distribution of scars was noted by Dr. D. Greifeneder on the Balinese sample of *O. reticulata* mentioned above (§ 4.1). Scars were present on 25 % of specimens of intermediate sizes (the great majority of the sample) but were absent on shells smaller than 20 mm, as well as on thick-lipped, large shells.

The efficiency of "crunchers" is certainly limited, as most specimens of *O. oliva* have survived at least one attack from these predators. Most of the massive mortality is probably due to the "gulpers". This hypothesis is supported by the high proportion (72.1 %) of "black" shells on Sisimangum beach. It is likely to result from a trade-off between being the choice target of rather inefficient predators (the "crunchers") and being to some extent protected from effective killers (the "gulpers"). More work on the nature and the extent of predation is certainly needed.

4.3. Colour changes.

The observation of induced changes in shell colour adds one more dimension to the already remarkable possibilities of variation and adaptation displayed by *Oliva* species. It corroborates the "habitat chronicle" hypothesis of GREIFENEDER (1981b) (see § 3.2.1). It also casts further doubts on the use of shell colour in *Oliva* taxonomy, where this has traditionally been a predominant character.

It is unlikely that the substrate changes we have used to induce changes in shell coloration are the only (or even the main) cause for the colour shifts observed in natural conditions. From what we know of the sedentary habits of *Oliva*, such events are probably exceptional. Colour shifts often coincide with a large scar, suggesting they could be caused by physiological stress.

Why did "white" specimens not change colour when kept on black sand? This is probably due to the simple fact that they did not experience any change of substrate ("spontaneous" colour shifts must be very infrequent, judging from the material collected at Sisimangum). One could check this explanation by changing the substrate of "white" *Oliva,* living in white sand, to black sand. We

did not run this experiment in Hansa Bay, for fear of depleting the small "white" population of Boro Beach.

How *Oliva* do estimate the colour (or more probably the albedo) of the substrate, and how they effect their colour adaptation remains a mystery. It is noteworthy that 3 species of anomuran decapods (genus *Hippa*) share the beaches of Hansa Bay with *O. oliva* and likewise have a cryptic coloration. Experimental changes of substrate also induced colour changes in these species, after moulting on the new substrate (BAUCHAU & PASSELECQ-GERIN, 1987). There is no indication that the mechanism should be the same as in *Oliva*.

4.4. Growth rate.

The growth rate obtained from the experiments on induced colour shifts is roughly 4.0 mm/year (max: 7.5; min: 3.0) (for shells in the size range H=13 to 22 mm). This is compatible with the slow growths of less than 0.5 mm/month (less than 6 mm/ year) casually observed by us in aquarium for specimens of several *Oliva* species, including *O. oliva* (unpublished observations).

The only comparable data we know for Olividae concern the somewhat distantly related Californian *Olivella biplicata*. For this species that reaches 26-28 mm, very slow growth (between 0.7 and 3.2 mm/year) has been observed, and longevity was estimated at 8-12 years (STOHLER, 1969). There is a very great individual variation in the growth rate of *Olivella biplicata*: it varies from 0.1 to 5.1 mm/year within the same size class (15.5 to 16 mm).

4.5. Conclusions.

The size frequency distribution of *O. oliva* at Sisimangum Beach is very sharp and was stable over 8 months.

Young individuals between 14 and 22 mm constitute over 75% of the population. The chances for a specimen of *O. oliva* to reach "adult size" are very dim: only about 1% of the population reaches 38-42 mm.

Most specimens of *Oliva oliva* has survived at least one unsuccessful attack from a scar-leaving predator.

Maximum predation by scar-leaving predators corresponds to the most abundant category: "black" shells between 16 and 22 mm.

Changes in shell colour have been experimentally induced. When black specimens (from black sand) are kept on white sand, over 80% shift their shell colour to white.

The growth rate of *O. oliva* (at least in the size range H=13 to 22 mm) is roughly 4.0 mm/year (max: 7.5; min: 3.0). It follows that the age of an "adult" specimen is at least 10 years.

We do not know yet if the above observations are general or constitute a particular case, possibly reflecting local conditions. The observations of Dr. Greifeneder on *O. reticulata* in Bali do however suggest that the distributions observed here are not restricted to Hansa Bay or to *O. oliva*.

REFERENCES

ALLEN, J.A., 1972. Evidence for stabilizing and apostatic selection by wild blackbirds. *Nature* 237: 348-349.

BALUKU, B. & M. LOREAU, 1989. Etude comparative de la dynamique des populations de *Biomphalaria pfeifferi* (Gastropoda, Planorbidae) dans deux cours d'eau au Zaïre oriental. *Revue de Zool. afr.- J. Afr. Zool.* (103): 311-325.

BAUCHAU, A. G. & E. PASSELECQ-GÉRIN, 1987. Morphological colour changes in anomuran decapods of the genus *Hippa*. *Indo-Malayan Zoology* 4: 135-144.

EDWARDS, D.G. 1968. Predators on *Olivella biplicata* , including a species-specific predator avoidance response. *The Veliger* 11(4): 326-333.

EDWARDS, D.G. 1969. Reproduction in *Olivella biplicata*. *The Veliger* 10(4): 297-304.

GREIFENEDER, D., 1981a. What do we know about Olividae. Contributions to the study of Olividae. *Acta Conchyliorum* 1: 1-90.

GREIFENEDER, D., 1981b. Die Farbmuster von *Oliva*-Gehaüsen. *Club Conchylia* (5/6): 53-65.

JONES, G.P., D.J. FERRELL & P.F. SALE, 1990. Spatial pattern in the abundance and structure of mollusc populations in the soft sediments of a coral reef lagoon. *Mar. Ecol. Prog. Ser.* 62: 109-120.

LOREAU, M. & B. BALUKU, 1987. Population dynamics of the freshwater snail *Biomphalaria pfeifferi* in Eastern Zaire. *J. Moll. Stud.* 53: 249-265.

PHILLIPS, D.D., 1977. Activity of the Gastropod Mollusk *Olivella biplicata* in response to a natural light/dark cycle. *The Veliger* 20(2): 137-143.

STOHLER, R., 1969. Growth study in *Olivella biplicata* (Sowerby, 1825). *The Veliger* 11(3): 259-267.

SMITH, D.A.S., 1975. Polymorphism and selective predation in *Donax faba* Gmelin (Bivalvia: Tellinacea). *J. Exp. Mar. Biol. Ecol.* 17: 205-219.

TURSCH, B., 1994. Studies on Olividae. XXI. The scale of sympatry in the genus *Oliva*. *Apex* 9(4): 131-142.

TURSCH, B. & L. GERMAIN, 1985. Studies on Olividae. I. A morphometric approach to the *Oliva* problem. *Indo-Malayan Zoology* (2):331-352.

VAN OSSELAER, C., 1992. Contribution a l'étude écologique du genre *Oliva* (Mollusca, Gastropoda a Hansa Bay (Papouasie-Nouvelle Guinée). Travail de fin d' Etudes, Université Libre de Bruxelles.

VAN OSSELAER, C., J. BOUILLON & B. TURSCH, 1993. Studies on Olividae XVII. Data on depth of burrowing, motion and substrate choice of some *Oliva* species. *Apex* 48(4): 151-158.

VAN OSSELAER, C., J. BOUILLON, J.M. OUIN & B. TURSCH, 1993. Studies on Olividae XVIII. The distribution of *Oliva* species and the variation of their colour patterns in Hansa Bay (Papua New Guinea). *Apex* 9(2/3): 29-46.

VERMEIJ, G.J., 1978. Biogeography and adaptation. Patterns of marine life. Harvard University Press.

VERMEIJ, G.J., 1982. Gastropod shell form, breakage and repair in relation to predation by the crab *Calappa*. *Malacologia* 23: 1-12.

WITTIG-SKINNER, R., 1981. Olividae of Indonesia. *Acta Conchyliorum* 1: 91-114.