HISTOIRE D'UNE MOULIERE.
Observations sur une phase de déséquilibre faunique

E. Fischer-Piette. 1935.

(History of a mussel bed. Observations on a phase of faunal disequilibrium)

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TRANSLATOR'S NOTES:

Purpurids- refers to drilling snails of the genus *Nucella*, in this case *Nucella lapillus*; in Fischer-Piette's time it was called *Purpura lapillus*

Astercanthion rubens- this species is currently known as *Asterias rubens*

Balanus balanoides- this species is currently known as *Semibalanus balanoides*

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1. Introduction - Historical

At the end of the last century, Fauvel devoted himself to a study of variations in the marine fauna around Saint-Vaast-la-Hougue. He was the first to practice observations of this type in an ample and continuous way; and in spite of the interest in facts obtained and the fact that one hears many naturalists wish this kind of research to be pursued, the course by Fauvel has not been followed since then except in brief and timid attempts.

Since 1929 I have regularly observed variations in the marine fauna of Saint-Malo, by visiting the same stations each year at the same seasons of the year.

My study, like that of Fauvel, will apply in principle to all the species; but, here as in Saint-Vaast, the most evident facts, the most easily followed and also the most interesting, relate to variations observed in the abundance of mussels (*Mytilus edulis*). The study of these variations permitted me to recognize the interactions of several species, mussels, purpurids and barnacles, following the disruption of the faunal equilibrium, interactions which have the effect of progressively bringing back the initial state of equilibrium. I present these facts in a special study, detaching them from the whole work related to the variations of all species, for which I continue to collect data each year.

Before presenting the data, we must recall the principal observations made up to now on the variation in mussel beds.

It has been recognized for a very long time that the abundance of mussels is liable to vary, and, as Fauvel recalls in 1901 "the periodicities of the mussel beds, in some places, is well recognized by the marine administration."

Fauvel has studied these variations and their effects from a biological point of view, in the region of Saint-Vaast-la-Hougue. He has reported that mussels of the bay of Isigny would rapidly colonize the region of St. Vaast from time to time, then disappear under the attacks of their enemies, man and especially starfish (*Astercanthion rubens*). Let us not fear to cite largely his work to demonstrate the complexity of the biological consequences of these variations: "when the mussel beds extend, the starfish arrive from all surrounding areas and, finding abundant food, grow and multiply with astonishing rapidity.

"Their voracity added to man's destructive activities does not take long to get the better of the mussels, but then when the prey begins to decline, the starfish, victims of famine, tends itself to disappear or at least diminish, soon leaving a field open to a new invasion of mussels. This is, without a doubt, one of the important causes of the periodicities of mussel beds on our coasts.

"The development of mussels on a rocky coast has other consequences. The slime which

collects between their shells and byssal threads does not take long to suppress the animals needing clean water, like many sponges, bryozoans, hydrozoans and colonial ascidians, and with them their associates. The invasion of the mussels is a disaster for the biologist . . .

. . . "After the death of the mussels, the soft slime disappears little by little and a coarse sand formed from remains of their shells settles between the rocks. This is a new, rather poor habitat, but sometimes containing special species. A certain length of time elapses before the rock surfaces, well cleared, are covered anew with a cloak of algae, sponges, ascidians and bryozoans, and that the coarse sand becomes a prairie of sea grass (Tr: 'zosteres'). Then, one fine day, a new invasion of mussels occurs, and the cycle begins again.

"Does it not seem that we have here a kind of cycle, if one may express it thus? We see the development of one species bring about the loss of a certain number of others at the same time as the multiplication of animals which live at its expense and bring about its destruction in turn.

"In many periodic appearances of certain species should we not discover thus a cycle of successive associations furnishing us with the explanation of these variations in the fauna of a locality?"

This work of Fauvel forms the essence of our biological understanding of the variations of mussel beds. I can see citing next only the work of Joubin (1910).

Joubin notes the weak development of mussel beds in the bay of Saint-Malo. He adds: "one attributes this fact to the great abundance of *Octopus vulgaris* which has been swarming in the bay for several years." Likewise, at Chausey, he remarks (1910) that the mussels "have diminished a lot this year because of the abundance of octopi". One can see that the case cited by Joubin is very different from that observed by Fauvel.

One will see likewise, that the case I have observed is very different from the two we have just recalled. Let us say right away that men, starfish and octopi, have not intervened in the present case to limit the extension of the mussel beds, and that this role has been fulfilled by the mollusc *Purpura lapillus* L.; but, here, as in the case observed by Fauvel, there is a cycle of variations which concerns several species.

These observations concern a long stretch of coast from Bréhat to Barfleur. But observations have not been made with continuity except on the rocks situated in front of Saint-Enogat and Saint-Lunaire (I. and V.), and in particular on the Décollé Point at Saint-Lunaire. This point has been chosen for these observations because its topography and its fauna were, for a long time (since 1925), known to me in all their details, for I had made them a basis of comparison for the population descriptions that appeared in my thesis work (1929). From 1925

to 1929 the state of the fauna of this station appeared stable. In 1929 began the expansion of the mussel beds, which is the object of this work.

We must therefore first recall the state of equilibrium existing until 1929. Then we will describe the observations since 1929.

2. Description of Décollé Point, and of its fauna in a period of equilibrium.

Décollé Point, situated at Saint-Lunaire, is elongated from south to north. The two flanks, east and west, rather steep, are very similar from a topographical point of view: compact granular gneiss forms the banks, rather regular overall because erosion of this gneiss gives relatively smooth and little tormented surfaces. The rocky crest is separated into three unequal sections, A, B and C (see the map) by two benches (Tr: 'seuils'- literally thresholds) which I will call proximal bench and distal bench.

From the population point of view, the two flanks, east and west, present certain differences, for the west flank is very battered, and the east flank is partially sheltered. These population differences have been described in my work of 1929: algae less rare on the east than west; *Balanus perforatus* (barnacles of large size) occurring on the west flank and in the benches, but not on the east flank; among the small barnacles, *Balanus balanoides* L. is very abundant on the two flanks, whereas *Chthamalus stellatus* Poli, very abundant on the west flank at all levels, does not exist on the east flank except above the level of the high tide at dead water.

But the difference which interests us the most concerns *Mytilus edulis* L. In this period (1925 - 1929), *Mytilus edulis* was entirely absent on the east flank (except in an isolated bed close to the beach of Saint-Lunaire, point *a*). On the west flank, the mussels exhibit a certain abundance, in particular in the vicinity of point h (map above), and principally from the level of mid-tide to high tide at dead water. These are individuals of a mediocre size (around 40 mm), strongly curved, with a stout shell ornamented with numerous growth lines, which fill the crevices and depressions but do not overflow them. As Joubin has already remarked (1910), the mussels of the region of Saint-Malo are scabby (Tr: 'galleuses'), that is to say covered with small barnacles.[1] Here these barnacles are principally *Balanus balanoides*, with some *Chthamalus stellatus*. These mussels, thus hidden in the crevices and clothed by barnacles, are not visible from far. I regret not having taken any photograph during the first years of these observations.

[1] The small barnacles are called "galls of the sea" by fishermen.

But photograph number 10, taken in 1933, reproduces well the appearance that this bed of mussels used to present, from 1925 to 1929. Over the course of these five years 1925 - 1929, this aspect did not change in any fashion.[2]

I will recall finally, that at this time the presence of *Purpura lapillus* was noted on the two flanks, east and west, with the notation "abundant".

3. Accounts of the mussels, purpurids and barnacles during the period from 1925 - 1929.

The barnacles *Balanus balanoides* and *Chthamalus stellatus* clothed the rock with an extremely crowded population, and formed thus the very base of the population, as they do moreover at all the unprotected stations of the region; they clothed equally the larger organisms attached to the rocks, principally limpets and mussels. These small barnacles served as nourishment for the purpurids.

To feed on a barnacle, the purpurid spreads the opercular plates with the aid of its proboscis. The proboscis is introduced through the orifice thus opened and consumes the flesh of the barnacle (see photo number 8). The purpurids disregard the very small barnacles, and do not attack them until they are 6 months to 1 year old.

Purpura lapillus had no apparent relation with the mussels. Never did I see a mussel drilled by a purpurid, although my attention had been drawn to this point by a work of P.-H. Fischer (1922). It was not rare to see the purpurids attached to mussels, but on separating them one saw barnacles interposed: the purpurid fed on balanids sitting on the mussel, and not on the mussel itself.

The state of the animal populations that we have just described, according to all appearance constituted a state of equilibrium, which already existed in 1925 (the beginning of my observations) and continued up to 1929. In 1930 I found that this state of equilibrium had come to an end, due to the settlement of a large quantity of juvenile *Mytilus edulis*. We shall report with some detail the stages of the expansion of the mussel beds and the various facts which accompanied it.

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[2] This state existed moreover probably since 1917: indeed, the fisherman of the region all recall that in 1916 the mussels were more abundant than normal, but they have not observed other phases of abundance since that time.

4. Extension of the mussel beds from 1929

The 16th of March 1930, I noticed at Décollé, that the mussels formed much thicker groups on the west flank than before, overflowing the crags, extending themselves progressively, and succeeding in covering rather extensive portions of the rocks; moreover, the mussels had invaded the benches (Tr: 'seuils') which traverse the point, and reached thus up to the east flank, without, however, spreading themselves out on this flank itself. The juveniles must have begun to settle in summer 1929.

At the end of summer 1930, a very abundant juvenile set reinforced the settlement of the already conquered surfaces, and carried out new conquests on all fronts.

In 1931, the juveniles having grown, one noticed that the mussels succeeded in covering extensive rock surfaces, being able in certain places, and particularly in the benches (Tr: 'seuils'), to form carpets of many square meters without interruptions. Moreover, the colonization had spread equally onto the east flank, up to that point completely devoid of mussels; it extended into the region marked *e* on the map, and still constituted there, in April, only a few groups (from 10 - 30) localized in the crevices; but in August, the appearance of the east flank succeeded at some points in reproducing the appearance which was observed from 1925 - 1929 on the west flank, and, moreover, the mussels began to appear on the south portion of this east flank (region *c*).

From 1932 on, the facts become more complex. The progression of the mussels continues on the east flank, particularly at the north extremity of this flank (region *g*) where very extensive populations are formed. But at other points a regression manifests itself that we must now look at, and which is due to the intervention of the purpurids which begin to drill the mussels. The effect of this regression is first felt at those points of the station which were the first colonized, that is to say on the west flank and in the benches.

Over the course of the study of these facts of regression, we will have to cite certain observations made at other stations on the rocks of the Grande Vidé and the Petit Vidé in front of Saint-Enogat. We must then, at first, mention the fact that these rocks (Fig. 2), nearly devoid of mussels from 1925 to 1929, were the site of an invasion of mussels parallel to that produced at Décollé, but which was delayed one year: the juveniles arrived there in the summer of 1930; in 1931 vast territories were covered with mussels; in 1932 this movement continued in considerable proportions; in 1933 one noted again an extension at one point, the north-west coast of Petit Vidé (point A); since then no extension has occurred.

Let us see thus what makes up the action of the purpurids on the mussels; but, to understand it well, it is necessary first to know that the mussels made the barnacles disappear,

and then to understand the circumstances in which this disappearance induced the release of the action of the purpurids.

5. Action of mussels on the barnacles

Before the arrival of the mussels, the rocks were, as we have said, almost completely covered with small barnacles, *Chthamalus stellatus* and especially *Balanus balanoides*. The mussels settled themselves on this carpet of barnacles. After awhile, under this covering of mussels and in the middle of the tangle of byssal filaments, the barnacles die. Most of them, pulverized by the growth of the mussels, disappear entirely. There remain meanwhile many empty shells, from which the inhabitants had perished probably from asphyxiation or by starvation. (Here, on these very battered rocks, it does not seem necessary to consider the action of the slime observed by Fauvel at Saint-Vaast on the other organisms).

One would think that, as compensation for the disappearance of this coat of barnacles covering the surface of the rocks, another cost would form on the surface of the carpet of mussels. Now this is not the case: the newly arrived mussels did not become "scabby" (Tr: 'galleuses'), they remained "clean" (see the plate, photo 3).

Explaining this cleanness moreover is not perfectly easy. Many factors come into play. First, there may be a question of incompatibility between the speed of growth of a barnacle and that of the mollusc upon which it is inserted. This incompatibility does not exist in normal times because the mussels grow slowly, but during the period of expansion of the mussel beds the mussels grew a great deal more rapidly. Second, this rapid growth is at the same time continuous: the growth lines are very little marks. Now it is along the growth striations that the cypris larvae used to fix themselves in normal times: on the very smooth surfaces these larvae are unable to hold. Finally and above all, the principal reason seemed to me to be the following. Over the course of the flourishing (Tr: 'pullulation') of the mussels, groups of them become so thick that the most external mussels do not have much connection with the rock, being driven out by the growth of others, and are peeled off by waves. This phenomena is the most evident. They carry away with them the newly attached barnacles; now, the attachment of the larval barnacles taking place only twice a year (spring for *Balanus balanoides*, autumn for *Chthamalus stellatus*, after Hatton and Fischer, 1932), and uniquely on the most external mussels, the young barnacles are rapidly swept away with these mussels; and the mussels left behind remain clean up to the following settlement of cypris larvae.

6. Action of purpurids on the mussels.

From the point of view of the relations between the purpurids and the mussels, nothing changed until the autumn of 1931, that is to say during the first two years of the extension of the mussel beds: the two species continued to coexist without a single drilling observed, the purpurids feeding themselves always on balanids without touching the mussels. At the end of 1931 some drill holes were seen, and from this moment on the purpurids are content with themselves to drill the *Mytilus* more and more frequently. This phenomenon took on such amplitude, that the movement of extension of the mussels gave place, we have said, to a brutal regression, but beforehand we must recall of what consists the act of drilling, and relate the observations that we have made on the drilling instinct.

To feed on a mussel, the purpurid applies its foot on the closed shell of the mussel, and places the extreme end of its proboscis in contact with the shell. At this place a perfectly regular excavation is produced, which is deepened little by little and becomes a cylindrical space traversing the entire thickness of the shell, that one could compare to a hole made by a punch, if it were a little contracted at its distal extremity (photo 6). It seems almost certain that it is the radula of the purpurid which is the essential agent of this boring. Other hypotheses have been put forth, in particular the intervention of an acid secretion. For all these questions I refer to the works of P. H. Fischer (1922) and of Pelseneer (1924). The drill hole once completed, the proboscis enters by this orifice and the purpurid devours the tissues of the mussel (photo 5). It leaves nothing from there which is for its support: the gonads when they are developed, and the other tissues, are always consumed by it.

7. The circumstances where the process of drilling is initiated by the purpurids.

How was the implementation of the drilling process initiated? Why did it not appear for such a long time after the beginning of the mussel bed extensions? It was easy for me to establish it without ambiguity.

I observed, in effect, that, among the first times where the drill holes appeared, *the purpurids which drilled the mussels were invariably purpurids entirely surrounded by mussels, and having no possibility of attaining a single barnacle. As long as barnacles remained in the proximity of a purpurid, it was able to feed itself, without attacking the nearby mussels.*

One can conceive how the purpurids occupied with feeding on balanids, can be progressively surrounded by mussels whose groups, overflowing the nearby crevices, come into

conflict, recovering and destroying the barnacles as it has been said. At some point, the purpurids, having relentlessly devoured the last barnacles in the limited domain which remains at their disposition, see this domain reduced to nothingness and find themselves in contact with the mussels. Their habitual food is entirely lacking because the mussels themselves do not carry any barnacles, contrary to that which exists normally. It is from this moment on that the purpurids attack the mussels.

8. Errors and correction of the drilling instinct.

It is rather curious to see thus developing at a given point, a phenomenon so complex as the act of drilling, in animals that had not exhibited this instinct until then, and would have been able besides not to exhibit it all. Because, it is necessary to insist, the purpurids whose generations succeeded one another at Décollé and in all the region from 1925 did not drill at any moment of their existence.[3] The capacity for drilling has therefore been transmitted through generations without being necessary.

Another curious fact is that, when the instinct of drilling begins to appear, it does not present its definitive perfection at first: errors are very frequent at the start, and one witnesses next a progressive correction. Here are some examples of their correction.

During the first months where the drill holes were able to be observed, it was not rare to see purpurids attacking empty and gaping mussels, and effecting there a complete drill hole, even though, according to all appearance, not trace of any flesh remained in the inside of that shell. At the same time it was not rare to find purpurids entered *in the interior* of the gaping valves and drilling a value *from the inside towards the outside*.[4] The observation of these imperfections at the beginning is interesting, for it has often been assumed that the instinct of drilling was quite certain, and that they did not drill except well knowingly.[5]

After the first year (after the end of 1932), such errors appeared no more. I saw nothing except the purpurids drilling, from the exterior to the interior, of living mussels, or at least

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[3] It is necessary to specify that the purpurids appeared to nourish themselves exclusively on barnacles, and that I have never seen them drilling any animal species whatever, before 1931. Moreover, after 1931, they drilled only mussels, and never limpets or other species.

[4] It is not a question of the purpurids simply taking refuge in these shells: on lifting the purpurid one saw it retract its proboscis and one could observe the presence of the drilling attempt.

[5] See Pelseneer, 1924.

containing flesh. Later the "instinct" continued to perfect itself: starting in autumn 1933, one could observe that, in the presence of a gaping mussel still containing flesh, the purpurids no longer practiced drilling: they only introduced their proboscis through the gape between the values and consumed the flesh directly. At the same time, from this moment on, one no longer saw the purpurids drilling very young mussels: they contented themselves with forcing apart the valves, with the aid of their proboscis, as they had done previously for the opercular plates of barnacles.[6]

We would have therefore before our eyes a sort of *apprenticeship* of the purpurids in their method of feeding on mussels.[7] But the notion of *individual* education does not suffice in the present case. It could not apply except to the first generations of purpurids which attempted to drill (1931-1932). In the following generations, the individuals knew right away to drill without errors, without passing through the stages of apprenticeship of which we have spoken above (the existence of these following generations makes no doubt: I will speak at length of the intense multiplication of the purpurids starting in 1932). Is it necessary to believe, over the course of the generations of purpurids which followed on the rocks of Décollé since 1931, that the transmission of the drilling instinct by a hereditary means had involved the transmission of acquired perfections? We do not maintain it strongly, for this would be to touch on the very difficult question of the inheritance of acquired characters (or, more precisely, it would concern here *re-acquired* characters, after having been *lost* during the numerous years where the generations followed one another without having an opportunity to drill. This loss of characters is no less curious than their re-acquisition).

What other hypotheses can we invoke? On the off chance I will suggest the following of which I am not certain: is it not possible that the instinct may be susceptible to varying in certain years more than others, and that the first drillings became apparent in our region in one year, or, by coincidence, the instinct finds itself particularly variable from the point of view of the choice of shells to drill and of the side, internal or external, to start drilling at. In the following years, simple coincidence again, the variation could carry itself to other things: the instinct not only

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[6] I observed to the same degree this mode of feeding in England, the 12th of May 1933, on the rocks of Pennance Point near Falmouth: in one whole region of shore, the heads of rocks, due to an uncemented crust, were entirely devoid of barnacles and carried nothing except mussels of very small size. On these mussels were numerous *Purpura lapillus* occupied at devouring them after having forced the valves.

[7] Pelseneer (1924, p 41) speaks of a case where *Natica* (penetrating *Donax* and *Tellina*) took advantage of the experience acquired at the end of a series of frustrations, which "is the criterion, generally accepted, of the existence of intelligence".

allows drilling, it also permits the direct introduction of the proboscis between the valves. In other words, the *apprenticeship* mentioned above will be the simple appearance of one of many possibilities. Once again, I am not certain of this.

9. Multiplication of the purpurids.

Some months after the purpurids had begun to drill, as far back as the spring of 1932, one was able to observe that their number had increased in enormous proportions. I had qualified the purpurids found on the Décollé from 1925 to 1929 as *abundant*. This abundance was relative, it consisted of seeing on the average many purpurids per square meter. But, from 1932 on, their number increased to the point that one easily counted hundreds and thousands of them per square meter (photo 7). Must we think, by comparison with the case of *Asterias rubens* cited by Fauvel, that this large number was due to a migration of individuals run up from all sides, attracted by the mussels? Certainly not. As a matter of fact, *after 1932 as before*, the purpurids, far from being attracted by the mussels, did not attack them except when constrained or forced, when they had no barnacles at their disposition. Moreover, one observed with one's own eyes, starting in 1931, an enormous increase in the amount of egg laying by purpurids. It seems thus certain that the purpurids were increasing in number by a very active multiplication.

One could consider this case as commonplace, because it is almost the rule that predators multiply when their prey have multiplied. It is nevertheless interesting to observe that *this diet to which the animal has not had recourse except when constrained and forced, is more profitable to it than the preceding regime to which it remained still faithful up to the limit of possibility*. Feeding on barnacles, the purpurids lived an inactive life. Why did they not profit as soon as possible from the new, infinitely more profitable regime which found itself in their immediate reach, *given that their species is precisely with a specialized means of attack for the regime in question*? There is here, at least in appearance, a singular failure of instinct.

But things go much further than that: we will see soon that following the destruction of the mussels by purpurids, the barnacles reappear on the locations stripped of mussels: now we will state that from this moment on, *the purpurids cease for the most part to feed on mussels, and return to their first diet* (photos 7 and 8). *There would be then a true preference in this species for the diet, apparently, the least profitable for the species*.

To explain this preference, one could invoke, at least humorously the "Law of Least Effort", the individual having greater ease sucking barnacles than drilling mussels. But the scientific explanation remains to be found.

10. Destruction of the mussels by purpurids; regression of the mussel beds.

The purpurids, surrounded by mussels, began their work at the underpinning: they drilled the mussels situated basally against the rock surface, in preference to the mussels situated superficially. When some mussels thus situated in contact with the rock were dead, they washed away in their decline (under cover of the first blows of the sea) all the mussels situated exterior to them, so that it is by large pieces that the mussels found themselves removed. One understands that under these conditions the mussel bed regressed very rapidly.

The work of the purpurids was manifested principally in the cracks of the rocks, then on the flat parts. After a certain time these regions were stripped, and no mussels subsisted except on protruding parts of the rocks. Thus an inverse distribution was achieved to that which existed at the beginning, where the mussels were contained in the cracks.

The mussels progressively diminishing in number, the purpurids succeed to be in certain beds, as numerous then later more numerous than the mussels (see the plate, photo 4). It was not rare, as far back as then, to see many purpurids simultaneously attacking a single mussel. The fact that one purpurid will have already achieved a perforation and commenced to devour the flesh of the mussel, does not hinder the other purpurids from achieving the perforations they have undertaken, and of taking their part of the remaining flesh. A bed having reached this point disappears with the greatest rapidity (plate, photo 4). But the destruction was not complete on all the beds making up the mussel bed: we will see further on under these circumstances an important number of mussels will escape from the massacre.

Photos 1, 2, and 3 of the plate present the aspects of destruction of a bed, situated at point *g* (map of Décollé).

11. Destruction of mussels by agents other than the purpurids.

Were the purpurids the sole agent of destruction of the mussels? What was the role of the mussel enemies cited by Fauvel and Joubin starfish, octopi, and man?

At no time have I seen starfish on the mussel beds studied from Bréhat to Contentin. In the effected (Tr: 'malouine') region, starfish were rare (except for the inoffensive *Asterina gibbosa*), and remained this way during the extension phase of the mussel beds.

At no time have I seen octopi on the mussel bed, nor on any of the exposed rocks of the region: they keep themselves in the more sheltered regions; at no time can the coastal natives be blamed for the destruction of the mussels in these last years. Finally, I will state precisely that, during the year 1932, where the destruction of the mussels was very active, the octopi were nearly non-existent in the region.[8]

These facts would not be understood to express the least doubt about the observations of Fauvel and Joubin. They show only that we have dealt with a different case from those that these authors have observed.

On the intervention of man here is what I can say.

The mussels of the region have never been the object of regular exploitations, except on the rocky reefs of cape Fréhel and at certain localities in the bay of Saint-Brieue. In the effected region properly speaking, it was only during the periods of abundance (1916; 1931-32), that profitable harvesting was done, and the only points where these harvestings were "profitable" were the rocky reefs situated in front of Paramé, where the mussels are particularly nice. But on the coastal rocks (among those which are studied), the mussels have always been neglected because of their small size and of their poor quality. Even at the time of the greatest abundance people carried out there only insignificant appropriations. The unemployed, the tourists, from time to time collected a basket of mussels; but the effects of these appropriations passed unnoticed. To prove this, I chose a place where people made particularly frequent collections (because of easy access) and where they were the only enemy of the mussels, the purpurids being

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[8] I have pointed out before (Bull. St. Servan, vol 10, p 28) that over the course of the year 1932 we were able to get only eight octopi total for the aquarium at Saing-Servan, in spite of frequent fishing with a trawl net and with a seine, and in spite of the promise of recompense which we made there to the sailors and children; this rarity moreover had been observed simultaneously in Bretagne, in Contentin and in Calvados.

diminished on this point. I made there, at regular intervals, successive photographs of a single bed (Figs. 3 and 4, and below): the appearance remained completely the same, which proves that the cleared spaces were rapidly filled up. One sees thus, that the intervention of people was negligible.

But the purpurids were nevertheless not the only agent of destruction of the mussels. Many mussels, as a matter of fact, were destroyed mechanically by the very fact of their abundance: I have already indicated strongly that the mussels situated superficially on a layer of their congeners, were eliminated in a regular fashion. But, moreover, it was common to see the *entire bed of mussels* detached from a rather large surface under the shock of a wave, because the very thickness of this bed presented an excellent grasp to the wave. It was very easy to observe this fact in regions deficient in purpurids, as well as in the regions provided with purpurids whose work at the underpinnings often only facilitated (in enormous numbers it is true) the action of waves. We must state precisely that this action of the waves was not capable by itself of wiping out a bed, but only of creating some clearings by removing the most heavily developed and most exposed groups. In summary, it acts there only to eliminate excess mussels.

12. Phases of activity and inactivity in the purpurids. Destruction of purpurids by mussels.

Purpurids are not always active. Under the influence of severe cold, and more again under the influence of heat, they become inactive for considerable lengths of time. Their repose resembles "aestivation": they are hidden in the cracks and depressions of the rocks, or else at the base of patches of mussels, often in very numerous groups. Those which are found on a smooth wall and without refuge, retract and fall to the base of the rocks, where the sea removes them.

On the days which represent the passage from inactive to active periods, the purpurids, active when the sea leaves them, remain that way as long as they are in the shade, and become inactive when the sun strikes them.

The inactivity which overtakes the purpurids is not known to overtake the mussels: the attachment of their young, and their growth, continues. The young mussels which attach around an immobile purpurid, succeed to clasp this purpurid in a lacework of byssal filaments, and the purpurid is bound shortly thereafter: when it revives, it is incapable of breaking the byssal filaments. Photo number 9 shows that byssal threads are sufficient to immobilize a purpurid.[9]

[9] The case represented by this photo is exceptional: in general the purpurid is enshrouded under a covering of byssal filaments, and concealed by a layer of newly arrived mussels. But it is in that case quite difficult to photograph.

The purpurids thus bound, dies of starvation. However, in the case where its aperture is against a mussel, it drills this mussel and devours it. Often it repeats the drilling act many times on the same valve, without benefit. It finishes always by dying.

The number of purpurids so sequestered by the mussels is considerable, one can count as many of them as one wants during the time of a low tide. But, relative to the prodigious number of purpurids existing in the mussel bed, it is unimportant, and one can say that this destruction of purpurids by mussels does not impede in a meaningful way the ravages made on the mussels by purpurids.

13. Cessation of mussel destruction by the purpurids. The role of barnacles.

The ravages carried out by the purpurids returned to nakedness, in a multitude of places, the rock previously covered by mussels. These cleared surfaces became populated with barnacles (photos 3 and 4) when the swarming of the latter comes about: spring for *Balanus balanoides*, autumn for *Chthamalus stellatus*.

The purpurids then cease to drill mussels and return to feeding on barnacles, when the latter have attained a sufficient size (after 6 months to 1 yr. of growth). The remaining mussels even then, are protected from destruction, the mussel bed is thus not totally annihilated.

The barnacles do not attach solely to the rock. They also attach, we have said, to mussels. We have stated how, at the time of the greatest extension of the mussel beds, the superficially situated mussels fell off and were carried away with the barnacles which covered them, leaving uncovered a layer of "clean" mussels. But then, at the time when the mussel bed is in great regression, the thickness of the bed of mussels returns to being slight and the elimination of which we have just spoken does not occur. In such a way the barnacles cover the mussels again in a durable fashion, and these latter merit anew the epithet "scabby" (Tr: 'galleuses').

Even then the purpurids finding themselves on the mussels, as well as the purpurids finding themselves on the rock, have barnacles at their disposition, and they generally cease drilling mussels to content themselves with sucking barnacles.

I say "generally" for nothing is absolute. For many months one could still see purpurids drilling the mussels even though barnacles of a sufficient size were at their disposition (photo number 6). But, overall, the drillings become more and more rare, and one can say that the purpurids return to their initial diet.

Consequently everything passes as if the reappearance of the barnacles had protected the mussels from total destruction.

Is this exactly the explanation of the disdain of the purpurids for the last mussels? One asks oneself if it was not necessary rather to see the proof that the mussels have lost their quality. Indeed, the active reproduction of the mussels (the production of a large quantity of juveniles), and their rapid growth, seems to have been only once. From 1933 on both of them slackened. The slackening of reproduction could only be due to an extrinsic cause, namely the progressive destruction of the mussel bed by purpurids. But the slackening of growth can not be explained except by a lesser vitality of the mussels (that this vitality was or not under the influence of external conditions), involving possibly a lesser nutritive quality. The mussels would not have in that case as much attraction for the purpurids.

I am not certain that this is the best explanation. Even if the mussels had less quality, the purpurids would truly complete the destruction of them if they had not had another food at their disposition. On the other hand, even at the height of the prosperity of the mussels, there existed numerous mussels of poor appearance, of gibbous shape and with slow growth marked by strong striations, and they were more often drilled than the others; inversely, during the later times, there were moreover numerous mussels with a good appearance, smooth and of large size, and the purpurids abandoned them as well as the mussels of size growth.

I admit thus that it is indeed the presence of barnacles which preserved the rest of the mussel beds from total destruction. Let us see now of what consists the rest.

14. Actual state of the bed (July 1934) after the unfolding of various phenomena mentioned above.

Presently, we observe the following state, which is variable depending on the stations since the date of mussel appearance has varied depending on the stations.

1° On the west side of Décollé, the only site that has had primitively a bed of mussels, and from which started the extension of these mussels, the actual state represents almost exactly the primitive state. We can say that the cycle is finished. The purpurids have all returned to their primitive food diet (barnacles); the mussels, again low in numbers, found in crevices[10], and

[10] We have said that the poupurids have first cleaned the crevices, and then attacked the mussels found on projecting site. It is likely that the crevices have been restocked during that time, favored to other regions, on which the newborns would have had difficulty to hang, since the rock would be too smooth because of the absence of Cirripedes. However, I have not watched closely the merchanisms of restocking of these crevices.

scabby (Tr: 'galleuses') again (picture no. 10); the barnacles have again colonized the site that was theirs. This state was found already during the summer of 1933, and since then, this aspect has not been modified: the stability has come back.

2° In the benches (Tr: 'seuils') and east side, the destruction goes on in certain places that are particularly well stocked, and lately stocked with mussels; elsewhere, in places where a low number of mussels were established, they have grown without being attacked; it will be interesting to see if the initial state (total absence of mussels on the east side) happens again. For that to occur, there should not be establishment of newborn mussels that would replace dying ones.

3° On the rocks of Saint-Enogat (Grand Vidé and Petit Vidé), the initial state has come back, or is being reconstituted, where the purpurids have intervened. However, there are places, on these reefs that have never borne many purpurids. In those places, mussels have developed freely, and still constitute discontinuous carpets (Figs. 3 and 4). However, they have the tendency to become "scabby", which proves that either their growth is being slowed or there are fewer newborns.

15. Summary of the interactions of the various species

We observe that the studied species act on one another in a complex manner.

Purpura lapillus on *Balanus balanoides* (and *Chthamalus stellatus*): they feed on them normally (before multiplication of mussels, and after their destruction).

Purpura lapillus on *Mytilus edulis*: they feed on it during great abundance of mussels.

Mytilus edulis on *Balanus balanoides* (and *Chthamalus stellatus*): destroy them by covering them up during expansion of the mussel bed.

Mytilus edulis on *Purpura lapillus*: the mussels confine and destroy a certain number of purpurids during the inactive time of the latter.

Balanus balanoides (and *Chthamalus stellatus*) on *Mytilus edulis*: indirect action: stop the destruction of mussels and prevent them from disappearing completely.

16. Conclusions. Reflections on faunal equilibrium

In the preceding pages, we have mentioned the various facts on fauna variations, as they relate to a mussel bed whose history has been followed for 9 consecutive years.

Now, we should separate these various facts, as far as interpretation is possible, in two

distinct categories: those whose cause is not apparent to us, and those that can be explained. The fact whose explanation is not apparent to us is the initial fact from which all others derive. It is the fixation of an abnormal quality of newborn mussels during several consecutive years.

The other facts derive from this one, and we can without simplifying too much, summarize in the following manner, the succession of facts.

a. - The arrival of a large number of newborn mussels induce death of small barnacles *Balanus balanoides* and *Chthamalus stellatus* on large surfaces where these barnacles are swamped by the encrustation of mussels.

b. - The *Purpura lapillus*, which were feeding on these barnacles, can no longer feed on them: they change diet and start perforating the mussels. At first, the perforating instinct is variable and produces interesting mistakes. An "apprenticeship" occurs. Everything happens as though the following generations benefit right away from this "apprenticeship".

c. - The *Purpura lapillus* multiply in large proportions: although they change their diet only when absolutely needed, the new diet is a lot more profitable than the old diet.

d. - From this multiplication of purpurids, a rapid decline of the bed of mussels, eaten by the purpurids, occurs.

e. - Surfaces stripped of mussels by the action of purpurids become colonized again with barnacles when the season of larval fixation of the latter occurs.

f. - As soon as those barnacles are of a sufficient size, purpurids start again to feed on them, thereby coming back to their original diet.

g. - The mussels, thus left alone by the purpurids, are no longer destroyed.

At the level of fauna equilibrium, this is, in a coarse manner, how we can represent the facts of this station where the mussels are generally limited in numbers:

If the mussels get to multiply in an abnormal way, thereby creating a strong disequilibrium, a *direct* consequence of the desequilibrium (suppression of barnacles) is *to trigger an antagonistic factor*, the purpurids, which start destroying the mussels by perforating them, whereas normally they would not touch them.

This destruction of mussels could lead to total disappearance if they did not *trigger* (by "liberation" of rock surfaces) another factor that *inhibits* the action of the first: the coming back of the barnacles that divert the purpurids from their prey.

Therefore, mussels survive in a limited number, and the various species that accompanied them have returned back to their respective places and normal interactions.

The final state is equivalent to the initial one.

The initial state was a state of equilibrium that had lasted for several years. It will be interesting to see if the final state also constitutes a state of persistent equilibrium.

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Figure Legends

Fig. 1. Map of Point Décollé, at Saint-Lunaire.

Fig. 2. Map of the rocks of Grand Vidé and Petite Vidé, at Saint-Enogat.

Fig. 3. Petite Vidé, September 23, 1933, point A. A rocky surface, formerly entirely lacking mussels, now covered. These mussels are not intermingled with purpurids (the white points visible are reflections from the very smooth shells of the mussels). The goal of this photo was to be able to verify ultimately if, in the absence of purpurids, the mussels were spared.

Fig. 4. The same view, July 15, 1934, that is to say ten months after. The mussels remain numerous. They are only whiter, because of the barnacles attached to them (barnacles aged 4 months).

Explanation of the plate III

N.B.-- It was not possible to take photographs during the first years of observation, but only since September 1933. Thus only the last stages of the evolution of the mussel bed are presented here.

Photo n° 1. -- Décollé, point *g*, 16 September 1933. This point though lacking mussels from 1925 to 1929, like the entire east side of Décollé, is now covered abundantly. The purpurids begin to attack them (one can see them as white spots); this photo was taken to permit a demonstration of the destruction much later.

Photo n° 2. -- The same point, 30 March 1934, that is to say six and one half months later. The mussels have in large part been destroyed. The purpurids are numerous.

Photo n° 3. -- The same prominent rock, seen clearly before (2 April 1934), to illustrate the purpurids at work on the mussels. The spaces stripped of mussels are covered with very young barnacles (forming white points) that settled less than three weeks before.

Photo n° 4. -- In the vicinity of the same station, 30 March 1934, the last stage of destruction of the bed of mussels. The purpurids having become more numerous than the mussels, the destruction is finished rapidly. The rock environment, freed from mussels, is covered with barnacles, but these are very young (less than 3 weeks) and do not distract yet the purpurids from their normal prey.

Photo n° 5. -- Décollé, point *b*, 2 April 1934. Three purpurids at work drilling. One of them, held apart by the hand of the investigator, exhibits its proboscis held in the drill hole it has produced (this proboscis retracted in one second). The mussels, along with the rock, carry young barnacles that attached three weeks previously.

Photo n° 6. -- Mussels harvested from Décollé, point *d*, the 15th of September 1933, each of them illustrating the drilling work of a purpurid. The drill holes are visible next to the apex of each mussel. On the left, an unsuccessful drill hole. On the right, a successful drill hole. These mussels are carrying barnacles that are below the size sufficient to serve as food for the purpurids, but these latter were not eaten (see section 13).

Photo n° 7. -- Décollé, in the vicinity of point *g*, 2 April 1934. A view of the swarming of the purpurids. Note in the right part of the photograph the absence of the purpurids from a place covered with very young barnacles (white points), and their presence on the rest of the surface, where barnacles of all ages are found (see the knob), and where they are feeding.

Photo n° 8. -- Petit Vidé, point *a*, 4 April 1934: on a point analogous to the preceding one, 70% of the purpurids are occupied feeding on *Balanus balanoides*. Each of these purpurids was

turned aperture up, and placed in a fashion that indicated the barnacle on which it had been feeding. The barnacles showing their opercular plates pushed aside (which proves the animal did not react anymore), but not missing as in barnacles dead a long time. One sees particularly well the opercular plates in the barnacle indicated by the purpurid second from the right (the first being one in which only the apex can be seen): the aperture of this barnacle is in the form of a slit, bordered by two bulging parts around the mouth that are formed by the opercular plates. In dead barnacles, the aperture is square, without bulging parts around the mouth: see those situated just to the left of the purpurid in question.

Photo n° 9. -- Décollé, 30 March 1934, point *f*. Purpurids on which the mussels have inserted byssal filaments during a period of inactivity. Three of these filaments (which are parallel) are visible. This purpurid is dead not having had the power to disengage itself and after having drilled (evidently at time of its rude awakening) the mussel to which it is attached.

Photo n° 10. -- Décollé, 16 September 1933, point *h*. Final state of the population of mussels on the west side of Décollé: scattered individuals, clustered in cracks in small groups, and rendered barely visible by the fact that they are covered with barnacles. (The black spots are tufts of the lichen *Lichina pyrgmaea*). From 1925 to 1929 the appearance of this point was exactly the same.