A Study of some of the reactions of the Whelk, *Buccinum undatum*.—By James Nelson Gowanloch, B. A., B. Sc., Head of the Department of Zoology, Dalhousie University, Halifax, N. S.

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The study of the reactions of animals to stimuli affords an instructive method of analyzing the mechanism of those organism-environment relations by means of which the living animal apparently free to wander through a wide and varying range of conditions is nevertheless normally restricted to those parts of its environment affording it appropriate conditions of moisture or of aridity, of sunlight or of darkness and of food. Properly controlled experiments on the response to gradients of light, of hydrogen ion concentration or some such chosen factor, provide a means of roughly measuring the directive value of these environmental elements whose aggregate effects may constitute, in the absence of such analyses, a complex and puzzling behaviouristic picture.

There exist however in addition to these directive responses on the part of the animal removed from its normal habitat a set of what may be termed "protective responses" which operating in an animal that has been displaced into a dangerous environment serve to reduce these dangers of its abnormal situation and thus aid in tiding the organism over this hazardous period of exposure. Such for example is the "clumping reaction" of the land isopods *Porcellio rathkei* when removed to abnormally dry surroundings, and such is the sealing up of the operculum that is performed by gasteropods when they are exposed to excessive loss of moisture.

It is the purpose of this paper to set forth briefly the facts of a case remarkable for the entire absence of these usual protective responses; an instance where in their stead a behaviour occurs that not only increases greatly the physiological dangers of the animal's situation but also actually causes the early death of the exposed individual. The case is that of the Common Whelk *Buccinum undatum L* under conditions of inter-tidal exposure.

Buccinum undatum is a marine gastropod, attaining a length of about six centimetres and with a shell grayish in colour exhibiting six whorls. The species is distributed from low water mark to a depth of at least 100 fathoms over the Atlantic, Arctic and Pacific coasts from the Atlantic coasts of North America to the coasts of Siberia. In Europe where the species appears to attain a larger size than in our waters, it is extensively used both as food and as cod-bait. Omnivorous in diet, the Common Whelk crawls about on the substratum by means of its muscular foot and when confined to an aquarium it will sometimes climb a few centimetres up the glass sides. Along coasts with average tidal changes *Buccinum* approaches exposure only during the dead low water of the spring tides. Thus the individuals of the species are never exposed under normal conditions to the danger of death from loss of moisture during inter-tidal desiccation.

Such, however, is not the case in the Bay of Fundy where the remarkable differences in tidal level of from eight to ten metres lay bare at one period of the month an area of the littoral zone that at other periods of the month is completely and even deeply submerged. Under these conditions species that rarely if ever become completely exposed by tidal change will through normal dispersal spread during one period of the month into an area of the submerged sea-bottom that in the course of the tide-cycle will at the spring phase become exposed for hours to the sunlight while the tide is out. While carrying out work at the Atlantic Biological Station situated at St. Andrews, New Brunswick, the writer became interested in the responses of *Buccinum* to these unusual conditions imposed upon it by the Bay of Fundy tides. The results of a few preliminary experiments proved to be so unexpected and stood so apart from the usual behaviour of inter-tidal forms that a brief investigation was undertaken of the normal dispersal behaviour of the species and the behaviour of individuals during normal and experimental exposure to desiccation. Data secured by these diverse methods supported the view that we are here dealing with the interesting case of an organism compelled by unusual

tidal conditions to meet with new and severe dangers and inasmuch as its phylogenetic history has not included exposure to such dangers, the species, responding with a set of reactions that are definitely deleterious and even fatal, perishes helplessly within a meter or two of conditions that would serve to shelter it until the tide again returns and the danger passes.

During other than the spring phases of tide *Buccinum undatum*, being a gastropod of more than ordinary motor activity becomes dispersed more and more in the shoreward direction together with such forms as the sea urchin, *Strongylocentrotus drobachiensis* and the starfish, *Asterias vulgaris*. When the tides pass into the spring phase and the amplitude of tidal change rapidly increases these shoreward migrants are suddenly thrust from conditions of continuous immersion in sea water at a temperature of eight degrees centigrade to conditions of daily exposure for hours to the summer sun.

To study the normal activity of *Buccinum* in this situation four series of animals aggregating 152 individuals were marked and released some at low tide level immediately following a spring tide, others at the upper limit of intertidal zone reached by *Buccinum* immediately after a spring tide. The methods of marking used were such that, as controls amply demonstrated, the animals were in every way physiologically normal. Subsequent careful searches were made for and records kept of these individuals. The results may be briefly summarized as follows. The released animals wandered in all directions there being no evidence of any shoreward or seaward directive influence. The rate of what may be termed "walking dispersal" varied greatly for individuals some of which remained near where they were liberated for as long as five weeks. There was an entire absence of any protective migration toward nearby areas offering optimal conditions of shelter. The most significant and unexpected result however occurred in the instance of the animals set free during spring tides at the upper level reached by *Buccinum*. Forty-eight hours later eighteen of the animals

were recovered, eleven of which were dead. Since it was evident that their death was in no way due to experimental treatment, an examination of the normal, unmarked *Buccinum* present at this level was immediately made with the surprising result that it was found that nine-tenths of these animals were also dead. The explanation of this heavy mortality must lie, it was thought, in some unusual failure of *Buccinum* to conserve its water-content during exsiccation and an experimental examination of the animal's behaviour during intertidal exposure was undertaken accordingly.

Ten *Buccinum* ranging in weight from 8.25 grams to 41.17 grams were weighed and exposed in a dry paraffined tray suspended over a water table which was covered with flowing seawater. These conditions thus reproduced very accurately those under which the animals would be exposed in nature during low water of a spring tide on a cloudy day. The animals were then weighed at intervals during the twenty-one hours and forty-five minutes that elapsed from the beginning of the period of exposure until the time when all the animals had died, there being seven successive weighings for each individual. The animals were then desiccated for three days in a drying oven and weighed again and subsequently a chosen group were macerated, the tissues other than the shell removed, the shells being again desiccated and weighed. From these data there was then calculated the rate of loss of water per hour in percentages of the initial total water content providing thus in exact terms the record of each individual's approach to the point where loss of water caused death. During the experiment the activities of the animals were constantly observed. The results may be concisely summarized as follows. When *Buccinum* is subjected to exsiccation it responds in a manner precisely the opposite from that exhibited by a gastropod such as *Littorina litorea*, a form occurring regularly far up into the zone of inter-tidal exposure. Instead of withdrawing into its shell and sealing up its operculum as does *Littorina*, *Buccinum* promptly extrudes its foot and head, exposes almost the maximum possible surface to the action of evaporation and, most disastrous of all, violently

expels all fluids that it can with the obvious end result that the organism's water-reserve is speedily lost, its water content sinks swiftly to the danger point and, if desiccation continues, the animal dies.

Since this series provides a representative range in size of the normal *Buccinum* population the average of these figures should give a reliable picture of the water-loss of the animals. When this average is calculated it is found that the average rate of loss of water per hour expressed in terms of percentage of initial total water content is as follows: for the first hour and a third, 4.19 per cent per hour; from the end of the first hour and a third to the end of two and a half hours, 3.55 per cent per hour; from the end of two and a half hours to the end of four hours 1.48 per cent per hour; from the end of four hours to the end of six hours, 0.77 per cent per hour; from the end of six hours to the end of eight hours and forty-five minutes, 0.51 per cent per hour; from the end of eight hours and forty-five minutes to the end of twelve and a half hours, 0.23 per cent per hour; from the end of twelve and a half hours to the end of twenty-one hours and forty-five minutes, 0.24 per cent per hour. Thus it is easily seen that the animals begin the dessication period with a relatively enormous rate of water loss that brings their reserve sharply downward to the danger point. Thus on the average during the twenty-one hours and forty-five minutes of desiccation the animals lost 18.07 per cent of their initial total water content but when considered hour by hour this loss shows an extraordinary and significant crowding of that loss into the early period of exposure. Thus, considered in terms of percentages of the entire water loss sustained, the animals lost 29 per cent during the first hour and a third of desiccation, 55 per cent during the first three hours and no less than 65 per cent during the first four hours of the twenty-one hour period over which water loss was taking place. During the last sixteen hours of the twenty-one hours the loss is, in sharp contrast, being only 16 per cent of the total loss that intervenes between the beginning of the exposure and the death of the organism.

Calculations of the total water content of the animals in per cent of total weight exclusive of shell gave remarkably uniform results, the percentages for five individuals with total weights of 38.35, 8.25, 13.97, 16.5 and 36.07 grams each being 79 per cent, 81 per cent, 79 per cent, 82 per cent and 81 per cent respectively.

The interpretation of this curious piece of ecology is apparently quite simple. In its normal habitat *Buccinum* does not become an inter-tidal animal since its upper limit of distribution brings it only to the edge of the lowest low tides. In the Bay of Fundy the exceptional tidal conditions created by the converging coasts produce a tidal change so great that during the spring phase those individuals of Buccinum that have wandered shoreward find themselves suddenly transformed from animals continuously submerged deeply under the waters of an unusually cold bay into animals exposed for hours to the desiccating action of the sun. The reactions that this exposure evokes from them are the reactions fitted for their normal submerged existence. In the new dangers of the inter-tidal zone exposure this behaviouristic response is the most disastrous one possible and leads to the early death of the individuals unless they are soon covered again by the incoming tide. This elimination of the upper, shoreward fringe of the *Buccinum* population exerts no permanent modifying selective action upon the species as a whole for the quite sufficient reason that it affects only some of the animals of one sharply local region.