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Implosion of living *Nautilus* under increased pressure

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Abstract.—In a hyperbaric chamber, a living mature specimen of Nautilus pompilius withstood a hydrostatic pressure of 8.05 MPa (80.5 kg/cm^2) equivalent to 785 m deep in the sea. Thereafter it was killed instantly by implosion of the shell. Before implosion, the animal reacted physiologically to increasing pressure. Therefore, the depth of 785 m can be assigned the depth limit of *N. pompilius*. The result bears on critical interpretations on the paleoecology and paleobiology of extinct nautiloids and ammonoids with similar shells.

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Introduction

Nautilus species have generally been regarded as "deep sea" chambered cephalopods. For example, N. pompilius Linné has been trapped in the Philippines at 61-310 m (Haven 1977); in Fiji at 100-550 m (Ward et al. 1977); N. macromphalus Sowerby in New Caledonia at 40-350 m (Hamada and Mikami 1977); the "Challenger Note" of 570 m was based on a single specimen of N. pompilius (Hoyle 1886); Griffin believed that the specimens of N. pompilius of the Menage collection was trapped between 360 and 540 m (Denton and Gilpin-Brown 1966). The strength of the shell and siphuncular tube have also been studied under atmospheric as well as increased hydrostatic pressure. The siphuncular tube of N. macromphalus withstood a pressure equivalent to more than 480 m (Collins and Minton 1967) and drifted, beached shells of this species imploded at equivalents to 530-730 m (Denton and Gilpin-Brown 1966). The drifted shells of another species, N. pom*pilius* failed at pressure equivalent to about 400-740 m (Raup and Takahashi 1966; Westermann 1973), but their young shells of 22-30 mm diameter withstood the pressure at 1360 m (Saunders and Wehman 1977). The loci of shell failure, however, were not specified. The calculated shell strength of the embryonic shell (<20 mm diameter) of these two species is only about half that of the mature shell (Westermann 1973). Most recently, Ward has lowered traps with living *N. pompilius* off Fiji and found that all specimens imploded at 750–900 m (G. E. G. Westermann and P. Ward, personal communication and 1980).

This study concerns the limiting pressure and behavior of a living specimen of N. *pompilius* under experimentally applied hydrostatic pressure.

Material and Methods

The specimen of N. *pompilius* was trapped on the 6th of December 1978, at 150 m depth 2 km off Bindoy, Negros Oriental, the Philippines, and experimented on five days later. It was a female with a mature shell of 167.5 mm in maximum diameter.

The specimen was kept in a 27 cm deep sea water tank of acrylic resin, thereafter it was placed in an "animal chamber" of the Japan Marine Science and Technology Center. The compression rate of ambient air was 0.1 MPa

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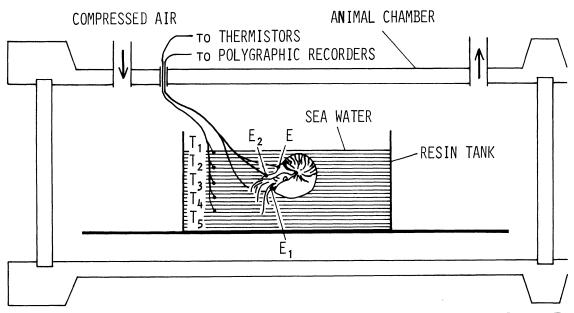


FIGURE 1. Nautilus pompilius in hyperbaric chamber. E, E_1 , E_2 : electrode-needles for funnel pulse; T_1 , ..., T_5 : thermistors for water temperature. Size of resin tank is 60 cm length, 30 cm width and 35 cm height.

(1 kg/cm² equivalent to 10 m in fresh water or 9.7 m in seawater, accuracy 0.25% on the pressure gage) per minute, corresponding to the heaving rate of the traps used in the Philippine sea. The electrode-needles (E and E_1 at hood, and E_2 at funnel in Fig. 1) were inserted into the specimen to measure its funnel pulse. The funnel pulse of *Nautilus* is assumed to correspond to the respiratory rate of the animal. The pulse was monitored by polygraphic recorder (type EEG-4113, Nihon Koden, Tokyo). The water temperature was recorded with thermistors (type K-730, Takara Kogyo, Tokyo) placed at intervals of 5 cm (T₁, ..., T₅ in Fig. 1).

Results

The specimen of *N. pompilius* withstood a hydrostatic pressure of 8.05 MPa corresponding to a water depth of 785 m (density of seawater 1.026 at 15°C) but was then killed instantly (E in Fig. 2) by implosion of the phragmocone of the shell. The septa and siphuncular tube were completely destroyed, but almost all parts of the living chamber remained, nearly intact at the anterior part of the animal (Fig. 3). The animal was alive until implosion of the shell. The rate of funnel pulse of *N. pompilius* was 42–47 per min before transfer into the pressure chamber

(A in Fig. 2), and the pulse rate was approximately the same before and after injection of oxygen gas in seawater. In the chamber the pulse rate at first fluctuated greatly, i.e. between 40 and 51 up to 28 kg/cm² corresponding to 273 m depth (B in Fig. 2), and between 42 and 74 with increasing mean up to 43 kg/cm^2 (419 m depth) (C in Fig. 2). The pulse rate then became less variable and to around 60 per min, and at 59 kg/cm² (575 m depth) began to slow down progressively up to the incidence of implosion (D in Fig. 2). The change of pulse rate of N. pompilius in the water tank (6000 m^3) of the Kamoike Marine Aquarium, Kagoshima 892, was also similar to this experiment, thus the rate was 42-43 at surface, 52 at 4 m depth, and 57-61 at 8 m, respectively (16.0°C of water temperature at 1:35-2:10 PM on 20th of January 1979). On the other hand, the hood of the animal unfolded, and did not react against increasing pressure on the miogram of the polygraphic recorder. The water temperature did not change significantly (14.4 to 15.6°C) during the experiment.

Discussion

Summarizing the above observations, the specimen of *N. pompilius* withstood a hydro-

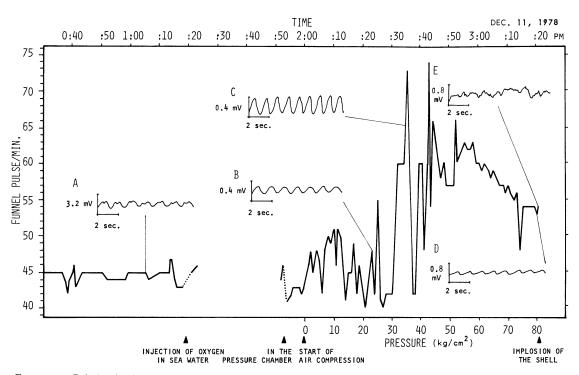


FIGURE 2. Relationship between funnel pulse of Nautilus pompilius and ambient pressure. A, . . . , E: funnel miograms.

static pressure of 8.05 MPa (785 m deep in the sea) and was then killed by implosion of the shell. The corresponding ocean depth of 785 m is greater than the catch records of living *Nautilus* (Hoyle 1886, Denton and Gilpin-Brown 1966; Hamada and Mikami 1977; Haven 1977; Ward et al. 1977; Westermann and Ward 1980) and also experimentally observed strength of the mature beached shells (Denton and Gilpin-Brown 1966; Raup and Takahashi 1966). This result approximately agrees with the implosion of living

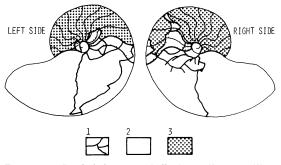


FIGURE 3. Imploded mature shell of *Nautilus pompilius*. 1: crack, 2: partial collapse, 3: complete collapse or powdered.

N. pompilius at the depth of 750–900 m in the Fiji sea by Ward. Consequently, the depth limit of mature N. pompilius can be assigned to the previous estimates of shell strength which have been used in the paleobathymetry of extinct nautiloids and ammonoids with similar shells. The animal can not prevent implosion by the cameral liquid removal system (Ward 1979) or increasing internal gas pressure with the simulated compression rate (9.7 m depth/min). The shell implosion has occurred at the last septum of the phragmocone or the siphuncular tube based on the imploded situation, which is therefore the weakest part of the shell. The collapse of the shell can be clearly distinguished from breakage due to wave action, the latter usually affecting the living chamber, then ventral and lateral walls of phragmocone (Hamada 1964). The funnel pulse corresponding to respiratory rate of N. pompi*lius* fluctuated greatly with pressurization, thus the animal violently reacted under increasing pressure including increased partial pressure of oxygen with this compression rate. This result suggests that *Nautilius* undergoes severe stress during rapid descent and ascent through the water column.

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