In Eq. 5 σ is the electrical conductivity of the medium (in siemens per meter); μ is the medium's relative magnetic permeability; ϵ_0 is the dielectric constant in free space (in farads per meter); and μ_0 is the magnetic permeability in free space (in henrys per meter). For soils low in magnetic material, $\mu = 1$ and Eq. 5 becomes

$$\alpha = \frac{60\ \pi\sigma}{\epsilon^{1/2}} \quad (6)$$

Combining Eq. 4 and 6 yields the medium electrical conductivity as

$$\sigma = \frac{\epsilon^{1/2}}{120\pi L} \ln \frac{V_T}{V_R} \quad (7)$$

Under conditions for which t is measurable, ϵ is known by Eq. 3. Equation 7 can then be used to calculate σ by TDR.

The relation between σ and soil water electrical conductivity, σ_w, is given by (*6*)

$$\sigma = \sigma_w \theta T(\theta) + \sigma_s \quad (8)$$

where θ, $T(\theta)$ and σ_s are, respectively, the soil water content, soil water transmission coefficient, and solid-phase conductivity. Values for these coefficients are available for a fine sandy loam (Indio, coarse-loamy, mixed, thermic haplic durixeralfs), which is similar to the soil used in this investigation (Arlington, coarse-silty, mixed hyperthermic typic torrifluvents), and are given by

$$T = 1.29\theta - 0.116 \quad (9)$$

and $\sigma_s = 0.25$ dS/m.

In order to compare the TDR determinations of the σ values as predicted from Eq. 7 with those described by Eq. 8, we brought ten soil columns to equal water contents, using waters of ten different σ values. Twenty-five days after infiltrating each column with waters of known electrical conductivities, we made TDR measurements of t, V_T, and V_R. Then we determined the average volumetric θ for each column by sampling in 5-cm depth intervals. In order to obtain the average σ_w value we took another set of soil samples and extracted the soil water by centrifuging. We then measured the σ_w values of the extracts by using a standard conductivity bridge.

During the time period allowed for each column to come to an equilibrium distribution of water content, a dissolution of residual salts occurred. This was reflected in a measured increase in the σ_w at the end of the experiment. The value of σ_w ranged from 0.8 to 11.1 dS/m, whereas the average volumetric θ for the ten columns was fairly constant at 0.34 ± 0.01. The average value of ϵ was 19.48 ± 0.53; this value is in good agreement with that determined by Topp *et al.* (*4*), (that is, 19.57), for a number of different soils, all at a $\theta = 0.34$. The effect of the large variations in the σ values of the media thus has a negligible effect upon the determinations of θ.

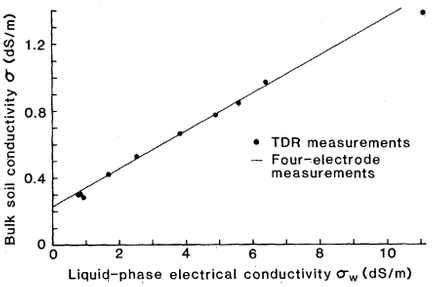

Fig. 2. The relation between bulk soil electrical conductivity and soil water electrical conductivity, as determined by four-electrode measurements (Eq. 8) and TDR measurements (Eq. 7).

Figure 2 compares the two determinations of σ as a function of σ_w. The solid line is a plot of Eq. 8; we calculated the positions of the data points from Eq. 7, using the values measured from the ten soil columns. The close agreement between the two determinations demonstrates that TDR can be used to obtain bulk medium σ and volumetric θ values with a single probe. Since the probe is spatially sensitive to the average ϵ and σ between the rods, water and solute distributions can be monitored if the probes are placed in a horizontal orientation at specified vertical intervals. Alternatively, vertical installations with probes of various lengths can yield average quantities over those lengths insofar as the soil σ does not completely attenuate the signal.

Only recently has bulk medium σ been used to estimate the pore-water σ. Even in the best instances, two separate measurements are necessary in order to determine θ and pore-water σ. Thus, when TDR is used in conjunction with known relations between medium σ and σ_w, it provides a powerful new tool in soil water research because a single measurement can yield both θ and the soil water salinity.

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References

1. W. H. Gardner, in *Methods of Soil Analysis*, C. A. Black, Ed. (American Society of Agronomy, Madison, Wis., 1965), vol. 1, pp. 82–127.
2. C. A. Bower and L. V. Wilcox, *ibid.*, vol. 2, pp. 933–951.
3. H. Fellner-Feldegg, *J. Phys. Chem.* **73**, 616 (1969).
4. G. C. Topp, J. L. Davis, A. P. Annan, *Water Resour. Res.* **16**, 574 (1980).
5. ———, *Soil Sci. Soc. Am. J.* **46**, 672 (1982).
6. J. D. Rhoades, P. A. C. Raats, R. J. Prather, *ibid.* **40**, 651 (1976).

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Nautilus Growth and Longevity: Evidence from Marked and Recaptured Animals

Abstract. *Study of* Nautilus belauensis *in its natural habitat in Palau, West Caroline Islands, shows that growth is slow (0.1 millimeter of shell per day on the average) and decreases as maturity is approached and that individuals may live at least 4 years beyond maturity. Age estimates for seven animals marked and recaptured between 45 and 355 days after release range from 14.5 to 17.2 years. These data indicate that the life-span of* Nautilus *may exceed 20 years and that its life strategy is very different from that of other living cephalopods.*

There has been considerable interest in the growth rate of *Nautilus* as a measure for estimating growth rates, lifespan, and timing of ontogenetic events in such fossil groups as the ammonoids and nautiloids. Diverse approaches have been used to estimate *Nautilus* growth rates; Oliver Wendell Holmes, for instance, suggested a rate of one chamber per year (or about 32 years to maturity) (*1*), which may be closer to fact than more recent projections. Other estimates, based on aquarium records of animals maintained in captivity (*2*), chamber partial gas pressures (*3*), shell radionuclide half-lives (*4*), and growth line counts (*5*), have ranged from 13 to 75 days per chamber (about 2 to 6 years to maturity). Longevity has not been the subject of such speculation; most cephalopods die after reproducing, and *Nautilus* has not been assumed to be an exception.

Reliable data on growth of animals in their natural habitat has not been available. The deep habitat of *Nautilus* limit-

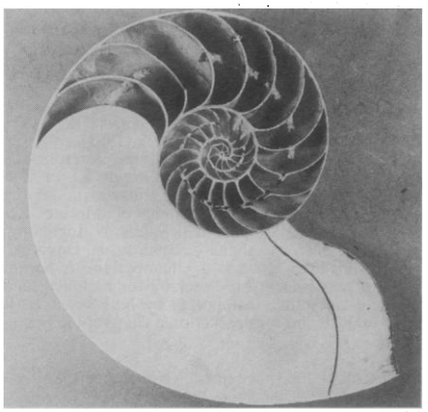

Fig. 1. Sectioned shell of *Nautilus belauensis* Saunders, 1981 (specimen E in Table 1), showing shell growth increment formed after the animal was tagged and released. Inked line marks aperture at time of release (5 July 1981); specimen was recaptured 342 days later.

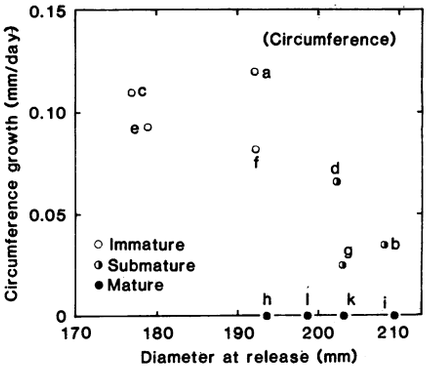

Fig. 2. Daily circumferential shell growth of *Nautilus belauensis* (growth increment/growth interval after release) as a function of shell diameter at release. Relative maturity at release is indicated by shaded circles. Animals h–l were mature at release and showed no growth when recaptured 3 and 4 years later.

ed direct study of these animals until it was discovered that *Nautilus* could be trapped at depth, released, and recaptured (*6*). Data on the capture, marking, and recapture of more than 2000 specimens of *Nautilus belauensis* Saunders, 1981, from 5 years (1977–1982) of study in Palau, West Caroline Islands (*7*), now provide information on growth and longevity of *Nautilus* in its natural habitat. *Nautilus* grows more slowly than had been thought, particularly as it approaches maturity, and lives for at least several years beyond maturity.

Seven animals that were immature or submature when released were recaptured after intervals ranging between 45 and 355 days (Table 1). Data on circumferential shell growth were recorded because this is readily measured and is the only measurement for which data on *Nautilus* held in aquariums are available. Shell growth varied from animal to animal, depending on relative maturity at release and duration of the growth interval (Fig. 1). Dated growth increments show that animals at similar stages of maturity grow at similar rates; average ventral shell growth for immature animals was 0.1 mm per day (a projected mean annual increment of 36.5 mm), whereas that for submature animals (nearly full size but lacking such mature characters as thickened aperture) (*6*, *7*) was 0.04 mm per day (or 14.6 mm annual increment).

A standard index of growth is the relative increase in size, which can be expressed as a percentage of size at release (*8*); from these values annual percentage rates can be estimated and used to compare shorter-term growth rates (45 to 82 days) with those for longer periods (330 to 355 days). Immature animals (at release) showed substantially higher relative annual growth (mean 6 percent) than those that were submature at release (mean 2.1 percent) (Fig. 2).

Because the growth rates were derived from relatively large specimens of *N. belauensis*, they must be used cautiously in estimating growth rates for very young animals and in projecting an overall growth rate. There is a rapid decrease in growth rate as maturity is approached, as shown by the relation of growth rates to diameter (a general measure of maturity). This indicates that neither absolute nor relative growth is constant and that the terminal portion of the growth curve of *Nautilus* decreases markedly during secretion of the last whorl.

Estimates of the rate of chamber formation in *Nautilus*, from specimens of *N. macromphalus* held in aquariums, are about 30 days per chamber and 70 to 120 days per chamber (*2*); radioisotope dating has yielded two estimates, 23 and 75 days, in *N. pompilius* (*4*). Among the specimens of *N. belauensis* described in Table 1, only two secreted septa after release. One, which was immature at release but fully mature when recaptured, had secreted and thickened the final septum in the 342-day interval after release, indicating that growth had stopped before recapture (Fig. 1). A second animal, submature when recaptured after 353 days, had added a single septum. Although apertural shell growth was still evident at the time of recapture, this animal had already deposited and thickened the final septum. Thus, an extensive period of time, approximately 1 year, is required for the final stages of growth.

Table 1. Records of growth data and calculated daily and annual growth and age estimates of seven *Nautilus belauensis* marked and recaptured in Palau, West Caroline Islands. The dates are those of release and recapture for each specimen. The relative stages of maturity at release and recapture are immature (I), submature (S), that is, immature but approaching maturity, or fully mature (M) with final growth achieved. The weight is that of body and shell in air; diameter is the maximum shell diameter; and circumference is the ventral shell circumference, aperture to protoconch (from cross section). Daily growth represents the absolute daily rate (growth increment/days). Estimated age is based on highest growth rate observed (total shell circumference, 43.8). Annual growth represents the absolute annual rate (growth increment/days) (365).

Specimen	Dates	Stage	Weight (g)	Diameter (mm)	Circumference (mm)	Age estimate (years)	Growth (mm)	
							Daily	Annual
A	25 May 1982	I	1185	192.2	680.2			
	14 August 1982	S		196.5	690.1			
(Net)	82 days			4.3	9.9	15.8	0.12	43.8
B	5 July 1981	S	1422	208.2	741.5			
	5 August 1982	M	1406	212.8	753.0			
(Net)	330 days		−16	4.5	11.5	17.2	0.035	12.7
C	30 May 1982	I	1064	177.0	627.9			
	15 July 1982	S	867	178.4	633.0			
(Net)	46 days		−164	1.4	5.1	14.5	0.11	40.15
D	29 May 1982	S	1270	202.3	726.3			
	17 July 1982	S	1244	203.0	729.3			
(Net)	45 days		−26	0.7	3.0	16.7	0.066	24.33
E	5 July 1981	I	1162	179.0	632.7			
	12 June 1982	M	988	189.8	664.5			
(Net)	342 days		−174	10.8	31.8	15.2	0.093	33.93
F	20 June 1981	I	1253	192.3	696.6			
	8 June 1982	S	1210	204.1	725.5			
(Net)	353 days		−43	11.8	28.9	16.6	0.082	29.88
G	8 June 1981	S	1230	203.0	700.6			
	29 May 1982	M	1298	204.8	709.6			
(Net)	355 days		68	1.8	9.0	16.2	0.025	9.25

It has been suggested that the external shell growth lines of *Nautilus* are laid down daily (and these lines have been used as a basis for arguments about lunar orbital evolution) (*5*). However, the growth lines are difficult to count because of the wide variation in relief and spacing. The number of growth lines on the dated increments of *N. belauensis* ranges from 1 to 2.7 per millimeter of shell across the venter. In time, these represent from 4 to 25.4 days per growth line (mean, 10.6 days); the four youngest animals (at release) show less variation—4 to 8.2 days per growth line (mean, 6.8 days). These values clearly contradict summary claims of daily growth lines in *Nautilus* (*5*).

These records show that in its natural habitat *Nautilus* grows more slowly than had been thought. Estimates derived from *Nautilus* growth rates in aquariums are higher than those reported here; daily rates of 0.15 mm (*2*), 0.25 mm (*2*), and 0.15 to 0.25 mm (*9*) were reported for *N. macromphalus* and *N. pompilius*, whereas the highest growth rate observed for a marked specimen of *N. belauensis* was 0.12 mm per day. The data from captive animals may be high because the animals had regular and often unlimited food and were all younger than the animals that were marked and released. Thus, the highest rate (0.12 mm per day or 43.8 mm per year) from a submature animal is used as an average approximation and gives age estimates ranging from 14.5 to 17.2 years for the seven specimens of *N. belauensis* in Table 1.

Nautilus exhibits determinate growth, reaching a mature stage after which there is no more growth. There is evidence of considerable longevity beyond maturity: one animal, caught 4 years after it had been logged as mature and released, had not grown during the intervening period. It is likely that *Nautilus* lives 5 to 10 years after reaching maturity, and its life-span may be greater than 20 years. This is in striking contrast to the relatively short life-span of most squids and octopods and provides another line of evidence of the great contrast in life strategies between the once successful and often dominant ectocochliate cephalopods and the modern dibranchiates (*10*).

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References and Notes

1. O. W. Holmes, *The Autocrat of the Breakfast Table* (Houghton Mifflin, Boston, 1858).
2. A. W. Martin *et al.*, *Neues Jahrb. Geol. Palaeontol. Abh.* **156**, 207 (1978); P. Ward *et al.*, *Paleobiology* **7**, 481 (1981).
3. E. J. Denton and J. B. Gilpin-Brown, *J. Mar. Biol. Assoc. U.K.* **47**, 723 (1966).
4. J. K. Cochran, D. M. Rye, N. H. Landman, *Paleobiology* **7**, 469 (1981).
5. P. G. K. Kahn and S. M. Pompea, *Nature (London)* **275**, 606 (1978).
6. W. B. Saunders and C. Spinosa, *Science* **204**, 1199 (1979).
7. In Palau, *N. belauensis* occurs on forereef slopes, at depths of 90 to 500 m. Of the 2387 animals trapped, processed, and released between 1977 and 1982, 300 were released in 1977, 424 in 1978, 233 in 1979, 452 in 1981, and 978 in 1982. All had first been weighed, measured, and sexed, and their relative maturity recorded. Each shell was numbered with an adhesive label or engraved number near the umbilicus. After processing, they were released at depths of 15 to 50 m on the reef face above the trap site [W. B. Saunders, *Veliger* **24**, 1 (1981); _____ and C. Spinosa, *Paleobiology* **4**, 349 (1978)].
8. W. H. Everhart and W. D. Youngs, *Principles of Fishery Science* (Cornell Univ. Press, Ithaca, N.Y., 1981); G. G. Simpson, A. Roe, R. C. Lewontin, *Quantitative Zoology* (Harcourt, Brace & World, New York, 1960).
9. P. D. Ward and J. Chamberlain, *Nature (London)* **304**, 57 (1983).
10. M. J. Wells, *New Sci.* **100**, 332 (1983).
11. This research was based at the Micronesian Mariculture Demonstration Center, Koror, Palau, West Caroline Islands, and was under the auspices of the Department of Marine Resources, with support of T. Paulis, N. Idechong, and F. Perron. I thank C. Spinosa, L. Davis, G. Heslinga, G. Monaco, J. Chamberlain, A. Swan, and particularly M. Weekley for technical and field assistance. Supported by NSF grant EAR 81-00629 and by the National Geographic Society.

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Inhibition of Aldosterone Production by an Atrial Extract

Abstract. *Crude extracts of rat atria reduced the basal amount of aldosterone released from rat zona glomerulosa cells and partially inhibited aldosterone stimulation by adrenocorticotropic hormone and angiotensin II. The destruction of this activity by trypsin suggests that the active factor is a peptide, possibly atrial natriuretic factor. These data suggest that atrial natriuretic factor affects sodium excretion by the kidneys both directly and through the inhibition of aldosterone production.*

Peptides contained in mammalian atria are reported to affect kidney function (*1–6*) and smooth muscle relaxation (*7, 8*). Atrial extracts injected into rats induce a prompt natriuresis and diuresis (*1–6*). The site of action of the atrial extracts in the kidney is primarily the medullary collecting duct (*2*). Mammalian atrial cardiocytes contain specific granules resembling those found in peptide-secreting cells of endocrine organs (*9*). These granules are probably storage sites for the atrial natriuretic factor (*10, 11*). In the rat, the number of granules changes when water and electrolyte balance are altered (*12, 13*). Adrenalectomy causes a slight increase in atrial granularity, and administration of 1 percent sodium chloride to adrenalectomized rats decreases atrial granularity (*12*). The atrial natriuretic factor is heat-stable and trypsin-sensitive (*3, 7, 13*). Recent characterization of this factor indicates that there are two low-molecular-weight peptides, atriopeptin I and atriopeptin II, containing 21 and 23 amino acids residues, respectively. Both of these peptides have potent natriuretic, diuretic, and vasorelaxant activities, and both appear to derive from a common precursor of molecular weight 20,000 to 30,000 (*8*).

Earlier studies on the control of aldosterone secretion suggested that an inhibiting system regulates secretion. In 1958, Mills *et al.* (*14*) reported increased aldosterone secretion in the dog during constriction of the inferior vena cava and decreased secretion when the constriction was released; sectioning the cervical vagi did not affect the increase in secretion but prevented the decrease. In 1959, Anderson *et al.* (*15*) showed that stretching of the right atria inhibited aldoster-

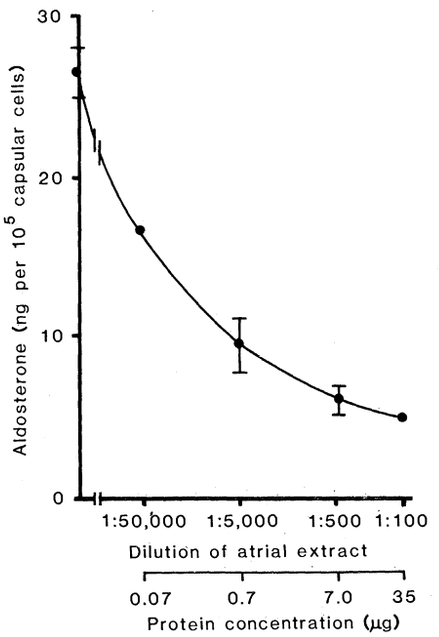

Fig. 1. Inhibition of secretion of aldosterone from unstimulated capsular cells by an atrial extract. The point without atrial extract and the points of 1:5000 and 1:500 dilution of the atrial extract each represent the mean ± standard error of five experiments. The other two points show the mean of duplicate incubations in one experiment. One milliliter of incubation Medium 199 contained a final dilution of atrial extract as indicated on the abscissa. Immediately beneath the dilution is shown the amount of atrial extract protein that was added to 1 ml of incubation media for a given dilution.