

# Allometric Changes During Growth and Reproduction in *Eleutheria dichotoma* (Hydrozoa, Athecata) and the Problem of Estimating Body Size in a Microscopic Animal

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**ABSTRACT** Changes in body morphology during growth and reproduction in the hydromedusa *Eleutheria dichotoma* are described in terms of variations in eight different characters: umbrella diameter, total surface area, tentacle area, umbrella area, tentacle knob diameter, number of embryos, and diameter and area of buds. Sexually (sex) and vegetatively (veg) reproducing medusae differ significantly in their body morphometrics. Statistically significant allometric relations exist between umbrella diameter and 1) central area (sex and veg); 2) tentacle area (veg); 3) total area (veg); 4) tentacle knob diameter (veg); 5) bud diameter; and 6) number of embryos. A significant correlation between umbrella diameter and area is also found in undetached buds. During sexual reproduction, umbrella area shows positive allometry and loses its correlations to total area, tentacle area, and tentacle knob diameter. Linear and nonlinear bivariate allometric coefficients allow estimation of total body size from only one or two easily measurable attributes, e.g., umbrella and tentacle knob diameter. Curve fitting by the classic allometric equation ( $y = bx^c$ ) is only negligibly worse than that obtained with a "full" equation ( $y = a + bx^c$ ), and statistical confidence is better.

Chemical analyses for carbon and nitrogen content allow estimation of biomass from the projection area of the body surface. The relation factors are  $1.06 \mu\text{gC mm}^{-2}$  (sex) and  $1.14 \mu\text{gC mm}^{-2}$  (veg) for carbon and  $0.293 \mu\text{gN mm}^{-2}$  (sex) and  $0.287 \mu\text{gN mm}^{-2}$  (veg) for nitrogen. The C:N ratios are 3.6 and 4.0 for sexual and vegetative medusae, respectively. The use of allometric regression formulas to calculate surface areas and to relate these to carbon content provides quick estimations of body size in a microscopic animal.

The size (magnitude of a given dimension) and the shape (the relation among dimensions) of organisms are important considerations for understanding morphology in a biological context. Allometric measurements are useful biological tools. They allow one to discriminate among species (e.g., Baxter and James, '86; Paine, '86) and to identify and understand specific functional adaptations (Strauss, '84) and nonadaptive variation (Gould, '84).

The medusa of *E. dichotoma* has an umbrella diameter of less than 0.5 mm and is one of the tiniest known species. This sessile anthomedusa lives attached to the green alga *Ulva* in very shallow coastal waters and is incapable of swimming. It reproduces both sexually by eggs and sperm and vegetatively (i.e., asexually by a polycytogenic process) by budding off young medusae from the

ring canal in the inter-radial areas of the exumbrella (Hauenschild, '56, '57b). Its unusual lifestyle and its capability of reproducing sexually as well as asexually are correlated to morphological attributes (e.g., Lengerich, '23). Only a few metazoan species have one individual capable of reproducing either by a sexual or by a vegetative asexual mode, i.e., displaying an "alternation of reproductive modes." In *E. dichotoma* the latter is integrated as a facultative element in the generally two-stage metagenetic alternation of generations. Recent discussions about "the evolution of sex" are mainly theoretical and lack an empirical basis, which is badly needed (for an overview, (see Stearns, '87; Michod and Levin, '88). If morphology has ecological

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consequences, morphometric studies on species like *E. dichotoma* might lead to an understanding of some basic advantages and disadvantages of sexual and asexual reproduction.

A "normal" medusa of *E. dichotoma* has six bifurcated marginal tentacles. Only Krumbach ('07) reports a prevalent number of five marginal tentacles for this species, whereas in my cultures specimens with five tentacles were rare and omitted from the investigations. From the two branches of each marginal tentacle, the orad-orientated "walking tentacle" ends in an adhesive disk that attaches the medusa to its substrate. The aborad-orientated "catching tentacle" ends in a knob of nematocysts and is responsible for catching the prey. The mesoglea is reduced, and an ectodermal umbrella cavity or a brood pouch is developed in which the embryos grow to the planula stage (see Fig. 1 below). As a result, the space between the ectodermal and entodermal layers does not allow the development of an antagonistic force during contractions of the epidermal muscular system, as needed for swimming.

Determination of body size, e.g., expressed as body weight in grams, is difficult to obtain for microscopically small animals when direct weighing on a balance is often not possible. (for reviews of the problem of expressing biomass, see Winberg, '71; Omori and Ikeda, '84). One often has to measure body surface areas to obtain an estimation of size. One common method is to photograph the animals, cut out the appropriate images, and measure the paper weight as an estimation of body surface area. The greatest disadvantage of this and other methods is that they are very time consuming. An alternative method, realized in this study, is to estimate body surface area from allometric equations derived by calculating the relevant allometric coefficients and exponents from measurements of various components of the organism. Here, the choice of an appropriate allometric model is important. Additional carbon and nitrogen analyses allow estimations of biomass.

The main aims of the present investigation were 1) to study the body morphometrics of *E. dichotoma* in detail and to provide simple allometric equations for obtaining rapid estimations of body size for further experimental studies, the main criterion therefore being utility (e.g., Gould, '66); 2) to estimate biomass from the surface area; 3) to compare the

usefulness of a simple classic allometric model (Huxley, '32; Huxley and Teissier, '36) with that of a so-called full model (e.g., Albrecht, '87); and 4) to study the impact of the mode of reproduction on body morphometrics.

#### MATERIALS AND METHODS

Measurements were performed on two different clones ( $\beta$  and  $\gamma$ ) of the medusa stage of *E. dichotoma* Quatrefages. The material was collected from the Mediterranean at Banyuls-sur-Mer (France) during August and September 1986. Culturing of each clone was started with one primary medusa, i.e., a medusa directly budded from the polyp. Feeding rate was set at four times per week until the clone size was about 50 animals. Feeding was then reduced to three times per week. Further details of culturing conditions are presented elsewhere (Hauenschild, '86). All measurements were performed on medusae that were starved for 24 to 28 hr.

Resting medusae in a normal position (see Fig. 1 below) were observed in vivo from the aboral side through a binocular microscope at  $\times 50$  magnification. There was no need to immobilize the motiveless sitting medusae. All line and area measurements were obtained with the aid of a graphic tablet. The tablet was connected to an IBM-compatible personal computer supplied with special "Hi-pad" software. It should be noted that the term *area* here means the two-dimensional projection area unless otherwise stated. The following dimensions were measured for each medusa: diameters of umbrella, tentacle knobs, and buds; areas of umbrella, tentacles, and buds; and lengths of the tentacles. In sexual medusae, the embryos in the brood pouch were also counted. Medusae were considered to be sexual if embryos but no buds were present; they were considered to be vegetative if only buds were present. Medusae in which both embryos and buds were present as well as those having neither buds nor embryos were omitted from the measurements since they were relatively rare (both together less than 10%).

For the statistical analysis, BMDP (Biomedical Computer Programs) software (BMDPAR, BMDP4R, BMDP3S) was used (e.g., Dixon, '83). The convergence criterion for nonlinear regressions was set to 0.00001. No constant limits were set to optimize curve fitting predominantly for the empirical measuring range. The Mann-Whitney U test

(one-tailed) was used to compare the different means between sexual and vegetative medusae. Parametric (Pearson) correlation coefficients and their levels of significance were calculated. To compare the curve fittings by the simple classic model with that by a "full" model, a deviation value (DV in %) was defined as follows:

$$DV = 100(\sqrt{RSS1} - \sqrt{RSS2}) / \sqrt{RSS1}, \quad (1)$$

where RSS1 is the higher value of the residual sum of squares, and RSS2 is the lower value.

Names and definitions used in the description of the morphological features of the medusa are as follows (Fig. 1): *Umbrella diameter* is the distance between two opposite ocelli; *tentacle knob diameter* is the diameter of the knob of the catching tentacle (since knob diameters of the walking tentacles were almost equal in size, but more difficult to see from an aboral view). *Area* always refers to the two-dimensional visible surface area (projection area) from an aboral

view; in vegetative medusae, areas are measured individually for buds and parent. *Tentacle area* is the sum of all six tentacles, unless otherwise stated. In those cases in which the walking tentacle branch was hidden by the catching branch, the area of the latter was measured twice. The hexagonal symmetry of the medusa shape is generally ideal, so that normally all three umbrella diameters as well as all six tentacle knob diameters are equivalent. Therefore, only two umbrella diameters and three tentacle knob diameters were measured for each medusa. The differences between these replicates were always less than 10% and on average less than 3%. Since one vegetative medusa had normally more than one bud, which were generally unequal in size, these had to be measured separately. *Bud diameter* is the largest diameter of the bud or its umbrella, in the case where tentacles were formed. All developmental stages of medusa buds, up to the final stages at which they are almost

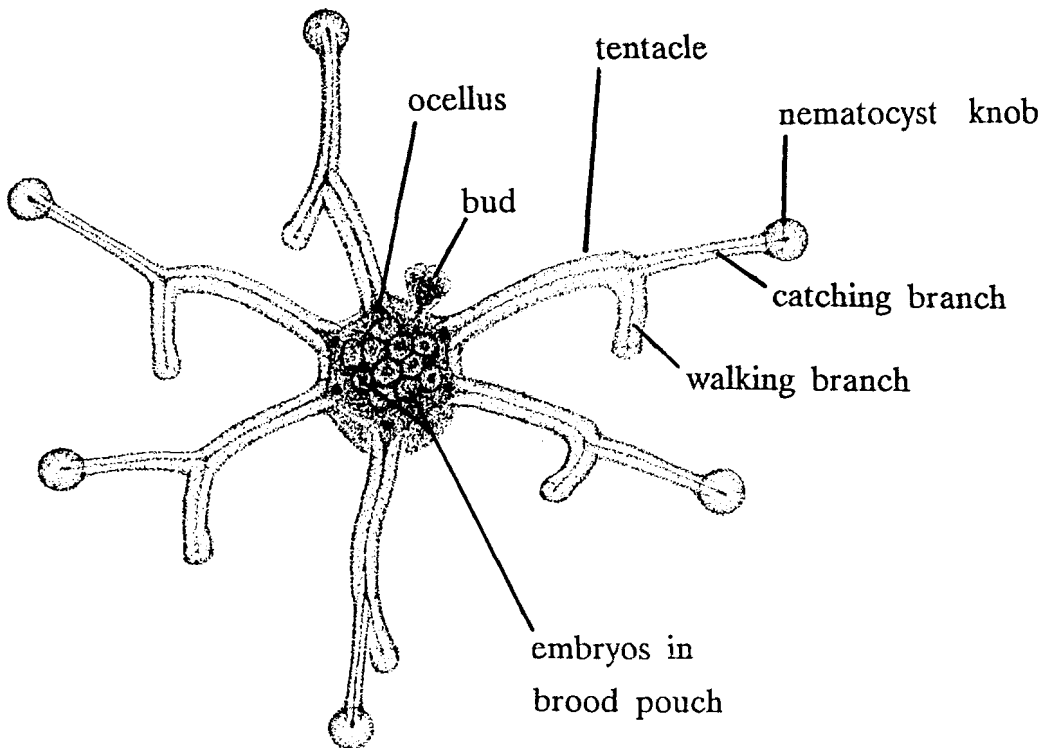


Fig. 1. Medusa of *E. dichotoma* reproducing both vegetatively and sexually at the same time, normally a rare event. Drawing from the aboral view of a living organism. About 25-fold magnification.

ready to separate from the parent, were included.

Determinations of carbon and nitrogen contents were performed with sample sizes between 24 and 38 medusae for one sample boat. The samples (whole aluminum boats) were oven-dried at 85°C for 5 hr, put into a chamber containing an atmosphere saturated with concentrated HCl for 8 hr, and then oven-dried again at 70°C for 8 hr before combustion. Samples were analyzed using a Perkin-Elmer 240C Elemental Analyzer. Results were recorded on a 0–1 mV recorder on a bar graph form (Fisher chart paper 13-939-37). When sample sizes of less than 0.5 mg dry weight were measured, carbon signals could be detected at 10-fold attenuation settings of the instrument, whereas nitrogen signals had to be measured at the highest sensitivity settings. Hydrogen signals were disregarded.

### RESULTS

No differences were detectable between the two clones  $\beta$  and  $\gamma$  ( $P > 0.05$ , U test), and the groups were pooled for statistical analyses.

As shown in Table 1, sexual (sex) medusae exhibit larger body sizes than do vegetative (veg) medusae. Enlargement is apparent not only in the umbrella (i.e., body center) but also in the tentacles. One-tailed Mann-Whitney U tests reveal that the difference in diameter between sexual and asexual medusae is significant at the  $P = 0.049$  level, while all the other differences in size presented in Table 1 are significant at  $P < 0.01$ . The mean tentacle length of vegetative medusae ( $0.76 \pm 0.220$  mm; range, 0.34–1.22 mm) does not differ significantly from that of sexual medusae ( $0.77 \pm 0.100$  mm; range, 0.55–0.95 mm); and the tentacle lengths do not show significant correlations to the diameters of either the umbrella or tentacles. The surface area covered by the tentacles is about 76 and 72%, respectively, for sexual and vegetative medusae. The umbrella area is only about 22% of the total area in both cases. The deviations of the total calculated areas from the theoretical 100% are taken to represent inaccuracies in the measurements.

Umbrella diameters range from 185 to 550  $\mu$ m in sexual medusae and from 211 to 437  $\mu$ m in vegetative medusae. In all cases a positive and statistically significant correlation exists between umbrella diameter and each of the other dimensions (see  $r$  values in Table 1). In asexual medusae, statistically significant

regression formulas exist for umbrella diameter versus umbrella area, tentacle area, total area, tentacle knob diameter, and bud diameter versus bud area (Figs. 2–7). Thus, the total area of an asexual medusa can be estimated by measuring the diameter of its umbrella and the diameters of its buds. In sexual medusae, regression formulas calculated for umbrella diameter versus tentacle area, total area, and tentacle knob diameter are not statistically significant (Figs. 3–5). However, the area of the umbrella is related significantly to the umbrella diameter (Fig. 2), and the area of the tentacles is related significantly to the tentacle knob diameter (Fig. 9). Thus, the total area of a sexual medusa can be estimated from combined measurements of the diameters of its umbrella and tentacle knobs. The statistically significant allometric coefficients and exponents required for the calculations are given in Table 2.

Comparison between the results obtained by applying the simple classic equation and those obtained with the “full” model equation is presented in Table 2. From the same data, the allometric exponents ( $c$ ) and the constants ( $a$  and/or  $b$ ), including their coefficients of variation, are given. As shown by the residual sums of squares (RSS), the mean square errors (MSE), and the deviation values (DV), nearly identical curve fittings are obtained with both models. The deviation values show that the mean distance between measurement values and regression curves is reduced on the average by less than 1% when the “full” model is used. Only the “full” model equation for  $TA_{veg} = f(UD)$  did not satisfy the convergence criterion because of reduction in the degrees of freedom.

The results of the carbon and nitrogen analyses are listed in Table 3. As indicated in Table 3, the nitrogen content per unit area is only 2% higher in sexual medusae, whereas the carbon content per unit area is about 9% lower. A statistical test to reveal possible differences between sexual and vegetative medusae could not be applied to the data since there are only three and four replicates, respectively. The given standard deviations provide estimations of the analytical measurement errors involved in the methods. The coefficients of variation are 13 and 9%, respectively, for nitrogen and carbon contents and are therefore higher than the observed differences between sexual and vegetative medusae.

TABLE 1. Summary statistics of measurements of sexual (sex) and vegetative (veg) medusae of *Eleutheria dichotoma*<sup>1</sup>

MR	N	Umbrella diameter (μm)	Umbrella area (μm <sup>2</sup> )	Tentacle area (μm <sup>2</sup> )	Total area (μm <sup>2</sup> )	Knob diameter (μm)	Embryos	Bud diameter (μm)	Bud area (μm <sup>2</sup> )
Sex	32	362.7 ± 73.87 <i>r</i> = 1.0	111,090 ± 42,396 <i>r</i> = 0.91**	387,286 ± 89,757 <i>r</i> = 0.55*	509,434 ± 122,642 <i>r</i> = 0.81**	113.7 ± 19.85 <i>r</i> = 0.74**	4.12 ± 1.88 <i>r</i> = 0.63**	—	—
Veg	45	334.9 ± 63.28 <i>r</i> = 1.0	86,798 ± 29,183 <i>r</i> = 0.91**	286,879 ± 158,921 <i>r</i> = 0.84**	395,982 ± 181,979 <i>r</i> = 0.89**	89.0 ± 20.31 <i>r</i> = 0.87** <i>n</i> = 27	—	134.1 ± 52.06 <i>r</i> = 0.50** <i>N</i> = 81	18,729 ± 16,718 <i>r</i> = 0.92** <i>N</i> = 81
U tests		<i>P</i> = 0.049	<i>P</i> = 0.006	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001	—	—	—

<sup>1</sup>MR, mode of reproduction; embryos, number of embryos in brood pouch. In the case of the tentacle knob diameters of vegetative medusae *N* is only 27 instead of 45 (18 values were lost because of a computer output error). Statistical parameters include means ± SD; *r* = correlation coefficient to umbrella diameter in all groups except bud area, in which *r* = correlation coefficient to bud diameter; *P* = level of significance.

\*Significance of *r* < .01.

\*\**r* < 0.001.

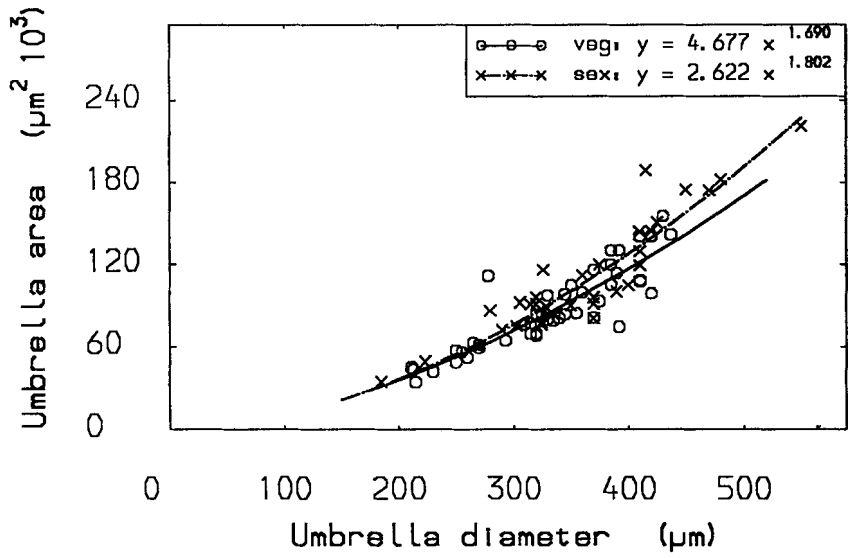


Fig. 2. *E. dichotoma*. Relation of umbrella area (projection area, see text) to diameter in vegetatively (veg) and sexually (sex) reproducing medusae. Each symbol represents one measurement; the equations for the nonlinear regression are given in the upper right corner.

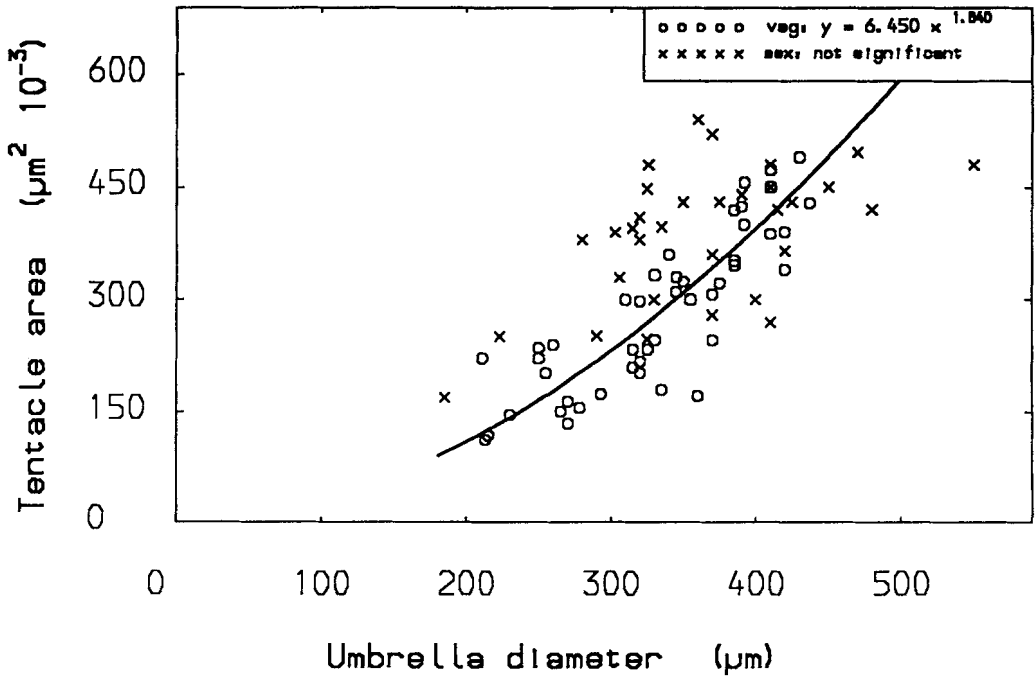


Fig. 3. Relation of tentacle area to umbrella diameter in vegetatively and sexually reproducing medusae of *E. dichotoma*.

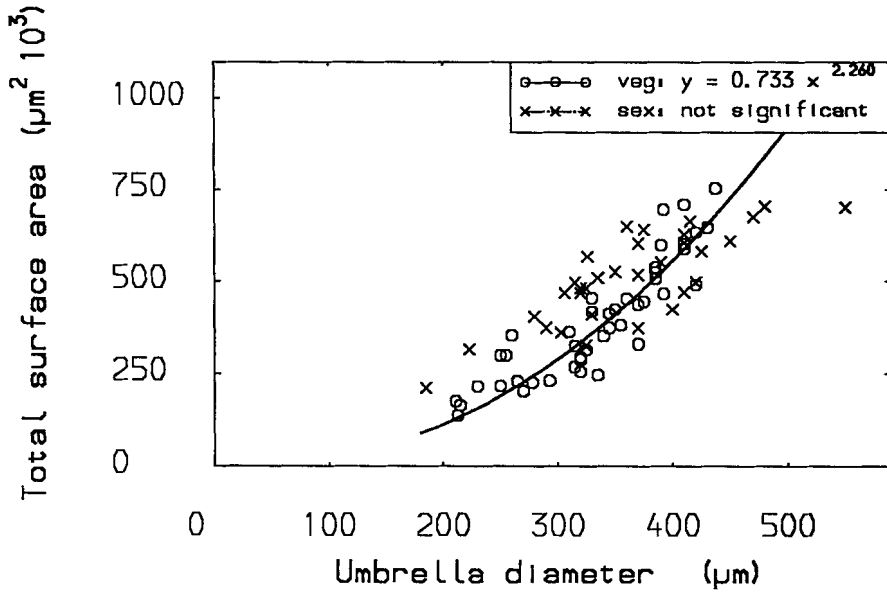


Fig. 4. Relation of total surface area (aboral view) to umbrella diameter in vegetatively and sexually reproducing medusae of *E. dichotoma*.

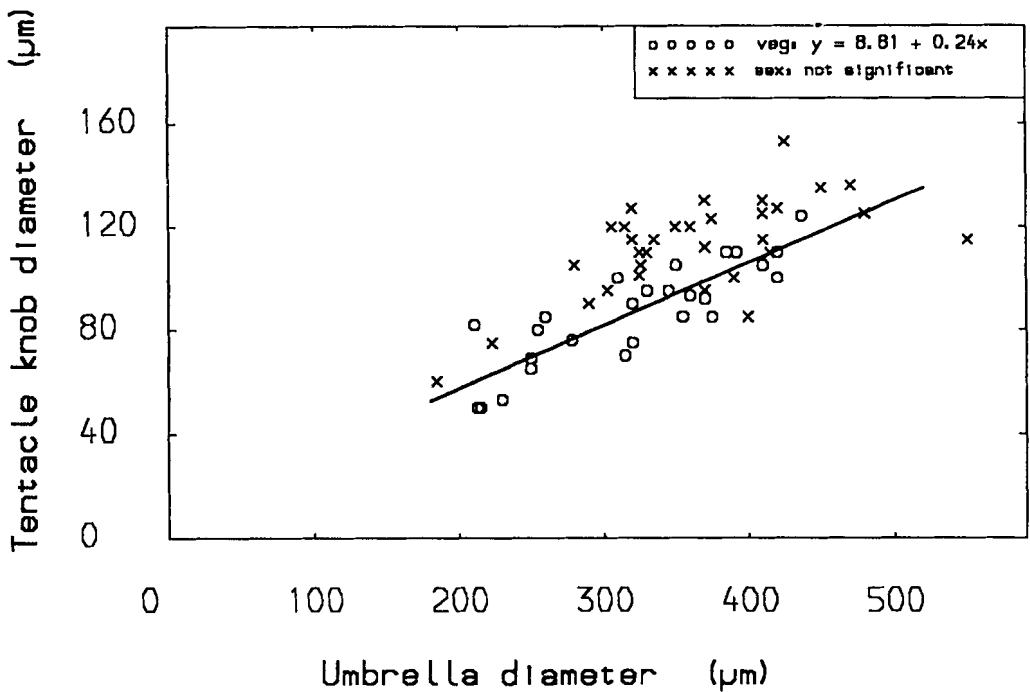


Fig. 5. Relation of tentacle knob diameter to umbrella diameter in vegetatively and sexually reproducing medusae of *E. dichotoma*.

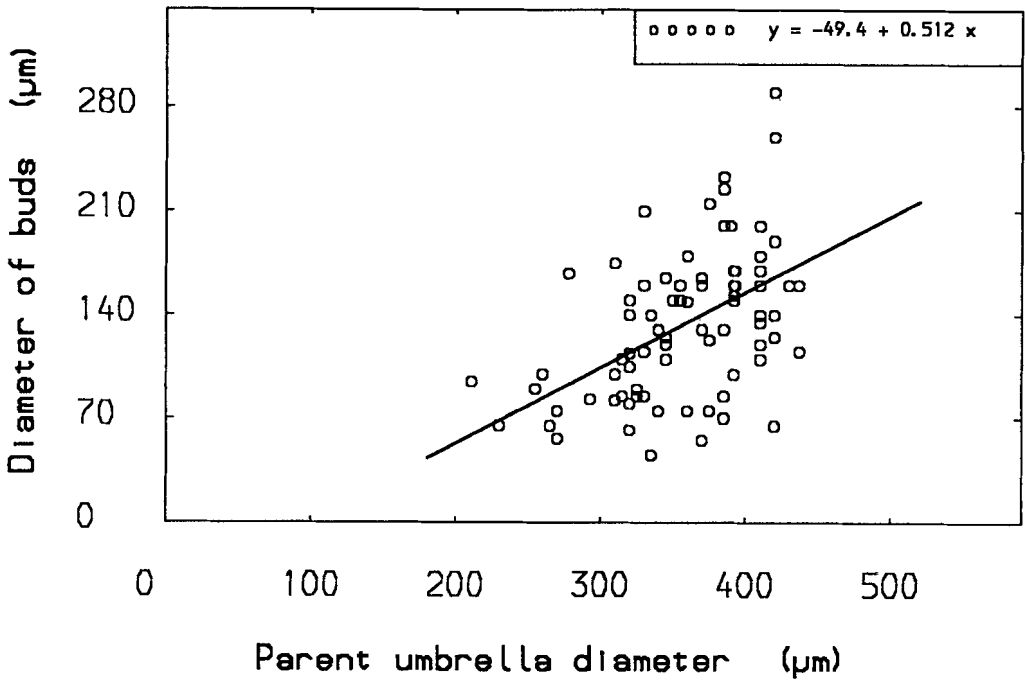


Fig. 6. Relation of bud diameter to parent diameter in vegetatively reproducing medusae of *E. dichotoma*.

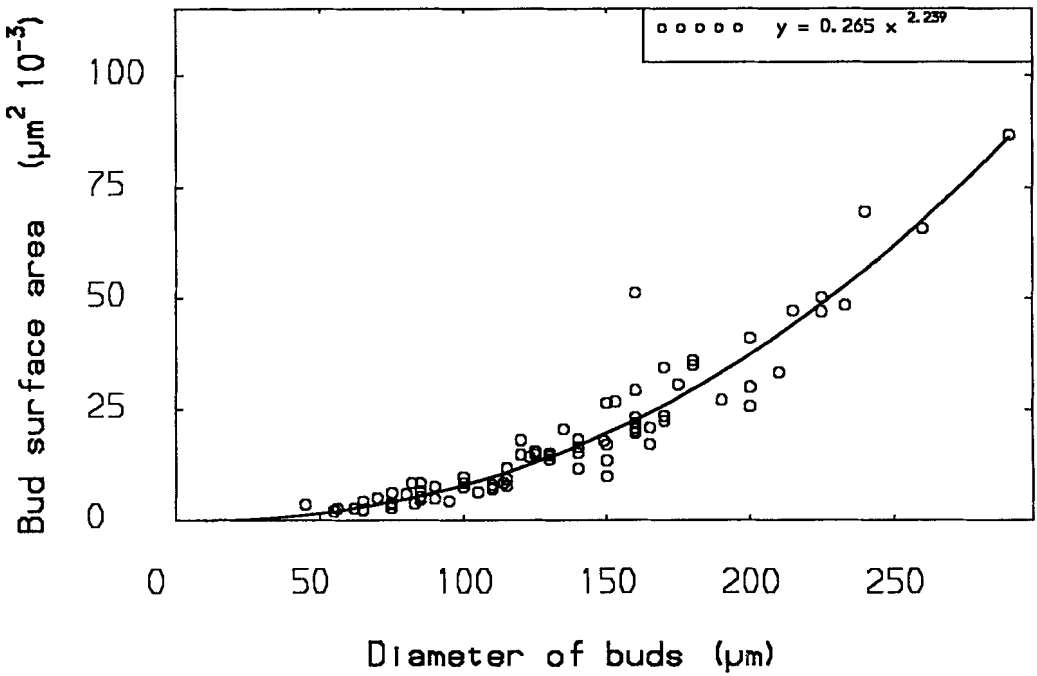


Fig. 7. Relation of bud surface area (lateral view) to bud diameter (buds attached to their parent).



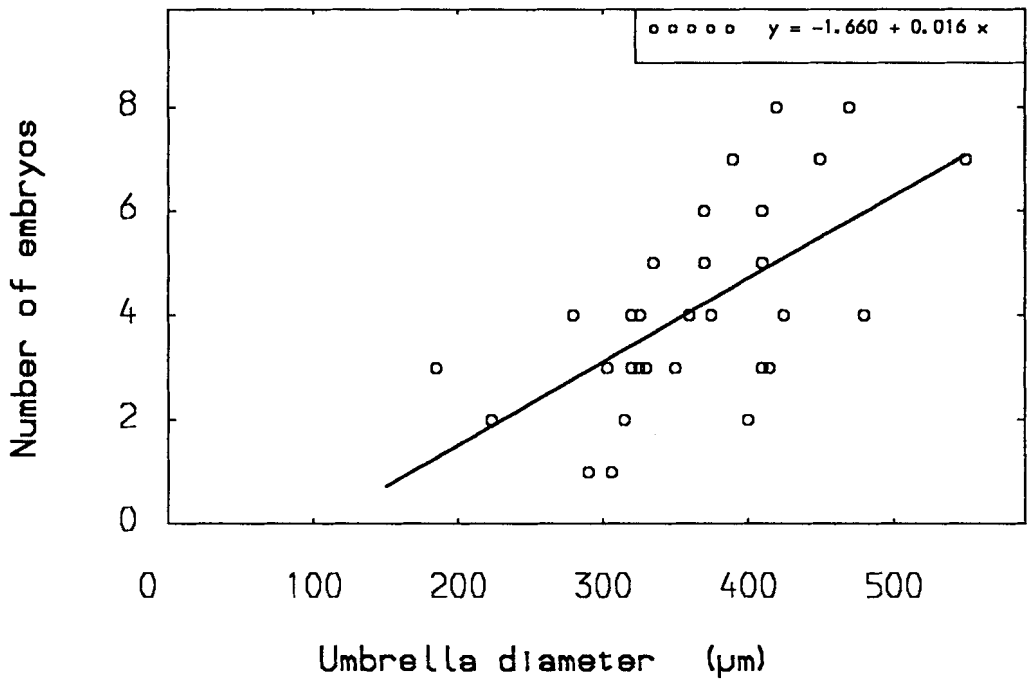


Fig. 8. Relation of number of embryos to parent umbrella diameter in sexual medusae of *E. dichotoma*.

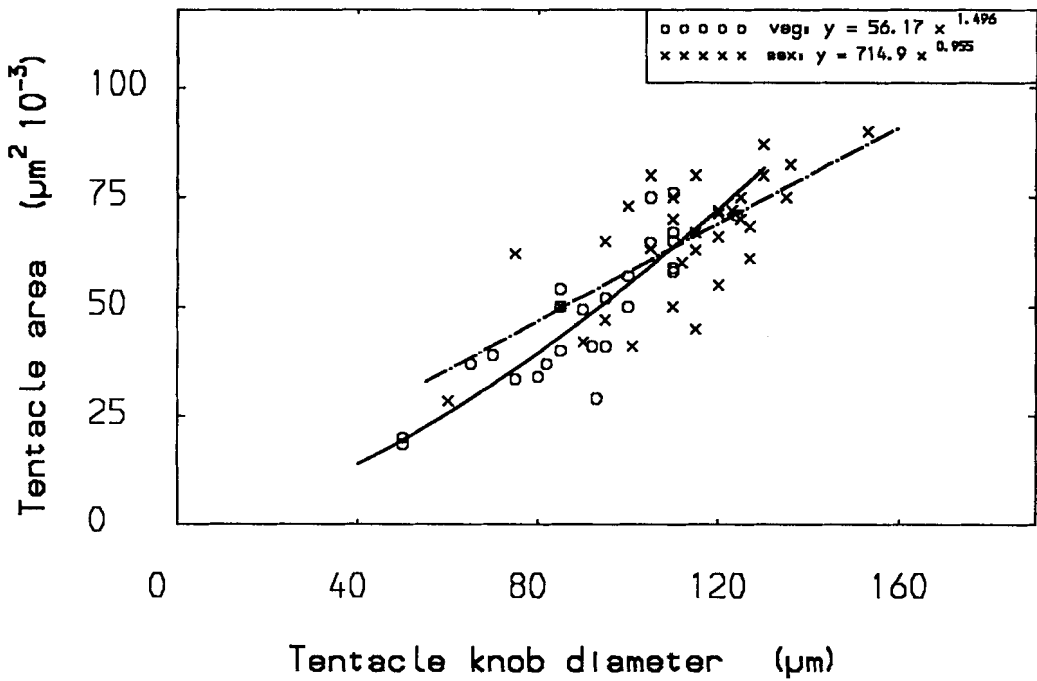


Fig. 9. Relation of tentacle area of a single tentacle to tentacle knob diameter in vegetative and sexual medusae of *E. dichotoma*.

TABLE 2. Comparison of the simple allometric model with a "full" exponential allometric equation for the statistically significant exponential relationships<sup>1</sup>

Allometric relation	Type of function	Parameter (cv)			RSS (10 <sup>11</sup> )	MSE (10 <sup>10</sup> )	DV (%)	DF
		a	b	c				
UA <sub>sex</sub> = f(UD)	y = a + bx <sup>c</sup>	11,855 (2.67)	0.783 (3.64)	1.990 (0.28)	30.83	10.63	0.21	29
	y = bx <sup>c</sup>		2.622 (0.82)	1.802 (0.08)	30.96	10.32		30
UA <sub>veg</sub> = f(UD)	y = a + bx <sup>c</sup>	25,510 (0.94)	0.046 (6.11)	2.422 (0.40)	31.76	7.563	0.64	42
	y = bx <sup>c</sup>		4.677 (0.17)	1.690 (0.10)	32.17	7.482		43
TTA <sub>veg</sub> = f(UD)	y = a + bx <sup>c</sup>	103,574 (0.61)	0.006 (6.65)	2.944 (0.37)	42.03	100.1	1.59	42
	y = bx <sup>c</sup>		6.450 (1.15)	1.840 (0.11)	43.40	100.9		43
TA <sub>veg</sub> = f(UD)	y = a + bx <sup>c</sup>	23,965 (6.45)	0.558 (29.4)	2.298 (0.45)	66.43	158.2	0.45	42
	y = bx <sup>c</sup>		0.733 (1.10)	2.260 (0.08)	67.03	155.9		43
BA = f(BD)	y = a + bx <sup>c</sup>	824 (2.71)	0.186 (1.09)	2.300 (0.08)	3.540	0.454	0.06	78
	y = bx <sup>c</sup>		0.265 (0.47)	2.239 (0.04)	3.544	0.449		79
TEA <sub>sex</sub> = f(TKD)	y = a + bx <sup>c</sup>	24,787 (1.50)	24.22 (7.84)	1.568 (0.94)	3.389	1.169	0.25	29
	y = bx <sup>c</sup>		714.9 (0.94)	0.955 (0.20)	3.406	1.136		30
TEA <sub>veg</sub> = f(TKD)	y = a + bx <sup>c</sup>	6,908 (3.36)	15.02 (5.27)	1.752 (0.59)	1.396	0.634	0.14	22
	y = bx <sup>c</sup>		56.17 (1.00)	1.496 (0.14)	1.400	0.609		23

<sup>1</sup>cv, Coefficient of variation; RSS, residual sum of squares; MSE, mean square error; DV, deviation value; DF, degrees of freedom; UA, umbrella area; UD, umbrella diameter; TTA, total tentacle area; TEA, tentacle area of a single tentacle; TA, total body area; BA, bud area; BD, bud diameter; TKD, tentacle knob diameter.

DISCUSSION  
*Allometric model*

The usefulness of allometric equations depends widely on the choice of the model, as shown in recent articles dealing with the relationship between processes of growth and evolution (e.g., Creighton and Strauss, '86; Somers '86; Blackstone, '87; Strauss, '85, '87) and the "sense and nonsense" of asymptotes in allometric growth equations (Knight, '68; Krüger, '69; Jean, '84; see also Ricker, '79).

The results presented in Table 2 indicate that the simple, classic model, as derived from Huxley ('32), can be more useful under some circumstances than a full model, as proposed, for example, by Albrecht ('87). Most of the published exponential allometric exponents were derived from the simple, classic model and are not directly comparable with the exponents derived from a full model. The use of the latter seems to be justified only when it leads to a distinct improvement in curve fitting.

TABLE 3. Relation of body surface areas to carbon and nitrogen contents in sexual and vegetative medusae of *Eleutheria dichotoma*<sup>1</sup>

MR	N	n	Area (mm <sup>2</sup> )	Nitrogen		Carbon		C:N
				µg ind <sup>-1</sup>	µg mm <sup>-2</sup>	µg ind <sup>-1</sup>	µg mm <sup>-2</sup>	
Sex	29 ± 6.4	3	0.501 ± 0.1203	0.147 ± 0.0115	0.293 ± 0.0229	0.530 ± 0.0608	1.058 ± 0.1210	3.6
Veg	26 ± 7.6	4	0.429 ± 0.0200	0.123 ± 0.0231	0.287 ± 0.0539	0.490 ± 0.0361	1.142 ± 0.0841	4.0

<sup>1</sup>Given are the means ± SD. MR, mode of reproduction; N, mean number of combusted animals per measurement; n, number of replicates; ind, individual; area, projection area, i.e., the total surface area as calculated from the simple classic allometric equations (2) and (3).

The allometric regression formulas depend on the geometrics of the body shape, which is the same for all observed clones of *E. dichotoma* over a broad range of body sizes. For the small percentage of individuals with abnormal tentacle numbers, however, the regressions are not valid.

#### Body size

Body size calculations are of basic importance for many kinds of physiological and ecological studies, e.g., productivity and respiration studies (e.g., McClatchie, '87; Grodzinski et al., '75). At present the controversy about the relationship between body size and basal metabolism is at one of its recurrent peaks (for review, see Donhoffer, '86a,b). It is unfortunate that until now measurements have been performed almost exclusively with certain protozoans and with a large number of coelomate metazoans, especially homeotherms. Hardly any data are available for the coelenterates, hydrozoa in particular (see also Hemmingsen, '60). This is probably due at least in part to the difficulties of determining body sizes in small hydrozoa. From all the normally used characters to express body size, e.g., body weight, body volume, and body surface area, the latter is used most often for very small organisms.

In medusae of *E. dichotoma*, the body morphometrics depend on the mode of reproduction. As stated in Results, the two-dimensional projection area of a vegetative medusa can be estimated from its umbrella diameter (UD) and from the diameters of its buds (BD;  $i = 1$  to  $n$ , where  $n$  is the number of buds per medusa). Therefore the suggested equation for a rapid in vivo estimation of the two-dimensional surface area derived from the simple, classic model is

$$\text{Area}_{\text{veg}} = 0.733 \text{ UD}^{2.260} + \sum_{i=1}^n 0.265 \text{ BD}_i^{2.239} (\mu\text{m}^2). \quad (2)$$

In sexual medusae the umbrella diameter as well as the tentacle knob diameter (TKD) have to be measured, and the suggested equation is the sum of umbrella area plus six times the area of one tentacle:

$$\text{Area}_{\text{sex}} = 2.622 \text{ UD}^{1.902} + 6(714.9 \text{ TKD}^{0.955}) (\mu\text{m}^2). \quad (3)$$

To estimate the real total surface area of the three-dimensional medusa body, its geometric simplicity allows an approximation of the body shape using simple geometric solids. If the tentacles are regarded as cylinders, the proportion between the two-dimensionally measured surface area and total cylinder area is given by the constant  $\pi$ . The umbrella can

be approximated by a short cylinder with a spherical cap at each end. Using longitudinal section drawings from Hartlaub (1886) and Lengerich ('23), as well as some videotapings, the total surface area of this solid was estimated to be about 3.8 to 4.3 times the two-dimensionally measured surface area of the umbrella. Thus values derived from the formulas (Fig. 2, 7, 9) can be transformed into three dimensional body areas simply by multiplying tentacle area by  $\pi$  and umbrella area by 4.

To obtain estimations of biomass from the calculated surface area one may use the carbon content to surface area relation, because carbon is the generally more constant fraction in animal composition and because of the smaller coefficients of variation for carbon determination in this study. The suggested equations for estimating biomass by carbon mass (CM) in *E. dichotoma* derived by multiplying the two-dimensional surface area (equations 2 and 3) by the determined carbon contents per unit area (Table 3):

$$\text{CM}_{\text{veg}} = \text{Area}_{\text{veg}} \times 1.142 [\mu\text{gC}] \quad (4)$$

$$\text{CM}_{\text{sex}} = \text{Area}_{\text{sex}} \times 1.058 [\mu\text{gC}]. \quad (5)$$

The absolute accuracy of these equations is limited by the statistical errors of the area calculations (see Table 2) and by the methodological inaccuracies of the chemical analysis, and it cannot be expected to be better than the highest observed coefficient of variation of 9% for carbon determination. The relative values for the comparison of sexual and vegetative medusae, however, should be more reliable.

Carbon and nitrogen contents of sexual individuals are 8 and 16%, respectively, higher than in vegetative medusae. This is in agreement with the approximately 14% higher surface areas of sexual individuals. Therefore, relating the values to one unit of surface area, the differences between both groups (7.9% for C and 2.1% for N) seem to be negligible. The observed C:N ratios of 3.6 in sexual medusae and 4.0 in vegetative medusae indicate a high protein content in both groups. This is in good agreement with the few other known values in the composition of medusae. An excellent overview of the chemical compositions of medusae is given by Larson ('86), who found average C:N ratios of 3.6 in hydromedusae. The difference in C:N ratios between sexual and vegetative medusae of *E. dichotoma* might be related to higher protein storage accompanying embryonic development.

For less gelatinous medusa species (*Aglantha digitale*, *Gonionemus vertens*), C composition equals 15% of dry weight and N composition equals about 4.5% of dry weight. These values might be used for rough estimations of dry weight from C and N composition in *E. dichotoma* (for general comments on the accuracy of determining dry weights in medusae, see Larson, '86).

#### Mode of reproduction

Depending on the mode of reproduction in medusae of *E. dichotoma*, the morphology of the body undergoes remarkable changes. These changes should have effects on the ecology of the medusae, since the morphology of the medusa affects its resistance to prevailing currents (Schierwater and Trager, '87; Denny et al., '85). As shown in Table 1, all five of the morphometric characteristics examined in sexually reproducing medusae exhibit significantly larger values than do those of vegetative medusae. The larger umbrella in sexual medusae of *E. dichotoma* might be explained, at least partially, by the filling of the brood pouch with embryos. In addition the larger tentacle sizes in sexual medusae might be related to the fact that sexual reproduction occurs later during ontogeny (Hauenschild, '56), i.e., that sexual medusae are generally older in age and have therefore grown to larger body sizes. It should be emphasized that the larger body size of sexual medusae is not apparent without measurement: There is no clear-cut distinction between the body sizes of sexual and vegetative medusae examined only by eye. As shown in Figures 2–5, body sizes overlap over almost the entire range. The fact, however, that sexual medusae are larger than vegetative ones seems to be of relevance in behavioral and ecological studies in general. For example, the active prey catching area is determined by body size up to a certain limit (Schierwater et al., unpublished data). From studies of the mechanical effects of currents on detaching the medusae from its substrate, it is known that the umbrella area is the most important parameter contributing to the water resistance of the medusa, i.e., the Reynolds numbers and the possibility of hiding the body center in the boundary layer are directly proportional to the umbrella diameters (Schierwater and Trager '87). In essence, an increase in body size, up to a certain limit, enhances the capacity of a medusa to catch prey; but beyond this limit it tends to

increase the risk that the medusa will be detached by currents.

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