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Growth, reproduction and mortality of the sea hare *Dolabella auricularia* (Gastropoda: Aplysiidae) in the Central Visayas, Philippines*

D. Pauly¹ and H. Calumpong²

¹ International Center for Living Aquatic Resources Management (ICLARM); MCC P.O. Box 1501, Makati, Metro Manila, Philippines

² Marine Laboratory, Silliman University; Dumaguete City, Philippines

Abstract

The growth parameters W_{∞} and K of the von Bertalanffy growth equation were estimated from size-frequency data of the sea hare *Dolabella auricularia* using an objective, computer-based method. The results obtained from two locations in the central Philippines were comparable, although based on only a few individuals; the means for both sites were $W_{\infty}=493$ g and $K=0.9$ (yearly basis). A value of $Z=3.66$, corresponding to an annual survival rate of 2.6%, was estimated for the juveniles and adults from a length-converted catch curve. Spawning and recruitment were found to occur throughout the year with peaks in May to July and September to October.

Introduction

This paper reports on a study of the growth of the gastropod *Dolabella auricularia* (Aplysiidae), a common and economically important species of sea hare from the central Philippines. The sea hares have, as a whole, received a lot of attention, but much of the work devoted to them has been devoted to members of the genus *Aplysia*, which have become well-investigated laboratory individuals (Kandel, 1979).

The present paper differs from other studies on sea hares in that methods developed by fishery biologists for the study of exploited fish populations are applied to animals usually studied by neurologists, physiologists or ecologists. Here, the demonstration is made that useful information on the life history of *Dolabella auricularia* can be obtained from field data by treating them as if they pertained to a fish.

Material and methods

The growth equation used here to describe the growth of *Dolabella auricularia* is the well-known von Bertalanffy growth function (VBGF) (for weight growth):

$$W_t = W_{\infty} (1 - e^{-K(t-t_0)})^3. \quad (1)$$

The exponent in Eq. (1) assumes that growth is isometric, i.e. that weight is proportional to length cubed. Since it is extremely difficult to take consistent linear measurements in aplysiid gastropods (which lack hard parts), the procedure used here was to take the cubic root of weights and to treat them – under the assumption of isometry – as length data; thus we assumed that

$$L \propto \sqrt[3]{W}, \quad (2)$$

and used a rewritten form of Eq. (1), i.e.

$$\sqrt[3]{W_t} = \sqrt[3]{W_{\infty}} (1 - e^{-K(t-t_0)}). \quad (3)$$

This study is based on specimens collected from 10 August 1979 to 18 March 1980 in Bais Bay (Lat. 9°35'44"N, Long. 123°09'30"E) and Siyt Bay (Lat. 9°04'13"N, Long. 123°09'00"E) in the central Philippines. A description of these bays is given in Calumpong (1979). The specimens were collected from quadrants set at regular intervals along a transect line, as described in Calumpong (1979).

The specimens found in the various quadrants were labelled individually and preserved in 10% formalin. They were subsequently washed with freshwater, blotted with paper towels and weighed to the nearest tenth of a gram. Table 1 gives the size-frequency distribution by sampling dates for the specimens collected.

In addition to the collection of juvenile and adult specimens, counts were made of the occurrence of egg masses during the transects. Altogether, 33 egg masses were sighted. Table 2 gives their seasonal distribution in Bais and Siyt Bays. To obtain an index of the seasonality of spawning in *Dolabella auricularia*, gaps in the monthly

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Table 1. *Dolabella auricularia*. Size distribution of specimens collected in Bais and Siyt Bays, Central Philippines, from August 1979 to March 1980^a

| Lower and upper weight class limits (g) | Midrange of $\sqrt[3]{W}$ classes | Bais Bay | | | | | | | | Total | Siyt Bay | | | | | | Total | Grand total | |
|---|-----------------------------------|-------------|---------|---------|---------|--------|---------|--------|--------|-------|----------|---------|---------|--------|-------|----|-------|-------------|---|
| | | 10 Aug | 15 Sept | 15* Oct | 17* Nov | 15 Dec | 18* Jan | 18 Mar | 18 Aug | | 22 Sept | 26* Oct | 30* Nov | 18 Dec | 5 Mar | | | | |
| 8 – 15 | 2.25 | 2 | – | – | – | – | – | – | 2 | – | – | – | – | – | – | – | – | – | 2 |
| 16 – 26 | 2.75 | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | 1 | 1 |
| 27 – 42 | 3.25 | 5 | – | – | – | – | – | – | 5 | – | – | 3 | – | – | – | 1 | 4 | 9 | |
| 43 – 64 | 3.75 | 4 | – | – | – | – | – | – | 4 | 3 | – | – | – | 2 | 2 | 7 | 11 | 11 | |
| 65 – 91 | 4.25 | – | – | – | – | – | – | – | – | 3 | 12 | 2 | – | 13 | 7 | 37 | 37 | 37 | |
| 92 – 124 | 4.75 | 1 | – | – | 2 | 1 | 1 | – | 5 | 6 | 3 | – | 1 | 13 | 11 | 34 | 39 | 39 | |
| 125 – 166 | 5.25 | 2 | – | 1 | – | 4 | – | – | 13 | 1 | – | – | – | 4 | 4 | 9 | 22 | 22 | |
| 167 – 215 | 5.75 | 6 | 2 | – | – | 1 | 1 | 18 | 28 | – | – | – | 1 | – | – | 1 | 29 | 29 | |
| 216 – 274 | 6.25 | 5 | 2 | – | – | 3 | – | 11 | 21 | – | – | – | – | – | 1 | 1 | 22 | 22 | |
| 275 – 342 | 6.75 | 1 | 1 | – | – | – | – | 5 | 7 | – | – | – | – | – | – | – | 7 | 7 | |
| 343 – 422 | 7.25 | – | 1 | – | – | – | – | 1 | 2 | – | – | – | – | – | – | – | 2 | 2 | |
| | | Σ 26 | 6 | 1 | 2 | 9 | 2 | 41 | 87 | 13 | 16 | 5 | 2 | 32 | 26 | 94 | 181 | | |

^a The small samples marked with an asterisk were not used for the estimation of growth parameters

Table 2. *Dolabella auricularia*. Number of egg masses collected during standard transects in Siyt and Bais Bays, June 1979 to March 1980, used for assessing seasonality of spawning (months arranged from January to December for convenience)

| Month | Numbers observed at each site α | | Interpolations for missing months | | Σ both sites | Running average (3 months) | Spawning pattern in % ^b |
|----------|--|------|-----------------------------------|------|---------------------|----------------------------|------------------------------------|
| | Siyt | Bais | Siyt | Bais | | | |
| J | – | 1 | 1.67 | 1 | 2.67 | 2.67 | 0 |
| F | – | 2 | 1.33 | 2 | 3.33 | 3.00 | 2.0 |
| M | 1 | 2 | 1 | 2 | 3 | 3.44 | 4.7 |
| A | – | – | 1.33 | 2.67 | 4 | 4.00 | 8.3 |
| M | – | – | 1.67 | 3.33 | 5 | 5.00 | 14.6 |
| J | 2 | 4 | 2 | 4 | 6 | 4.67 | 12.5 |
| J | – | – | 1 | 2 | 3 | 3.00 | 2.0 |
| A | 0 | 0 | 0 | 0 | 0 | 3.33 | 4.1 |
| S | 4 | 3 | 4 | 3 | 7 | 4.67 | 12.6 |
| O | 4 | 3 | 4 | 3 | 7 | 6.33 | 23.1 |
| N | 1 | 4 | 1 | 4 | 5 | 4.66 | 12.6 |
| D | 2 | 0 | 2 | 0 | 2 | 3.22 | 3.5 |
| Σ | 14 | 19 | | | | | 100.0 |

^a –: month with no data collection

0: no egg masses observed

^b Obtained by subtracting lowest monthly value (January) from each of the 12 monthly values of the preceding column and expressing the remainder in %. This procedure allows direct comparison of the spawning pattern with a recruitment pattern (see Fig. 2)

egg masses counts were filled in by interpolation between adjacent months. Then, the data for Bais and Siyt Bays were pooled and smoothed by taking running means (over 3 months). The lowest of the resulting smoothed counts was then subtracted from each of the 12 monthly values, and the remainders expressed as percentages. The results (see Table 2), which reflect the overall seasonality of spawning in *D. auricularia*, have a form which allows direct comparison with the "recruitment pattern" obtained from the length-frequency data (see below).

The computer-based method used here to estimate the parameters W_{∞} (actually $\sqrt[3]{W_{\infty}}$, see above) and K of the

VBGF, based on the size-frequency data in Table 1, has been described in detail in Pauly and David (1981), Pauly and Ingles (1981) and Pauly (1982); it will suffice, therefore, to mention briefly the main features of the method:

– It is entirely objective, i.e. does not require external inputs, such as assumed number of age classes or number of recruitment events per year;

– it makes use of a growth function which has been shown to apply to a vast number of organisms (including aquatic gastropods) and uses the interpolative power of the equation to bridge gaps in the size-frequency data, and hence

– it can be used with very limited data sets, given that the data do reflect some of the growth processes occurring in the population.

To estimate the parameter t_0 of the VBGF (which expresses the age the specimens would have had at length zero, had they always grown according to the equation), an indirect method was used as follows:

(i) Using at first a value of $t_0 = 0$, the size-frequency data of Table 1 were projected back onto the time axis using the growth curve described by the values of W_∞ and K presented below;

(ii) the mismatch between the resulting "recruitment pattern" (Pauly, 1982) and the spawning pattern presented in Table 2 was then determined, and the value of t_0 assessed thus making the two patterns overlap as much as possible;

(iii) the operation in step (i) was then repeated using the new value of t_0 , then the mismatch evaluated, a new value of t_0 computed, etc., until the value of t_0 could not be improved further.

The computations involved in Steps 1, 2 and 3 were performed using the computer program ELEFAN II (Pauly, 1982).

Pauly (1982) showed how, given a set of size-frequency data and estimates of L_∞ and K , an estimate of instantaneous rate of total mortality can be obtained from a "length-converted catch curve".

Total mortality (Z) is defined by

$$N_t = N_0 e^{-Zt}, \quad (4)$$

where N_0 and N_t are numbers of specimens at the beginning and end, respectively, of a time period t . A "length-converted catch curve" is obtained by summing up available size-frequency data over a certain period of time to smooth out the effect of recruitment pulses and of small sample sizes. An estimate of Z can thus be obtained, based on the righthand, fully selected side of a catch curve and under the assumption of a steady state (growth, mortality and recruitment constant) from

$$\log_e (N_i / \Delta t_i) = a - Z \cdot t_i', \quad (5)$$

where N_i is the number of specimens in a given size class (i), Δt_i is the time needed to grow through size class (i) and t_i' is the relative age corresponding to the midrange of size class (i). Z is estimated as the slope (with sign changed) of a linear regression of the form $y = a + bx$, where $\log_e (N_i / \Delta t_i) = y$ and $t_i' = x$, while the values of t_i' and Δt_i are estimated from

$$t_i' = \frac{-\log_e \left(1 - \frac{\sqrt[3]{W}}{\sqrt[3]{W_\infty}} \right)}{K} \quad (6)$$

and

$$\Delta t_i = \frac{\ln \left(\frac{\sqrt[3]{W_\infty} - \sqrt[3]{W_1}}{\sqrt[3]{W_\infty} - \sqrt[3]{W_2}} \right)}{K}, \quad (7)$$

where $\sqrt[3]{W_1}$ and $\sqrt[3]{W_2}$ correspond to the lower and upper size limits of a class, respectively.

Results and discussion

Figure 1 shows plots of the size-frequency data in Table 1, with growth curves super-imposed. The two sets of growth parameter values estimated were similar; the values of W_∞ are 512 g for Bais Bay and 475 g for Siyt Bay, while the values of K are 0.8 and 1.0 for Bais Bay and Siyt Bay, respectively. The geometric mean of the two W_∞ values (493 g) was also very close to the maximum weight of 500 g reported by Calumpong (1979) for *Dolabella auricularia*. Noteworthy also is the fact that *D. auricularia* are smaller in Siyt Bay, where the population density is higher than in Bais Bay (Calumpong, 1979).

The best match between recruitment and spawning patterns was obtained with a value of $t_0 = -0.33$ yr, or -4 months. As might be seen (Fig. 2) both patterns suggest that *Dolabella auricularia* spawns and recruits twice a year in May to July and September to October.

Total mortality was estimated as $Z = 2.81$ in Bais Bay, and $Z = 5.44$ in Siyt Bay. This high mortality may also be attributed to density effects. However, the estimates are based in both cases on only a few specimens, and it was thought appropriate to combine the samples from the two Bays, using average growth parameter values ($W_\infty = 493$ g and $K = 0.9$, see above) for the analysis of the combined sample. Figure 3 shows the resulting length-converted catch curve, which provides an estimate of total mortality of $Z = 3.66$, corresponding to a survival rate of 2.6% per year.

The value of Z estimated here is also an estimate of natural mortality, since it is only the eggs of *Dolabella auricularia* which are collected for food (Calumpong, 1979).

As a whole, both the growth parameter values and the estimates of Z correspond to such values as obtained from small tropical fishes. Indeed, fishes with growth parameters similar to those estimated here generally reach maturity at the age (L_m) of one year and a weight (W_m) about equal to about 30% of their value of W_∞ (Beverton and Holt, 1959).

Thus, carrying the analogy between fish and sea hare one step further, one can estimate t_0 by solving Eq. (1) for this parameter, i.e.

$$t_0 = \frac{-\log_e \left(1 - \left(\frac{W_m}{W_\infty} \right)^{1/3} \right)}{K} + t_m, \quad (8)$$

and inserting 493 g for W_∞ , 148 g for W_m , 1 yr for t_m and 0.9 for K (see above), which gives $t_0 = -0.23$. This value is close to that of $t_0 = -0.33$ estimated from the pattern of occurrences of egg masses. The complete equation describing the growth of *Dolabella auricularia* is thus

$$W_t = 493 (1 - e^{-0.9(t+0.33)})^3. \quad (9)$$

Fig. 4 gives a pictorial representation of Eq. (9).

While Carefoot (1967a, b) presented the results of his growth experiments in a fashion that renders comparison

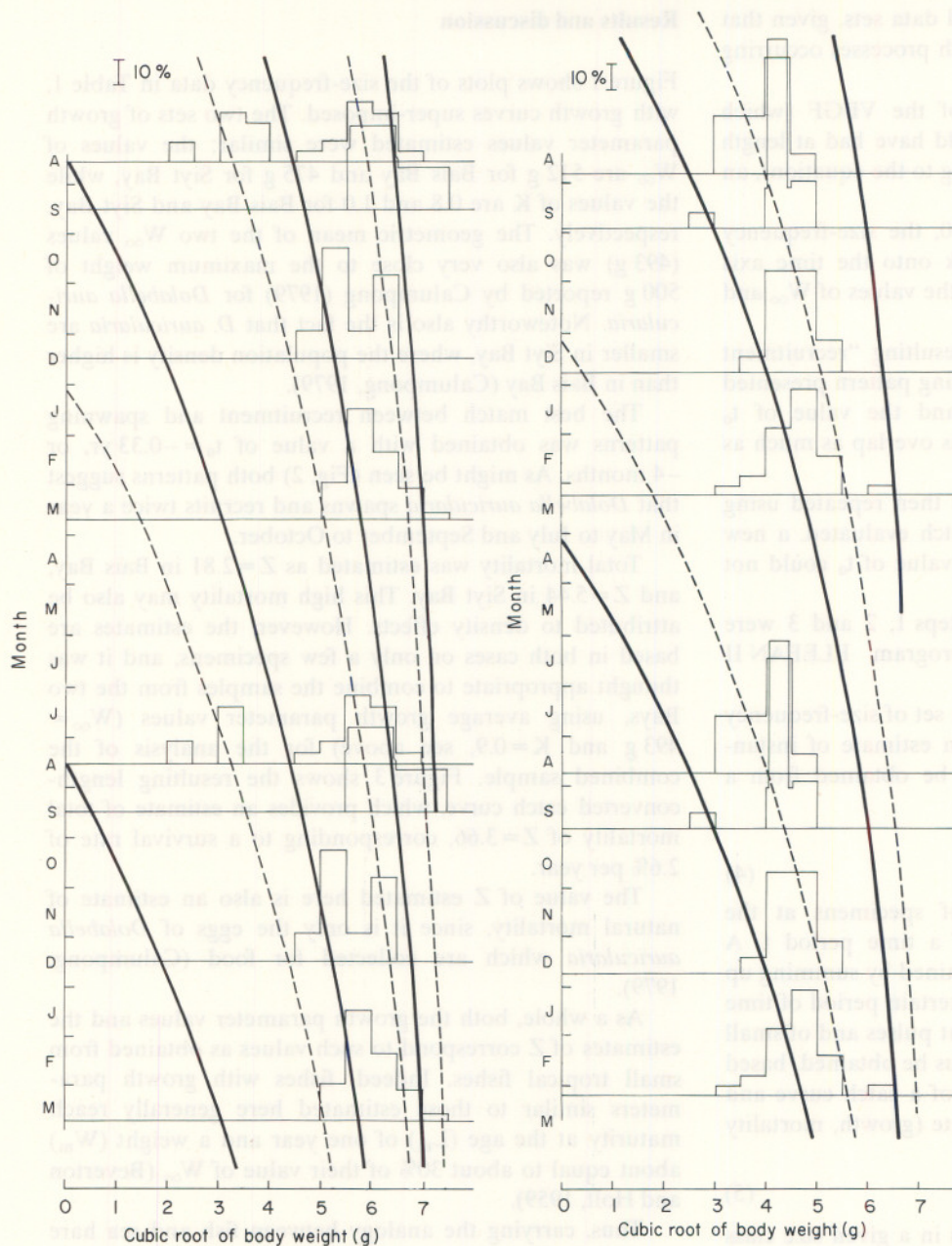


Fig. 1. *Dolabella auricularia*. Size-frequency data in Bais Bay (left) and Siyt Bay (right), Central Philippines, with super-imposed growth curves estimated by the ELEFAN I method. (See text)

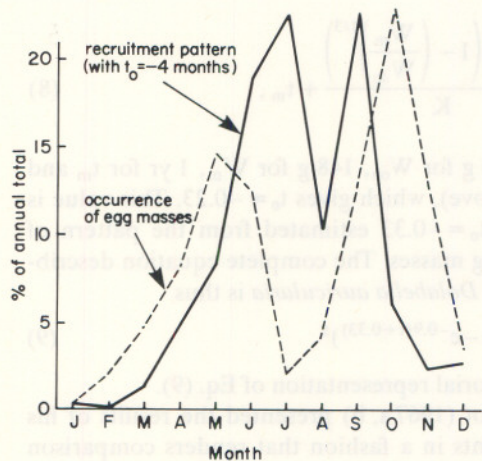


Fig. 2. *Dolabella auricularia*. Solid line: recruitment pattern in Bais and Siyt Bays, obtained by projecting size-frequency data of Table 1 onto time axis, with $t_0 = -4$ months. Dotted line: spawning pattern reflecting the seasonal occurrence of egg masses in Bais and Siyt Bays (see also Table 2). Note that the patterns largely overlap, with minima in December to February and July to August, and maxima apart by only one month in both cases

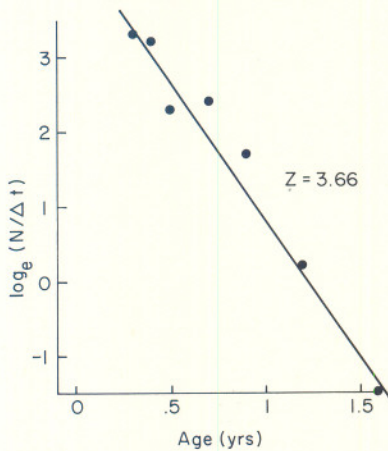


Fig. 3. *Dolabella auricularia*. Descending, right side of catch curve in Bais and Siyt Bays. The slope of this catch curve is an estimate of the instantaneous rate of mortality Z . (See text)

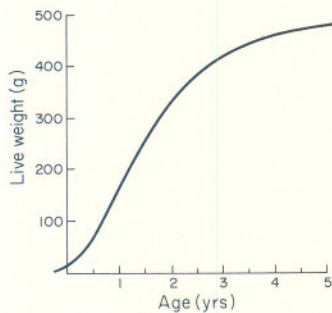


Fig. 4. *Dolabella auricularia*. Growth in Bais and Siyt Bays, Central Philippines ($W_{\infty}=493$ g, $K=0.9$ and $t_0=0.33$ yr)

with our results impossible (he expresses growth as body weight increase "plus" weight of shed gonadal products), at least two papers by other authors have presented data which can be compared with those obtained here.

The data in Beeman (1970, Fig. 7) and Nishiwaki *et al.* (1975, Figs. 5, 6) suggest that the temperate species they investigated (*Phyllaplysia taylori* and *Aplysia kurodai*) differ markedly from the tropical *Dolabella auricularia* in that growth in the temperate forms is faster than in *D. auricularia*, but limited to a short season of about 3 to 4 months, after which spawning and adult mortalities drastically reduce mean individual weights in the populations.

Beeman (1970) on the other hand, using both the occurrence of egg masses and size-frequency distributions, found in *Phyllaplysia taylori* a bimodal pattern of spawning and recruitment similar to the one we report from

Dolabella auricularia. The longevity of about nine months suggested by Beeman (1970) for *P. taylori* suggests, finally, that our estimated annual survival rate of 2.3% in *D. auricularia* might not be far off the mark.

It thus seems, in summary, that the application to invertebrates, such as aplysiid gastropods, of at least some of the methods developed for the study of fish populations does lead to conclusions comparable to those obtained by invertebrate specialists.

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