Reproductive Energetics of Two Species of Dorid Nudibranchs with Planktotrophic and Lecithotrophic Larval Strategies

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Abstract

Onchidoris muricata (Müller) and *Adalaria proxima* (Alder and Hancock) are sympatric, potentially competing species of dorid nudibranchs, which preferentially graze the cheilostome polyzoan *Electra pilosa* (L.). *O. muricata* is small and lays small eggs which hatch as poorly-developed planktotrophic veliger larvae. *A. proxima* is larger and reproduces by means of larger eggs which hatch as well-developed lecithotrophic larvae, that can metamorphose within approximately 24 h of release. *A. proxima* larvae can feed in the plankton, but do not require extrinsic nutrition to undergo complete development. Both species spawn in February–April, and have a strictly annual life-cycle. Comparisons of the calorific content of spawn have shown that *A. proxima* apportions a greater number of calories to reproduction, but that *O. muricata* makes a greater relative effort. *A. proxima* shows considerable individual variability in reproductive effort, which fails to correlate with body size or rate of spawning. A more deterministic situation applies to *O. muricata*, because body size and fecundity follow an allometric relationship. It appears that there is a threshold of absolute energy required to support the lecithotrophic larval strategy in nudibranchs, and that this is not attained by the smaller species, *O. muricata*. *A. proxima* thus appears to have both reproductive strategies open to it, and to have adopted lecithotrophy in order to offset the unpredictability of energy available for reproduction.

Introduction

In spite of the considerable current interest in life-histories and reproductive strategies (see Chia, 1974; Giesel, 1976; and Stearns, 1976 for reviews), particularly amongst marine invertebrates (e.g. Vance, 1973; Crisp, 1974a, 1976; Menge, 1975; Clark and Goetzfried, 1978), comparatively few studies have investigated the relationship between larval type and the absolute and relative amounts of energy apportioned to reproduction (Menge, 1975; Grahame, 1977). It is likely that the particular life-history of any one marine invertebrate species — that is, whether an animal has an annual, biennial, perennial or ephemeral life-cycle, and whether it is iteroparous or semelparous (Stearns, 1976) — and the larval type adopted, will be the resultant of the complex of ecological pressures and restrictions placed upon that species. Moreover, it is improbable that the particular larval type possessed by that species (i.e., pelagic or non-pelagic; planktotrophic or lecithotrophic, and — in the case of non-pelagic development — whether or not there is brood-protection) can be explained in terms of simplistic relationships such as body size (e.g. Menge, 1975). However, in searching for a "rule" which might have general applicability, Chia (1974) suggests that the quantities of energy available for reproduction over and above that required for somatic growth, respiration and maintenance, may be the fundamental determinant of the particular larval strategy adopted.

The present paper is concerned with reproduction of two littoral dorid nudibranchs, *Onchidoris muricata* (Müller) and *Adalaria proxima* (Alder and Hancock) which, like all opisthobranchs, are hermaphrodites. These are sympatric, potentially competing species, both preferentially grazing the cheilostome polyzoan *Electra pilosa* (L.). Both species are strictly annual, spawning in late winter/early

Table 1. *Onchidoris muricata* and *Adalaria proxima*. Summary of contrasting characteristics of the two nudibranch species

Characteristic	*O. muricata*	*A. proxima*
Life-cycle:	Annual	Annual
Distribution:	Lower intertidal/upper subtidal on macroalgae and on/beneath rocks	Lower intertidal/upper subtidal on macroalgae and on/beneath rocks
Diet:	Wide range of Polyzoa, but preferentially *Electra pilosa*	Wide range of Polyzoa, but preferentially *Electra pilosa*
Spawning period:	February-April	February-April
Egg diameter:	Approximately 90 μm	Approximately 180 μm
Larval strategy:	Planktotrophic	Lecitotrophic

spring, although they differ in larval type. *O. muricata* is small (8 to 14 mm) and lays small (80 to 100 μm) eggs which hatch as small, poorly-developed veliger larvae requiring an extended planktotrophic existence prior to settlement and metamorphosis (Table 1). *A. proxima*, on the other hand, is larger (13 to 20 mm) and produces relatively few, large eggs (approximately 180 μm in diameter) hatching as well-developed lecithotrophic veligers with eyes and a pronounced propodium (Table 1). Although they are capable of feeding, extrinsic nutrition is not necessary for the developmental processes to reach completion: settlement and metamorphosis can occur within approximately 24 h of release on encountering live *E. pilosa* (Thompson, 1958a).

The objective of this study is to compare the absolute and relative amounts of energy apportioned to reproduction, and the number of larvae produced, in order to attempt to explain the striking differences in reproductive strategy of these two species, despite their considerable morphological and ecological proximity.

Materials and Methods

The spawning of *Onchidoris muricata* (Müller) was followed in the laboratory at Robin Hood's Bay, North Yorkshire (England) between February and May 1977. Adults were collected several weeks prior to the commencement of spawning, and were maintained in pairs (A, B and C) in plastic mesh cages. *Electra pilosa* (L.) encrusting *Fucus serratus* L. was supplied to excess as food, and was regularly changed. All cages were floated in a 20 l aquarium with re-circulated, aerated seawater. Temperature was not regulated, and was invariably a few degrees above ambient

seawater, ranging from 9.3° to 13.4°C at the end of the experiment.

Spawning of *Adalaria proxima* (Alder and Hancock) was followed in the laboratory at Menai Bridge, Gwynedd (N. Wales) between February and May 1978 (Pairs 15, 16, 17 and 19). Adults were collected from the Menai Straits approximately 1 month prior to spawning, and were maintained in the same manner as *Onchidoris muricata*. Temperature was again not regulated, and ranged from 4.1° to 13.6°C (Fig. 4).

The eggs of both species are laid in gelatinous masses and attached to the substratum. These are easily removed by means of fine forceps and a sharp scalpel. The cages were checked at least once daily, when records of copulatory or spawning activity were made. Eggs were allowed to commence cleavage before being counted so that infertile (non-cleaving) eggs could be noted. Egg-counts were made using a camera-lucida attachment to a Wild stereomicroscope which thus permitted precise enumeration.

Dry weights of representative egg-masses were obtained for masses of known egg-number. These were counted, damp-dried and weighed, and dipped in isotonic (0.9%) ammonium formate, to remove surface salts, prior to freeze-drying and re-weighing. This enabled dry weight (and thence caloric) conversions of total spawn output from the counts of egg numbers for all pairs. Similar data were obtained from live adults (collected prior to the commencement of spawning) after damp- and dry-weighing.

Ash determinations of both whole adults and spawn were obtained from pills of freeze-dried, powdered material incinerated in a muffle-furnace at 550°C for 5 h. Percentage mineral ash contents were determined microgravimetrically.

All calorimetry was carried out using a Phillipson oxygen micro-bomb calorimeter calibrated with benzoic acid standard (6318 calories g^{-1}). Lipid determinations for *Adalaria proxima* spawn and body samples were obtained microgra... metrically using a 1:2 methanol:chloroform extraction solvent. The small amount of available freeze-dried material obtained from the smaller species, *Onchidoris muricata*, precluded comparative lipid analyses.

Results

The linear regression equations describing the egg number:dry weight relationships for spawn masses of both species

are given in Table 2. Fig. 1 presents the cumulative spawn weight production-curves for the three pairs of *Onchidoris muricata*. Each plot has been fitted with a power-curve regression (see Table 3 for equations), a model which was found to accurately describe spawn production curves for *O. bilamellata* (L.) (Todd, in press b). Overestimations by the model are, however, inevitable, as the spawning rate decreases at the end of the reproductive period. The corresponding data for *Adalaria proxima* are presented in Fig. 2 (as egg numbers), along with the changes in body weight of the spawning individuals. In contrast to *O. muricata* and *O. bilamellata*, the cumulative spawn production-curves for *A. proxima* follow a sigmoid relationship with time, and can be efficiently described by linear regression analysis after transforming the ordinate data to $\log_e (p/1-p)$ (Fig. 3). The regression equations are given in Table 3, and show the regression coefficients to be very similar (0.085 - 0.137). The mean regression coefficient is 0.106, and a Student's t-test showed that the regression coefficients for Pairs 15 and 16 do not differ significantly from the mean value ($t = -1.37$ and -0.22, respectively), while those for Pairs 17 and 19 differ significantly ($t = 3.73$ and -5.11, respectively). For *A. proxima* no correlation between the regression coefficient ($\equiv$ rate of spawning), body size, or total number of eggs produced is detectable, suggesting that, within any one population, there will be considerable individual variability in fecundity. Table 4 summarises the body size and fecundity data for both species.

It is apparent that there is a relationship between body size and fecundity, but not between body size and rate of spawning for *Onchidoris muricata*; in con-
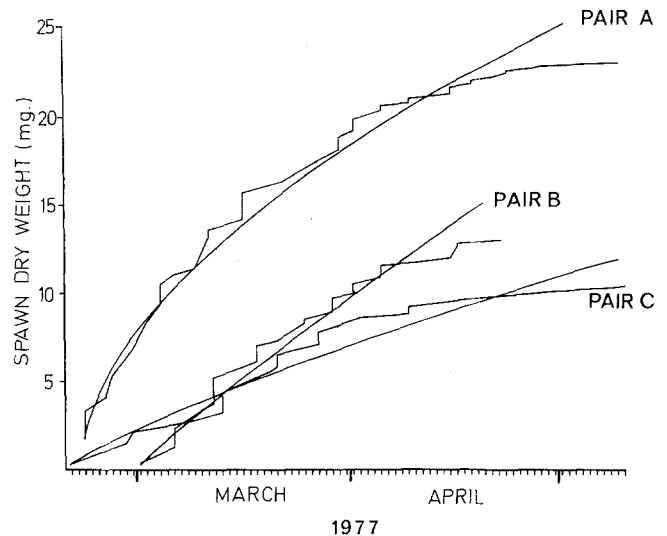

Fig. 1. *Onchidoris muricata*. Cumulative spawn dry-weight production curves for 3 pairs of nudibranchs in laboratory. Each data set is fitted with power-curve regression ($y = ax^b$) (see Table 3 for regression equations)

Table 2. *Onchidoris muricata* and *Adalaria proxima*. Regression equations for spawn and adult body weight conversions

Species	Regression equations
O. muricata	Linear regression ($y = a + bx$) Egg number:spawn mass dry weight $y = 0.0678 + 0.0003x$, $n = 10$, $r = 0.990^{***}$
	Power curve regression ($y = ax^b$) Body length:body dry weight $\log_e y = \log_e 0.042 + \log_e x\ 2.659$, $n = 213$, $r = 0.971^{***}$
A. proxima	Linear regression Egg number:spawn mass dry weight $y = 0.248 + 0.0072x$, $n = 14$, $r = 0.998^{***}$
	Body damp weight:body dry weight $y = 2.72 + 0.224x$, $n = 15$, $r = 0.984^{***}$

Table 3. *Onchidoris muricata* and *Adalaria proxima*. Regression equations for cumulative spawn production curves for both species, and changes in adult body weight during spawning for *A. proxima*

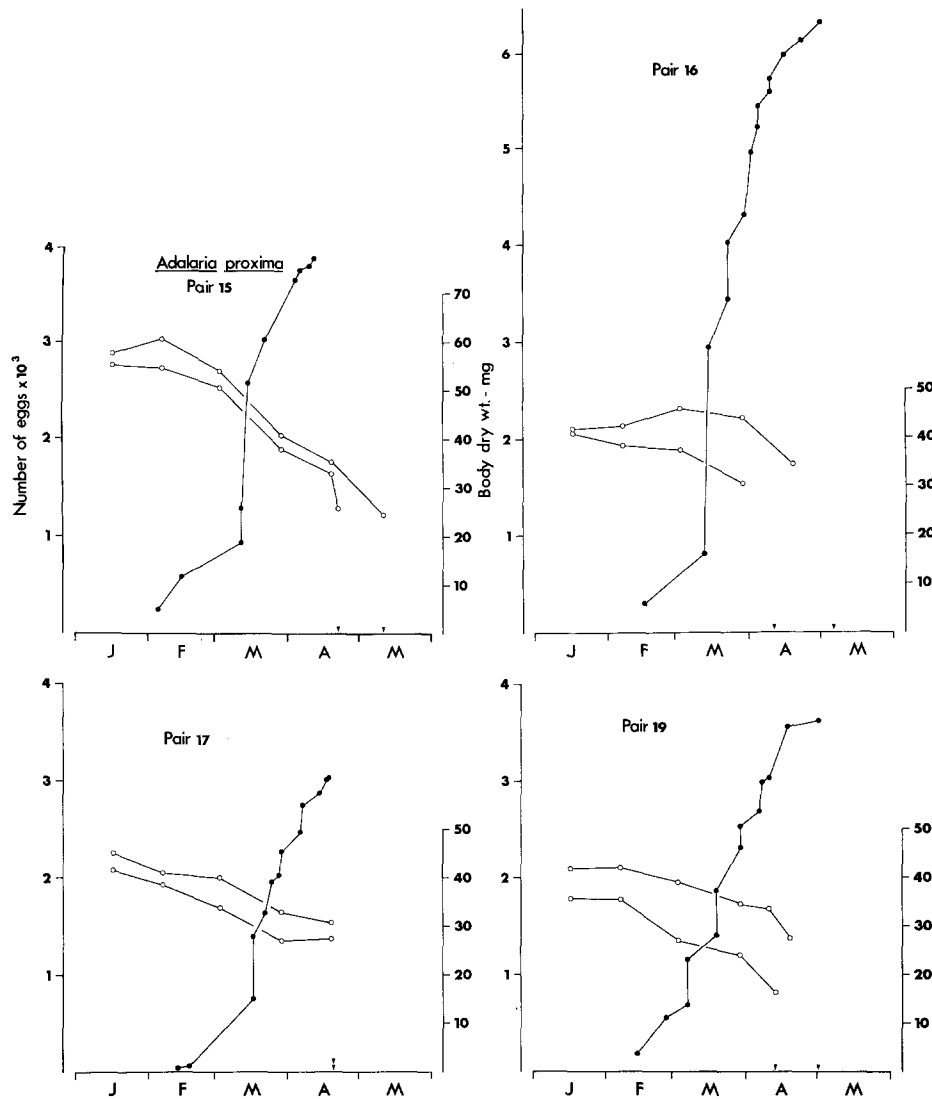| Species	Regression equations
O. muricata	Power curve regression ($y = ax^b$), cumulative spawn production
Pair A	$\log_e y = \log_e 2.395 + \log_e x\ 0.522$, $r = 0.986^{***}$
Pair B	$\log_e y = \log_e 0.402 + \log_e x\ 0.992$, $r = 0.984^{***}$
Pair C	$\log_e y = \log_e 0.348 + \log_e x\ 0.805$, $r = 0.981^{***}$
A. proxima	Linear regression ($y = a + bx$), cumulative spawn production (transformed data)
Pair 15	$y = -3.314 + 0.100x$, $r = 0.950^{***}$
Pair 16	$y = -3.382 + 0.103x$, $r = 0.985^{***}$
Pair 17	$y = -4.999 + 0.137x$, $r = 0.977^{***}$
Pair 19	$y = -3.040 + 0.085x$, $r = 0.980^{***}$
	Linear regression ($y = a + bx$), changes in body dry weight
Pair 15	$= 59.23 - 0.38x$, $r = -0.970^{***}$
Pair 16	$= 41.85 + 0.086x$, $r = -0.427$
Pair 17	$= 40.30 - 0.168x$, $r = -0.853^{**}$
Pair 19	$= 38.68 - 0.192x$, $r = -0.650^{*}$

Fig. 2. *Adalaria proxima*. Cumulative egg production curves for 4 pairs of nudibranchs in laboratory. Changes in adult body dry weights estimated from live weight measurements are also shown (see Tables 2 and 3 for regression equations)

trast to the total lack of correlation for *Adalaria proxima*. It is possible, therefore, that there is a degree of unpredictability in the relative and absolute amounts of energy available to individual *A. proxima* for reproduction, while the situation for *O. muricata* is rather more deterministic, as suggested by the allometric relationship between body size and fecundity in the latter species.

Synchronous spawning of both individuals in pairs of both species was frequently observed (Figs. 1, 2 and 4), and probably results from entrainment of ovulation of individuals following (reciprocal) copulation. In recognising a similar situation, Thompson (1958b) sug-

gested that not only was spawning synchronous in *Adalaria proxima*, but that the periodicity of spawning was determined by temperature. Fig. 4 shows the incidence of copulation and spawning in *A. proxima*, and indicates a degree of synchrony, but a lack of periodicity of spawning. Although individuals held under constant conditions may well undergo a temperature-determined cycle of spawning activity, this is unlikely to occur in the field. The duration of copulation was observed to range from a few hours to several days in the case of *A. proxima*. *Onchidoris muricata* copulated frequently between spawnings, but only for a few hours at a time. The significance of extended copulation in *A. proxima* is un-
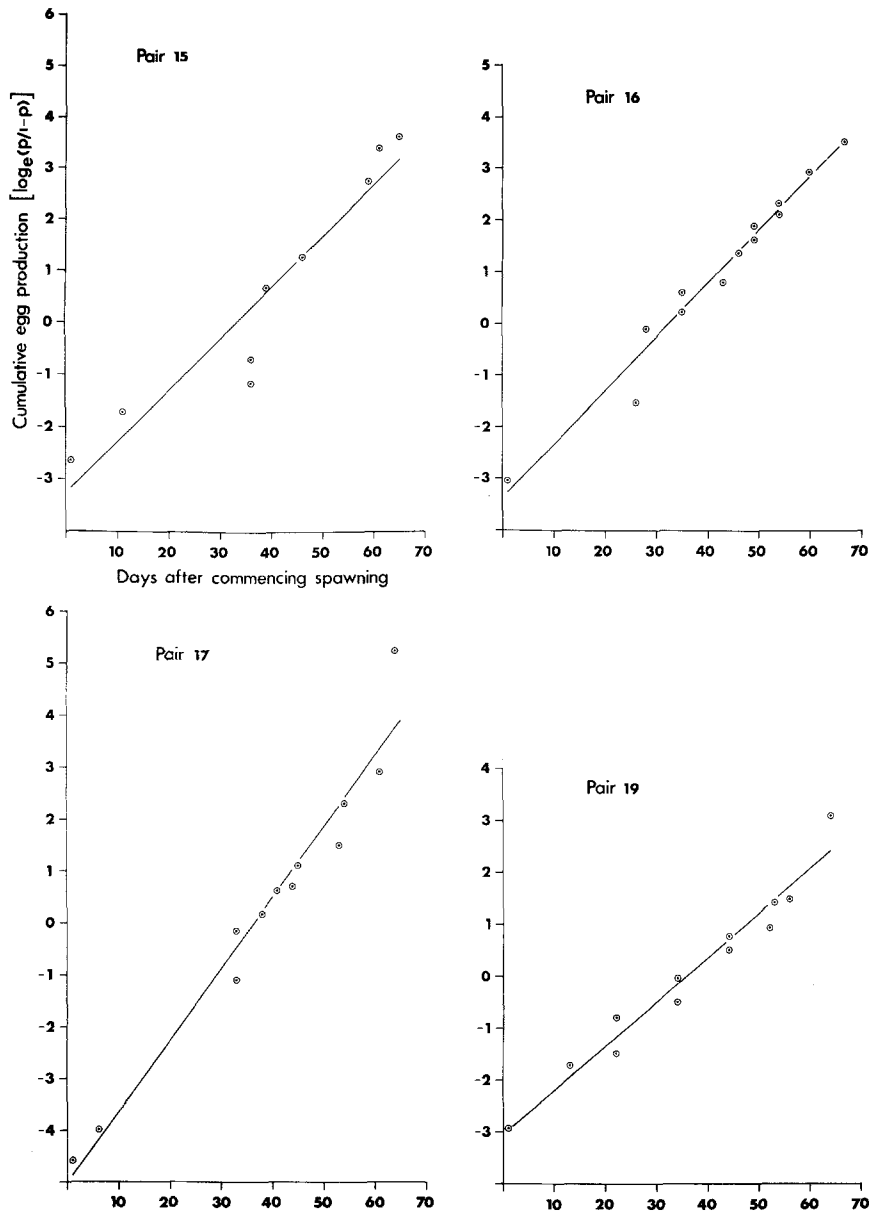
Fig. 3. *Adalaria proxima.* Cumulative egg production curves for 4 pairs of nudibranchs after transformation of the *y* axis (see Table 3 for regression equations)

Table 4. *Onchidoris muricata* and *Adalaria proxima.* Adult body size and reproduction data

Species	Combined maximum dry weight of nudibranchs	Total no. of eggs laid	Estimated no. of eggs mg^{-1} dry weight of adults	Estimated egg output for each individual (body dry weight in parentheses)
O. muricata				
Pair A	22.72 mg	68,073	2996.2	29,632 (9.89 mg) 38,441 (12.83 mg)
Pair B	19.49 mg	37,710	1934.8	17,239 (8.91 mg) 20,471 (10.58 mg)
Pair C	17.86 mg	30,309	1697.0	14,085 (8.30 mg) 16,224 (9.56 mg)
A. proxima				
Pair 15	114.78 mg	3,863	33.66	1,832 (54.43 mg) 2,031 (60.35 mg)
Pair 16	83.55 mg	6,293	75.32	2,828 (37.55 mg) 3,465 (46.00 mg)
Pair 17	86.56 mg	3,029	34.99	1,455 (41.58 mg) 1,574 (44.98 mg)
Pair 19	77.61 mg	3,712	47.83	1,699 (35.53 mg) 2,013 (42.08 mg)

clear, particularly in view of the fact that only a few hundred eggs are laid at any one spawning.

Table 5 shows the results of the calorific determinations for whole adults and spawn of both species, in addition to the dry weight and ash determinations.
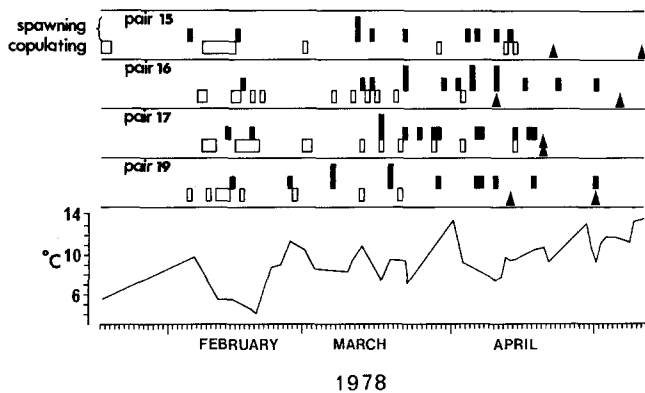

Fig. 4. *Adalaria proxima*. Observations of copulatory (open bars) and spawning (shaded bars) activity for 4 pairs of nudibranchs in laboratory. Arrowheads indicate times of death of the individuals. Seasonal changes in experimental temperature are also shown

The high ash values for whole adults of both species was anticipated due to the presence of large quantities of endoskeletal calcareous spicules. The correspondingly high ash values for the spawn material are, however, somewhat surprising, although Thayer *et al.* (1973) quote ash values in excess of 50% dry weight for ctenophores and an ascidian species (both with high "jelly" contents), in addition to 3 ophiuroid species, and a polychaete. In view of the high mineral ash contents of all samples, a correction factor for the endothermic conversion of $CaCO_3$ (presumed to be the major ash component) to CaO and CO_2 has been applied. An endothermy of 0.43 cal mg^{-1} $CaCO_3$ was allowed for, according to the theoretical thermochemical values quoted by Paine (1966), although he found average heat loss of only 0.14 cal mg^{-1} on ignition of artificial samples.

The low calorific values for all determinations are somewhat enigmatic, and worthy of comment. Since the calibration line for the micro-bomb was precise (y = $0.227 + (0.527x)n = 10$, $r = 0.977***$) and since the y-axis intercept did not differ significantly from the origin ($t = 0.319$), sensitivity of the calorim-

Table 5. *Onchidoris muricata* and *Adalaria proxima*. Results of mineral ash and calorific determinations of adult body and spawn. $n = 5$ in all cases

Species	Mineral ash (% of dry weight)	Calories
O. muricata		
Body	48.90 ± 0.70%	1457 ± 40.3 cal g^{-1} dry weight
		2850 ± 79.3 cal g^{-1} ash-free dry weight
		3261 ± 79.3 cal g^{-1} ash-free "corrected" dry weight
Spawn	45.44 ± 0.17%	2184 ± 97.9 cal g^{-1} dry weight
		4006 ± 178.9 cal g^{-1} ash-free dry weight
		4364 ± 178.9 cal g^{-1} ash-free "corrected" dry weight
A. proxima		
Body	42.82 ± 0.26%	1899 ± 27.5 cal g^{-1} dry weight
		3561 ± 140.4 cal g^{-1} ash-free dry weight
		3937 ± 161.8 cal g^{-1} ash-free "corrected" dry weight
Spawn	53.54 ± 1.66%	1743 ± 66.2 cal g^{-1} dry weight
		3781 ± 148.6 cal g^{-1} ash-free dry weight
		4284 ± 150.2 cal g^{-1} ash-free "corrected" dry weight

Table 6. *Adalaria proxima*. Results of total lipid analysis for adult body and spawn. Extraction solvent was 2:1 mixture of chloroform and methanol

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3.168 mg of lipid extracted from 29.964 mg freeze-dried body tissue
        Total lipids = 10.57% of total body dry weight
                     ≡ 18.49% of total ash-free body dry weight
              29.964 mg of body tissue = 66.52 cal (by calorimetry)
              (assuming 9.45 cal mg⁻¹ lipid)
              Total lipid = 29.94 cal
                          ≡ 45.01% of total body calories

3.301 mg lipid extracted from 25.998 mg freeze-dried spawn
        Total lipids = 12.70% of total spawn dry weight
                     ≡ 27.33% of total ash-free spawn dry weight
              25.998 mg spawn = 51.65 cal (by calorimetry)
              (assuming 9.45 cal mg⁻¹ lipid)
              Total lipid = 31.19 cal
                          ≡ 60.40% of total spawn calories
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eter was considered satisfactory. Furthermore, ignition of a freeze-dried sample of mullet [*Crenimugil labrosus* (Risso)] muscle rendered a calorific value of 5003 cal g^{-1} without conversion to ash-free dry weight, or correction for endothermy. Clearly, the low calorific values observed for the nudibranchs and their spawn are a real result, and fall within the range of some of the data reported by Thayer et al. (1973); the high levels of mineral ash probably affect the operation of the calorimeter. Examination of the potentiometer traces shows a slow rise to peak deflection, and a slower cooling curve on ignition of biological samples, in comparison with the benzoic acid standard. It appears, therefore, that the endothermic reactions on burning biological samples with high ash content result not only in endothermic "loss" of heat, but also in a more protracted combustion. Having calibrated the apparatus for a particular mode of combustion (in the present case, very rapid combustion of benzoic acid), an intrinsic error is probably interpolated on burning samples with different thermochemical combustion characteristics. Further work in this respect is currently in progress. In spite of the possible error involved in the absolute calorific determinations, the present data are considered reliable for comparative purposes.

As a further check on the calorific determinations, a total lipid analysis of *Adalaria proxima* adults and spawn samples was undertaken, on the basis that lipids would probably account for the bulk of the total calories. The results are presented in Table 6, and show the absolute amounts of total lipids, and

their proportion of the total calories estimated from the microbomb calorimetry. The results compare very favourably with other data for molluscs and crustaceans reviewed by Holland (1978). The quantities and calorific proportions accounted for by lipids are very similar for bodies and spawn (45.01 and 60.40% of dry weight, respectively), although somewhat higher for the spawn, as might be anticipated.

Two measures of reproductive effort are presented. The first relates to the total dry weight of spawn, expressed as a percentage of the maximum available body dry weight, while the second (and more important) concerns these same data converted to total calories. Clearly, in a situation where no significant difference in calorific value of somatic and spawn material occurs (e.g. *Adalaria proxima*, in the present case), reproductive effort can be adequately and rapidly measured in terms of dry weight alone (see Gadgil and Solbrig, 1972; Gaines et al., 1974; Menge, 1974; Grahame, 1977). However, in cases where there are large discrepancies in calorific values (e.g. *Onchidoris muricata*, in the present case) such a measure is quite inappropriate.

Table 7 summarises the reproductive effort data expressed as both dry weight and calories for both species. The discrepancies in the two estimates of reproductive effort for *Onchidoris muricata* arise from the calorific differences between the body and the spawn discussed above. The absolute quantity of energy apportioned to reproduction by *Adalaria proxima* (51.42 to 100.18 cal), considerably exceeds that by *O. muricata* (24.36 to 54.07 cal); although, in relative terms, the position is reversed (as a result of

Table 7. *Onchidoris muricata* and *Adalaria proxima*. Summary of reproductive effort and egg calorific contents

	O. muricata (planktotrophic)			A. proxima (lecithotrophic)			
	Pair A	Pair B	Pair C	Pair 15	Pair 16	Pair 17	Pair 19
Combined maximum body dry weight (mg) for each pair	22.72	19.49	17.86	112.64	81.15	86.56	77.49
Total body calories	37.87	32.48	29.76	253.57	182.68	192.24	174.44
Total dry weight (mg) of spawn output for each pair	22.71	12.87	10.23	30.64	49.27	25.29	30.40
Total spawn calories pair^{-1}	54.07	30.64	24.36	62.30	100.18	50.28	61.81
Reproductive effort (dry weight)	99.96%	66.03%	57.28%	27.20%	60.71%	29.22%	39.23%
Reproductive effort (calories)	142.82%	94.33%	81.85%	24.57%	54.84%	26.16%	35.43%
Total no. of eggs pair^{-1}	68,073	37,710	30,309	3,863	6,293	3,029	3,712
No. of calories egg^{-1}	0.79 x 10^{-3}	0.81 x 10^{-3} ($\bar{x}$ = 0.89 x 10^{-3})	0.80 x 10^{-3}	16.13 x 10^{-3}	15.92 x 10^{-3} ($\bar{x}$ = 16.42 x 10^{-3})	16.60 x 10^{-3}	16.65 x 10^{-3}
Diameter of ova	90 µm			180 µm			
Approximate egg volume	3.81 x 10^5 µm^3			3.05 x 10^6 µm^3			
Calories µm^{-3} for individual eggs	2.10 x 10^{-9}			5.38 x 10^{-9}			

species body-size differences) with O.
muricata making the larger reproductive
effort. Moreover, in spite of the dif-
ferences in relative and absolute quan-
tities of energy output, the number of
eggs produced differs by an order of
magnitude between species. A reproduc-
tive effort in excess of 100% (i.e., O.
muricata) can only be attained by con-
tinued feeding and immediate diversion
of assimilated products to gametogenesis
during the spawning period. In addition,
these nudibranchs also undergo atrophy
of the digestive gland tissues and pre-
sumably also divert these products to
gametogenesis (Todd, 1978).

It is apparent that, for the larger
species (Adalaria proxima) there is no re-
lationship between body size, fecundity,
and rate of spawning (Figs. 2 and 3) or
between body size and reproductive ef-
fort ($r = -0.27$, $n = 4$, not significant)
(Fig. 2 and Table 7), while for Onchidoris
muricata there appears to be a close al-
lometric relationship between body size
and reproductive effort ($r = 0.99$, P
<0.01) (Fig. 1 and Table 7). This latter
relationship is corroborated by the ob-
servation that larger O. muricata have re-
latively larger gonads (Todd, 1978), and
suggests that selection ought to tend
towards a larger body size.

Table 7 also presents data concerning
the number of calories invested egg^{-1},
and shows that Adalaria proxima (with its
few, large eggs and lecithotrophic lar-
vae) apportions approximately 20 times
as much energy egg^{-1} than does Onchidoris
muricata. Consideration of the egg vol-
umes of each species in relation to cal-
orific investment indicates that A. prox-
ima eggs are approximately 156% richer
in calories than are O. muricata eggs.
Such an interpretation would, however,
be both misleading and incorrect, since
the relative amounts of mucopolysaccha-
ride gel matrix associated with each in-
dividual egg are considerably greater in
A. proxima, and probably account for a
large part of the extra 3.28×10^{-9} cal
μm^{-3} for individual eggs. It is sug-
gested that the eggs of both species
probably have similar relative calorific
values (i.e., calories μm^{-3}) (see Strath-
mann and Vedder, 1977), but that A. prox-
ima invests relatively more energy in
the protective gel matrix. It seems
likely that an animal will invest more
energy in protective mechanisms for the
eggs if the period of embryonic develop-
ment is extensive. O. muricata larvae
hatch after 14 days at 9° to 10°C (Mil-
ler, 1958), while A. proxima requires 36
to 42 days (Thompson, 1958a) to hatch at
the same temperature. In consequence, a
more durable gel matrix, and/or a great-

er proportion of mucopolysaccarides per
egg might be anticipated for A. proxima
egg masses, both at increased energetic
cost. In this particular instance, ex-
tra protection appears to be obtained
solely by increasing the quantity of the
gel matrix.

Discussion

The results show that Onchidoris muricata
produces a large number (approximately
15,000 to 34,000) of small eggs at a
considerable reproductive effort (81 to
142% in calorific terms). These data
compare well with O. bilamellata, which was
found to exert a reproductive effort of
between 119 and 157% (calories) depend-
ing on body size (Todd, in press a). O.
bilamellata possesses a planktotrophic
larva, and adults are considerably larg-
er than either O. muricata or Adalaria prox-
ima, attaining maximum sizes of up to
40 mm in length.

The eggs of Onchidoris muricata develop
comparatively quickly, are lightly pro-
tected, and hatch as poorly-developed
veligers, which require an extended
planktotrophic existence prior to meta-
morphosis. The duration of the pelagic
phase is as yet unknown, but is likely
to be similar to that of its congener,
O. bilamellata. In the case of the latter
species, the larva requires approximate-
ly 32 days (at 15°C) to complete growth
and development in culture (Todd, in
press a). From a temperature-coefficient
estimation of 2.19 for the phase of em-
bryonic development, it was estimated
that the larvae of O. bilamellata are pe-
lagic for some 10 to 12 weeks in the
field. Application of this conversion to
O. muricata suggests that the plankto-
trophic phase should be of approximately
8.5 weeks duration in the field, result-
ing in a total development phase of some
11.5 weeks (Fig. 5).

Adalaria proxima, on the other hand,
produces comparatively few (approximate-
ly 1500 to 3000) large well-protected
eggs at a substantially greater energet-
ic cost egg^{-1}, although, in relative
terms, reproductive effort is consider-
ably less than for Onchidoris muricata. It
would appear, therefore, that lecitho-
trophy demands a higher energetic out-
put, in absolute terms, than plankto-
trophy for successful reproduction. Al-
though the embryonic development period
of A. proxima is $2\frac{1}{2}$ to 3 times that of
O. muricata, and consequently A. proxima
eggs might be subjected to greater prob-
abilities of pre-hatch mortality, it is
certain that the brief pelagic phase of
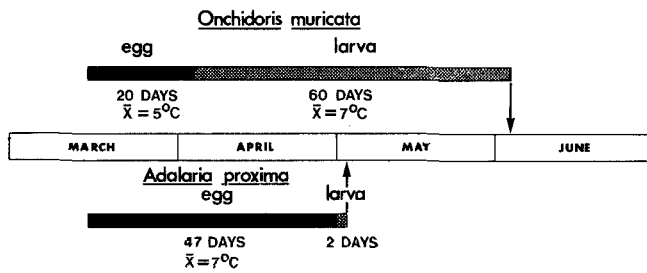the A. proxima larva (approximately 24 to

Fig. 5. *Onchidoris muricata* and *Adalaria proxima*. Schematic representation of developmental phases of nudibranchs. Shaded area represents duration of respective pelagic phases. Since peak spawning activity occurs in mid-March, this is taken as starting date for both species. Arrows indicate different times of metamorphosis

Table 8. *Onchidoris muricata* and *Adalaria proxima*. Conversion of mean calorific reproductive effort of each species to corresponding egg number for the alternative reproductive strategy

	O. muricata	A. proxima
Mean total calories per spawn pair	36.36 ± 9.04	68.93 ± 10.72
Mean total no. of eggs per pair	45,011 ± 11,787	4,224 ± 713
Mean egg total per individual	22,682	2,112

Given that 1 planktotrophic egg requires 0.80×10^{-3} cal, and 1 lecithotrophic egg requires 16.42×10^{-3} cal,

then, for *O. muricata*:
36.36 cal = 45,364 planktotrophic eggs = 2,214 lecithotrophic eggs per pair = 1,107 lecithotrophic eggs per individual

for *A. proxima*:
68.93 cal = 4,224 lecithotrophic eggs = 86,163 planktotrophic eggs per pair = 43,081 planktotrophic eggs per individual

48 h) results in considerably greater individual probabilities of survival to metamorphosis. Herein lies the ecological and energetic compromise between the two reproductive strategies in terms of the numbers of eggs produced, the duration of the embryonic and larval phases, individual probabilities of survival, and the relative and absolute costs in calories. The conversions in Table 8 indicate that the mean calorific output of spawn by *A. proxima* could be partitioned into approximately 43,081 planktotrophic eggs individual^{-1}, which considerably exceeds the mean output observed for *O. muricata* (22,682 eggs). The caloric output of spawn for *O. muricata* could, however, only be partitioned into approximately 1107 lecithotrophic eggs, i.e., just over half the mean number actually observed for *A. proxima*. On the assumption that the observed egg-counts approximate to the optimum numbers re-

quired to maintain steady populations (i.e., for each individual to reproduce itself once to spawning), *A. proxima* would have both reproductive strategies available to it. *O. muricata*, on the other hand, is forced into planktotrophy, since it could not produce a sufficient number of lecithotrophic eggs to maintain its populations. Moreover, it has to be stated that the reproductive output measured in the laboratory represents the reproductive "potential" for each species, and that, as a result of adult mortality, and time required to find mates between spawnings in the field, the "realised" reproductive output will be considerably curtailed. Todd (in press a, b) has shown that the reproductive "potential" of *O. bilamellata* corresponds to an effort of 114 to 150%, while the "realised" reproductive effort in the field was only 48 to 64%.

It has been shown that *Adalaria proxima* apportions greater absolute quantities of energy to reproduction, and sustains a larger body size, than does *Onchidoris muricata*. Differences in growth rate and body size are attributable to differences in feeding strategy: *A. proxima* consumes *Electra pilosa* by using the radula in a rasping motion, removing individual polypides with only a few "strokes". *O. muricata* removes individual polypides suctorially, consuming approximately 0.4 to 5.2 polypides h^{-1} in contrast to 2.3 to 17.8 polypides h^{-1} for *A. proxima* (own personal observations). These differences in mode of feeding are manifest in different radula structures. The reduced relative quantities of energy apportioned to reproduction by *A. proxima* possibly reflects relatively greater maintenance demands for its larger body size, or unpredictability in its capacity to attain a net flux of assimilated energy during the spawning period. *O. muricata* does, however, attain a predictable flux during the spawning period, as shown by the close relationship between body size and fecundity.

The reason for *Adalaria proxima* opting for lecithotrophy, rather than planktotrophy, seems to lie in the previous observations that the absolute and relative amounts of energy available for reproduction are unpredictable. By adopting the lecithotrophic strategy, and thereby increasing the individual probabilities of survival of the larvae, the effects of unpredictability of reproductive output and success may be damped. Clearly, a species with a strictly annual life-cycle, and exhibiting semelparity, cannot afford reproductive failure throughout its geographic range in any one year.

A further speculation is that a species ought to switch strategies in instances of abnormally high or low energy availability. There are many intimations of invertebrates switching larval type, especially amongst polychaetes (e.g. Rasmussen, 1973; Curtis, 1977), but perhaps the more relevant in the present context are those described by Thorson (1946) for the prosobranch *Natica catena* (da Costa), and by Clark and Goetzfried (1978) for the sacoglossan nudibranch *Elysia cauze* Marcus. In the case of *N. catena*, developing embryos are furnished with a number of nutritive "nurse" eggs upon which the larvae subsist prior to hatching as fully-developed juveniles, i.e., development is entirely benthic. Instances are, however, recorded of embryos only being provided with a very few nurse eggs, resulting in hatching of poorly-developed pelagic larvae. *E. cauze* embryos obtain additional nutrition from a granular ribbon which ramifies through the egg-mass. Development appears to vary seasonally, and is controlled by variable utilization of the ribbon material, resulting in both pelagic lecithotrophic, and direct development. The genetic and selective possibilities of such strategy-switching are inviting; if a parent is confronted with a suboptimal environment, it produces dispersive, planktotrophic larvae at low individual energetic cost. Conversely, if the environment is super-optimal, there seems to be little advantage in dispersing the offspring and unnecessarily exposing them to the rigours of pelagic life.

Vance (1973) has suggested that only either planktotrophy or lecithotrophy are evolutionarily stable. Furthermore, he proposes selection would favour that strategy which provides the greatest number of surviving offspring per calorie devoted to reproduction. The number of surviving offspring (as an expression of "fitness") might be considered the "currency" of natural selection and, on this basis, I suggest that selection will tend towards that strategy which results in the greatest absolute number of surviving offspring — even if these are produced comparatively inefficiently in energetic terms.

The advantages and disadvantages of having dispersive, pelagic, larvae have been considered by several authors (e.g. Thorson, 1946; Scheltema, 1971; Crisp, 1974a, 1976; Doyle and Todd, in preparation). For sessile species with pelagic larvae, it is apparent that selective settlement in the presence of conspecifics ("gregarious" settlement; Crisp, 1974b) is necessary to reduce the isolation of those which survive to settle. For mobile species, this is not so important to consequent reproductive success if a means of finding a mate is available. In the case of nudibranchs, many species exhibit very restricted dietary requirements: selective settlement on the preferred diet ("associative" settlement; Crisp, 1974b) thus enhances the probability of settlement within the proximity of other individuals of the same species.

It is of interest that the duration of the pre-benthic developmental phases conferred by these two reproductive strategies should differ so greatly (Fig. 5). As described above, the duration of the larval phase for *Onchidoris muricata* has been estimated from comparative data for *O. bilamellata*. Both *O. bilamellata* and *Adalaria proxima* juveniles measure approximately 500 μm in length following metamorphosis, and it is likely that *O. muricata* will do so similarly, after its appropriate planktotrophic existence. Field observations at Robin Hood's Bay indicated that *O. muricata* post-metamorphic juveniles feed on the small anascan polyzoan *Callopora aurita* (Hincks) before moving on to the preferred diet of *Electra pilosa* and *Alcyonidium* spp. Juveniles of 0.8 to 1.2 mm in length were detected in late June/early July, which would concur with the proposed time of settlement (Fig. 5) after allowing for growth from 0.5 mm at settlement.

Thompson (1967) has shown that the dorid nudibranch *Cadlina laevis* (L.) has direct (non-pelagic) development, and that from oviposition to hatching of the juvenile nudibranch requires approximately 50 days at 10°C. Comparison with the data for the duration of the planktotrophic and lecithotrophic strategies of *Onchidoris muricata* and *Adalaria proxima* (Fig. 5), shows that planktotrophy (at least in these opisthobranchs) results in the longest pre-benthic development phase, while lecithotrophy represents the shortest, with direct development being intermediate. Although comparative reproductive effort data are not yet available for a nudibranch species with direct development, it would appear that the lecithotrophic reproductive strategy represents the supreme compromise in terms of total energy demand, duration of the pre-benthic phase, numbers of eggs and individual probabilities of survival to metamorphosis, and the advantages and disadvantages of dispersal. In the case of *A. proxima*, the obligatory swimming phase (approximately 24 to 48 h, during which the larva is incapable of metamorphosis) enforces limited pelagic

dispersal away from the adult microhabitat.

Adult body size becomes important in that a small species may be incapable of attaining the (higher) absolute energy output required to reproduce by means of a lecithotrophic strategy. Furthermore, body size may become important in cases of very small species which might encounter greater difficulty in producing relatively large eggs. In such cases, it may be of adaptive significance to strike a compromise between reducing egg-size (and thereby individual probabilities of survival) whilst maintaining numbers. Those large species with considerable surfeits of energy available for reproduction would have all larval options open to them; there would be no restriction on egg-size which could be produced, and numbers of larvae could be extremely high. Perhaps most important of all is the suggestion that large species with considerable excesses of energy might opt for an inefficient means of reproduction — in terms of the number of calories devoted to each surviving offspring — yet still maintain the number of offspring. Whilst the particular reproductive strategy adopted by any one species will presumably depend upon the specific combination of ecological pressures and demands exerted upon that species, larval dispersal, with all its concomitant ecological and genetic implications, and the quantities and predictability of available energy are perhaps the most important. It remains of interest, therefore, that the majority of shallow-water, temperate marine invertebrates reproduce by means of planktotrophic larvae, and that lecithotrophy is comparatively poorly represented.

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