



Figure 2. Live Doto amyra (7 mm long) and egg masses on heavily fouled Abietinaria sp. Specimens from Middle Cove, Cape Arago, Oregon (June, 1985).

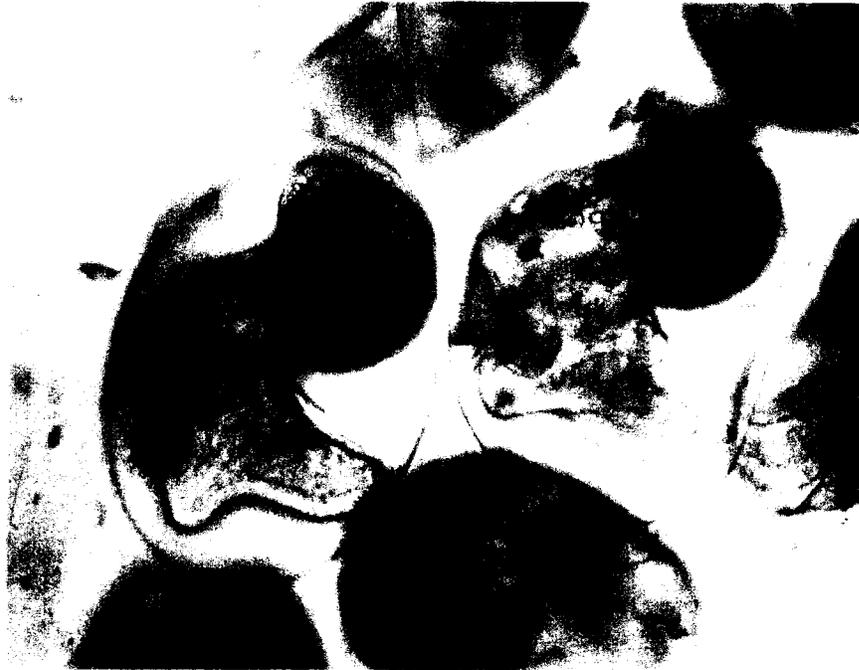


Figure 3. Live embryonic veligers of *Doto amyra* two days before hatching. Shell of specimen on left is 250 μm long.

Figure 4. Newly hatched veliger larva of Doto amyra, right lateral aspect. Drawn from photographs and life. Shell length about 250 μ m.

The following abbreviations are used in figures 4-9:

A	anus
BM	buccal mass
CA	ciliary arc
DD	digestive diverticulum
DG	digestive gland
E	eye
ESO	esophagus
INT	intestine
LK	larval kidney
M	metapodium
OP	operculum
P	propodium
RAD	radula
RCG	right cerebral ganglion
RH BUD	rhizophore bud
S	shell
STA	statocyst
STOM	stomach
V	velum

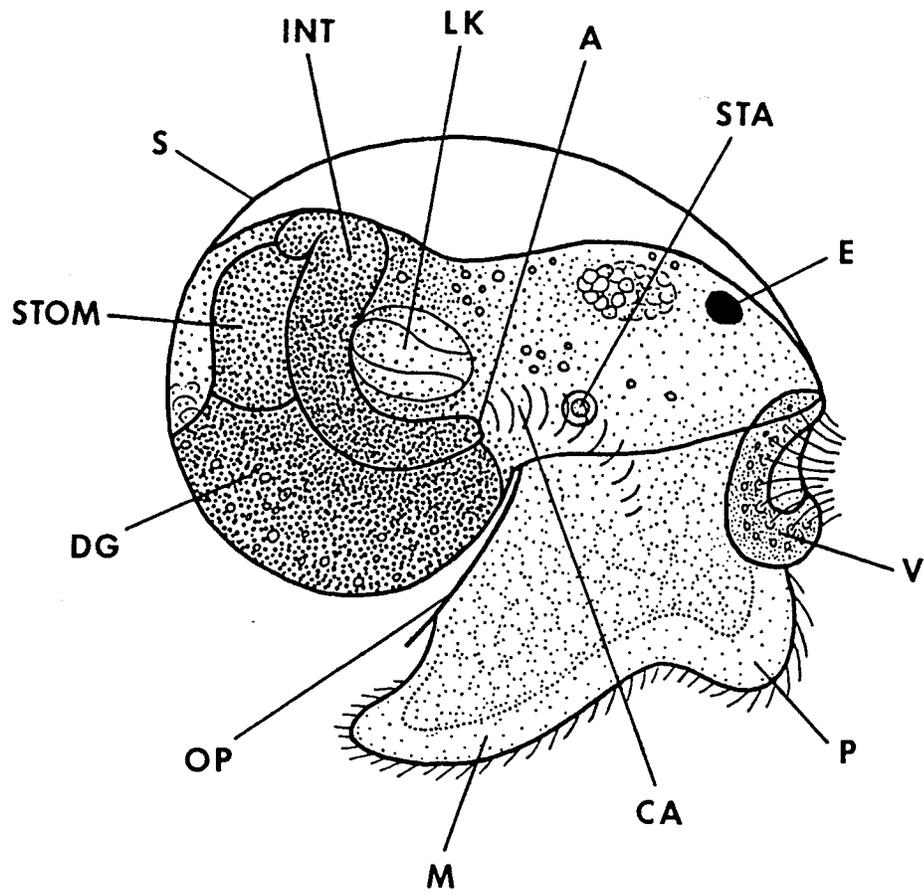


TABLE 1. Egg size and embryonic development
of Doto amyra from Cape Arago, Oregon.

Egg Mass	Egg diameter (μm)			Embryonic period (days)	Temp. ($^{\circ}\text{C}$)	Shell size at hatching (μm)		
	\bar{X}	SD	n			\bar{X}	SD	n
1	145.1	3.1	10	21	15-17			
2	149.6	5.5	10					
3	149.8	2.9	5	20	15-17	236.0	5.3	10
4	151.6	3.1	10	28	11-13	233.6	4.6	10
5	152.1	4.5	10					
6	153.9	3.4	10	20-21	15-17	238.5	5.4	10
7	154.3	2.4	10					
8	157.6	3.3	20	29	11-13	246.1	4.1	7
9				19-20	15-17			
\bar{X}	151.8					238.6		

velum. The clear shells (type 1 of Thompson, 1961) ranged in length from 233.6 μm in one egg mass to 246.1 μm in another, with a grand mean of 238.6 μm (Table 1). I did not observe a mantle fold in the newly hatched larvae, and the shell appeared to be attached to the body only in the region of the visceral mass, particularly on the left side. The large digestive gland was well endowed with yolk reserves, and consequently quite opaque. No radula was observed at this stage. A large, clear larval kidney was present on the right side, next to the anus, and appeared composed of a number of large, flask-shaped cells.

A remarkable band of cilia originated just anterior to the anus, curved and tapered antero-ventrally, and terminated on the right side of the foot (CA, Figure 4). The cilia in this band were observed beating rapidly in wave-like synchrony, creating a current that ventilated the space between the shell and body and probably removed wastes. Bonar & Hadfield (1974:236) described a similar band of cilia on the lecithotrophic larvae of the aeolid nudibranch Phestilla sibogae.

Larvae hatching in the presence of Abietinaria sp. crawled out of the egg mass and onto the hydroid or bottom of the vials. Many were then observed alternately crawling and then swimming just above the bottom of the vials. Some became trapped in the surface film of the water within one day of hatching, presumably after swimming there. No

morphological or qualitative behavioral differences were observed between hatching larvae that had developed in the presence of Abietinaria and those that had developed in its absence. However, a higher proportion of the latter appeared trapped in the water surface film within a day of hatching, suggesting they had spent more time swimming.

Metamorphosis, Feeding, and Post-Larval Growth

The following description is based on observations made in 1983 at temperatures of 15-17°C.

Within one day of crawling and swimming in the presence of Abietinaria sp. some of the larvae anchored themselves to the hydroid perisarc, presumably with pedal gland secretions, and began metamorphosis. They appeared to prefer newly grown (and relatively unfouled) basal stolons for attachment sites, but some were also observed on the branches and stalks of the hydrocaulus. Two days after hatching, these larvae were in the same positions, had lost the velum, and had developed a small radula. Shell loss occurred 3 to 5 days after hatching. At this stage the visceral mass was still in a posteriorly directed hump, the ciliary arc was still visible on the right side, and the radula of one individual was 80 μm long and had 11 teeth (Figures 5 and 6). Closer examination of the eyespots at this stage of development revealed them to be composed of minute grains of dense black pigment overlain with a clear

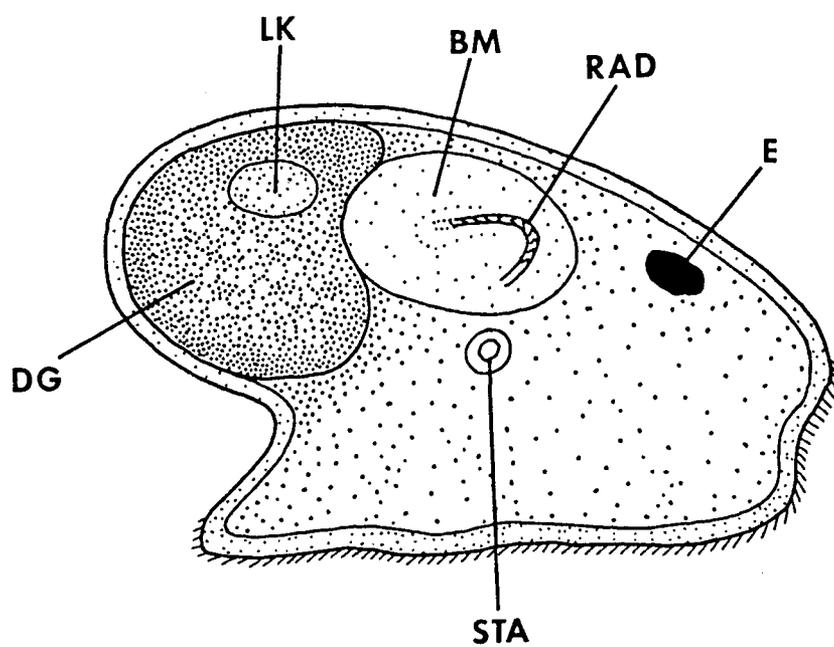


Figure 5. Post-larva recently after exit from shell, right lateral aspect. Body is 265 μm long. Drawn from life.

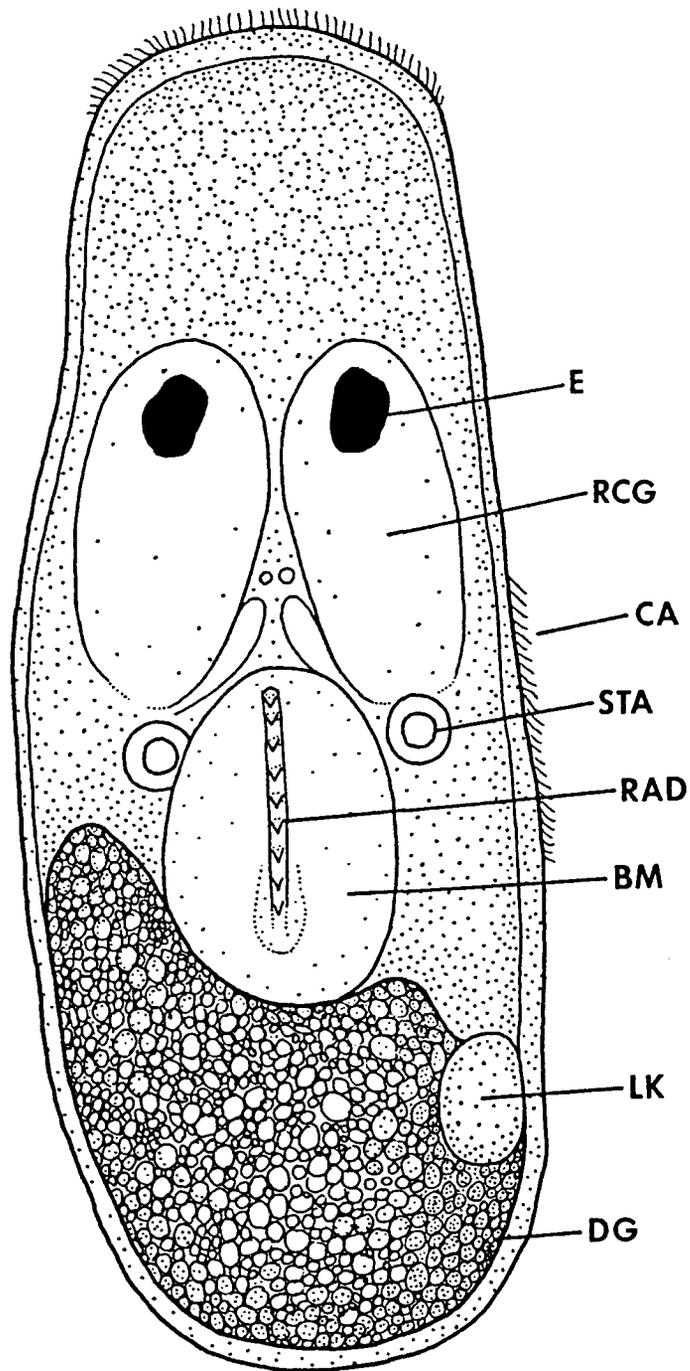


Figure 6. Post-larva, 265 μm long, recently after exit from shell. Dorsal aspect. Same specimen (at same time) as in Figure 5.

lens one fourth the diameter of the pigmented area. Metamorphosis appeared complete 1 to 2 days after shell-loss and resulted in a juvenile about 275 μm superficially resembling a small acoel turbellarian flatworm (Figure 7).

Feeding on Abietinaria sp. was first observed in juveniles about 290 μm long and 7 days post-hatching (it may have commenced one or two days earlier). Feeding entailed repeated protraction of the radula to drill a hole in the hydroid perisarc, followed by retraction of the radula and rhythmic contractions of muscles in the foregut and buccal mass to suck out hydroid coenosarc. Feeding did not appear very efficient in recently metamorphosed individuals: as soon as contractions of the foregut ceased, ingested coenosarc was observed to reverse direction and run out of the nudibranch's alimentary canal and back into the hydroid (one wonders if some hydroids, using their gastrodermal cilia, might be capable of forming localized internal negative pressures as one defense against small suctorial predators).

Twelve days after hatching four juveniles ranged in length from about 280 μm to 390 μm and possessed two pairs of cerata buds, but no external signs of the rhinophores (Figure 8). One of these individuals (390 μm long) had a radula 214 μm long with 47 teeth.

Only one individual was examined at a post-hatching age of more than 12 days. Twenty-five days after hatching this

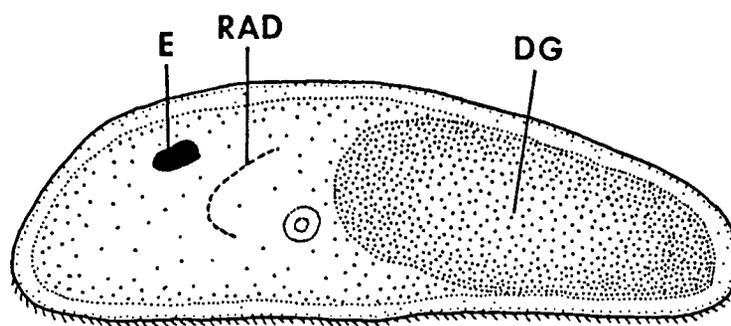


Figure 7. Juvenile *Doto amyra*, 290 μm long, 7 days after hatching. Left lateral aspect. Drawn from life.

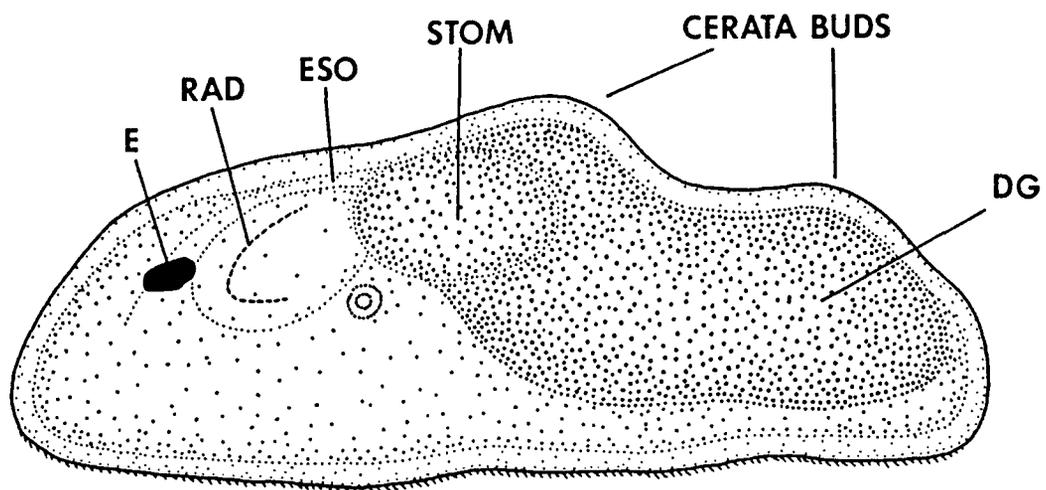


Figure 8. Juvenile *Doto amyra*, 390 μm long, 12 days after hatching. Left lateral aspect. Drawn from life. The radula of this specimen had 47 teeth.

specimen was 480 μm long and had small rhinophore buds and two pairs of cerata. After 38 days it had a third pair of cerata (each ceras had a visible extension of the digestive gland) and measured 750 μm in length (Figure 9). At an age of 46 days it was still about 750 μm long, but had four pairs of cerata, longer rhinophores (still sheathless), and a considerably fuller body that gave a more adult-like appearance. This individual died of unknown causes some time between 46 and 53 days after hatching.

Discussion

The larval development described above is not limited to populations of Doto amyra from Cape Arago. I have observed virtually identical development in Doto amyra from the open coast of Santa Cruz County, California (unpublished observations), and S. Millen (personal communication) describes similar development in Doto amyra from the Vancouver Island region. She observed eggs 140 μm in diameter that developed into hatching larvae after 38 days (at 10°C). Newly hatched larvae alternated every few minutes between swimming and crawling, and shell-loss occurred three days after hatching.

In the presence of Abietinaria sp. some of the larvae observed in this study began metamorphosis within a day of hatching (at 15-17°C). Other larvae did not appear to begin metamorphosis for another day or two, and in one case some

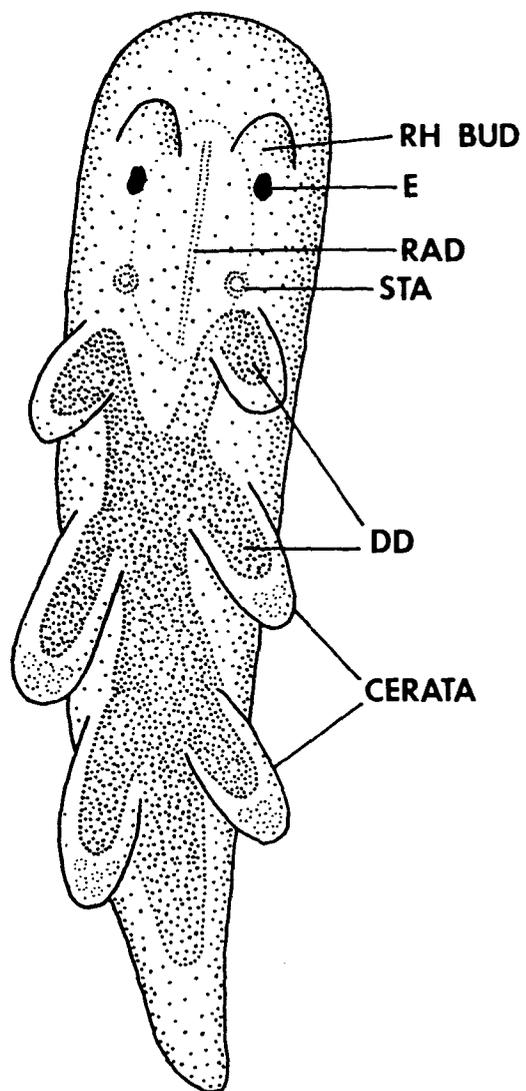


Figure 9. Juvenile *Doto amyra*, 750 μm long, 38 days after hatching. Dorsal aspect. Drawn from life.

larvae (in the presence of a small amount of Abietinaria as well as newly metamorphosed siblings) had not metamorphosed after 9 days. This variation in onset of metamorphosis might have resulted from: (1) normal variation in the length of an obligatory or pre-competent phase (during which larvae are incapable of metamorphosis, even in the presence of the adult food (see reviews by Todd, 1981 and Hadfield & Switzer-Dunlap, 1984)) or (2) from increased searching time under laboratory conditions (which included the presence of only small amounts of Abietinaria).

Morphologically, the larvae of Doto amyra appear competent to metamorphose upon hatching. Other lecithotrophic larvae possess a mantle fold that fuses with the perivisceral membrane either during the obligatory period (e.g. see Thompson, 1958; Todd, 1981) or during metamorphosis itself (e.g. Bonar & Hadfield, 1974; Rose, 1983). Hatching Doto amyra lack a mantle fold (it recedes late in embryonic development) and thus appear ready for metamorphosis, if not already in the process.

During this study larvae of Doto amyra were not held more than one day in the absence of Abietinaria sp. Consequently, I do not know if this hydroid is necessary to induce metamorphosis. Likewise, little can be said about the ability of the larvae to delay metamorphosis and disperse in search of hydroids, and nothing is known about their ability to feed in the plankton as observed in some

other lecithotrophic larvae (e.g., Kemp & Hadfield, 1985). The relatively small velum probably limits swimming and feeding behaviors, but yolk reserves are considerable (the viscera are semi-opaque) and can probably support competent veligers for an extended period. Possession of the ciliary arc, shell, and operculum (structures for the maintenance and protection of the larvae respectively) also suggest the potential for a prolonged larval period. Larvae hatching in the absence of Abietinaria did appear to swim more than those hatching in its presence, and, as mentioned above, some larvae held with Abietinaria remained unmetamorphosed 9 days after hatching. However, observations were not continued on these latter individuals, and I do not know if they were still capable of metamorphosis.

In this study few Doto amyra survived more than a week or two beyond metamorphosis. However, only small pieces of hydroid were available to the larvae and juveniles, and the relatively stagnant conditions in the vials holding them may have fostered a community of micro-organisms detrimental to their survival. And while Abietinaria may induce metamorphosis in the larvae (and is the only known prey of Doto amyra from Cape Arago), metamorphic success and (or) juvenile survival might be higher on other hydroids. Feeding by recently metamorphosed juveniles did not appear very efficient, but this may be fairly common among individuals just beginning to feed, even on optimal

prey.

Because hatching and metamorphosis in Doto amyra are so closely timed (at least in the presence of Abietinaria sp.), it seems possible that hatching sometimes might be delayed until after metamorphosis. However, this could occur only if: (1) the late embryos are competent (see above), (2) induction of metamorphosis in Doto amyra is not dependent on external factors such as Abietinaria, or (3) the factor(s) inducing metamorphosis can permeate through the egg mass and capsules. Other species of opisthobranchs with short-term lecithotrophic larvae (including one species of Doto) are known to hatch either as veliger larvae or as juveniles, the stage at hatching depending in part on differences in embryonic period (e.g., Schmekel & Kress, 1977; Harris et al., 1980; Gibson & Chia, 1989; Carrol & Kempf, 1990). Harris et al. (1980) suggested that some of the variability in the embryonic period of the hydroid-feeding nudibranch Tenellia fuscata is caused by external factors, such as water motion and colonization of the egg masses by micro-organisms, contributing to the breakup of the egg mass. In addition, Gibson & Chia (1989) present strong evidence that a diffusible compound in the egg mass jelly of Haminoea callidegenita induces intracapsular metamorphosis. This stimulus might be reduced or eliminated with an early breakup of the egg mass, especially for embryos whose capsules become separated

from the egg mass.

Variability in stage of development at hatching caused by differences in condition of the egg mass could be advantageous to species with lecithotrophic larvae if the condition of the egg mass is correlated with the quality or accessibility of the prey of the juveniles. For hydroid-feeding species like Doto amyra and Doto acuta, fouled egg masses might mean that nearby hydroid colonies are also fouled and (or) senescent. These might be nutritionally inferior to relatively unfouled colonies or less vulnerable to predation by newly metamorphosed nudibranchs (especially drilling and sucking predators like Doto amyra). Fouled hydroids might also harbor higher densities of predators of the post-larval nudibranchs. Embryos in heavily fouled egg masses would hatch earlier (as larvae) and thus be more likely to disperse farther and find less fouled prey -- especially if the cue for settlement emanates from the prey and is stronger in unfouled colonies (as reviewed by Todd, 1983; Hadfield & Switzer-Dunlap, 1984; and Hadfield & Miller, 1987, most nudibranchs will settle and metamorphose only in the presence of the adult prey). The potential for externally caused variation in developmental state at hatching -- especially that caused by seasonally correlated factors -- needs to be examined in Doto amyra and other species of opisthobranchs.

Although Abietinaria sp. is subject to seasonal fouling

by epifauna and flora (Ricketts et al., 1985; personal observations), as well as predation by Doto amyra and other dendronotacean nudibranchs (McDonald & Nybakken, 1978; Goddard, 1990), patches of this hydroid ($\leq 0.25\text{m}^2$) have persisted for at least 10 years at Middle Cove, Cape Arago (personal observations). Thus, it seems likely that Doto amyra hatching at Cape Arago will often be close to exploitable Abietinaria sp. Moreover, predation by Doto amyra appears to be partial (the thick perisarc of the hydroid is damaged little, and only coenosarc is consumed (Goddard, 1984; present study)). Enough coenosarc may remain after bouts of predation to fuel either the growth of new stolons and hydrocauli or the regeneration of existing ones (e.g., see Hughes, 1977; 1986), especially if population densities of Doto amyra are kept low by other factors such as predation.

This apparent predictability in local food supply, combined with the lower probability of reaching more distant patches of the hydroid (especially if Abietinaria sp. is patchily distributed on a scale of kilometers or more), may have been important in the evolution of lecithotrophic development in Doto amyra (see next section). However, more information is needed on the population dynamics of Abietinaria, on the effects of predation by D. amyra, and on the dietary composition of D. amyra over a larger portion of its range.

Comparisons of feeding methods, effects on prey, and developmental mode between Doto amyra and two much larger nudibranch predators of Abietinaria, Dendronotus albus and Dendronotus diversicolor, would be useful in illuminating some of the factors important in the life-history evolution of D. amyra. However, little is known about the biology of these two species. Based on observations available for other hydroid-feeding species of Dendronotus from the northeastern Pacific (see Hurst, 1967; Robilliard, 1970 and Strathmann, 1987), it seems likely that one or both of these species produce planktotrophic larvae and are more detrimental in their effects on colonies of Abietinaria than Doto amyra. Dendronotus diversicolor is known to produce eggs 96 μm in diameter (Strathmann, 1987), just under the 100 μm minimum size known for nudibranch species with non-planktotrophic development (Hadfield & Miller, 1987).

It might be argued that lecithotrophy evolved in Doto amyra as a way of increasing larval survivorship in the face of the reduced fecundity associated with small adult size (e.g., Chia, 1974; Menge, 1975). While this may be important given the much larger size (and fecundities) of potential competitors such as the above species of Dendronotus, consideration of adult size and developmental mode in other species of Doto (see below) suggest that the present adult size of D. amyra does not impose any absolute

limitations on fecundity precluding planktotrophy. Many species of Doto smaller than D. amyra and having planktotrophic larvae (including some sympatric species) appear to be just as successful (albeit on different hydroids).

Development in the Genus

Species of Doto prey suctorially on the coenosarc of hydroids and as a consequence (Goddard, unpublished) are smaller than most other nudibranchs (adults rarely exceed 10 - 15 mm in length) (Lemche, 1976; Todd, 1981; Thompson & Brown, 1984). Because small adult size is associated with a reduced pelagic phase in the life history of many benthic marine invertebrates (e.g., Chia, 1974; Menge, 1975; Strathmann & Strathmann, 1982; Strathmann, 1985), one might expect a higher incidence of lecithotrophy and (or) direct development in the genus Doto compared to the Nudibranchia as a whole, more than two-thirds of which produce planktotrophic larvae (Hadfield & Miller, 1987). On the other hand, the opportunistic and ephemeral nature of many hydroids (e.g., Clark, 1975; Hughes, 1977; 1986; Boero, 1984; Harris, 1987) might be exploited best by predators with short generation times and good powers of dispersal. For small benthic predators with limited dispersal abilities as adults (like most nudibranchs) the latter can be facilitated by planktotrophic or pelagic lecithotrophic larvae adapted for locating the prey of the adults.

Data presented in recent analyses of developmental patterns in the Opisthobranchia (see Ros, 1981; Hadfield & Switzer-Dunlap, 1984; Hadfield & Miller, 1987) suggest most species of Doto have planktotrophic development. However, patterns of development have not been examined in detail in this genus, and considerably more data have recently become available (e.g., Fernandez-Ovies & Ortea, 1981).

The purposes of this section are to: (1) summarize data available on larval development in the genus Doto; (2) determine the predominant mode of development, and (3) attempt to gain some understanding of the factors and constraints shaping patterns of development in the genus.

Based on observations of the size, morphology, and behavior of hatching veliger larvae, developmental mode can be determined directly for 11 species of Doto (Table 2). Nine of these have planktotrophic larvae; D. amyra produces short-term lecithotrophic larvae from eggs averaging 152 μm in diameter (present study); and D. acuta hatch as either short-term lecithotrophic larvae or as newly metamorphosed juveniles (both from eggs 110 to 120 μm in diameter) (Schmekel & Kress, 1977). All larvae have coiled type 1 shells (see Thompson, 1961).

Egg diameter appears to be a relatively good predictor of shell size at hatching in the genus (Figure 10). However, of the planktotrophic species, D. yongei is reported to produce the largest hatching veligers from the

TABLE 2. Development in the genus Doto. Values for egg diameter and shell length at hatching are means or grand means. All larvae have type 1 shells (Thompson, 1961).

Species ¹	Egg diameter (µm)	Embryonic period (days)	Temp. (° C)	Shell length at hatching (µm)	Type of devel. ²	Reference
<u>D. japonica</u>	80	5	26-30	145	(P)	Hamatani (1963)
<u>D. yongei</u>	64	---	---	168	P	Thompson (1972)
<u>D. coronata</u>	72	13	10-12	116	(P)	Kress (1975)
<u>D. fragilis</u>	83	18	10-12	145	(P)	Kress (1975)
<u>D. pinnatifida</u>	95	16	10-12	160	(P)	Kress (1975)
<u>D. acuta</u>	115	16-20	16	---	L or D	Schmekel & Kress (1977)
<u>D. amyra</u>	152	19-21 28-29	15-17 11-13	239	L	Goddard (1984, present study)
<u>D. kya</u>	78	7	15-17	133	P	personal
<u>D. lancei</u>	---	---	---	---	P	personal ³
<u>D. sp. A</u> ⁴	76	12	11-13	123	P	personal
<u>D. sp. B</u> ⁴	70	11	11-13	122	P	personal

TABLE 2. Continued.

- 1 D. acuta Schmekel & Kress 1977; D. amyra Marcus, 1961; D. coronata (Gmelin, 1791); D. fragilis (Forbes, 1838); D. japonica Odhner, 1936; D. kya Marcus, 1961; D. lancei Marcus & Marcus, 1967; D. pinnatifida (Montagu, 1804); D. yongei Thompson, 1972.
- 2 P = planktotrophic, L = lecithotrophic, D = direct (capsular metamorphic or ametamorphic).
If not stated in the original reference, developmental type was determined using descriptions and figures of hatching veliger larvae and the criteria described by Thompson (1967, 1976), Bonar (1978), Todd (1983) and Hadfield & Switzer-Dunlap (1984). Developmental types determined in this manner are placed in parentheses.
- 3 Specimens from Bahia de Concepcion, Baja California Sur, and Matanchen Beach, Nayarit, Mexico.
- 4 See appendix for description of these species.

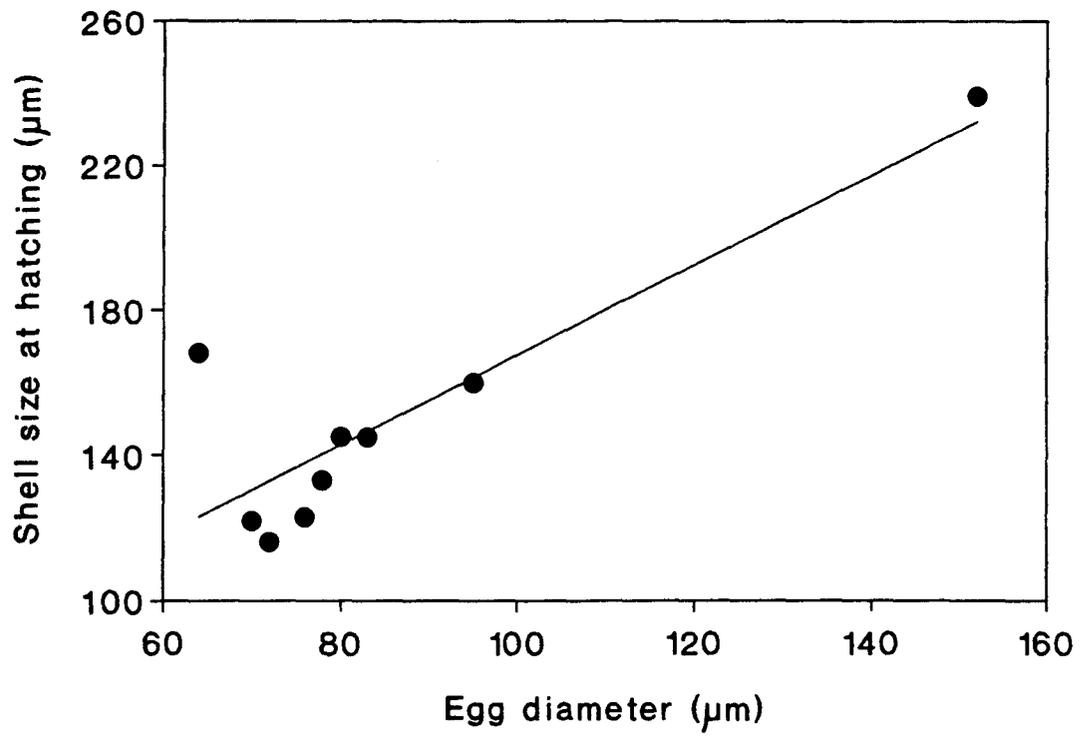


Figure 10. Relation between mean egg diameter and mean shell size at hatching for 9 species of *Doto*. Data from Table 2.

smallest eggs -- if omitted from the regression analysis summarized in Figure 10, r^2 would increase to 0.98 ($p \ll 0.005$). The eggs and hatching larvae of this species should be re-examined for idiosyncrasies in morphology and development as well as to confirm the original size measurements.

Egg diameter varies widely within different taxonomic groups, including genera, and can be used to distinguish between planktotrophic and non-planktotrophic modes of development in the Nudibranchia (Hadfield & Switzer-Dunlap, 1984; Hadfield & Miller, 1987). Including the species in Table 2, egg diameters are known for a total of 26 species of Doto (Table 3) and range from 64 to 230 μm . Their frequency distribution is skewed to the right and has a mode of 75 μm (Figure 11). Twenty-one (81%) of these species produce eggs under 100 μm , the minimum diameter known for nudibranch species with lecithotrophic or direct development (Hadfield & Miller, 1987).

Of the five species of Doto with eggs larger than 100 μm , D. amyra and D. acuta have already been discussed, D. fragaria produces eggs averaging 110 μm in diameter (Ortea & Bouchet, 1988), the eggs of D. tuberculata are 126 μm in diameter (Fernandez-Ovies & Ortea, 1981), and D. ussi from the Comoro Islands in the Indian Ocean is reported to lay eggs 210 to 250 μm in diameter (Ortea, 1982) (however,

TABLE 3. Egg size and maximum adult length in the genus Doto. Values given for eggs are means or, if more than one mean was available for a species (i.e. for different egg masses and localities, or from different references), grand means.

Species ¹	Egg diameter (μ m)	Maximum adult length (mm)	Source ²	
			egg size	adult size
<u>acuta</u>	117	7	16	16
<u>amyra</u>	152	14	6,22	22
<u>chica</u>	77	10*	4	11
<u>coronata</u>	70	15	5,9,16,18,23	20
<u>doerga</u>	83	6	16	17
<u>eireana</u>	81	7	5,10	20
<u>fluctifraga</u>	97	8	14	14
<u>fragaria</u>	110	8	13	13
<u>fragilis</u>	81	40	9,16	16
<u>japonica</u>	80	12	8	1
<u>koenneckeri</u>	68	8	5,24	15
<u>kya</u>	78	10	22	2
<u>lemchei</u>	74	10	5,21	20
<u>maculata</u>	72	9	5	20
<u>millbayana</u>	66	14	5	20
<u>oblicua</u>	73	9.5	15	15
<u>paulinae</u>	70	7	16	16
<u>pinnatifida</u>	97	29	5,9,16	20

TABLE 3. Continued.

Species ¹	Egg diameter (μm)	Maximum adult length (mm)	Source ²	
			egg size	adult size
<u>rosea</u>	70	12	16	16
<u>tuberculata</u>	127	19	5	20
<u>ussi</u>	230	10	12	12
<u>verdicioi</u>	67	6	15	15
<u>yongei</u>	64	6	19	19
sp. A of present study ³	76	7	22	22
sp. B of present study ³	70	11	22	22
sp. (<u>coronata</u> of Clark, 1975) ⁴	89	12	3	7

¹ Doto acuta Schmekel & Kress, 1977; D. amyra Marcus, 1961; D. chica Marcus & Marcus, 1960; D. coronata (Gmelin, 1791); D. doerga Marcus & Marcus, 1963; D. eireana Lemche, 1976; D. fluctifraga Ortea & Perez, 1982; D. fragaria Ortea & Bouchet, 1988; D. fragilis (Forbes, 1838); D. japonica Odhner, 1936; D. koenneckeri Lemche, 1976; D. kya Marcus, 1961; D. lemchei, Ortea & Urgorri, 1978; D. maculata (Montagu, 1804); D. millbayana Lemche, 1976; D. oblicua Ortea & Urgorri, 1978; D. paulinae Trinchese, 1881; D. pinnatifida (Montagu, 1804); D. rosea Trinchese, 1881; D. tuberculata Lemche, 1976; D. ussi Ortea, 1982; D. verdicioi Ortea & Urgorri, 1978; D. yongei Thompson, 1972.

² 1, Baba (1949); 2, Behrens (1980); 3, Clark (1975); 4, Clark & Goetzfried (1978); 5, Fernandez-Ovies & Ortea (1981); 6, Goddard (1984); 7, Gosner (1971); 8, Hamatani (1963); 9, Kress (1975); 10, Lemche (1976); 11, Marcus (1972); 12, Ortea (1982); 13, Ortea & Bouchet (1988); 14, Ortea & Perez (1982); 15, Ortea & Urgorri (1978); 16, Schmekel & Kress (1977);

TABLE 3. Continued.

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- ² (Continued)
17, Schmekel & Portmann (1982); 18, Thompson (1967); 19, Thompson (1972); 20, Thompson & Brown (1984); 21, Thompson et al. (1990); 22, present study (see appendix); 23, Miller (1958) in Thompson (1967); 24, Ballesteros (1980) in Fernandez-Ovies & Ortea (1981).
- ³ See appendix, present study.
- ⁴ According to Thompson & Brown (1984:29) Doto coronata reported from the east coast of the United States are "distinctive and may be another species". The large differences in egg size between European D. coronata and the D. coronata of Clark (1975) (see above) support this hypothesis. D. coronata of Clark (1975) is thus considered a separate species in the present study.
- * Length of a preserved specimen (an estimate of 15 mm was used in statistical analyses).

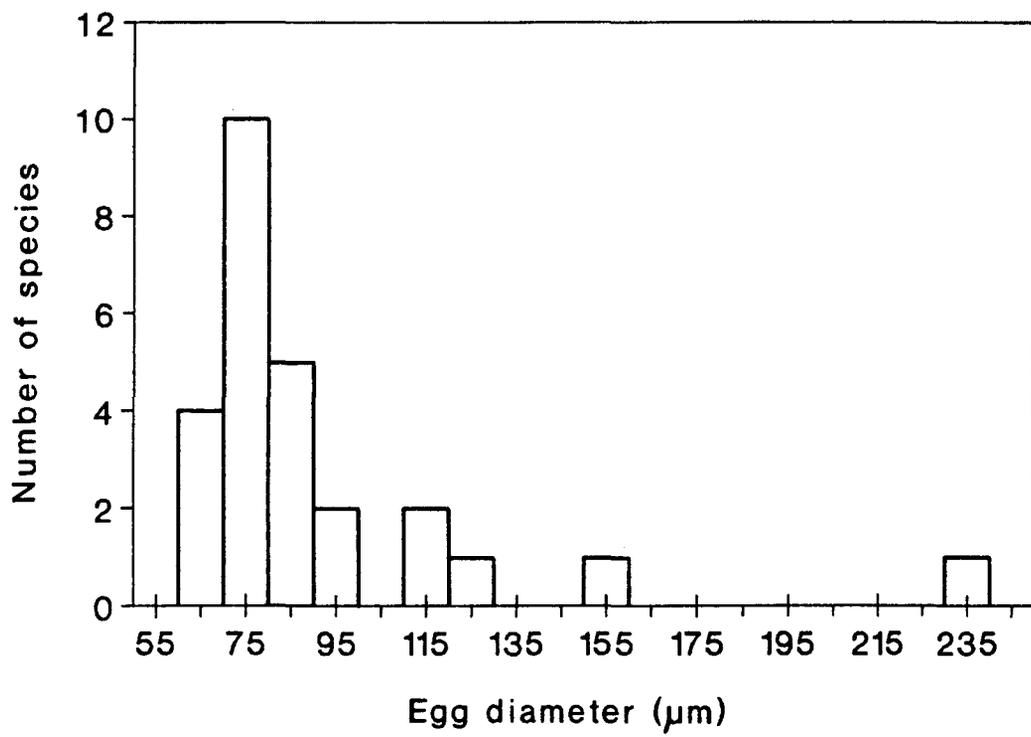


Figure 11. Egg size distribution for 26 species of *Doto*. Data from Table 3.

Ortea's drawing of the egg mass of D. ussi and scale bar indicate an egg diameter of about 130 μm). Mode of development has not been described for the latter three species. However, based on the egg size distributions reported by Thompson (1967) and Hadfield & Miller (1987), D. fragaria and D. tuberculata most likely have planktotrophic or lecithotrophic development, and D. ussi probably has direct development. Observations on the hatching larvae or juveniles of these three species are needed.

Species of Doto usually deposit one egg per capsule, but pairs are occasionally seen, especially in D. fragilis (Kress, 1975:696). There are no reports of egg masses containing extra-zygotic yolk.

The largest range in egg size reported for a species of Doto (all localities and egg masses combined) is 40 μm for D. ussi, followed by 25 μm for D. pinnatifida and 22 μm for D. amyra, D. coronata, and D. maculata (Fernandez-Ovies & Ortea, 1981; Kress, 1975; present study). Using standard deviations in egg diameter reported for individual egg masses or eggs from a given locality by Kress (1975), Clark (1975) and the present study, the average coefficient of variation in egg diameter for a species of Doto is about 3% (range, 0.8% - 9.4%; data for 8 species), a value similar to those for other nudibranchs (Goddard, unpublished data; and see, for example means and standard deviations in egg

diameter reported by Clark, 1975; Eyster, 1980; Williams, 1980; and Ros, 1981).

As might be expected given the limited intraspecific variation in egg size, no examples of poecilogony, or polymorphism in type of development (see Hoagland & Robertson, 1988), have been reported in the genus. As mentioned above, Doto acuta from different egg masses hatch as either short-term lecithotrophic larvae or newly metamorphosed juveniles (Schmekel & Kress, 1977). However, this appears to result more from a variable embryonic period rather than significant differences in egg size and (or) developmental pathways (both types developed at the same temperature from eggs of the same size, and individuals hatching as juveniles had a longer embryonic period than those hatching as larvae).

Developmental mode can be inferred for six additional species of Doto. Based on sizes of egg capsules early in development reported by Garcia Gomez & Lopez de la Cuadra (1988) for D. furva, and on ratios of capsule length to egg diameter that can be derived from Kress (1975) and Schmekel & Kress (1977) for five other European species of Doto, D. furva most likely has eggs between 80 and 95 μm in diameter and thus probably has planktotrophic development. Descriptions and depictions of egg masses (especially their size and approximate number of eggs) in Just & Edmunds (1985) suggest that D. columbiana O'Donoghue, 1921, D.

dunnei Lemche, 1976, D. onusta Hesse, 1872, and their Doto sp. E have planktotrophic development, and that development in Doto sp. C is either planktotrophic or lecithotrophic. Just & Edmund's Doto sp. D, which has "small eggs", is probably the same species as the Doto sp. B of the present study (see Table 3 and Appendix A) and thus already has been included in the present analysis.

Based on the data in Tables 2 and 3, and including the observations on the above six species, between 82% (27/33) and 91% (30/33) of species of Doto have planktotrophic development, at least as high a proportion as the 66 to 80% known for the Nudibranchia as a whole (Hadfield & Miller, 1987). There is no relationship between maximum reported adult length and egg diameter (and thus mode of development) for the species listed in Table 3 ($r^2 = 0.003$, $n = 26$, $p > 0.25$). Moreover, the maximum reported adult lengths of the planktotrophic species ($n = 27$ or $n = 30$) do not differ significantly from those of the non-planktotrophic species ($n = 6$ or $n = 3$, respectively) ($p > 0.4$ for both comparisons; Mann-Whitney U test)*.

A pelagic larval stage has probably been maintained so strongly in the Genus Doto partly as a means for colonizing

*Adult lengths used for Doto columbiana, D. dunnei, D. furva, D. onusta, and D. spp. C and E of Just & Edmunds (1985) were 14, 25, 15, 11, 4, and 10 mm, respectively (see Garcia-Gomez & Lopez de la Cuadra, 1988; Just & Edmunds, 1985).

their hydroid prey, many of which are widely dispersed, fast-growing occupants of ephemeral substrata (Hughes, 1977; 1983; 1986; 1987; Boero, 1983; Harris, 1987). Some hydroids can be quickly depleted by nudibranch predators (Miller, 1962; Thompson, 1964; Clark, 1975; Harris, 1987); others acquire epifaunal communities that probably harbor predators and (or) competitors of the nudibranchs, especially the juveniles (e.g. Hughes, 1975; Lagardere & Tardy, 1980; Highsmith, 1982). Epifaunal communities may also hinder detection of the hydroids by nudibranchs, as well as impede feeding by suctorial predators like the Doto. Thus, the susceptibility of many hydroids to predation by nudibranchs probably declines rapidly as the generally short-lived hydroids age, and subsequent generations of nudibranchs must be deposited on, or find, the new patches of prey that are continually forming. However, the small adult size of most Doto (which could be an adaptation for feeding efficiently on the coenosarc of hydroids) must severely limit their chances of finding new patches of prey, especially compared with pelagic larvae adapted for locating the prey of the adults (but see Martel & Chia, 1991). Pelagic larvae, especially those capable of feeding and delaying metamorphosis for long periods, may also be important in surviving seasonal or unpredictable lows in hydroid availability. When the hydroids resume growth and (or) become accessible again, the veliger larvae

(now competent and finding the appropriate cues) settle, metamorphose, and commence benthic feeding. In the absence of suitable stimuli (such as the adult prey) the larvae of many opisthobranchs can delay metamorphosis for long periods (see review by Hadfield & Switzer-Dunlap, 1984).

Why planktotrophy over lecithotrophy? Given adequate supplies of planktonic food, as well as the ancestral and conservative nature of feeding larval forms (e.g. Strathmann, 1986; Hadfield & Miller, 1987), planktotrophy should be maintained in a species of Doto as long as its hydroid prey are widely dispersed and larval mortality rates do not offset the higher fecundities associated with planktotrophy (e.g. Strathmann, 1985; Levin & Hugget, 1990). Even if larval mortality (from non-food related causes) were to increase dramatically, selection probably has other aspects of the larval stage to act on (e.g. behavioral and structural defenses against predators), not just the size of their yolk reserves and degree of dependence on planktonic food for growth.

All of the Doto included in the present review are from coastal waters with moderate to high levels of annual primary production (see, e.g., figures in Raymont, 1980). Consequently, larval mortality from lack of food (and the resulting selection against planktotrophy) is probably uncommon in these species. Pelagic lecithotrophy should be more common in species of Doto from regions with low

primary production.

If pelagic development is advantageous in exploiting hydroids, then the incidence of pelagic development in other groups of nudibranchs specializing on hydroids should be comparable to that seen in the Doto. A survey of the literature appears to confirm this, at least for members of the Aeolidacea. To my knowledge only five species of aeolids specializing on hydroids are known to have non-pelagic development (see reviews by Thompson, 1967; Thompson & Brown, 1984; Todd, 1981, 1983; Hadfield & Switzer-Dunlap, 1984; Hadfield & Miller, 1987). Two of these species (belonging to the genus Tenellia) occur in restricted estuarine habitats, and another two (Cuthona nana and C. pustulata) reportedly have planktotrophic development over parts of their range. No aeolids specializing on hydroids are known to have direct development, and the vast majority, like the Doto, appear to have planktotrophic development (op. cit.).

The high incidence of planktotrophy and lack of relationship between adult size and mode of development in the Doto indicate that fecundities, even in the smallest species, have not been limited in a way that might have favored (owing to planktonic mortality and relatively low densities of settling larvae) an evolutionary shift towards the reduced larval periods and reduced dispersal associated with non-planktotrophic modes of development. Either

spawning is synchronous enough to ensure adequate densities of settling larvae, or benthic populations are dense and widespread enough (and juvenile mortality rates low enough) that recruits from the plankton, however few, have a good chance of reaching maturity, encountering mates, and successfully reproducing. Early maturity, a relatively prolonged reproductive period, and overlapping generations would probably enhance an individual Doto's chances even more under the latter circumstances. Individuals appear to begin mating at small sizes (Miller, 1962; Clark, 1975; personal observations of northeastern Pacific species), and Miller (1962) provided evidence suggesting that Doto coronata from Britain live from 5 to 10 months depending on the season and have up to 4 overlapping generations per year.

Non-planktotrophic development might be selected for in a nudibranch specializing on hydroids under one or more of the following ecological conditions:

- 1) Consistently high larval mortality rates (due to predation, food scarcity, or transport away from habitats conducive to settlement).
- 2) Increased persistence (on a seasonal time scale) of local hydroid populations. This could occur if colonies were longer-lived, or through greatly reduced dispersal of hydroid propagules and multiple generations per year. Even if the hydrocauli are ephemeral, the stolons may not be,

and these could be utilized by suctorial predators like the Doto. Of course, persistent hydroids would also have to be apparent and accessible to the nudibranchs (especially the juveniles), as well as provide adequate refuges from predators and other sources of mortality. As alluded to previously, this combination of conditions may be uncommon in hydroids.

The next two conditions assume increased persistence (combined with accessibility) of the hydroid prey of the nudibranchs.

3) The hydroids are so rare, patchy, or confined to such restricted habitats that planktotrophic larvae lacking finely tuned sensory and behavioral adaptations would have little chance of encountering them. This might explain lecithotrophy in estuarine species such as the Tenellia spp.

4) Predation or some other factor limits the population size of the nudibranchs so that local populations of hydroids are usually not overgrazed. However, occasional declines in hydroid abundance (due to seasonal and (or) stochastic factors) would require relatively long distance dispersal by the nudibranchs. Lecithotrophic larvae with a short obligatory phase but also with the potential for feeding and an extended pelagic phase would seem an ideal strategy under these circumstances.

Some combination of (1), (2), and (3) might result in

selection for direct development, especially if juvenile mortality rates are consistently high and there is selection for larger juveniles. As shown by Hadfield & Miller (1987, Figure 13), direct development (especially ametamorphic development) usually results in considerably larger juveniles than either of the other modes of development.

More observations and data on the population dynamics and life histories of Doto species and their hydroid prey are needed to refine and then test these hypotheses.

Appendix

Varieties of Doto currently Referred to as Doto amyra

The four varieties of Doto that in my opinion would be identified as Doto amyra based on the descriptions and synonymies in Beeman & Williams (1980), Behrens (1980), McDonald & Nybakken (1980), and McDonald (1983) are as follows (descriptions are of live adults):

1) Doto amyra of Goddard (1977, 1984, 1987, 1990, and present study). The following description of the external morphology and color of this species expands on that given by Goddard (1984) for specimens from Cape Arago, Oregon and is based on additional specimens from that locality.

Adults (figures 1 and 2 of this paper) feed on the hydroid Abietinaria sp. (A. anguina of Ricketts & Calvin,

1985) and reach a length of 14 mm, though most are under 10 mm. The body and head are translucent white and occasionally have an irregular scattering of fine-grain, subcutaneous brown to black pigment. The gonads are yellow and show clearly through the body wall. The rest of the viscera are cream-colored. The 5 to 8 pairs of cerata have pale yellow to light pinkish-orange or orange-brown colored cores, possess 4 to 7 rings of tubercles, and lack dark pigment. The tubercles vary from low to elongate in different individuals and contain semi-translucent white glands (possibly defensive in nature). Longer tubercles point upward; all are rounded at their ends. The accessory gills (pseudobranchs) interrupt the lower rings of tubercles and are clear, branched, and often contain a few minute, opaque white grains. The rhinophores and their sheaths are translucent like the body and contain opaque white grains, especially distally. The anal papilla is distinct and located between the right members of the first and second pairs of cerata. Specimens of this variety closely resemble Doto amyra as described and depicted in McDonald & Nybakken (1980:58-59).

In addition to Cape Arago, I have also found this species at: (1) Scott Creek, Santa Cruz County, California where it feeds on Sertularia furcata growing on an unidentified red alga and on the proximal parts of the leaves of the surfgrass Phyllospadix torreyi; these

specimens have development virtually identical to that described in the present paper (Goddard, 1977; personal observations), (2) at Punta Gorda, Humboldt County, California (Goddard, 1987), and (3) on the southern Oregon coast (Goddard, 1990). This species has also been found in the Vancouver Island region where it also has short-term lecithotrophic development (see discussion) and has been observed on hydroids of the genera Coryne, Abietinaria, and Garveia (S. Millen, personal communication).

2) Doto species A of the present study. Specimens of this variety were found among small athecate hydroids on the undersides of intertidal boulders at the mouth of Drake's Estero, Marin County, California. They measured up to 7 mm long and were similar to Doto amyra in color, but none had dark pigment. They closely resemble the individual pictured in photograph number 91 of Behrens (1980). There are 5 to 6 pairs of cerata, with longer tubercles than D. amyra. Unlike D. amyra, this variety produces small planktotrophic larvae from eggs averaging 76 μ m in diameter (see Table 2 of the present study). Seven specimens of this species have been deposited in the invertebrate collection of the California Academy of Sciences (voucher number 056222).

3) Doto species B of the present study. This variety occurs on species of Aglaophenia growing on various algae, especially species of Laminaria. I have observed it at the

mouth of Drake's Estero, Marin County, California; on the southern Oregon coast; and at the south jetty of Coos Bay, Oregon. Specimens from Drake's Estero and the south jetty have been deposited in the California Academy of Sciences (voucher numbers 056216 and 056217 respectively).

This variety differs from the above two in having cerata with dark pigment and low to medium-length tubercles (the cerata of some individuals are almost smooth). The dark pigment may be scattered over the entire cerata (including the tubercles) or concentrated between the tubercles. Specimens lack the opaque white grains found in the accessory gills, rhinophores and rhinophore sheaths of varieties 1) and 2) (however, one larger specimen from the south jetty did have these grains in the rhinophore sheaths). The ground color of the body and cerata is pale yellow; the cerata of specimens from south jetty were pinkish-orange. The body, head, and rhinophore sheaths of most individuals have subcutaneous brown to black pigment. Specimens from Drake's Estero measured up to 8 mm in length and produced small planktotrophic larvae from eggs averaging 70 μm in diameter (Table 2, present study).

This may be a light form of Doto columbiana O'Donoghue, 1921 (which is how I referred to specimens from the southern Oregon coast (Goddard, 1990)) and may well be the same as the Doto amyra reported by McDonald (1983) on Aglaophenia struthionides. Individuals of Doto sp. B

closely resemble the individual pictured by McDonald & Nybakken (1980:59) for D. columbiana, and their morphology and egg masses are also very similar to those of Doto sp. D in Just & Edmunds (1985: 40-41)

4) A variety from the La Jolla, California area that James Lance (personal communication) refers to as Doto amyra but which he states produces planktotrophic larvae. In addition, Dr. Hans Bertsch has sent me a photograph of what he calls D. amyra, also from the La Jolla area. The photograph shows adults (very similar in appearance to 2) above) and their egg masses among short hydroids. These egg masses contained small embryos that clearly developed into planktotrophic larvae. This variety may be the same as 2) above or may be a different species.

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CHAPTER III

UNUSUALLY LARGE POLAR BODIES IN AN AEOLID NUDIBRANCH:
A NOVEL MECHANISM FOR PRODUCING EXTRA-EMBRYONIC
YOLK RESERVESIntroduction

The polar bodies of molluscs and most other animals are: 1, normally small compared to the egg; 2, often short-lived, and 3, not known to influence embryonic development after their formation (Conklin, 1915; Morgan, 1927; Wilson, 1928; Raven, 1966; Kume & Dan, 1968; Austin, 1969; Longo, 1983; Wourms, 1987). However, in some animals polar bodies are not formed during meiotic maturation of the egg, and the unextruded polar nuclei play a role in later development. For example, polar nuclei contribute to the formation of: 1, the trophamnion in the parasitic Hymenoptera (Chapman, 1971; Ivanova-Kasas, 1972); 2, the mycetome organ in scale insects (Homoptera) (Austin, 1969; Counce, 1973), and 3, mosaic individuals of the silkworm Bombyx (Lepidoptera) (Swanson, 1957; Counce, 1973). Finally, in some animals reproducing by meiotic (automictic) parthenogenesis (e.g., certain nematodes, insects, crustaceans, and asteroids) the polar nuclei fuse with each other or with the female pronucleus to restore the somatic number of

chromosomes, thus effectively replacing the male pronucleus of sexually reproducing species (Wilson, 1928; Austin, 1969; Chapman, 1971; Counce, 1973; Hope, 1974; Nicholas, 1984; Schwalm, 1988).

In this paper I report the consistent formation of unusually large, yolk-filled polar bodies in the aeolid nudibranch Cuthona lagunae (O'Donoghue, 1926) and discuss their apparent function as extra-embryonic food reserves for the late embryos.

Cuthona lagunae occurs uncommonly along the Pacific coast of North America from northern Baja California (McDonald, 1983) to southern Oregon (Goddard, 1990). Little is known about the biology of this distinctive species, and nothing is on record concerning its embryonic development.

Methods

Seven individuals of Cuthona lagunae were collected in July 1987 from the low-intertidal zone at two wave-exposed, rocky localities: 1, 20 km north of Brookings, on the southern Oregon coast, and 2, 200 km south of Brookings at Punta Gorda, northern California. In the field and during transport specimens were held in jars in a cooler kept at about 13°C; in the laboratory they were maintained in a beaker (250 ml) of unfiltered seawater held in a water bath at 12-14°C. Egg masses deposited on the sides of the beaker were removed intact, examined with a compound microscope

equipped with an ocular micrometer, and then transferred to separate vials of unfiltered seawater and held in the above water bath. Seawater in all containers was changed once or twice daily, and egg masses were examined daily until the veliger larvae hatched. Photographs and size measurements were made using live material and bright field microscopy.

For comparative purposes the uncleaved ova and polar bodies of 8 additional species of nudibranchs were examined. These species (see Table 1) were collected during winter 1988 from the low, rocky intertidal zone at Cape Arago, Oregon and were selected only on the basis of their availability (i.e., without regard for type of embryonic development). Their egg masses were treated as above (temperature of the water bath was 10-12°C); for the larger dorids, however, only small portions of the egg mass were used for culture and observation.

Observations

The earliest stage at which the ova of Cuthona lagunae were observed was after completion of egg-laying and between extrusion of the polar bodies and first cleavage (Figures 1 and 2). At this stage mean diameters of the ova from two egg masses were 93.9 μm (SD = 1.6 μm , n = 10) and 102.3 μm (SD = 5.6 μm , n = 15) respectively. The first polar body had presumably divided (a common phenomenon in the mollusca (Raven, 1966)), resulting in the two outermost

Table 1. Sizes of polar bodies and uncleaved eggs of some opisthobranch molluscs. Diameters originally reported as means are listed to one decimal place; other diameters (estimations either stated directly in original reference or calculated using published photographs and scale bars) are listed to nearest integer. Midpoints were used in calculations whenever a range was given.

Species ¹	Egg diameter (µm)	Polar bodies			Source
		diameter (µm)	number	% volume of egg ²	
NUDIBRANCHIA					
Dendronotacea					
<u>Doto coronata</u>	72.5	4.8-7.2	2-3	0.1	Kress (1975)
<u>Doto fragilis</u>	83.0	7.2-9.6	2-3	0.3	Kress (1975)
<u>Doto japonica</u>	84	7	2	0.1	Hamatani (1963)
<u>Doto pinnatifida</u>	95.5	9.6	2-3	0.2	Kress (1975)
Doridacea					
<u>Aldisa sanguinea</u>	90.7	10.4	2	0.30	present study
<u>Archidoris montereyensis</u>	90.4	8.9	2	0.19	present study

Table 1. Continued.

Species ¹	Egg diameter (μm)	Polar bodies			Source
		diameter (μm)	number	% volume ² of egg	
<u>Archidoris odhneri</u>	96.1	9.1	2	0.17	present study
<u>Cadlina marginata</u>	94.0	10.1	2	0.25	present study
<u>Discodoris heathi</u>	78.8	8.4	2	0.25	present study
<u>Discodoris sandiegensis</u>	83.0	8.5	2	0.21	present study
<u>Doridella steinbergae</u>	65	6	2	0.2	Perron & Turner (1977)
<u>Onchidoris muricata</u>	79.5	6.3	2	0.10	present study
<u>Rostanga pulchra</u>	80	6	2	0.1	Chia & Koss (1978)
Eolidacea					
<u>Aeolidia papillosa</u>	73.7	5	3	0.2	Williams (1980)
<u>Catriona columbiana</u>	100.0	8.9	2-3	0.18	present study
<u>Cuthona lagunae</u>	102.3	18.3	3	1.72	present study

Table 1. Continued.

Species ¹	Egg diameter (µm)	Polar bodies			Source
		diameter (µm)	number	% volume ² of egg	
<u>Hermisenda crassicornis</u>	64.7	8	2	0.3	Williams (1980)
SACOGLOSSA					
<u>Limapontia capitata</u>	82	9	2	0.3	Chia (1971)
<u>Limapontia depressa</u>	80	15	2	1.3	Chia (1971)

¹ Doto coronata (Gmelin, 1791); Doto fragilis (Forbes, 1838); Doto japonica Odhner, 1936; Doto pinnatifida (Montagu, 1804); Aldisa sanguinea (Cooper, 1863); Archidoris montereyensis (Cooper, 1863); Archidoris odhneri (MacFarland, 1966); Cadlina marginata MacFarland, 1905; Discodoris heathi MacFarland, 1905; Discodoris sandiegensis (Cooper, 1863); Doridella steinbergae (Lance, 1962); Onchidoris muricata (Muller, 1776); Rostanga pulchra MacFarland, 1905; Aeolidia papillosa (Linnaeus, 1761); Catriona columbiana (O'Donoghue, 1922); Hermisenda crassicornis (Eschscholtz, 1831); Limapontia capitata (Muller, 1774); Limapontia depressa Alder & Hancock, 1862.

² Combined volume of polar bodies as percent volume of the egg; calculated from: $(\text{diameter p.b.}/\text{diameter egg})^3 \times (\# \text{p.b.}) \times (100)$.



Figure 1. Uncleaved eggs and polar bodies of Cuthona lagunae. Ova in this egg mass averaged 102 μm in diameter.

Photomicrographs in Figures 1-6 made using bright field optics and live eggs, embryos, and larvae of Cuthona lagunae.



Figure 2. Uncleaved egg (100 μm in diameter) with polar bodies. The outermost polar body measured 17.5 μm in diameter.

cells. These were of similar size, together averaging 18.3 μm in diameter in one egg mass (SD = 1.2 μm , n = 22), and clearly were packed with yolk droplets (for sake of convenience, all cells produced by division of the polar bodies will also be referred to as polar bodies). Measurement of the diameter of the second, or innermost, polar body was hindered by its compression between the outer polar bodies and the egg. The second polar body, however, was also packed with yolk and appeared to be slightly larger than the outer ones. Assuming a uniform density of yolk in both the egg and polar bodies, the three polar bodies together contained about 2% of the amount of yolk remaining in the egg. Polar bodies of similar size and appearance were observed in every egg capsule examined in 10 egg masses.

At the blastula stage the three polar bodies of Cuthona lagunae remained undivided and were still attached to the embryo in either one or two groups. By the time gastrulation was completed (3-4 days after oviposition) some of the polar bodies had divided so that up to six polar bodies could be observed, still attached to the embryo. These began to separate from the embryo after this stage, probably as a result of the early movements of the embryos, but some appeared to remain attached as late as the early veliger stage. Loose polar bodies, moving in the egg capsule as a result of the action of the velar cilia, were observed

well into the development of the veligers (Figure 3).

Eight to nine days after egg-laying, spherical bodies similar in size and appearance to the polar bodies were observed in the stomachs of some of the embryonic veligers (Figure 4), along with a concurrent decrease in the number of polar bodies present in the capsular fluid. Up to three spherical bodies per stomach were seen; other stomachs contained only small particles. By the time the veligers were ready to hatch both the spherical bodies and loose polar bodies had virtually disappeared (Figures 5 and 6). In one egg mass containing fully developed veligers I could find only one capsule still containing loose polar bodies.

Veliger larvae hatched after an embryonic period of 10-11 days (at 12-14°C). They possessed small eyespots, a moderately long foot lacking a propodium, and clear, elongate shells (type 2 of Thompson, 1961) averaging 261.8 μm in length (SD = 6.5 μm , n = 15 [5 measurements from each of 3 egg masses]) (Table 2, Figures 5 and 6). Although eyespots at hatching normally indicate lecithotrophic development in opisthobranchs (Thompson, 1967; Bonar, 1978; Todd, 1981; Hadfield & Switzer-Dunlap, 1984), the relatively transparent visceral mass and lack of both a propodium and extensive yolk reserves clearly reveal the planktotrophic nature of these larvae. Other species of Cuthona with planktotrophic larvae also hatch with visible eyespots (see Table 2 and Hurst, 1967, pp. 280-281; Todd



Figure 3. Embryos and loose polar bodies 7 days after oviposition. The polar bodies were moving inside the egg capsules as a result of the action of the velar cilia of the embryos. The shells of these embryos averaged 261 μm in length.

Figure 4. Right latero-ventral view of a 9 day old embryo. Note the spherical body (SB) inside the stomach. The spherical body measured 14.4 μm in diameter and was rotating as a result of the motion of the cilia lining the inside of the stomach.

The following abbreviations are used in Figures 4-6:

DO	dark mantle organ
E	eyespot
F	foot
INT	intestine
KR	rudiment of adult kidney
LDD	left digestive diverticulum
LK	larval kidney
OP	operculum
R	retractor muscle
RDD	right digestive diverticulum
SB	spherical body
SH	shell
ST	stomach
V	velum



and Havenhand, 1985, p.97; Strathmann, 1987, p. 293).

The hatching larvae of Cuthona lagunae are distinctive in their possession of two mantle organs, one dark and one clear, on the right side, adjacent to the anus (Figures 4 - 6). The dark organ is semi-opaque owing to its high density of yolk droplets. At hatching the larvae of most nudibranchs possess a single developed mantle organ - the so-called "larval (or secondary) kidney" - next to the anus (Thompson, 1958, 1976; Raven, 1966; Hurst, 1967; Bonar & Hadfield, 1974; Bonar, 1978; Bickell & Chia, 1979, Strathmann, 1987, personal observations). In nudibranchs this organ is usually colourless and backed with an undifferentiated mass of tissue (the "kidney rudiment" that will eventually become the "adult kidney" (op. cit.; also see Robertson, 1985). A small irregular mass of tissue, which may correspond to the kidney rudiment, appears to overlie part of the clear mantle organ in C. lagunae (see Figure 6), suggesting that this organ is equivalent to the "larval kidney" of the above authors. However, the identity and function of the dark organ is unclear. Even if part of the "larval kidney", its concentration of yolk suggests a role as some kind of nutritional reserve for the newly hatched larvae. Larvae were observed for only a short while after hatching; consequently, nothing is known about the fate of the dark organ and its contents.



Figure 5. Lateral views of two veligers at hatching (11 days after oviposition). Note small eyespot in the upper specimen. The shell of the lower specimen measured 275 μm .

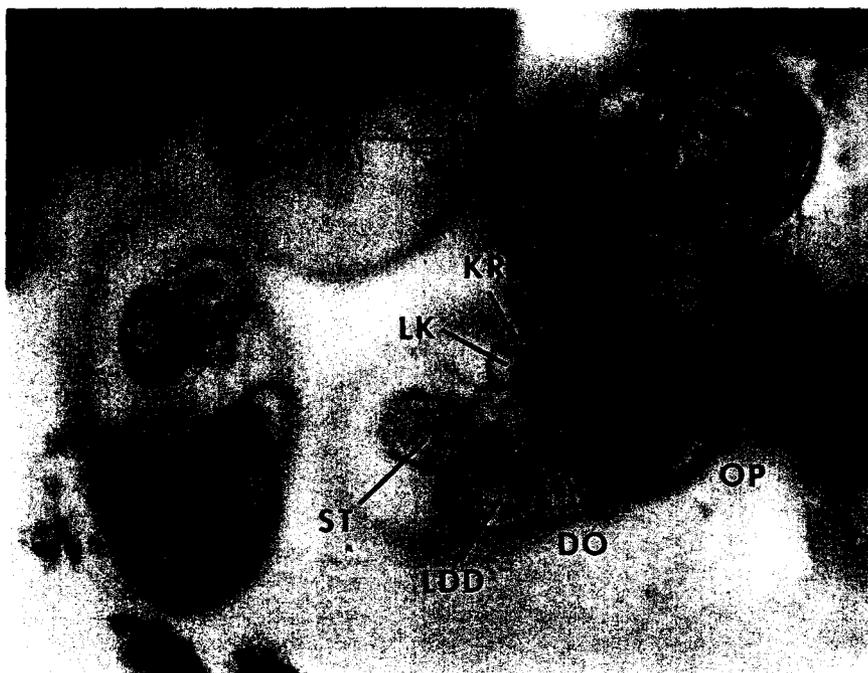


Figure 6. Ventral views of three veliger larvae at hatching. Note the two organs, one clear (probably the larval kidney - see text) and one dark, on the right side adjacent to the anus.

Discussion

Together, the three polar bodies of Cuthona lagunae contain approximately 2% of the amount of yolk remaining in the egg. A sampling of the literature and examination of the polar bodies of eight species of nudibranchs collected from Cape Arago reveals that, relative to the volume of the egg, the polar bodies of members of the Nudibranchia are typically an order of magnitude smaller than those of C. lagunae (Table 1). Moreover, the polar bodies of the species listed in Table 1 are usually transparent and appear to contain little, if any, yolk. In addition, I have not noticed consistently large and (or) yolk-filled polar bodies during observations of egg size and embryonic development in 36 other species of northeastern Pacific opisthobranchs, including 31 nudibranchs, 3 sacoglossans, 1 notaspidean, and 1 cephalaspidean (Goddard, 1984, 1987, and unpublished data). The polar bodies of these species, like those of the species in Table 1, are usually small, clear, and inconspicuous.

Of the species listed in Table 1 only the polar bodies of the sacoglossan Limapontia depressa approach the size of those produced by Cuthona lagunae. However, as seen in figures 7-11 of Chia (1971), they are relatively transparent and appear to contain little yolk compared to those of C. lagunae. Except noting the time of their

formation, Chia did not describe any aspect of the polar bodies of L. depressa.

According to Raven (1966), the first polar body divides once in many molluscs; the second, only rarely. Multiple division of the polar bodies, as observed in the present study, appears to be unusual in any kind of animal. Hoadley (1930) reported that in the squid Loligo pealei LeSueur, 1821 either one or both of the daughter cells of the first polar body could divide once again, contributing to the total of up to six polar bodies observed in that species (and here, for C. lagunae). The polar bodies of C. lagunae do not, however, undergo their final divisions until sometime between the blastula and gastrula stages, while those of L. pealei apparently complete their divisions soon after extrusion. Further study is needed to determine if the second polar body of C. lagunae divides, exactly when the polar bodies divide, and why there is such a long interval between their extrusion and final divisions.

The disappearance of the polar bodies of Cuthona lagunae before hatching, combined with the brief appearance of similar bodies in the stomachs of some of the embryos, suggests that the polar bodies are ingested orally by the embryonic veligers and then digested. However, the possibility remains that some of the polar bodies break apart in the capsular fluid (owing to their motion in the capsular fluid, occasional compression between the capsule

walls and embryos, or some inherent degradational process) and that their soluble contents are then either assimilated by the embryos or lost when the veligers hatch. Any particles resulting from such a breakup would almost certainly be ingested by the embryos as a result of the functioning of their ciliary feeding mechanisms prior to hatching. Particles were observed in the stomachs of some embryos but not in the capsular fluid, suggesting that the polar bodies are not breaking up before ingestion. However, more observations (including counts and size measurements of all bodies in the capsular fluid) at shorter intervals are needed to confirm this.

Even if some polar bodies are disintegrating in the capsular fluid, it appears likely that most, if not all, of the contents of the polar bodies of Cuthona lagunae are being consumed by the embryonic veligers. Ingestion of polar bodies by embryonic opisthobranch veligers has been previously observed (and undoubtedly occurs in other animals with encapsulated embryos and feeding larvae), but these were minute and contained a negligible amount of yolk (T. E. Thompson, personal communication).

As stated by Hadfield & Switzer-Dunlap (1984, p.281), "Most opisthobranchs develop to hatching nourished only by the yolk contained within the fertilized ovum." Others provision their egg masses with additional supplies of yolk that are utilized by either the developing embryos or the

newly hatched larvae (see reviews by Boucher, 1983 and Hadfield & Switzer-Dunlap, 1984). These yolk supplies may be located inside or, more commonly, outside the egg capsules and can be referred to collectively as extra-zygotic yolk or EZY. The provisioning of EZY presumably requires specialization of the reproductive tract, allowing some yolk to be withheld from the developing oocytes and then deposited as EZY during formation of the egg mass. Nurse- or food-eggs, which may be considered another type of EZY and are produced by some prosobranchia (reviewed by Fretter, 1984), are not known in the Opisthobranchia.

In Cuthona lagunae changes in the processes underlying the maturation divisions of the ova have led to the evolution of large, yolk-filled polar bodies - a novel mechanism for the production of EZY that avoids the potentially costly modifications of the adult reproductive system mentioned above. Although fewer changes in development are probably required to produce yolk-filled polar bodies than other forms of EZY, those changes, occurring so early in development, could disrupt other processes upon which the rest of development depends, a constraint that might help explain the apparent rarity of polar bodies as a source of EZY.

In oviparous species, placement of yolk supplies external to the zygote is thought to accelerate early development (less yolk to cleave) and thus reduce mortality

caused by exposure of embryos to predators and physical stresses (Spight, 1975; Clark & Goetzfried, 1978; Thompson & Salghetti-Drioli, 1984; Thompson & Jarman, 1986). Spight (1975), examining the relationship between embryonic period and yolk volume (roughly estimated by hatching size) in muricacean prosobranchs, found that "on average, the nurse-egg feeders require only about 60% as long to develop as do the other species." However, as noted by Thompson & Jarman (1986), no study has yet quantified the effect of EZY on the developmental rates of opisthobranchs, and, as stated by Boucher (1983) "The advantages gained by placement of yolk external to the ovum are not clear, as no obvious features of ecology or life history, or patterns of development are unique to these species" [of opisthobranchs]. Clark & Goetzfried's (1978) suggestion that EZY might also serve to divert predators from the embryos obviously applies only to extracapsular yolk supplies.

The advantages, if any, of EZY to Cuthona lagunae are not readily apparent. Inspection of the available data on egg size, embryonic period, and size at hatching of C. lagunae and some closely related sympatric aeolids (Table 2) does not reveal significant differences between C. lagunae and the other species in these traits. Variable culture temperatures and relatively infrequent observations (times of egg-laying and hatching were recorded only to the

Table 2. Embryonic development of Cuthona lagunae and six other species of the family Tergipedidae from southern Oregon. All of these species have larvae with inflated, egg-shaped shells (type 2 of Thompson, 1961). Values given for egg diameter and length of veliger shell are means based on at least 10 measurements from each of one or more egg masses. Data from Goddard (1984, and unpublished) and present study.

Species ¹	Egg diameter (µm)	Shell length at hatching (µm)	Embryonic period (days)	Temp. (°C)	Eyespots at hatching ²
<u>Cuthona fulgens</u>	94.3	252.0	9	10-12	+
<u>Cuthona abronia</u>	94.8	223.8	10	12-14	+
<u>Cuthona cocoachroma</u>	95.4	276.8	9	12-13	+ or -
<u>Cuthona albocrusta</u>	97.2	280.9	10	12-14	+
<u>Cuthona lagunae</u>	98.1	261.8	10-11	12-14	+
<u>Catriona columbiana</u>	99.7	273.9	10	15-17	+
<u>Cuthona divae</u>	107.1	249.1	7-8	15-17	-

¹ Cuthona fulgens (MacFarland, 1966), Cuthona abronia (MacFarland, 1966), Cuthona cocoachroma Williams & Gosliner, 1979, Cuthona albocrusta (MacFarland, 1966), Cuthona lagunae (O'Donoghue, 1926), Catriona columbiana (O'Donoghue, 1922), Cuthona divae (Marcus, 1961).

² + = present, - = absent.

nearest day) might have obscured possible differences in development time. While the polar bodies of Cuthona lagunae are an order of magnitude larger than those of other nudibranchs, they still contain only a small fraction (about 2%) of the yolk available to the developing embryo - the effects on development of partitioning this yolk as EZY may not be easily detected.

The hatching larvae of Cuthona lagunae are distinctive in their possession of an extra supply of yolk (in the dark mantle organ next to the anus), and preliminary observations suggest that they have a relatively larger foot than some of the other species in Table 2 (Figures 5 and 6). Combined with the data in Table 2 on embryonic periods, possession of these traits raises the possibility that C. lagunae are hatching after the same embryonic period as the other species, but in a slightly more advanced stage of development (see Bonar, 1978 and Bickell & Chia, 1979 for discussion of morphological indicators of stage of development in opisthobranch veliger larvae). By accelerating early development (or increasing its efficiency) without affecting hatching time, EZY would in this case effectively be reducing the larval period (and presumably the larval mortality rate) more than the embryonic period.

Experimental removal of the polar bodies from the egg capsules of Cuthona lagunae (and, if possible, the removal

of an equivalent amount of yolk from the eggs of other species), combined with a more careful comparative approach, should help reveal some of the effects of EZY on the development of C. lagunae (attempts to collect more C. lagunae for further observations on its development have thus far been unsuccessful). However, the larvae of Cuthona lagunae may be virtually identical to those which develop from an equivalent amount of yolk contained entirely within the developing embryo. That is, the production of large, yolky polar bodies could be a potentially maladaptive, developmental aberration that the late embryos, by virtue of their already functioning ciliary feeding mechanisms, are able to "correct" before the displaced yolk is lost at hatching. Organisms that spawn their eggs directly into the water-column without any form of encapsulation clearly would be under stronger selective pressure not to produce such large polar bodies (unless the cast-off polar bodies served another function, such as diverting predators from the newly released eggs).

Adaptive or not, the evolution of polar bodies as a source of EZY is not difficult to imagine. Unusually large polar bodies are known to occur at low frequency in populations of oocytes normally producing small polar bodies (Francotte, 1898; Conklin, 1915; Braden, 1957; Donahue, 1970; Wourms, 1987; personal observations). Assuming that polar body size and yolk content are

genetically controlled and that the separation of some yolk from the egg does not result in inviable embryos, all that is needed is a mechanism for the assimilation of the EZY by the embryos (already in place and functioning in the late embryos of many species with planktotrophic larvae), followed by one of the various mechanisms of evolution. Division of the polar bodies (known to occur in some organisms; e.g., Wilson, 1928; Hoadley, 1930; Raven, 1966) may also be required if they are ingested whole by the embryos.

The polar bodies of Cuthona lagunae are among the largest known in the animal kingdom, especially the invertebrates (in addition to the references cited in the introduction, also see reviews of early development in Kume & Dan, 1968; Reverberi, 1971; Giese & Pearse, 1974-1979; Tsafiriri, 1978, and Harrison & Cowden, 1982). If found to confer some developmental advantage to C. lagunae, they would represent the first molluscan example known in which the polar bodies play a role in development beyond maturation of the egg and, to my knowledge, one of the few examples known in the animal kingdom.

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