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Cover Page Footnote

BG thanks the captain and crew of the Truth Aquatics dive boat Vision, as well as John Yasaki, Brynn Hooton, Terry Strait, Kim Mitchell and Brian Swift. We also thank Jack Engle for permission to use his image of *Felimare californiensis*, Maya Wolf for sharing with us her fine images of the hatching larvae of *Janolus fuscus*, and Craig Hoover for sharing his in situ observations on the egg masses of *Felimare californiensis*. Two anonymous reviewers commented on the manuscript, and we are thankful for their efforts. Some of the specimens documented in this study were collected during a study of intertidal nudibranchs funded by grant R/OPCENV-08 from the California Ocean Protection Council and California Sea Grant to JHRG.

Developmental Mode in Opisthobranch Molluscs from the Northeast Pacific Ocean: Additional Species from Southern California and Supplemental Data

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Abstract.—We document development type for 33 species of benthic opisthobranch gastropods – 15 for the first time – collected mainly from the Southern California Bight. Fourteen of the newly examined species had planktotrophic development, while the dorid nudibranch *Atagema alba* had capsular metamorphic development, the first example of direct development in a non-dendrodoridid nudibranch known from the northeast Pacific Ocean. For the remaining 18 species our new data are either consistent with earlier determinations of development type, or confirm previous inferences. The new data also broaden geographic coverage for some species, and for the sacoglossan *Stiliger fuscovittatus* and the nudibranch *Melibe leonina*, suggest that egg size is inversely related to temperature. We correct the previous erroneous identification of nephrocysts as eyespots in the hatching planktotrophic larvae of the nudibranchs *Tritonia festiva* and *Janolus fuscus*. These results further highlight the predominance of planktotrophic development in benthic opisthobranchs from the northeast Pacific Ocean.

Introduction

Mode of development has been determined for approximately two-thirds of the over 300 species of opisthobranch molluscs known from the northeast Pacific Ocean (Goddard 2004, 2005; Goddard and Hermosillo 2008). Small eggs and planktotrophic development predominate among these species; so far, only 14 species from the region are known to hatch from their egg coverings as either lecithotrophic larvae or juveniles (Goddard and Hermosillo 2008). The four species of nudibranchs known to bypass a free-living larval stage and hatch as juveniles all belong to a single family, the Dendrodorididae (Goddard, 2005).

Developmental mode in opisthobranchs is most reliably documented when based on observations of the morphology of hatching veliger larvae - particularly the presence or absence of eyespots and propodium - accompanied by measurements of egg size, embryonic period and temperature, and size and type of shell at hatching (Bonar 1978; Goddard 2004). However, these parameters are not always readily measured or reported in the literature, and developmental mode has previously been inferred for some species based on subsets of the above information. For example, Goddard (2004) characterized as planktotrophic the development of the nudibranchs *Polycera tricolor* Robilliard, 1971 and *Dirona picta* MacFarland in Cockerell & Eliot, 1905, based on, respectively, (1) a comparison of the embryonic period reported for *P. tricolor* by Robilliard (1971) with those of congeners of known developmental type, and (2), qualitative observations, combined with a measurement of the preserved embryos reported by Marcus and Marcus (1967). As

Table 1. Collection localities.

Site	GPS coordinates	Depth (m)/habitat
Whittier, Alaska	60.7778, -148.6903	Floating docks
Monterey Bay	36.6088, -121.8797	Subtidal, 16 m
Monterey Harbor	36.6043, -121.8912	5 m, dock pilings
Asilomar, Pacific Grove	36.6272, -121.9408	Rocky intertidal
Sand Dollar Beach, Monterey Co.	35.9217, -121.4717	Rocky intertidal
Cayucos	35.4478, -120.9100	Rocky intertidal
Hazard Canyon, Montana de Oro State Park	35.2897, -120.8839	Rocky intertidal
Naples, Santa Barbara Co.	34.4339, -119.9514	Rocky intertidal
Naples Reef	34.4218, -119.9523	Subtidal, 15 m
Santa Barbara Harbor	34.4067, -119.6892	Floating docks
Tarpits Reef, Carpinteria	34.3869, -119.5164	Rocky intertidal
Laguna Beach	33.5429, -117.7906	Rocky intertidal
La Jolla	32.8549, -117.2680	subtidal, 17 m
South Casa Reef, La Jolla	32.8434, -117.2814	Rocky intertidal
Bird Rock, La Jolla	32.8144, -117.2739	Rocky intertidal
San Clemente Island	32.8134, -118.3626	subtidal, 20 m
Mission Bay, San Diego	32.7642, -117.2172	Floating docks
Point Loma, San Diego	32.6664, -117.2450	Rocky intertidal
Punta Rosarito, Baja California	28.5672, -114.1597	Rocky intertidal
El Tomatal, Baja California	28.4869, -114.0694	Rocky intertidal

opportunities have arisen, we have endeavored to fill some of these gaps in the available embryological data, as well as sample across more of the geographic range of some species. Aside from providing confirmation or not of previous inferences, this will enable more robust comparative studies, help distinguish closely related species, and increase our understanding of geographic variation in the life history traits of opisthobranchs.

Here we document mode of development for species not previously examined, most of which are from southern California, and fill existing gaps in the embryological data for others. We include species rarely observed or mainly subtidal in distribution, two undescribed species, and document a new example of rare direct development in a nudibranch from the northeast Pacific Ocean. We discuss discrepancies between our observations and those reported in the literature and also correct the previous erroneous identification by the senior author of the paired larval structures known as nephrocysts (e.g., Thompson 1976; Bonar 1978) as eyespots in the hatching larvae of two common planktotrophic species.

Collection Sites and Methods

Adult opisthobranchs, or portions of their egg masses in the process of being deposited, were collected by hand from subtidal and intertidal sites along the Pacific coast of North America (Table 1). Adults were held in containers (250 to 1000 ml) of unfiltered seawater at near ambient ocean temperatures until they laid egg masses. Recently laid egg masses were examined using a compound microscope equipped with an ocular micrometer. If first cleavage had not commenced, the diameters of a random sample of 10 zygotes were measured in each egg mass; otherwise, an upper limit on zygote size was estimated by measuring the dimensions of a few randomly selected embryos at or before the gastrula stage. We then isolated individual egg masses, or approximately 1 cm long sections of larger egg masses, into separate, labeled vials (20 ml) and changed and gently swirled the seawater in these once or twice daily. We examined the egg masses daily until hatching

and then measured the longest dimension of their shells and assigned mode of development (planktotrophic, lecithotrophic or direct) and larval shell type (coiled type 1 or egg-shaped, inflated type 2) as in Goddard (2004). After obtaining the above egg masses, adult specimens were relaxed in 7.5% MgCl₂, fixed in 70% ethanol, and deposited as voucher specimens in the California Academy of Sciences. Some of these vouchers included pieces of egg masses and were supplemented by digital images of adults. We used an underwater data logger (StowAway Tidbit, Onset Computer Corp.) to record temperature at 10 min. intervals in our holding containers.

For the dorids *Geitodoris mavis* Marcus & Marcus, 1967 and *Taringa aivica* Marcus & Marcus, 1967, we examined preserved specimens originally collected in 1994 and 2000, respectively, and following Goddard (2004), inferred their mode of development based on the relatively small size of their embryos. For the chromodorid *Felimare californiensis* (= *Hypselodoris californiensis*) (Bergh, 1879) we inferred mode of development based on estimates of embryonic period and egg size. We estimated the latter by measuring the zygotes in an image of an adult laying its egg ribbon (Figure 2A) and assuming an egg ribbon width of 6 mm (adjusted to 4.243 mm to account for the approximately 45° viewing angle of the segment of the egg ribbon containing the zygotes we measured), based on the measurement reported by Ingram (1935). Craig Hoover (personal communication to JG, 30 Sept 2012) provided information on the embryonic period of *F. californiensis*, based on subtidal observations he made in September 2012 of three egg masses laid by *F. californiensis* in Big Fisherman Cove, Santa Catalina Island.

JG identified the egg mass of *Atagema alba* (O'Donoghue, 1927) from Bird Rock, La Jolla (see Table 2) based on original 35 mm slides, including close-ups of sections of egg ribbon, in the James R. Lance collection at the California Academy of Sciences (CAS) in San Francisco.

We follow the taxonomic nomenclature of Behrens and Hermosillo (2005), and for the Chromodoridae, Johnson and Gosliner (2012).

Results

We obtained results on the development of 33 species, 15 for the first time (Table 2). Eleven of these 15 laid small eggs and developed into hatching planktotrophic larvae (Table 2). Planktotrophic development was inferred for an additional three of them (*Geitodoris mavis*, *Felimare californiensis*, and *Flabellina pricei*), based on the small size of their embryos, and for *Felimare californiensis*, the length of its embryonic period as well (Table 2). Finally, *Atagema alba* from La Jolla developed from relatively large eggs and had capsular metamorphic development (Table 2, Figure 1). The juveniles of this species exited their shells while leaving the egg capsules, and one day after hatching had rhinophore buds and an oval notum reinforced by calcareous spicules and edged with secretory glands (Figure 1B & C). Five days after hatching, the juveniles had two to three notal caryophyllidia (papillae surrounded by crowns of spicules; Figure 1D). A radula with three pairs of hamate teeth was visible two days after hatching (Figure 1F) and appeared to have approximately six rows of teeth after seven days (Figure 1E).

Of the remaining 18 species examined, hatching planktotrophic larvae were observed in 15, and this same mode of development was inferred for the remaining three based on the small size of their embryos (Table 2).

Discussion

Thirty-two of the 33 total species we examined were found to have planktotrophic development, consistent with prior compilations of developmental mode in benthic

Table 2. New data on embryonic development of opisthobranch molluscs from California. Mode of development: P = planktotrophic, CM = capsular metamorphic, with modes inferred based solely on size of zygotes or early embryos in parentheses. An asterisk (*) preceding a species name indicates a species whose mode of development has not previously been determined, and a dash (—) indicates no data. Values for egg diameter and shell length at hatching are means \pm 1 SD, and sample size (n).

Taxon	Egg Diameter (μ m)	# eggs per capsule	Embryonic		Shell type	Shell length at hatching (μ m)	Eyespots at hatching	Mode of		Locality
			period (days)	Temp. ($^{\circ}$ C)				Develop-	ment	
Sacoglossa										
<i>Stiliger fuscovittatus</i> Lance, 1962, CASIZ 182713	58.8 \pm 1.1 (10)	1	4.5	15–20	1	104.3 \pm 3.3 (22)	no	P		Mission Bay
	60.9 \pm 0.9 (10)	1	4.5	15–20	1	108.3 \pm 2.8 (22)	no	“		Mission Bay
	59.6 \pm 2.1 (9)	1	—	—	1	—	—	“		Monterey Harbor
	—	1	—	—	1	102.7 \pm 6.1 (11)	no	“		Monterey Harbor
Anaspidea										
<i>Aphysia vaccaria</i> Winkler, 1955, CASIZ 189306	—	>50	19+	—	1	143.8 \pm 3.1 (5)	no	P		Laguna Beach
Nudiopleura: Pleurobranchidae										
<i>Berthella strongi</i> (MacFarland, 1966), CASIZ 182722	89.3 \pm 0.8 (10)	1	16	12–16	1	137.0 \pm 3.1 (10)	yes	P		El Tomatal
	—	1	—	—	1	137.1 \pm 7.9 (5)	yes	“		Naples
Nudiopleura: Doriidina										
* <i>Acanthodoris lutea</i> MacFarland, 1925	69.5 \pm 1.1 (10)	1	8	15	1	132.4 \pm 4.0 (10)	no	P		Monterey Bay
* <i>Ancula lentiginosa</i> Farmer in Farmer & Sloan, 1964, CASIZ 182719	<60	1–2	10	13–18	1	99.3 \pm 3.1 (10)	no	P		Naples
* <i>Atagena alba</i> (O'Donoghue, 1927), CASIZ 186493	156.6 \pm 1.7 (3)	1	>>14	18–20	1	210–218 ^a	yes	CM		Bird Rock, La Jolla
<i>Doriopsilla albopunctata</i> (Cooper, 1863)	—	1–3	—	—	1	193.0 \pm 7.0 (5)	no	P		Cayucos
* <i>Doris pickensii</i> Marcus & Marcus, 1967, CASIZ 189305	77.2 \pm 1.2 (10)	1	13	14–20	1	132.6 \pm 2.2 (10)	no	P		Naples
* <i>Felimare californiensis</i> (Bergh, 1879)	\approx 100 ^b	—	>7, <12 ^c	17–19 ^c	—	—	—	(P)		Santa Catalina Island
* <i>Geitodoris mavis</i> Marcus & Marcus, 1967, CASIZ 186482	<85 ^d	1	—	—	—	—	—	(P)		Punta Rosarito
<i>Okenia rosacea</i> (MacFarland, 1905)	—	1	—	—	1	129.8 \pm 1.0 (10)	no	P		Point Loma

Table 2. Continued.

Taxon	Egg Diameter (μm)	# eggs per capsule	Embryonic			Shell type	Shell length at hatching (μm)	Eyespots at hatching	Mode of Develop- ment		Locality
			period (days)	Temp. ($^{\circ}\text{C}$)	Shell type				(P)	(P)	
<i>Patio dubia</i> (M. Sars, 1829), CASIZ 182721	<75 ^d	1	—	—	—	—	—	—	(P)	(P)	Whittier, Alaska
<i>Polycera tricolor</i> Robilliard, 1971	78.0 \pm 1.7 (10)	1	7	18	1	120.0 \pm 5.5 (10)	no	no	P	P	San Clemente Island
<i>Taringa avica</i> Marcus & Marcus, 1967, CASIZ 186481	<70 ^d	4-6	—	—	—	—	—	—	(P)	(P)	Punta Rosarito
* <i>Thoridisa bimaculata</i> Lance, 1966, CASIZ 182715	79.6 \pm 2.0 (5)	1	9	15-19	1	122.8 \pm 6.3 (10)	no	no	P	P	Point Loma
<i>Triopha maculata</i> MacFarland, 1905, CASIZ 184514	70.1 \pm 1.1 (10)	1	11	12-17	1	116.5 \pm 1.8 (10)	no	no	P	P	Naples
Nudipleura: Dendronotina											
<i>Dendronotus subramosus</i> MacFarland, 1966 CASIZ 184512	—	1	8	10-20	2	223.2 \pm 9.6 (10)	no	no	P	P	Asilomar
<i>Doto Columbiana</i> O'Donoghue, 1921, CASIZ 186483	73.6 \pm 1.9 (5)	1	7	—	1	120.1 \pm 2.7 (10)	no	no	P	P	Hazard Canyon
<i>Melibe leonine</i> (Gould, 1852), CASIZ 186815	70.4 \pm 1.6 (10)	2-5	4	—	1	120.9 \pm 3.6 (10)	no	no	P	P	Santa Barbara Harbor
Nudipleura: Arminina											
<i>Dirona picta</i> , MacFarland in Cockerell & Eliot, 1905, CASIZ 182714	70.1 \pm 1.5 (10)	4-5	4	15-21	1	114.7 \pm 3.5 (10)	no	no	P	P	Point Loma
* <i>Janolus anulatus</i> Camacho-Garcia & Gosliner, 2006, CASIZ 189420	66.7 \pm 1.4 (10)	1	6-7	12-18	1	110.7 \pm 2.7 (10)	no	no	P	P	Tarpoons Reef
<i>Janolus barbarensis</i> (Cooper, 1863), CASIZ 184513	95.4 \pm 1.3 (10)	15-20	8	16-24	1	187.1 \pm 5.3 (10)	no	no	P	P	San Diego
Nudipleura: Aeolidina											
* <i>Austracolis stearnsi</i> (Cockerell, 1901), CASIZ 186486	81.4 \pm 2.2 (10)	1	7	18	1	122.0 \pm 7.3 (10)	no	no	P	P	La Jolla
* <i>Babakina festiva</i> (Roller, 1972), CASIZ 182204	72.2 \pm 2.2 (10)	1	7.5	13-17	1	115.8 \pm 1.1 (10)	no	no	P	P	Naples

Table 2. Continued.

Taxon	Egg Diameter (µm)	# eggs per capsule	Embryonic			Shell type	Shell length at hatching (µm)	Eyespots at hatching	Mode of Development	Locality
			period (days)	Temp. (°C)	2					
<i>Cuthona laganae</i> (O'Donoghue, 1926), CASIZ 182716	94.9 ± 1.1 (10)	1	8	—	2	262.1 ± 2.5 (7)	yes	P	Hazard Canyon	
<i>Cumanotus</i> sp. CASIZ 191891	<80	1	—	—	—	—	—	(P)	Santa Barbara Harbor	
* <i>Eubranchius</i> sp. 2 of Behrens & Hermosillo (2005), CASIZ 189422	<100	1	6	12–19	2	210.4 ± 6.4 (10)	yes	P	South Casa Reef, La Jolla	
* <i>Flabellina cooperi</i> (Cockerell, 1901), CASIZ 186489	65.4 ± 2.0 (10)	1–6	5	18	1	101.0 ± 6.9 (10)	no	P	La Jolla	
* <i>Flabellina goddaradi</i> Gosliner, 2010, CASIZ 182590	—	2–4	—	—	1	105.9 ± 4.2 (12)	no	“	La Jolla	
<i>Flabellina iodinea</i> (Cooper, 1862), CASIZ 182717	65.2 ± 0.5 (10)	1	7	11–21	1	102.4 ± 2.3 (10)	no	P	Tarpits Reef	
* <i>Flabellina pricei</i> (MacFarland, 1966), CASIZ 186485	—	1–2	—	—	1	155.0 ± 4.3 (3)	no	P	Sand Dollar Beach	
<i>Flabellina trilineata</i> (O'Donoghue, 1921), CASIZ 182718	64.2 ± 1.0 (10)	1	—	—	1	157.2 ± 3.2 (6)	no	P	Naples Reef	
CASIZ 189421	—	—	—	—	1	—	—	(P)	La Jolla	
* <i>Flabellina</i> sp. (cf. <i>F. trilineata</i>), CASIZ 182720	—	1	7.5	12–19	1	103.7 ± 1.9 (10)	no	P	Naples	
	64.0 ± 2.5 (20)	1–2	—	—	1	—	no	“	Naples	
	62.8 ± 2.2 (10)	1	8	9–15	1	105.6 ± 2.8 (10)	—	(P)	Santa Barbara Harbor	
	—	1	—	—	1	107.6 ± 2.0 (10)	no	P	Naples	
	63.8 ± 1.5 (6)	1	8	9–15	1	110.8 ± 2.2 (10)	no	“	Naples	
	—	1	5.5	13–17	1	112.4 ± 3.8 (8)	no	“	Naples	
	—	1	5	13–17	1	108.7 ± 1.3 (10)	no	“	Naples	
	—	1	6	13–17	1	110.2 ± 1.5 (10)	no	“	Naples	

^a Shells left behind while hatching from egg capsules.

^b Estimate based on image of egg ribbon (see Methods and Figure 2A).

^c C. Hoover, personal communication to JG, 30 Sept 2012.

^d Measurements of early embryos preserved in 70% ethanol.

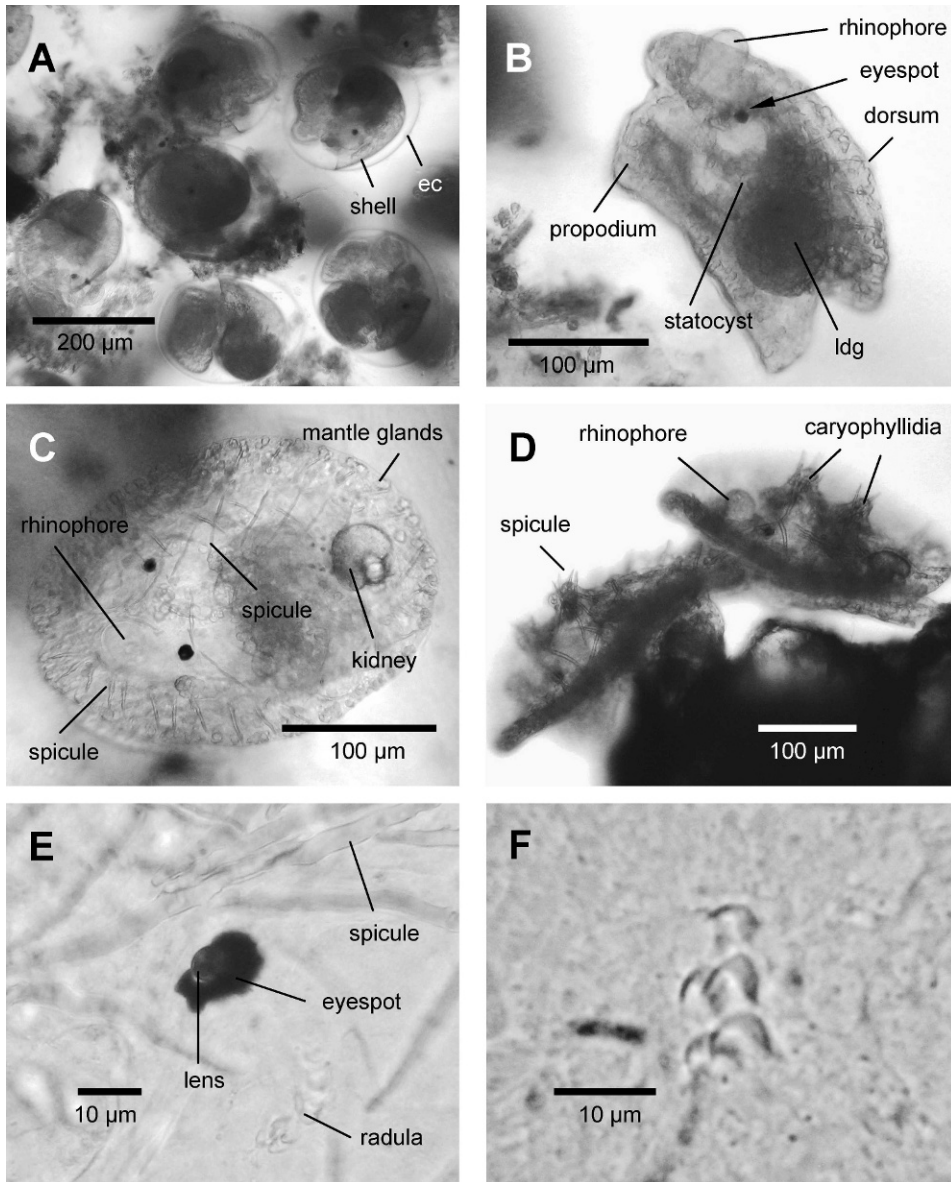


Fig. 1. Live embryos and newly hatched juveniles of *Atagema alba* from Bird Rock, La Jolla. **A.** Embryos, still encapsulated, on day of hatching. **B.** Juvenile, left lateral view, one day after hatching. **C.** Juvenile, dorsal view, one day after hatching. **D.** Two juveniles, five days after hatching. **E.** Eyespot, with overlying lens, and radula from juvenile, 7 days after hatching. **F.** Radula from juvenile, two days after hatching. Note three pairs of hammate teeth. E and F from squashed specimens. Abbreviations used in figure: ec = egg capsule; ldg = left digestive gland; rhinophore = rhinophore bud.

opisthobranchs from both the temperate and tropical northeast Pacific Ocean (Goddard 2004; Goddard and Hermosillo 2008). *Atagema alba*, with capsular metamorphic development, was the only species we observed in this study with non-feeding development. It represents the first example of direct development in a non-dendrodorid nudibranch from the region. For each of the 18 species previously

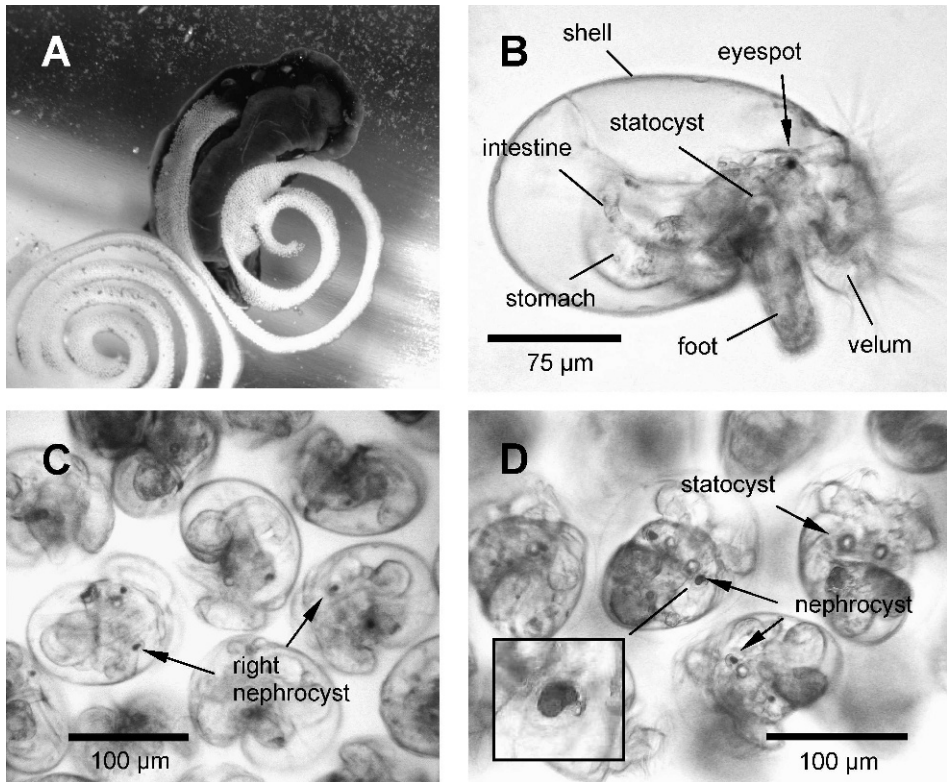


Fig. 2. Nudibranch egg masses and veligers. A. *Felimare californiensis* laying an egg ribbon in the laboratory at the USC Marine Laboratory on Santa Catalina Island, September 1972. Image by John Engle. B. Newly hatched veliger larva of *Eubranchus* sp. 2 of Behrens and Hermosillo (2005), right lateral view. C. Near-hatching veligers of *Tritonia festiva* from Cape Arago, Oregon, July 1987. D. Near-hatching veligers of *Janolus anulatus*, showing (inset) higher magnification of a nephrocyst.

examined, including *Polycera tricolor* and *Dirona picta*, our new data either support earlier determinations of development type, or confirm previous inferences (see Goddard 2004, Table 1). Below we (1) discuss individual species, including discrepancies with previously reported embryological data, and (2) correct the previous erroneous identification by one of us (JG) of nephrocysts as eyespots in two species.

Stiliger fuscovittatus Lance, 1962

Case (1972) studied this diminutive sacoglossan in San Francisco Bay and reported an uncleaved egg diameter of 70 μm and shell-size at hatching of 110 μm , similar to the values reported here for specimens from San Diego and Monterey. In contrast, Strathmann (1987) reported values of 95 μm and 150 μm for eggs and hatching larvae, respectively, from specimens from the San Juan Islands, Washington. A similar size discrepancy exists between our values for the eggs and larvae of *Melibe leonina* (Gould, 1852) from Santa Barbara (Table 2) and those reported by Strathmann (1987) for this species from the Washington and British Columbia. These size discrepancies are consistent with the inverse relationship between temperature and egg and larval sizes known for some marine invertebrates (discussed by Moran & McAlister 2009), and might be worth investigating experimentally.

Atagema alba (O'Donoghue, 1927)

The egg mass of this species was found under an intertidal cobble at Bird Rock, La Jolla. The egg mass was a fairly stout ribbon 3 mm high, coiled in 1.3 turns, with a simple (not wavy) free edge and a total diameter of 6.5 mm. The zygotes and embryos were white. Compared to the images in the Lance collection at CAS of an egg mass laid in captivity by an *A. alba* collected intertidally in San Diego in July 1969, the egg mass we found had one less turn, but was otherwise virtually identical in appearance, including the relatively large size and spacing of the embryos. In the northeast Pacific Ocean, only *Dendrodoris behrensi* Millen & Bertsch, 2005 deposits a similar egg mass, but its embryos are significantly larger than those of *A. alba*, are deposited in thicker-walled capsules, and undergo ametamorphic direct development (Goddard 2005). Our voucher specimens (CASIZ 186493) of *A. alba* consist of post-metamorphic juveniles as pictured in Figure 1D.

Doris pickensi Marcus & Marcus, 1967

This species, previously known only from the northern Gulf of California to Costa Rica (Behrens and Hermsillo 2005; Camacho-Garcia et al. 2005), laid its egg ribbon flat, rather than on edge like most other dorids. The yellow ribbon, pictured in Goddard (2012a), measured up to 2.3 mm wide and was laid in a loose coil of three turns.

Felimare californiensis (Bergh, 1879)

Our estimate of 100 μm for the egg diameter of this species is based on Ingram's (1935) measurement of a single egg ribbon, applied to Figure 2A, and therefore depends on variability in egg ribbon width in *F. californiensis*, which is unknown. However, the estimate is similar to the 95 μm egg size of another chromodorid, the sympatric *Felimida macfarlandi* (Cockerell, 1902), a known planktotroph (Goddard 2004), as well as planktotrophic representatives in the northeastern Pacific Ocean of the closely related genus *Cadlina* (Goddard 2004).

Based on *in situ* observations by Craig Hoover of three egg masses in Big Fisherman Cove, Santa Catalina Island, *F. californiensis* developed to hatching at 17–19°C in at least seven days, but not more than 12 days (Table 2). At these temperatures, this range in embryonic period falls within that typical of dorid nudibranchs with similarly sized eggs and planktotrophic development and is also at least a week shorter than embryonic periods known for species with non-feeding modes of development in the NE Pacific Ocean (Hadfield and Switzer-Dunlap 1987; Goddard 1996; Goddard and Hermsillo 2008). We therefore conclude that *F. californiensis* has planktotrophic development. Based on an image in (Kopp 2008), a smaller congener of *F. californiensis*, *F. porterae* (Cockerell, 1901) also lays relatively small eggs and likely has planktotrophic development.

Although the information we present here on the development of *F. californiensis* is incomplete and less precise than for other species, we have included it to help assess the cause of the loss of this species from the mainland of southern California. *Felimare californiensis* was once common throughout the Southern California Bight, but in contrast to other Californian nudibranchs in the region, has not been sighted on the mainland in over three decades (M. Miller *in* Behrens 2001; Goddard et al. 2013).

Palio dubia (M. Sars, 1829)

The size of the embryos from Alaska is consistent with measurements of the eggs and embryos of this species from the North Atlantic Ocean (Hamel et al. 2008; Goddard 2011a).

Triopha maculata MacFarland, 1905

Mulliner (1972) reported that an 80 mm long *Triopha grandis* MacFarland 1966 “produced 400,000 eggs per egg-mass” and hatched after 6 days (at an unspecified temperature) into “free swimming, planktotrophic veligers.” Because both the large brood size and short hatching time are entirely consistent with planktotrophic development, Goddard (2004) followed Mulliner’s (1972) determination of developmental mode for this species, which was synonymized, along with *Triopha occidentalis* (Fewkes, 1889), with *T. maculata* by Ferreira (1977). Behrens (1991) and Goddard (2004) followed Ferreira (1977), but not McDonald (1983, 2007), who considers *T. grandis* a junior synonym of *T. occidentalis*, separate from *T. maculata*. Our finding that the eggs deposited by a 50 mm long *T. maculata* were encapsulated singly (Table 2) contrasts with Mulliner’s (1972) report of an average of 18 eggs per capsule for *T. grandis*. This large difference between egg masses in the number of eggs per capsule suggests that *T. grandis* may indeed be separate from *T. maculata*, as argued by McDonald (1983, 2007).

Doto columbiana O’Donoghue, 1921

This species feeds on hydroids of the genus *Aglaophenia* and has previously been referred to by the senior author as *Doto* form B (Goddard, 1996, 2004). The sizes of the eggs and hatching larvae reported here from Hazard Canyon are similar to those reported from northern California by Goddard (1996).

Janolus anulatus Camacho-Garcia & Gosliner, 2006

The cream to white egg strings of this species (see Goddard 2012b) contained embryos encapsulated singly. This contrasts with other species of *Janolus* known from the northeast Pacific Ocean, including *J. barbarensis* (Cooper, 1863), with 15 to 20 embryos per capsule (present study, Table 2), and *J. fuscus* O’Donoghue, 1924, with an average of 66 embryos per capsule (Wolf and Young 2012). The zygotes and hatching larvae of *J. anulatus* were also significantly smaller than those of the above two congeners (Goddard 2004; Wolf and Young 2012; present study, Table 2).

Cumanotus sp.

Following Behrens (1991), Goddard (2004) referred to this species, which feeds on *Ectopleura crocea* (Agassiz, 1862) in bays and harbors, as *Cumanotus fernaldi* Thompson & Brown, 1984. However, as pointed out by S. Millen (personal communication to JG, 8 Jan 2012), Thompson and Brown (1984) in their brief description of *C. fernaldi* were referring to the larger, soft-sediment dwelling species studied by Hurst (1967) that is ecologically and morphologically similar to the north Atlantic *C. beaumonti* (Eliot, 1906). Hurst (1967) used the name *C. beaumonti* for her specimens from Washington and reported that they laid corkscrew shaped egg masses with 4–14 eggs per egg capsule. *Cumanotus* sp. consistently has one egg per capsule (Goddard 1992; present study, Table 2), is ecologically and morphologically similar to the north Atlantic *C. cuenoti* Pruvot-Fol, 1948, and is undescribed (S. Millen, personal communication to JG, 8 Jan 2012). It is pictured as *C. fernaldi* in Behrens and Hermosillo (2005, species number 244), but that name actually applies to species number 245 in Behrens and Hermosillo (2005). (S. Millen, personal communication to JG, 8 Jan 2012).

Unaware that two species of *Cumanotus* exist in the northeast Pacific Ocean, Goddard (2004, Table 1) lumped development data for both species. The complete and correct

breakdown is as follows. Based on Hurst (1967), *C. fernaldi* (as *C. beaumonti*) deposits corkscrew-shaped egg masses with 4–14 eggs per capsule that hatch after 10 days at 8–11°C with type 1 shells averaging 119 µm long. Based on Goddard (1992, 2011b) and the present study, *Cumanotus* sp. also deposits corkscrew-shaped egg masses, but with one egg (averaging 73 µm in diameter) per capsule, hatching after 9–10 days at 12–16°C with type 1 shells averaging 130 µm long.

Cuthona lagunae (O'Donoghue, 1926)

The egg masses and embryonic development of specimens of *C. lagunae* collected from Hazard Canyon in central California were virtually identical to those described by Goddard (1991) for specimens from northern California and southern Oregon, including the extrusion from the zygotes of unusually large, yolk-filled polar bodies.

Eubranchus sp. 2 of Behrens and Hermosillo (2005)

This species laid small, C-shaped egg masses characteristic of the genus. The embryos developed into planktotrophic veligers with type 2 shells, a small foot, eyespots, and minimal yolk reserves (Figure 2B).

Flabellina goddardi Gosliner, 2010

The developmental data for this species in Table 2 were obtained from the coiled and secondarily looped, white egg string and near-hatching veligers pictured without size or scale information in Gosliner's (2010) original description of this distinctive species. Since finding the first specimen in May 2008, we have found 14 additional specimens of *F. goddardi*, all in May and June at Tarpits Reef in Carpinteria, California, the type locality of this species.

Flabellina trilineata (O'Donoghue, 1921)

Two specimens found feeding on *Ectopleura crocea* in the Santa Barbara Harbor in January 2012 each laid egg strings with most capsules containing 2 eggs (Table 2). Previously, only one egg per capsule has been recorded for this species, including for specimens from the outer coast of Santa Barbara County (Bridges and Blake 1972; Strathmann 1987; Goddard 1992; present study).

Flabellina sp.

Adults were collected intertidally at Naples, on the south coast of Santa Barbara County. They closely resembled *F. trilineata* collected from the same locality in overall shape, but had smooth to slightly wrinkled rhinophores, more irregular white lines on the body, and white cnidosacs. Instead of a thin white line down the middle of the notum as in *F. trilineata*, some of our specimens of *Flabellina* sp. had a notum mostly covered with white pigment. *Flabellina* sp. deposited egg masses similar to those of *F. trilineata* collected from the same locality, but the ribbons of *Flabellina* sp. had a smaller diameter. The eggs were similar in diameter to those of *F. trilineata*, but the shells of the hatching veligers were slightly larger (Table 2). Preliminary genetic evidence suggests *Flabellina* sp. is distinct from *F. trilineata* (R. Johnson, personal communication to JG, 23 June 2010).

In his description of *Coryphella piunca*, Marcus (1961, Fig. 163) illustrated smooth to lamellate rhinophores. Steinberg (1963) synonymized *C. piunca* with *C. trilineata* O'Donoghue, 1921, and later, Roller (1970) synonymized *C. fisheri* MacFarland, 1966 with *C. trilineata*. Because both MacFarland's (1966) description of *C. fisheri* and

O'Donoghue's description of *C. trilineata* only mention annulate or lamellate rhinophores, it appears that Marcus's *C. pinca* likely included specimens of both *F. trilineata* and *Flabellina* sp. as recognized here.

Goddard (1984, Table 1) reported that dendronotid *Tritonia festiva* has eyespots at hatching, and Strathmann (1987, p. 291) and Goddard (2001b, Appendix A) repeated this. Reexamination of JG's original notes from 1981 and photomicrographs taken by JG in 1987 of the hatching larvae of this species revealed the paired structures were not eyespots, but rather nephrocysts (see Thompson 1976; Bonar 1978; Bickell and Kempf 1983) containing unusually large and dense, irregularly shaped, semi-translucent granules. At low magnification and certain angles of view and illumination, these structures can appear to be eyespots (Figure 2C). However, larval eyespots in opisthobranchs consist of thin patches of opaque black pigment, develop an overlying hyaline lens, and are located anterior to the nephrocysts (Thompson 1976; Bonar 1978). Goddard (1992, 2001b) also mistook dense nephrocysts for eyespots in the arminid nudibranch *Janolus fuscus*, but these have also been confirmed to be nephrocysts in both this species (Wolf and Young 2012; pers. obs.), as well as its congener, *J. anulatus* (present study, Figure 2D).

The combined presence of eyespots and a propodium is a reliable indicator of metamorphic competence in opisthobranchs (Bonar 1978), and most planktotrophic nudibranchs hatch without eyespots (Bonar 1978; Hadfield and Switzer-Dunlap 1984; Goddard 2004). However, exceptions are known from the northeast Pacific Ocean, including species of Eubranthidae and Tergipedidae (Hurst 1967; Strathmann 1987; Goddard 1991; present study, Figure 2B) and the dorid *Aegires albopunctatus* MacFarland, 1905, which has unusual larval development (Goddard 2001a).

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