Reference: *Biol. Bull.* **216:** 355–372. (June 2009)

Not My "Type": Larval Dispersal Dimorphisms and Bet-Hedging in Opisthobranch Life Histories

PATRICK J. KRUG

Department of Biological Sciences, California State University, Los Angeles, Los Angeles, California 90032-8201

Abstract. When conditions fluctuate unpredictably, selection may favor bet-hedging strategies that vary offspring characteristics to avoid reproductive wipe-outs in bad seasons. For many marine gastropods, the dispersal potential of offspring reflects both maternal effects (egg size, egg mass properties) and larval traits (development rate, habitat choice). I present data for eight sea slugs in the genus *Elysia* (Opisthobranchia: Sacoglossa), highlighting potentially adaptive variation in traits like offspring size, timing of metamorphosis, hatching behavior, and settlement response. *Elysia zuleicae* produced both planktotrophic and lecithotrophic larvae, a true case of poecilogony. Both intracapsular and post-hatching metamorphosis occurred among clutches of "*Boselia" marcusi*, *E. cornigera,* and *E. crispata*, a dispersal dimorphism often misinterpreted as poecilogony. Egg masses of *E. tuca* hatched for up to 16 days but larvae settled only on the adult host alga *Halimeda*, whereas most larvae of *E. papillosa* spontaneously metamorphosed 5–7 days after hatching. Investment in extracapsular yolk may allow mothers to increase larval size relative to egg size and vary offspring size within and among clutches. Flexible strategies of larval dispersal and offspring provisioning in *Elysia* spp. may represent adaptations to the patchy habitat of these specialized herbivores, highlighting the evolutionary importance of variation in a range of life-history traits.

Introduction

When environmental conditions change unpredictably in space and time, variation in life-history traits can be an adaptive response to selection (Meyers and Bull, 2002). For instance, stable dispersal dimorphisms can evolve when the quality of habitat patches varies over time and there is spatial heterogeneity in environmental fluctuations (Mathias *et al*., 2001). High-dispersal morphs like winged insects trade off costs of migration against the opportunity to locate new habitat or mates, whereas wingless morphs have more energy for reproduction but suffer if local conditions deteriorate (Roff and Fairbairn, 1991; Mole and Zera, 1993; Roff, 1994; Crnokrak and Roff, 1995, 1998; Denno *et al*., 1996; Zera and Denno, 1997; Langellotto and Denno, 2001).

Unpredictable environments can also drive the evolution of bet-hedging strategies, which incur reduced reproductive success in good conditions to avoid reproductive wipeouts in bad times (Seger and Brockmann, 1987; Phillipi and Seger, 1989; Crean and Marshall, 2009). By always producing a few well-suited individuals, bet-hedging genotypes have reduced variance in fitness across generations, which increases the geometric mean fitness of a genotype and hence its rate of increase in a population (Gillespie, 1974, 1976). If mothers cannot predict the environment their offspring will experience, they can vary offspring characteristics within a clutch by altering egg size or other maternal effects (Marshall and Keough, 2008; Marshall *et al*., 2008; Crean and Marshall, 2009). For instance, mothers may respond to uncertain conditions by producing a single phenotype that avoids risk—for example, making bigger eggs than necessary to hedge against offspring mortality (conservative bet-hedging; Einum and Fleming, 2004). However, environmental fluctuations can alter the size-fitness relationship of offspring, and bigger offspring are not always better (Parker and Begon, 1986; Bernardo, 1996a, b; Kaplan and Phillips, 2006). If mothers cannot anticipate the optimal size for their offspring, they may instead increase within-brood variance (Crean and Marshall, 2009). Such tactics are termed diversified bet-hedging, when a single genotype

Received 24 November 2008; accepted 7 April 2009.
E-mail: pkrug@calstatela.edu

produces multiple phenotypes but only one will have high fitness under a given set of conditions (Cooper and Kaplan, 1982).

Mothers can also risk-spread by producing offspring that vary in their emergence time or dispersal potential. Variation in the timing of diapause or seed germination scatters individuals that share a genotype through time to escape drought or resource limitation (Clauss and Venable, 2000; Menu *et al*., 2000; Simons and Johnston, 2006; Venable, 2007). In birds, hatching asynchrony within a clutch may produce siblings that differ in dispersal potential (Laaksonen, 2004). Many plants express dimorphic seeds or fruits that differ in structures affecting buoyancy or drag, such that one morph has greater potential for transport by wind or water (Payne and Maun, 1981; Morse and Schmitt, 1985; Venable, 1985; Telenius and Torstensson, 1989; Imbert, 1999).

Dispersal in many marine invertebrates occurs during the larval planktonic period, which is influenced by both maternal effects and larval genotype. Mothers control the development mode of their offspring *via* egg energy content, and determine whether embryos have a period of benthic development in protective capsules (Strathmann, 1985, 1990, 1995; Levin and Bridges, 1995; Moore and Manahan, 2007). Larval genotype can affect metabolic efficiency and pelagic period (Levin *et al*., 1991; Pace *et al*., 2006; Hedgecock *et al*., 2007; Pace and Manahan, 2007), as well as habitat choice behavior (Toonen and Pawlik, 2001a). There is thus considerable potential for adaptive variation in traits related to larval size, hatching, dispersal, and habitat selection in marine life histories. However, variation in such traits within and among broods has received little attention, despite its potential importance as a target of selection (Doyle, 1975, 1976; Raimondi and Keough, 1990; Hadfield and Strathmann, 1996; Krug and Zimmer, 2000, 2004; Toonen and Pawlik, 2001a; Marshall *et al*., 2008). Variation within and among clutches can also result from functional constraints or developmental instability, but may be of adaptive value for organisms that face uncertain environments.

A few invertebrates express an extreme developmental dimorphism, producing distinct types of embryos that develop into either long-lived larvae with an obligate feeding period or short-lived larvae that can settle without feeding in the plankton. Termed poecilogony, such stable polymorphisms in development are rare and have been controversial since the first putative cases were proposed (Levin, 1984; Hoagland and Robertson, 1988; Bouchet, 1989). Their potential adaptive significance was highlighted by Giard (1905), who coined the term; he argued that poecilogony presents an opportunity to study how selection acts on larval stages, by considering the environmental context in which different embryos are generated:

> Chez d'autres animaux, les divers individus ou les diverses générations d'une même espèce considérés aux divers points de la distribution géographique, aux diverses saisons de l'année, ou dans des conditions de nutrition différentes, ont des larves qui ne se ressemblent pas, bien que l'adulte reste constamment semblable à lui-même, ou ne présente que des modifications très légères. C'est la particularité que j'ai désignée naguère, sous le nom de pœcilogonie. Les larves sont devenues divergentes en s'adaptant à des milieux différents. L'hérédité a maintenu la similitude des adultes. (Giard, 1905)
>
> In other animals, various individuals or generations of the same species from various points along their geographical distribution, various seasons of the year, or under different nutritional conditions, have larvae which do not resemble each other, although the adult always looks the same, or exhibits only slight modifications. This is the characteristic that I recently described under the name poecilogony. The larvae diverged while adapting to different environmental conditions. Heredity maintained the similarity of the adults. (author's translation)

Giard discussed cases where brooding appeared in broadcast-spawning lineages, or viviparity in oviparous groups, but his examples were cryptic species. Modern studies have focused on the production of planktotrophic and lecithotrophic larvae by polychaetes in the family Spionidae and by opisthobranch sea slugs (Hoagland and Robertson, 1988; Bouchet, 1989). For instance, the polychaete *Streblospio benedicti* produces both larval types in the western Atlantic (Levin, 1984; Levin and Bridges, 1994; Schulze *et al*., 2000). Larval development is invariant among broods of a given female even when maternal condition is manipulated, and quantitative genetic studies indicate that poecilogony in *S. benedicti* reflects a stable polymorphism maintained by trade-offs between two suites of correlated life-history characters (Levin and Creed, 1986; Levin and Huggett, 1990; Levin *et al*., 1991; Levin and Bridges, 1994).

Poecilogony also occurs among herbivorous sea slugs in the opisthobranch group Sacoglossa, which differ from polychaetes in several key respects (Krug, 2007). Sacoglossans are specialized herbivores that feed on coenocytic algae, with most species restricted to one algal genus (Jensen, 1997). Slugs depend on spatially patchy resources that fluctuate markedly over time, which could favor bet-hedging strategies (Clark, 1975; Clark and DeFreese, 1987; Trowbridge, 1992, 1993, 2002). Embryos develop inside benthic egg masses; planktotrophic larvae settle after an extended planktonic period, whereas lecithotrophic larvae metamorphose (a) after hatching, if cues from host algae are present; (b) after hatching, with no inductive requirement; or (c) prior to hatching (intracapsular metamorphosis) (Krug, 2007). The Pacific species *Alderia willowi* expresses all four of those dispersal strategies, and individual adults can vary larval type among and within clutches (Krug, 1998, 2001; Smolensky *et al*., 2009). Two populations of *Elysia chlorotica* express different larval types but are interfertile (West *et al*., 1984). The Caribbean *Costasiella ocellifera* was thought to be two species differing in devel-

opment (Miles and Clark, 2002), but poecilogony was confirmed by genetic analyses and breeding studies (Ellingson, 2006; Ellingson and Krug, unpubl. data). Sacoglossans may therefore be an ideal study taxon for testing hypotheses about the adaptive value of variation in key life-history traits, given the frequency of poecilogony in this group.

However, some published claims of poecilogony among opisthobranchs reflect confusion over what constitutes a "type" of larval development. Thompson (1967) coined Type 2 development to describe the release of swimming lecithotrophic veligers, but noted that some Type 2 larvae undergo intracapsular metamorphosis. In contrast, he labeled species that develop through a reduced larval stage into crawl-away juveniles as Type 3 (Thompson, 1967). Bonar (1978) sought to distinguish intracapsular metamorphosis from ametamorphic (direct) development, where larval structures are vestigial and transient and no clear metamorphosis separates the juvenile stage. Unfortunately, he introduced confusion into the literature by classifying development into a fully formed veliger followed by intracapsular metamorphosis as "Type 3 with capsular metamorphosis," disregarding Thompson's standard that Type 3 species have a reduced larval stage.

I aim to show that Thompson's Type 2 and Bonar's Type 3 with capsular metamorphosis are not different types of development, but merely points on a spectrum of dispersal strategies accessible to lecithotrophic opisthobranchs. Larval dispersal potential can vary within and among clutches due to flexibility in time to hatching and metamorphosis (Eyster, 1979; Chester, 1996), attainment of competence (Gibson and Chia, 1995), or settlement cue requirements (Gibson, 1995; Krug, 2001). Many authors have erroneously classified species in which *some* lecithotrophic larvae hatch, but *others* undergo encapsulated metamorphosis, as poecilogonous (Clark *et al*., 1979; Clark and Jensen, 1981; Marin and Ros, 1993; Clark, 1994; Gibson and Chia, 1995; Jensen, 2001). As noted by Bouchet (1989), such species do not produce two types of embryos and do not meet the definition of poecilogony. However, such dispersal dimorphisms may be adaptive solutions to environmental challenges and should be studied to understand the role of variation in marine life histories. I present data for eight Caribbean sacoglossans in the genus *Elysia* to illustrate how offspring size and dispersal potential may vary within a species, and to highlight the ecological and evolutionary importance of such variation.

Materials and Methods

Study taxa

Adult sea slugs were collected from the field on trips between 2004 and 2009, with permission of the host country and the State of Florida (Table 1). About 1 kg of the host alga for each species was collected by snorkeling and placed in aerated bins overnight; slugs were removed as they crawled off the algae, and transferred to plastic bins for oviposition. After a few days, small pieces of algae were provided to allow slugs to feed. Some measurements of clutch characteristics were made at the collection location. For settlement experiments and hatching-time measurements, I transported slugs and algae to California State University, Los Angeles, where most species continued reproducing for 2–3 months. Algae were grown in aquaria under ambient light and room temperature. Slugs and egg masses were kept in an incubator at 25 °C on a 14:10 h light/dark cycle. Filtered seawater (FSW), prepared by filtering ocean water from the Cabrillo Aquarium's system (San Pedro, CA) to 0.22 μm, was used for culturing egg masses and in larval settlement experiments.

Pilot studies in 2003 showed that eight Caribbean sacoglossans had lecithotrophic development: *E. crispata* Morch 1863*, E. subornata* Verrill 1901, *E. pratensis* Ortea and Espinosa 1996, *E. cornigera* Nuttall 1989, *E. zuleicae* Ortea and Espinosa 2002, *E. papillosa* Verrill 1901, *E. tuca* Marcus and Marcus 1967, and "*Boselia*" *marcusi* Marcus 1972. Species were identified from original descriptions based on morphology of the dorsal vessels, radulae, and parapodia. As part of a molecular phylogenetic study of the Placobranchacea, portions of two mitochondrial and two nuclear genes were also sequenced from multiple specimens of all

Table 1

Collection localities and dates for specimens that produced clutches used in this study

Location	Date(s) sampled	Latitude, Longitude	*Elysia* spp. sampled
Bahamas			
Sweetings Cay	6/03, 6/04, 7/07	26°37′N, 78°05′W	*tuca, zuleicae, crispata, pratensis, subornata*
Little San Salvador	6/03, 6/04, 7/07	24°40′N, 76°00′W	*tuca, crispata, pratensis*
San Salvador	6/03, 6/04, 7/07	24°01′N, 74°33′W	*tuca, zuleicae, marcusi*
Plana Cays	6/04, 7/07	22°36′N, 73°33′W	*tuca, zuleicae*
Discovery Bay, Jamaica	3/06	18°28′N, 77°24′W	*zuleicae, marcusi, crispata*
Key West, Florida, USA	10/06, 6/07, 8/07	24°30′N, 81°39′W	*tuca, zuleicae, marcusi, papillosa, cornigera, pratensis, subornata*
Spanish Waters, Curaçao	1/09	12°04′N, 68°51′W	*crispata*

species (A. Rodriguez, E. Hidalgo, D. Trathen, R. Ellingson, and P. Krug, unpubl. data). Results of molecular studies will be reported elsewhere, but were used to confirm conspecificity of morphologically similar specimens, species identity of field-collected egg masses, and differences among species lumped by previous workers. Of particular note, the species currently named *Boselia marcusi* is not a *Boselia* but rather a derived *Elysia*; I refer to it as "*Boselia*" *marcusi* to avoid introducing taxonomic confusion, but it is congeneric with other *Elysia* spp. No developmental data have been reported for this poorly studied species.

At least four species have been called *E. papillosa*, due to a poor initial description and missing type material (Verrill, 1901; Thompson, 1977; Clark, 1984; Ortea *et al*., 2005). I follow the first detailed description (Marcus and Marcus, 1967). The taxonomic confusion makes published reproductive data on *E. papillosa* unreliable. Clark (1984) acknowledged that what he called *E. papillosa* was a complex of species; on the basis of drawings in Clark (1984), he lumped both *E. patina* and *E. zuleicae* with the species redescribed as *E. papillosa* by Marcus and Marcus (1967). Further, both Thompson (1977) and Ortea *et al*. (2005) referred to an undescribed member of the *E. tomentosa* species complex as *E. papillosa*, but this species does not swim when disturbed and hence does not match the original description of *E. papillosa* (Verrill, 1901; P. Krug, unpubl. data). The Caribbean *E. cornigera* was synonymized with its Mediterranean sister taxon *E. timida* (Ortea *et al*., 1998), but molecular and morphological data confirm it is a distinct species (P. Krug, unpubl. data).

Reproductive traits

Although there is an extensive literature on egg size for Caribbean sacoglossans, some species were misidentified or unknown to earlier researchers, and hatching larval size was not reported for most species (*e.g*., Clark and Jensen, 1981; Ortea *et al*., 1998). In all *Elysia* spp., eggs develop within individual capsules embedded inside a jelly string, deposited in a tight spiral and surrounded by a tough outer membrane. Egg masses were carefully cut free from the substrate with a scalpel and transferred to individual petri dishes with 4 ml FSW. Presence of extra-capsular yolk globules, or ribbons, a common feature in this family, was recorded. Egg diameters were measured for uncleaved ova in newly laid egg masses of *E. pratensis*, *E. subornata*, "*B*." *marcusi*, *E. zuleicae* (planktotrophic), *E. crispata*, and *E. papillosa*, species for which such data were previously unreported or unreliable due to taxonomic confusion—*e.g.,* Clark *et al*. (1979) lumped three species as *E. cause*; see Clark (1984). Literature values were used for *E. cornigera*, for which proper identification was not a concern, and are included for *E. crispata* for comparison with new measurements. Number of eggs per clutch was scored for all species except *E. crispata* and planktotrophic clutches of *E. zuleicae* (see Results).

Each day, egg masses were transferred to a new dish with fresh FSW and checked for stage of development, encapsulated metamorphosis, and hatching of larvae or juveniles. Time to hatching and percent intracapsular metamorphosis were determined for replicate egg masses of all species. Maximum larval shell dimension was measured from the aperture to the opposite side of the coiled shell for larvae at hatching; as many larvae as possible were measured from a given clutch, and for multiple clutches when possible for a species. Size of newly metamorphosed juveniles was measured for *E. tuca*, "*B*." *marcusi, E. crispata*, and *E. pratensis*. For size measurements, a high-resolution digital image was taken at maximum magnification, using an Olympus 5060 camera mounted on a Zeiss Stemi stereomicroscope. Images were calibrated by photographing a hemocytometer grid at the same magnification and determining the number of pixels per micrometer in Adobe Photoshop ver. 7.0. Sizes were measured from images, using the ruler tool in Photoshop. All eggs or larval shells in an egg mass were measured where possible, although for clutches of more than 200 eggs only a subset were measured.

Numbers in the text are mean values ± one standard error (SE). For sizes of eggs, larval shells at hatching, and juveniles, the mean value of each clutch was first calculated; the overall mean of clutch means was then computed for each species. To compare variance within and among clutches in offspring size, I calculated the coefficient of variation (CV) for egg, larval, and juvenile size from each clutch, and then determined the mean within-clutch CV for each species. I also calculated the among-clutch CV for egg, larval, and juvenile size for each species from the corresponding mean size for each clutch.

Within a species, variation in mean larval size per clutch was determined using a one-way ANOVA with *post hoc* Scheffé tests for unplanned comparisons (Day and Quinn, 1989). For comparison across species, the mean larval size for each clutch was the level of replication, and a one-way ANOVA was used to test for significant variation in mean size per species with *post hoc* Scheffé tests.

Variance in time to hatching

Pilot studies indicated that the egg masses laid by large specimens of *Elysia tuca* hatched over an extended period of time; larvae in the outermost whorls of the egg spiral hatched days before siblings developing in inner whorls. I therefore isolated egg masses ($n = 19$) laid by specimens of *E. tuca* from the Florida Keys, and determined the number of larvae emerging from the egg mass each day once hatching commenced. The cumulative proportion of hatched larvae was tracked until all larvae had emerged. The relationship between duration of the hatching period and (a) egg

number per clutch, or (b) time to first hatching, was determined by calculating Pearson's correlation coefficients in SPSS ver. 16.0.

Spontaneous metamorphosis

Lecithotrophic larvae may undergo "spontaneous" metamorphosis in culture dishes containing only FSW, with no exogenous substrate added (Pawlik, 1992). In some species, larvae are more likely to settle spontaneously over time, a so-called desperate larvae effect (Toonen and Pawlik, 2001b; Marshall and Keough, 2003). However, most spontaneous metamorphosis occurs in the first 2 days after hatching in the sacoglossan *Alderia willowi* (Krug, 2001; note recent name change: Krug *et al*., 2007). The proportion of larvae that metamorphosed spontaneously in FSW was therefore scored for one week post-hatching for replicate egg masses of the following species, in which most larvae hatched as swimming veligers: *Elysia papillosa* ($n = 5$), *E. tuca* ($n = 14$), and "*B*." *marcusi* ($n = 4$). Egg masses were incubated in individual culture dishes until hatching. All veligers that emerged on the day hatching began were transferred to a new culture dish. On each successive day, the number of larvae that had died or metamorphosed since the previous day was scored, and swimming veligers were transferred to a clean dish.

Settlement cue specificity

Sufficient larvae were available only from *E. tuca* and the lecithotrophic morph of *E. zuleicae* (see Results) to perform settlement experiments with newly hatched larvae. To test whether larvae selectively metamorphosed in the presence of the adult host alga, larvae from 2–4 egg masses were pooled and then subsampled, adding 10–20 larvae to each replicate dish (3–8 dishes per treatment, depending on larval availability). Negative controls were dishes with FSW only. Treatments included a small piece of suitable adult host algae and 2–3 alternative algae not utilized by the adult, as indicated by field collections and laboratory choice assays (P. Krug, unpubl. data). Adult *E. tuca* are abundant on the calcified green algae *Halimeda incrassata* and *H. monile*, and are occasionally found on *H. opuntia*; no specimens were collected over a 5-year period on *Batophora oerstedii*, *Caulerpa verticillata*, or *Udotea flabellum*. In contrast, *E. zuleicae* is a specialist on the green algal genus *Udotea* and is found mainly on large stipes of *Udotea flabellum*; no specimens were collected from *Penicillus capitatus* or *C. verticillata*, which are fed on by other Caribbean sacoglossans (P. Krug, unpubl. data). Settlement assays started within a day of hatching. Larvae were scored daily for metamorphosis, death, or continuation of the swimming veliger stage over 3 days after the initiation of the experiment. Pilot studies indicated that larvae often settled on inductive algae on the first day of exposure, but required up to 2 days to complete metamorphosis. The percentage of initial larvae that successfully metamorphosed after 3 days was arcsine(square-root)-transformed to normalize data; transformed percentages were compared by a one-way ANOVA in SPSS ver. 16.0, using a *post hoc* Dunnett's t test to compare metamorphosis in algal treatments against negative controls (FSW-only).

Results

Elysia tuca

Egg masses contain ribbons of bright orange extra-capsular yolk (ECY) contacting every egg capsule, within which the veligers develop (Table 2). Some veligers were observed to ingest granules of ECY that entered their individual capsules through minute tears at the point of contact with the yolk ribbon; the larvae take on an orange hue during development as ECY is either absorbed or directly consumed. Mean number of eggs per clutch did not differ between adults from the Bahamas (113.7 ± 20.2 SE; $n = 7$; range = 32–194) or the Florida Keys (177.3 ± 32.7 SE; $n = 19$; range = 6-580).

Mean time to first hatching was 18.1 days (±0.7 SE; $n = 19$) for clutches from Florida slugs, and 17.7 days (±0.3 SE; $n = 3$) for egg masses from Bahamas slugs. However, there was wide variation among clutches in the time until hatching was complete; larvae in the outermost whorl of an egg mass hatched days or weeks before siblings from inner whorls (Fig. 1). Mean time from initial hatching until the last veliger emerged from the egg mass was 8.6 days (±3.9 SD; $n = 19$; range = 2-16). Larger clutches took longer to complete hatching; the number of eggs per clutch was significantly correlated with the duration of the hatching period ($r = 0.576$, $P < 0.01$). There was no correlation between time to first hatching and the period until hatching was complete ($r = 0.293$, $P = 0.22$).

No intracapsular metamorphosis occurred in egg masses of *Elysia tuca* (Table 2). When held in FSW, only 4 out of 866 larvae ($n = 13$ clutches) metamorphosed spontaneously in the week after hatching (Fig. 2). Larval mortality increased linearly after day 3 post-hatching and exceeded 50% by day 7, but some larvae survived and successfully metamorphosed after 12 days in FSW with no food.

Recently hatched larvae of *E. tuca* showed significant variation in metamorphosis when exposed to six potential host algae (Fig. 3A, and results of a one-way ANOVA: $F_{7,34} = 43.63$, $P < 0.0001$). Only the adult host algal genus *Halimeda* induced significant metamorphosis compared to negative controls (Dunnett's t test, $P < 0.0001$). Among the three assayed species of *Halimeda*, the least inductive was *H. opuntia* (Fig. 3A), which is also the *Halimeda* sp. preferred least by adult slugs.

Mean larval shell size was 275.8 μm (±3.9 SE; $n = 5$ clutches) in maximum dimension, but among clutches

Table 2

Characteristics of egg masses, larvae, and juveniles for eight Caribbean sacoglossans

Species	Extra-capsular yolk	Egg diameter (μm)	# Eggs per clutch	Larval shell size (μm)	Time to hatching (days)	% Intracapsular metamorphosis	Juvenile size (μm)
E. tuca	thick orange ribbon	104.8 ± 0.5	160.2 ± 20.9 (26)	275.8 ± 3.9 (5)	18.0 ± 0.6 (22)	0% (27)	358.2 ± 30.5 (2)
E. zuleicae							
planktotrophic	thin white zig-zags	66.1 ± 1.6 (2)	n.d.	109.5 ± 6.2	5.7 ± 0.7 (3)	not applicable	n.d.
lecithotrophic	thick white ribbon	n.d.	104.0 ± 10.4 (4)	253.9 ± 4.5 (4)	18.5 ± 0.5 (2)	0% (4)	n.d.
"*B.*" *marcusi*	pale yellow blobs	103.9 ± 1.0 (8)	22.6 ± 3.5 (16)	190.3 ± 6.2 (5)	14.1 ± 0.7 (9)	12.4% ± 0.5 (11)	316.6 ± 2.5 (2)
E. papillosa	orange ribbon, top face of egg mass	116.3 ± 0.9	45.0 ± 20.0 (2)	337.3 ± 1.6	19.5 ± 0.5 (2)	0% (2)	n.d.
E. crispata	none	110.0 ± 3 205[a], 209[c]	1020[c]	279.9 ± 13.9 (4)	14.9 ± 0.4 (9)	100% (9), 0% (2)	517.1 ± 64.6 (2)
E. cornigera	pale yellow ribbon	105[b]	20.5 ± 1.5 (2)	248.4 ± 4.8 (2)	16.7 ± 1.2 (3)	95.8% ± 4.2 (3)	n.d.
E. pratensis	thick orange ribbon	117.9 ± 2.2 (5)	146.6 ± 106.4 (11)	321.2 ± 2.9 (12)	23.3 ± 1.0 (6)	100% (22)	651.9 ± 42.0 (5)
E. subornata	thick orange ribbon	119.2 ± 0.4	470[c]	306.6 ± 4.6 (2)	14.8 ± 0.9 (4)	100% (4)	n.d.

Data are means ± standard errors, with clutch as the unit of replication; as many eggs, larvae, or juveniles as possible were used to determine the mean for each clutch, then a mean-of-means was calculated. The number of clutches on which a mean is based is given in parentheses unless measurements were for a single clutch, in which case the standard error is for that clutch and no sample size is given. n.d. = not determined.

[a]Clark and Jensen, 1981; [b]Nuttall, 1989; [c]Defreese and Clark, 1983.

ranged from 261.9 μm ± 1.7 SE to 284.1 μm ± 2.0 SE. There was significant variation in offspring size among clutches (Fig. 4A, and results of a one-way ANOVA: $F_{4,172} = 19.14$, $P < 0.0001$). Larval size was significantly lower in the clutch with the smallest larvae compared to all other clutches (*post hoc* Scheffé test, $P < 0.05$), which did not differ in mean shell size ($P > 0.20$). Juveniles measured 358.2 μm in length (±30.5 SE; $n = 2$ clutches) when extended and crawling.

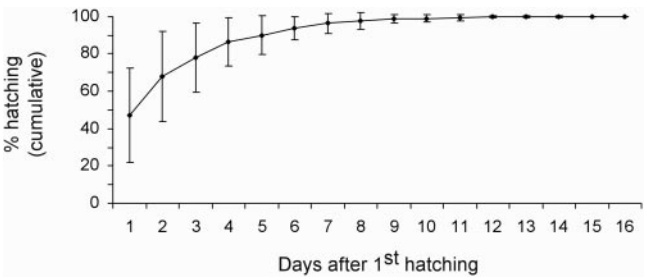

Figure 1. Extended hatching period for egg masses of *Elysia tuca*. Data are the daily mean cumulative percentage of total larvae (±1 SD) that hatched from replicate ($n = 19$) egg masses laid by a collection of specimens from the Florida Keys. Error bars are standard deviation to illustrate the variation among egg masses in the proportion of larvae that had hatched by a given day. Time until all larvae had hatched ranged from 2 to16 days.

Elysia zuleicae

Most *Elysia zuleicae* from Bermuda, Florida, Jamaica, and the Bahamas produced white planktotrophic eggs measuring 66.1 μm (±1.6 SE; $n = 2$). A thin ribbon of white ECY was woven unevenly through planktotrophic egg masses (Fig. 5A). Larvae measured 109.5 μm (±6.2 SE) at hatching, which occurred 5–7 days after egg mass deposition (Table 2).

Unexpectedly, a few individuals collected from the Bahamas in 2004 laid lecithotrophic egg masses in the laboratory, and two lecithotrophic egg masses were collected in the field from Plana Cays, Bahamas, in 2007 (Fig. 5B). A thick ribbon of white ECY contacted every capsule, in which embryos developed over 18.5 days ± 0.5 days into larvae with a mean shell size of 253.9 μm (±4.5 SE, $n = 4$) (Table 2). There was significant among-clutch variation in larval size (Fig. 4B, and results of a one-way ANOVA: $F_{4,90} = 45.07$, $P < 0.0001$).

All adults had the diagnostic morphological features of *E. zuleicae*, including a species-specific dorsal vessel pattern. Further, a portion of the mitochondrial cytochrome oxidase I gene was sequenced from more than 100 specimens collected across the Caribbean, along with field-collected egg masses, and confirmed that slugs producing planktotrophic and lecithotrophic larvae were conspecific (D. Trathen and

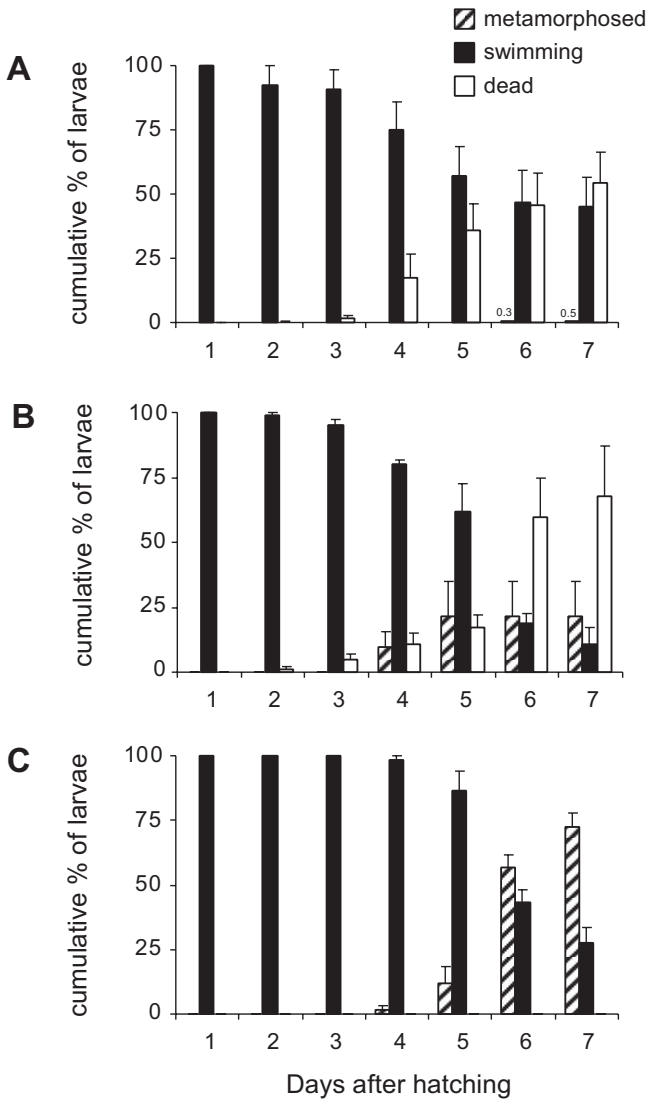

Figure 2. Larval survival and spontaneous metamorphosis over 7 days post-hatching. Data are mean daily cumulative percentages ± standard errors of swimming veligers, mortality, and metamorphosis in the absence of any inductive substratum. Each replicate comprised the larvae released on the first day of hatching from one clutch. Larval survival and spontaneous metamorphosis for (A) *Elysia tuca* ($n = 14$); (B) "*Boselia*" *marcusi* ($n = 4$); (C) *E. papillosa* ($n = 5$).

P. Krug, unpubl. data). Thus, *E. zuleicae* is a true case of poecilogony, producing two distinct kinds of embryos.

Lecithotrophic clutches hatched over 4–5 days. No intracapsular metamorphosis occurred in five egg masses; a single larva metamorphosed in FSW from a clutch of 105 eggs, and no larvae from a further 4 clutches metamorphosed spontaneously. Significant metamorphosis was induced only by the adult host alga *Udotea flabellum* (Fig. 3B, and results of a one-way ANOVA: $F_{4,11} = 30.24$, $P < 0.0001$; Dunnett's t test, $P = 0.002$). No metamorphosis occurred after exposure to *Penicillus capitatus*, host of the related species *E. patina*, and larval response to *Caulerpa verticilata* did not differ from FSW controls (Dunnett's t test, $P = 0.57$).

"Boselia" (= Elysia) marcusi

Specimens from Jamaica, San Salvador (Bahamas), and the Florida Keys produced lecithotrophic offspring. In most egg masses, each egg capsule was provisioned with a discrete globule of pale yellow ECY matching the egg color (Fig. 5C); in one egg mass, all ECY globules were connected by a thread of yolk. Mean egg diameter was 103.9 μm (±1.0 SE; $n = 8$ clutches), but there was significant variation in egg size among clutches (one-way ANOVA: $F_{7,120} = 13.82$, $P < 0.0001$). Mean egg size was more variable among three clutches from Jamaica (range: 99.5 μm ± 0.6 to 108.5 μm ± 0.8) than among five clutches from Florida (range: 102.9 μm ± 1.0 to 106.3 μm ± 1.4 SE). Mean fecundity was 22.6 eggs per clutch (± 3.5 SE; $n = 16$) and did not differ among the three populations.

Embryos developed over 14 days to hatch into veligers with mean shell sizes ranging from 175.5 μm ± 1.7 SE to 210.3 μm ± 2.7 SE (Table 2), which included the smallest lecithotrophic larvae among the taxa examined in this study. There was significant among-clutch variation in larval size

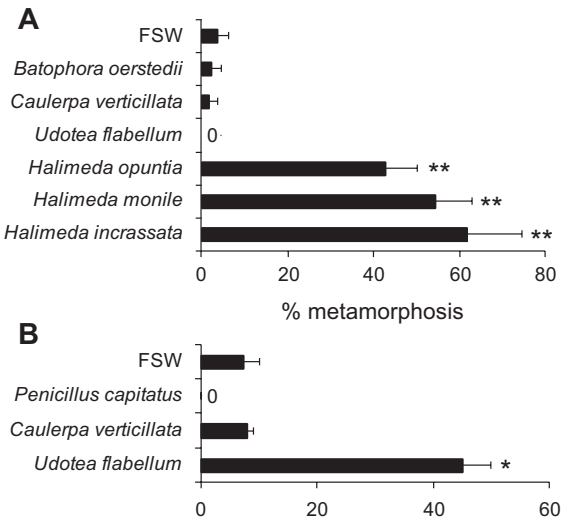

Figure 3. Induction of metamorphosis in newly hatched larvae of two *Elysia* spp. by host *versus* non-host algae. Algae used in assays are co-occurring, and each is the host of at least one sacoglossan; all therefore represent potential settlement substrata. Data are mean percentages of metamorphosis + standard errors after 3 days of exposure to a piece of the indicated algae, or in filtered seawater (FSW) controls. Asterisks denote means that differed significantly from negative controls, after transformation and comparison by ANOVA with *post hoc* Dunnett's t tests; $^*P < 0.005$, $^{**}P < 0.0001$. (A) Larval metamorphosis in *E. tuca*. Adult slugs feed on the algal genus *Halimeda*, preferring *H. incrassata* and *H. monile*. (B) Metamorphosis in lecithotrophic larvae of *E. zuleicae*. Adults specialize on the alga *Udotea flabellum*; a close relative feeds on *Penicillus*.

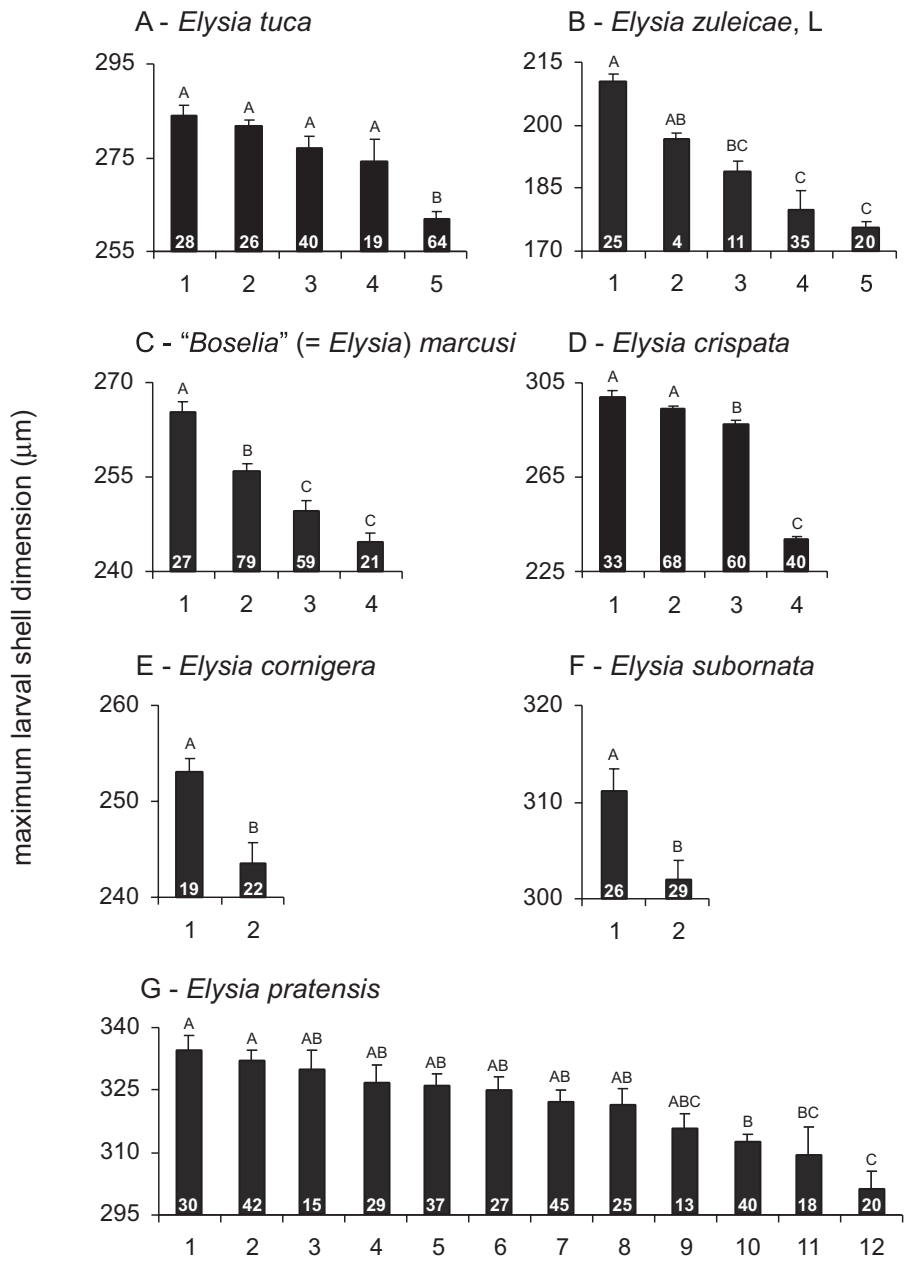

Figure 4. Among-clutch variation in larval size for seven *Elysia* spp. "L" indicates lecithotrophic clutches for the poecilogonous species *E. zuleicae*. Data are mean maximum larval shell sizes + one standard error. Sample size for each clutch is given on the bar, with numbers below the *X*-axis indicating different egg masses. In each species, there was significant variation among clutches; means labeled with the same letter did not differ significantly at the $P < 0.05$ level, either by *post hoc* Scheffé test after a significant one-way ANOVA or by an unpaired two-tailed *t* test.

for five egg masses produced by Florida specimens (Fig. 4C, and results of a one-way ANOVA: $F_{3,182} = 65.52$, $P < 0.0001$).

There was no intracapsular metamorphosis in five egg masses from Florida slugs, but 22.8% ± 15.9% SE of larvae metamorphosed prior to hatching in egg masses from Jamaican slugs ($n = 6$; range = 0–100%). After hatching, there was no spontaneous metamorphosis from Florida egg masses over 4 days, but 21.3% ± 13.9% SE of larvae had metamorphosed after 7 days in FSW (Fig. 2B). Most remaining larvae died without metamorphosing over a week post-hatching (Fig. 2B). Juveniles were the smallest of the four species examined in this study (Table 2).

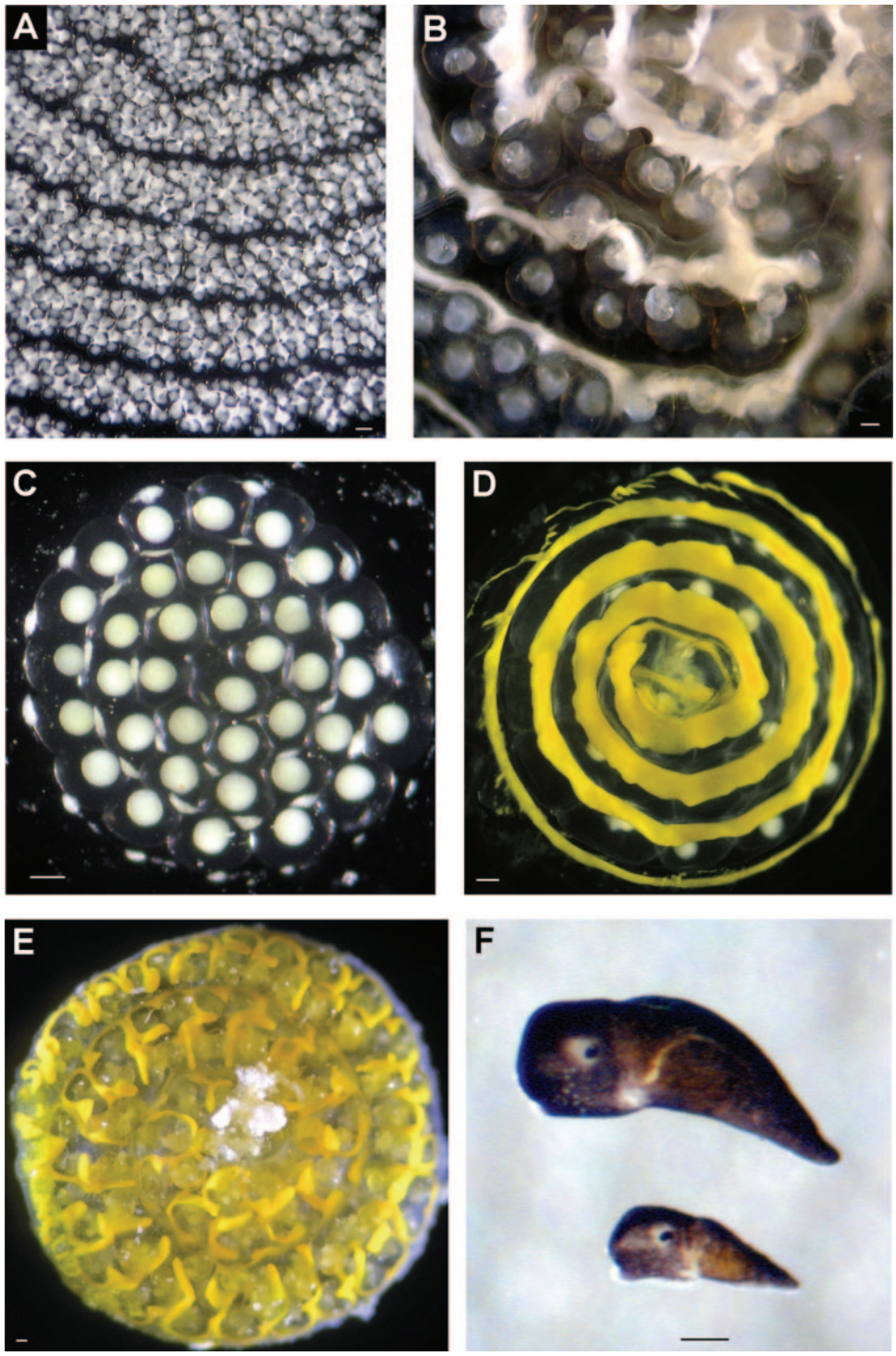

Figure 5. Previously undescribed egg masses of four *Elysia* spp. included in the present study. All scale bars are 100 μm. (A) Close-up of a planktotrophic egg mass from *E. zuleicae*, showing irregular deposition of white extra-capsular yolk (ECY) around capsules containing early-stage embryos. (B) Close-up of a lecithotrophic egg mass from *E. zuleicae* (Plana Cays, Bahamas) containing well-developed veliger larvae. Note size of larvae and capsules and thickness of ECY ribbon, compared to conspecific planktotrophic egg mass in A. (C) Egg mass containing uncleaved ova of "*Boselia*" (= *Elysia*) *marcusi* from Jamaica, showing a discrete globule of ECY attached to the outer face of each egg capsule. (D) Freshly deposited egg mass of *E. papillosa*, showing orange ECY ribbon on the upper face of the egg mass. (E) Egg mass of *E. pratensis* containing early-stage veligers; orange ECY ribbon meanders throughout egg mass, wrapping around all capsules. (F) Juvenile *E. pratensis* from the same egg mass, showing the size variance among siblings that is caused by differential consumption of ECY. The smaller juvenile crawled out of the egg mass after metamorphosing, whereas its larger sibling remained in the egg mass feeding on ECY for several days post-metamorphosis.

Elysia papillosa

Development was lecithotrophic, with a flat ribbon of bright orange ECY deposited inside the egg mass on the surface pointing away from the substratum (Fig. 5D). Mean egg diameter in one clutch was 116.3 μm ± 0.9 SE (n = 15 ova). Two clutches had 65 and 25 eggs, respectively; embryos developed over 19–20 days into larvae with a mean shell size of 337.3 μm ± 1.6 SE, the largest in this study (Table 2). When disturbed, larvae released white mucous strands from pedal glands, a possible defensive reaction.

No larvae underwent intracapsular metamorphosis. However, larvae held in FSW began to metamorphose spontaneously after 4 days (Fig. 2C); after a week, over 75% of larvae had metamorphosed in the absence of any inductive substratum, and none had died. Juveniles fed immediately on *Halimeda opuntia*, the adult host alga.

Elysia crispata

No ECY is produced by *E. crispata*. In the field, egg masses were frequently found on flat, upright algae such as *Udotea*, and slugs in aquaria preferentially oviposited on upright algae or structural mimics (plastic aquarium plants) instead of the glass. Mean egg diameter was 106.1 μm ± 0.3 SE for one clutch from Curaçao, and a significantly greater 113.8 μm ± 1.5 SE for one clutch from the Bahamas (unpaired two-tailed t test: df = 72, t = 8.25, $P <$ 0.0001).

Embryos developed over about 15 days into larvae with a mean shell size of 279.9 μm (±13.9 SE; n = 4 clutches) (Table 2). There was significant variation in larval size among four clutches (Fig. 4D, and results of a one-way ANOVA: $F_{3,167}$ = 282.15, $P <$ 0.00001). Mean larval size from Curaçao (238.7 μm ± 0.9 SE) was smaller than the larval size of all three Bahamanian clutches, which ranged from 287.7 μm to 299.2 μm (*post hoc* Scheffé test, $P <$ 0.0001); one Bahamanian clutch had a significantly smaller mean larval size than the other two clutches, which did not differ (*post hoc* Scheffé test, $P <$ 0.0001).

In nine egg masses laid by Bahamas slugs, 100% of larvae metamorphosed prior to hatching and emerged as crawl-away juveniles. Two egg masses were collected from the field in Sweetings Cay, Bahamas, in 2007, from which hatched free-swimming veligers that settled after one day and had metamorphosed by the second day post-hatching. Newly metamorphosed juveniles were about a half-millimeter in size (Table 2).

Elysia cornigera

Egg masses contain a thin ribbon of partially clear, pale yellow ECY. Mean development time was 16.7 days ± 1.2 SE. Embryos developed into veligers capable of swimming if artificially freed from their egg capsules, but 95.8% (±4.2% SE; n = 3) of larvae underwent intracapsular metamorphosis and emerged as crawl-away juveniles when egg masses were undisturbed. The few veligers that did hatch underwent spontaneous metamorphosis within 1–2 days. Mean larval size differed significantly between two clutches (Fig. 4E, and results of an unpaired two-tailed t test: df = 39, t = 3.60, $P <$ 0.001).

Elysia pratensis and *Elysia subornata*

Development in *E. subornata* was described in detail by Clark *et al*. (1979) under the synonym *E. cause*. Mean larval shell size differed among two clutches of *E. subornata* (Fig. 4F, and results of an unpaired two-tailed t test: df = 53, t = 2.97, $P <$ 0.005).

Clutches from *E. pratensis* developed similarly to those of *E. subornata*, its sister species. A wide, flat ribbon of orange ECY weaves around each individual capsule in the egg mass (Fig. 5E). Egg size was comparable for *E. pratensis* and *E. subornata* (Table 2). For *E. pratensis*, mean egg number per clutch was 146.6 (±106.4 SE; n = 11; range = 13–1209); when the largest clutch was excluded, mean egg number per clutch was 40.4 ± 6.2 SE.

Encapsulated larvae of *E. pratensis* completed metamorphosis after 18.4 days (±0.7 SE; n = 13 clutches), at which point mean larval shell size was 321.2 μm (±2.9 SE; n = 12). However, it took another 4.8 days (±0.7 SE; n = 6) for juveniles to begin emerging from the egg mass, at which point hatching continued for about another 5 days. There was significant among-clutch variation in larval shell size for *E. pratensis* (Fig. 4G, and results of a one-way ANOVA: $F_{11,329}$ = 7.77, $P <$ 0.0001). There was no geographical trend in larval size when comparing parents from Florida and two Bahamas sites.

After metamorphosis, some juveniles of *E. pratensis* and *E. subornata* stayed inside the egg mass and consumed ECY. In *E. pratensis*, varying degrees of juvenile feeding on ECY led to marked size variation among siblings from one clutch (Fig. 5F), which had a CV of 23.4% for juvenile size compared to a mean within-clutch CV 13.3% ± 1.2% SE for four other clutches.

Among-species comparisons of egg and offspring size

Mean lecithotrophic egg size varied relatively little among surveyed species, ranging from 103 to 119 μm (Table 2). Within-clutch coefficients of variation for egg size were similar for the five species for which data were available (Fig. 6A).

Larval size varied more than egg size across species; the largest larvae (*E. papillosa*) were 77% larger than the smallest lecithotrophic larvae (*"B." marcusi*) (Table 2). Larval size was also more variable than egg size within and among clutches, as indicated by coefficients of variation and ANOVA results for all species. *"Boselia" marcusi* had little

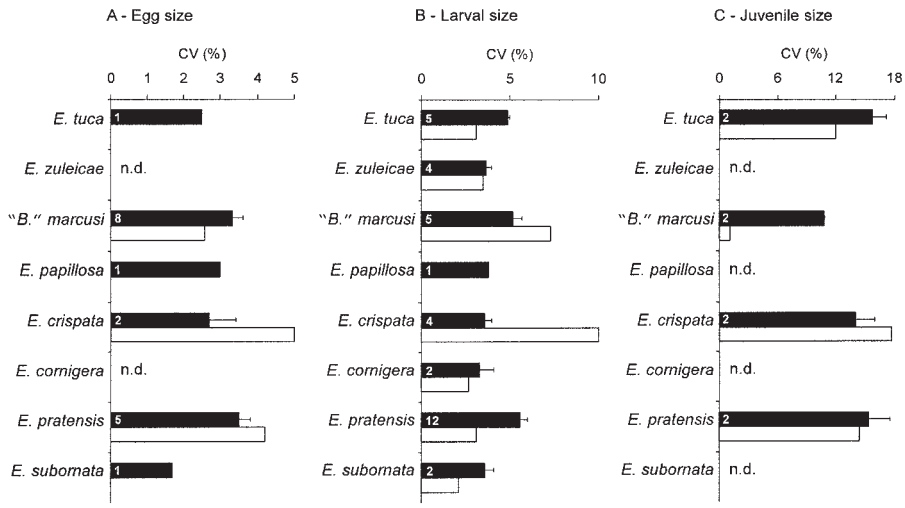

Figure 6. Variation in offspring characteristics within and among clutches for eight *Elysia* spp. Data are coefficients of variation (CV) expressed as percentages for (A) egg size, (B) larval size, or (C) juvenile size. The within-clutch coefficient of variation (solid bar) was calculated for each clutch. If data were available for multiple clutches, the mean within-clutch CV was then determined and plotted plus one standard error. White bars are among-clutch CVs calculated from standard deviations about the mean size of eggs, larvae, or juveniles when data were available for multiple clutches. The number of clutches used in calculations is indicated on the solid bar for each species. n.d. = no data available.

among-clutch variation in egg size but the second highest among-clutch CV for larval size, and the second highest mean within-clutch CV for larval size (Fig. 6A, B). *Elysia crispata* had the highest CV for larval size among clutches (10%) due to the small size of larvae from Curaçao, but a mean within-clutch CV for larval size comparable to that of the other species (Fig. 6B). The among-clutch CV for larval size was low in *E. pratensis*, but the mean within-clutch CV for larval size (5.6% ± 0.4% SE) was the highest out of the eight species studied.

Juvenile size varied 2-fold among four species for which data were obtained. Mean juvenile size varied significantly among *E. pratensis*, *E. subornata*, *E. crispata*, and *"B." marcusi* (Table 2, and results of a one-way ANOVA: $F_{3,7} = 11.35$, $P < 0.005$). Juvenile *E. pratensis* were larger than juveniles of *E. tuca* and "*B.*" *marcusi* (*post hoc* Scheffé test, $P < 0.05$); no other pairwise comparisons were significant. Mean within-clutch CV for juvenile size ranged from 10.8% (±0.5% SE) for *"B." marcusi* to 15.7% (±1.4% SE) for *E. tuca*, but did not vary significantly among species ($F_{3,7} = 0.681$, $P = 0.59$) (Fig. 6C). The among-clutch CV for mean juvenile size was far lower for *"B." marcusi* (1.1%) than for the other three species, which ranged from 12.0% (*E. tuca*) to 17.7% (*E. crispata*).

Discussion

Bet-hedging in opisthobranch life histories

Traits that vary larval planktonic period or offspring size warrant attention as potential targets of selection, especially when mothers cannot predict their offspring's environment (Marshall *et al*., 2008). Selection can increase trait variance at the individual level (within a genotype) if fitness is maximized by diversified bet-hedging strategies, which trade off reduced fitness under predictable conditions to avoid reproductive failure when the environment fluctuates (Meyers and Bull, 2002; Simons and Johnston, 2006; Crean and Marshall, 2009). Sacoglossan opisthobranchs inhabit the intertidal zone or shallow waters where conditions fluctuate on time scales ranging from daily tidal cycles to seasonal rainfall patterns. Further, as specialist consumers, they are ecologically tied to host algae that are often a patchy and unpredictable resource (Clark, 1975, 1994; Clark and DeFreese, 1987; Trowbridge, 1992, 1993, 2002). Variation in clutches may thus reflect selection for risk-spreading that allows mothers to modulate offspring traits and hedge against uncertain local conditions.

Hopper *et al*. (2003) distinguished two forms of bet-hedging that differ in their dependence on population size. Between-generation bet-hedging occurs when different phenotypic variants are produced, only some of which will survive the conditions in a particular season. In contrast, within-generation bet-hedging operates when mothers scatter a single offspring phenotype to escape localized disasters that could otherwise wipe out a whole brood—for instance, spreading offspring among multiple resource patches. In such cases, there is heterogeneity in selection acting on a single phenotype (Hopper *et al*., 2003). The fitness advantage of within-generation bet-hedging decreases as population size increases, making it unlikely to evolve unless

Table 3

*Timing and induction of metamorphosis in some sacoglossans (*Elysia *spp. and* Alderia willowi*) and the cephalaspidean* Haminoea japonica

Species	Intracapsular	|← Early spontaneous	Post-hatching delayed spontaneous	→| Substrate-induced
E. pratensis	√			
E. subornata	√			
E. crispata	√	√		
E. cornigera	√	√		
E. papillosa			√	?
"*B.*" *marcusi*	√		√	?
A. willowi[a]	√	√		√
H. japonica[b]	√		√	√
E. zuleicae				√
E. tuca				√

Check denotes the presence of the indicated category of metamorphosis in lecithotrophic larvae of a particular species. Question mark indicates taxa for which there were insufficient larvae to test for substrate-induced metamorphosis.

[a]Krug, 2001.

[b]Gibson, 1995, as the junior synonym "*Haminoea callidegenita*."

populations are very small or selection is severe (Gillespie, 1974). The dispersal strategies discussed in the present study represent between-generation bet-hedging, as larvae express different phenotypes (for example, pre- *versus* post-hatching metamorphosis) that will vary in fitness depending on whether selection favors local retention or dispersal away from the natal habitat. Within-generation bet-hedging could potentially occur in sacoglossans with intracapsular metamorphosis if slugs oviposit several small clutches onto different algal patches rather than laying one large egg mass, but this has not yet been investigated.

The sacoglossans studied here expressed a variety of mechanisms that can vary the dispersal potential or size of their offspring, including a new case of poecilogony (Table 3). Outside of polychaetes, confirmed cases of poecilogony are restricted to opisthobranchs and may be limited to the Sacoglossa. Morphologically identical, co-occurring specimens of *Elysia zuleicae* produced either planktotrophic or lecithotrophic larvae, making *E. zuleicae* the fourth case of poecilogony in the Sacoglossa (Table 4). Confirmed examples include *E. chlorotica* (West *et al*., 1984), *Alderia willowi* (Krug *et al*., 2007), and *Costasiella ocellifera* (Ellingson, 2006; Ellingson and Krug, unpubl. data); claims of

Table 4

Poecilogony versus *dispersal polymorphisms in opisthobranchs*

Species	Poecilogony	Dispersal dimorphism	Cryptic species	Mechanism varying planktonic period	Reference
Sacoglossa					
Alderia willowi	√	√		variable settlement requirements (among lecithotrophic larvae)	Krug, 1998, 2001; Krug *et al.,* 2007
Costasiella ocellifera	√				Ellingson, 2006
Elysia chlorotica	√				West *et al.,* 1984
E. zuleicae	√				present study
E. tuca	—	√		variable hatching time	present study
E. crispata	X	√		pre- *vs.* post-hatching metamorphosis	Clark and Jensen, 1981; Clark, 1994
E. cornigera	—	√		″	present study
E. timida	X	√		″	Marin and Ros, 1993
E. evelinae	X	√		″	Clark and Jensen, 1981
"*B.*" *marcusi*	—	√		″	present study
E. subornata, as *E. cauze*	X		√		Clark *et al.,* 1979; Clark, 1994
Cephalaspidea					
Haminoea japonica	X	√		variable attainment of competence	Gibson and Chia, 1989b; Gibson, 1995
Nudibranchia					
Tenellia adspersa	—	√		pre- *vs.* post-hatching metamophosis	Chester, 1996
T. pallida	?	√		″	Eyster, 1979
Dendronotus frondosus	X		√		Sisson, 2002

Confirmed cases of poecilogony have a checkmark in the 2nd column. Claims that do not meet the definition of poecilogony are indicated by an X; a horizontal strike indicates no prior claim of poecilogony. Cases of dispersal dimorphism within or among lecithotrophic clutches are indicated with a checkmark in the 3rd column, along with how variation in the larval planktonic period is achieved. Claims of poecilogony that turned out to be cryptic species have a checkmark in the 4th column.

poecilogony in *E. subornata* resulted from taxonomic confusion surrounding three distinct species (Clark, 1984, 1994).

Changes in development occur seasonally in *Alderia willowi*, and within the lifetime of individual slugs. Slugs produce lecithotrophic larvae in the summer but most switch to planktotrophic eggs in winter, and some produce mixed clutches containing both larval types when transitioning between development modes (Krug, 1998; Ellingson and Krug, 2006; Smolensky *et al*., 2009). Individual slugs can produce planktotrophic larvae with a pelagic period exceeding one month, lecithotrophic larvae that spend hours to days in the water column, and crawl-away juveniles—in some cases, all from the same egg mass (Table 4; Krug, 1998, 2001). Poecilogony thus confers an exceptional degree of life-history flexibility and could represent a bet-hedging mechanism to cope with the unstable conditions on the estuarine mudflats where *A. willowi* occurs (Chia *et al*., 1996; Krug, 2007). It is unknown whether specimens of other poecilogonous sacoglossans such as *Elysia zuleicae* can similarly vary the development of their offspring, or if larval type is fixed within individuals as in *Streblospio benedicti* (Levin and Creed, 1986; Levin and Bridges, 1994).

In both *Alderia willowi* and *Streblospio benedicti*, the larger larval morph is facultatively planktotrophic (Botello and Krug, 2006; Pernet and MacArthur, 2006). Opisthobranch researchers have long followed Thompson (1959, 1967) in defining lecithotrophy as the production of larvae that do not *need* to feed prior to metamorphosis, regardless of whether facultative planktotrophy is possible (Hadfield and Miller, 1987). Some gastropod and polychaete larvae use the same ciliary bands for particle capture and swimming, which may favor the retention of feeding ability in larger larvae with limited dispersal potential (Thompson, 1959; Kempf and Todd, 1989; Miller, 1993; Allen and Pernet, 2007; Collin *et al*., 2007). Retaining the term lecithotrophic emphasizes the ecological difference among larval morphs that vary dramatically in their minimum planktonic lifespan and hence dispersal potential, by distinguishing larger larvae that can settle before or immediately after hatching from those that drift for weeks while feeding in the plankton.

Outside of the Sacoglossa, a few nudibranchs were proposed to exhibit poecilogony but the data are equivocal (Table 4). Clark and Goetzfried (1978) reported that fed specimens of *Spurilla neapolitana* produced 90-μm eggs that developed into lecithotrophic larvae, but after 5 days of starvation, slugs laid 82-μm eggs that hatched as planktotrophic larvae. No data were provided, however, and it is unresolved whether the small larvae could attain competence; further study is needed before this can be accepted as a case of poecilogony. The nudibranch *Tenellia pallida* produced 72-μm eggs developing into hatching veligers, and 103-μm eggs developing into larvae that underwent intracapsular metamorphosis (Eyster, 1979). Hatching larvae were assumed to be planktotrophic because they lacked eyespots, but larvae of both types measured 195 μm and two "planktotrophic" veligers metamorphosed spontaneously. Embryos developing from smaller eggs may have been supplemented with extra albumen (nutritive material in capsular fluid), allowing them to reach the same size as embryos from larger eggs; it is possible that all larvae were lecithotrophic but at different stages of development, or with alternative settlement requirements that inhibited some from settling in the absence of their host. Variation among clutches may thus represent a hatching dimorphism like that expressed by the congener *T. adspersa* (Chester, 1996), without constituting a case of poecilogony.

Bet-hedging dispersal strategies in lecithotrophic opisthobranchs

Only free-swimming larvae were produced by *E. tuca*, *E. papillosa,* and *E. zuleicae*, while egg masses of *E. subornata* and *E. pratensis* had 100% intracapsular metamorphosis. In contrast, there was variation in dispersal potential among offspring within or among clutches of *E. crispata*, *E. cornigera*, and "*Boselia*" *marcusi*, because some larvae metamorphosed prior to hatching while the others had a brief swimming phase. Some intracapsular metamorphosis occurred in half the clutches of "*B.*" *marcusi* from Jamaica, but not in clutches from Floridian slugs. In *E. cornigera*, one clutch produced a few swimming larvae, but most veligers metamorphosed prior to hatching. Most clutches of *E. crispata* had 100% intracapsular metamorphosis under laboratory conditions, but two released all swimming larvae that settled after a day. Each species produced only one type of embryo, so none are examples of poecilogony. However, a variable proportion of intracapsular metamorphosis within clutches may spread risk by ensuring that some offspring disperse while others are retained in the natal habitat.

The occurrence of both pre- and post-hatching metamorphosis is a common dispersal dimorphism among opisthobranchs, especially when larvae do not require a specific substrate to induce settlement (Tables 3, 4). In addition to the above examples, *Elysia evelinae* (Clark and Jensen, 1981), *E. timida* (Marin and Ros, 1993), and the nudibranch *Tenellia adspersa* (Chester, 1996) exhibit a similar strategy. Some reports claim these species are poecilogonous because they make two "types" of larvae, but in fact only one type of embryo is produced in each case (Clark *et al*., 1979; Clark and Jensen, 1981; Bouchet, 1989; Marin and Ros, 1993; Clark, 1994; Jensen, 2001). However, they do represent dispersal dimorphisms that retain a swimming phase in the life cycle, providing opportunities for gene flow and colonization of new habitat patches. Larvae entrained in a fast-moving current could travel a substantial distance and

encounter a range of potential juvenile habitats even in the course of one day, so these dimorphisms may be ecologically and evolutionarily significant.

In some lecithotrophic clutches of *Alderia willowi*, a few larvae metamorphose before hatching, but about a third metamorphose 1–2 days after hatching in the absence of any inductive cues; the remainder delay settlement until they encounter the adult host alga *Vaucheria* or exhaust their energy reserves and die (Krug, 2001). The proportion of larvae that undergo spontaneous metamorphosis after hatching is highly variable among clutches. This strategy ensures that some offspring do not disperse (intracapsular metamorphosis), others travel only a limited distance (metamorphosis after 1–2 days with no cue requirement), and still others disperse until locating a suitable juvenile habitat (*Vaucheria*-dependent metamorphosis). Such bet-hedging strategies likely reduce variance in breeding success across generations by ensuring a mixture of local recruitment and migration to new habitat patches from each batch of offspring. Patches of *Vaucheria* disappear on time scales well within the lifespan of individual slugs (P. Krug, unpubl. data), which may select in favor of such risk-spreading strategies.

A different mechanism to vary offspring dispersal is employed by the cephalaspidean *Haminoea japonica*, an invasive population of which was described as *H. callidegenita* in Washington, USA. (Gibson and Chia, 1989a; Gosliner and Behrens, 2006). This species is strictly lecithotrophic, but sibling larvae vary widely in their rate of attaining competence. About half the larvae in a clutch reach competence prior to hatching and metamorphose in response to the egg mass jelly (Gibson and Chia, 1989b, 1995). Their siblings hatch and take up to 16 days to attain competence, and can delay metamorphosis a further 4 days in the absence of settlement cues (Gibson, 1995). Two elements vary dispersal in this species: (1) rate of attainment of competence, and (2) response to cues in egg jelly *versus* in the juvenile environment. As a result, most egg masses release crawl-away juveniles as well as planktonic larvae with considerable dispersal potential. This versatile colonization strategy may contribute to invasion success in *H. japonica*, which has become established in Puget Sound, northern California, Italy, and Spain (Gosliner and Behrens, 2006).

Variation in the proportion of offspring that undergo intracapsular metamorphosis may be an anticipatory maternal effect, allowing a mother to adaptively adjust the dispersal potential of her offspring after assessing local conditions (Marshall and Uller, 2007). Starved slugs produce fewer crawl-away juveniles in *Tenellia adspersa* (Chester, 1996) and *Haminoea japonica* (Gibson and Chia, 1995). Maternal starvation also reduces spontaneous metamorphosis in lecithotrophic clutches of *Alderia willowi*, increasing the proportion of larvae that disperse until locating a new food patch (Krug, 2001). The proportion of intracapsular metamorphosis varies seasonally in *Elysia timida*, which may reflect changes in the availability of host algae (Marin and Ros, 1993) or maternal condition. Mothers could potentially achieve such variance within and among broods by manipulating the material properties of the egg mass itself or by changing the energy content of eggs to delay hatching or attainment of competence.

Time to hatching may also vary the dispersal potential of siblings in species that do not exhibit intracapsular metamorphosis. In *E. tuca*, most egg masses released larvae for over a week, and in one case for 16 days. Staggered hatching from benthic egg masses may be analogous to asynchronous hatching in birds, which alters the resources available to siblings and increases within-clutch variation (Laaksonen, 2004). Larvae that spend more time in the egg mass may have greater access to extra-capsular yolk (ECY), potentially affecting growth and energy reserves. Alternatively, staggered hatching may expose sibling larvae to different flow regimes and thus increase variance in the direction and magnitude of larval transport. Notably, *Elysia tuca* frequently oviposits on blades of sea grass, which are easily uprooted and buoyant (P. Krug, pers. obs.). An egg mass on floating sea grass that gradually released larvae for 2 weeks could potentially increase the dispersal potential of veligers substantially beyond what could be achieved during their larval lifespan alone. The greater aeration and microbial degradation an egg mass experiences in the field may produce more uniform hatching than occurs when egg masses are held under static laboratory conditions. However, the substantial variation in hatching time within most clutches suggests this may be a potentially adaptive mechanism to vary the distribution of offspring in space and time.

Larval selectivity and habitat choice

Some species in this study produced larvae that metamorphosed less selectively over time as their energy reserves were depleted, while larvae of other species remained largely dependent on induction by host-associated cues over time. In *E. tuca*, mortality rose dramatically over time, but almost no larvae metamorphosed without exposure to the adult host alga *Halimeda*. In contrast, larvae of *E. papillosa* did not metamorphose for 3 days after hatching in FSW, but over 75% metamorphosed over the next 4 days, a classic "desperate larva" response (Toonen and Pawlik, 2001b; Marshall and Keough, 2003). During the initial planktonic period, larvae presumably delayed settlement in the absence of habitat cues, but eventually metamorphosed when energy levels dropped below a threshold. A different strategy was expressed by "*B.*" *marcusi*: some larvae metamorphosed prior to hatching, then there was little spontaneous metamorphosis for 3 days after hatching, and finally some "desperate" larvae metamorphosed at the end of the week in the absence of substrate cues. However, most larvae died with-

out metamorphosing. A similar pattern occurs in lecithotrophic clutches of *Alderia willowi*: larvae that do not metamorphose just after hatching usually die after a week unless triggered to settle by the host alga (Krug, 2001). Older larvae of *A. willowi* will accept weaker cues of habitat suitability, however, if unable to supplement their energy levels with planktonic food (Botello and Krug, 2006). Thus, in addition to flexibility in time to hatching and metamorphosis, sacoglossans exhibit remarkable variation in larval traits affecting planktonic period and habitat choice behavior, both within and among clutches. Further, even related and ecologically similar species differ in their host-colonization strategies, evidenced by the variation in settlement requirements of lecithotrophic larvae among *Elysia* spp.

Offspring size and extra-capsular yolk

Maternal control over variance in egg size and offspring size at independence may allow bet-hedging when offspring size-fitness relationships are unpredictable (Marshall *et al*., 2008; Crean and Marshall, 2009). In the present study, coefficients of variation for egg size were relatively low and constant across five species with lecithotrophic development. Mean egg sizes for two clutches of *E. crispata* were much smaller than published values of 205 and 209 μm (Clark and Jensen, 1981; Defreese and Clark, 1983). The two clutches of *E. crispata* used here for egg measurements were collected 5 years apart at different sites, yet they yielded similar egg sizes. Clark and co-workers published means with no variances, so it is unclear how much egg size varied among clutches. One possibility is that *E. crispata* from Florida lay bigger eggs due to local adaptation, as there is little gene flow among most populations of *E. crispata* (Hidalgo, 2007; E. Hidalgo and P. Krug, unpubl. data).

Despite the small size range of lecithotrophic eggs produced by these eight study species, mean larval and juvenile sizes varied considerably among species. Offspring size at independence is thus functionally decoupled from egg size, likely due to maternal provisioning of the benthic egg mass with extra-embryonic nutritional reserves that augment energy invested in the eggs themselves. Additionally, there was significant among-clutch variation in larval size in all seven species for which data were available. By varying offspring size within or among clutches, mothers may spread risk when faced with fluctuating environments that prevent them from accurately predicting the optimal offspring size (Crean and Marshall, 2009). Experimental manipulation of maternal conditions are needed to test this hypothesis for sacoglossans.

Many elysiids and some nudibranchs deposit ECY within the egg mass but outside the egg capsules (Clark and Jensen, 1981; Boucher, 1983). Both planktotrophic and lecithotrophic species produce ECY, presenting a conundrum: Why invest energy in ECY instead of producing more eggs? It is particularly hard to reconcile allocating resources to ECY in species that produce planktotrophic larvae with an extended feeding period and high planktonic mortality. Clark and Jensen (1981) hypothesized that ECY was an adaptation to accelerate cleavage by reducing egg size, allowing embryos to grow faster by shifting yolk outside of the ovum. Strathmann *et al*. (2002) found no correlation between egg size and early cleavage rate in gastropods; however, Spight (1975, 1976) reported a correlation between egg size and overall development time among gastropod species, and Marshall and Bolton (2007) found a strong effect of egg size on development time within lecithotrophic broods of three broadcast-spawning taxa. There was no apparent relationship between egg size and development time among taxa studied here, and it remains unclear whether ECY is a mechanism for accelerating the rate of development to a given larval size.

Ribbons or globules of ECY gradually diminish during embryonic development, suggesting that yolk is absorbed by larvae. I also observed larvae of several species ingesting granules of ECY, and the larval gut of species with orange ECY takes on an orange color as veligers mature. These observations suggest ECY provides supplemental larval nutrition. One hypothesis is that ECY may increase larval size relative to egg size. The ratio of larval shell to egg size ranges from 1.83 ("*B*." *marcusi*) to 2.91 (*E. papillosa*) among species in this study (mean = 2.45). The shell:egg ratio of *E. crispata* (no ECY) was only 2.25 for one clutch from Curaçao, the second-lowest ratio in this study; for lecithotrophic *A. willowi* (which also lack ECY) the ratio is 1.77 (Krug, 1998). Although the ratio for "*B*." *marcusi* larvae is also low, the overall trend supports the hypothesis that investment in ECY allows mothers to increase larval size without increasing egg size, and possibly without increasing benthic development time.

In addition to a possible role in larval nutrition, ECY was consumed by juvenile *E. pratensis* and *E. subornata* inside the egg mass, which has not been previously reported for an opisthobranch. Thus, ECY may be more akin to nurse eggs of caenogastropods than previously thought. In *E. pratensis*, juvenile consumption of ECY led to high variance in size at hatching in one clutch, and likely contributed to the production of very large juveniles compared to other *Elysia* spp. Thus, in species with intracapsular metamorphosis, ECY may influence offspring size both before and after metamorphosis. Control over allocation of ECY could allow mothers to vary larval and juvenile sizes among clutches while holding egg size constant; however, among-clutch CVs were higher for *E. crispata* than for any species with ECY, indicating that other mechanisms can also vary offspring characteristics among clutches.

Although preliminary, these data suggest that species with ECY bolster the size of offspring at independence.

Most species with ECY are tropical; extra energy reserves may buffer planktotrophic larvae against the oligotrophic conditions of tropical waters. In lecithotrophic species, ECY may be a response to selection for post-settlement fitness benefits of larger offspring (Marshall *et al*., 2003, 2006). Due to the prevalence of intracapsular metamorphosis among lecithotrophic sacoglossans, ECY may both increase larval size pre-hatching and also provide nutrition to post-metamorphic juveniles, before they begin feeding on their calcified host algae. Future studies will test this proposed link between ECY and offspring size; data for more species are needed, together with a robust phylogeny allowing the use of comparative methods to correct for phylogenetic effects and test for correlated trait evolution.

Acknowledgments

This study was supported by awards to PJK from the U.S. National Science Foundation programs in Biological Oceanography (OCE 02-42272 and OCE 06-48606), Systematics and Biodiversity Inventories (DEB 08-17084), and the Human Resources Division (HRD 03-17772). I thank J. Pawlik for the opportunity to participate in research cruises (funded by NSF awards OCE 0095724 and PEHS 0550468), and the governments of the Bahamas, Bermuda, Curaçao, and Jamaica for permission to collect in their territorial waters. I thank C. Blackburn, R. Collin, A. Debrot, R. Ellingson, K. Eve, T. Eve, M. Ilan, T. Justins, S. Pierce, M. Romero, Á. Valdes, and D. Willette for help with collection, logistics, or maintenance of animals.

Literature Cited

Allen, J. D., and B. Pernet. 2007. Intermediate modes of larval development: bridging the gap between planktotrophy and lecithotrophy. *Evol. Dev.* **9:** 643–653.

Bernardo, J. 1996a. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am. Zool.* **36:** 216–236.

Bernardo, J. 1996b. Maternal effects in animal ecology. *Am. Zool.* **36:** 83–105.

Bonar, D. B. 1978. Morphogenesis at metamorphosis in opisthobranch molluscs. Pp. 177–206 in *Settlement and Metamorphosis of Marine Invertebrate Larvae,* F.-S. Chia and M. E. Rice, eds. Elsevier, New York.

Botello, G., and P. J. Krug. 2006. Desperate larvae revisited: Age, energy and experience affect sensitivity to settlement cues in larvae of the gastropod *Alderia* sp. *Mar. Ecol. Prog. Ser.* **312:** 149–159.

Boucher, L. M. 1983. Extra-capsular yolk bodies in the egg masses of some tropical opisthobranchia. *J. Molluscan Stud.* **49:** 232–241.

Bouchet, P. 1989. A review of poecilogony in gastropods. *J. Molluscan Stud.* **55:** 67–78.

Chester, C. M. 1996. The effect of adult nutrition on the reproduction and development of the estuarine nudibranch, *Tenellia adspersa* (Nordmann, 1845). *J. Exp. Mar. Biol. Ecol.* **198:** 113–130.

Chia, F.-S., G. D. Gibson, and P.-Y. Qian. 1996. Poecilogony as a reproductive strategy of marine invertebrates. *Oceanol. Acta* **19:** 203–208.

Clark, K. B. 1975. Nudibranch life cycles in the Northwest Atlantic and their relationship to the ecology of fouling communities. *Helgol. Wiss. Meeresunters.* **27:** 28–69.

Clark, K. B. 1984. New records and synonymies of Bermuda opisthobranchs (Gastropoda). *Nautilus* **98:** 85–97.

Clark, K. B. 1994. Ascoglossan (=Sacoglossa) molluscs in the Florida Keys: rare marine invertebrates at special risk. *Bull. Mar. Sci.* **54:** 900–916.

Clark, K. B., and D. DeFreese. 1987. Population ecology of Caribbean Ascoglossa (Mollusca: Opisthobranchia): a study of specialized algal herbivores. *Am. Malacol. Bull.* **5:** 259–280.

Clark, K. B., and A. Goetzfried. 1978. Zoogeographic influences on development patterns of North Atlantic Ascoglossa and Nudibranchiata with a discussion of factors affecting egg size and number. *J. Molluscan Stud.* **44:** 283–294.

Clark, K. B., and K. R. Jensen. 1981. A comparison of egg size, capsule size, and development patterns in the order Ascoglossa (Sacoglossa) (Mollusca: Opisthobranchia). *Int. J. Invertebr. Reprod.* **3:** 57–64.

Clark, K. B., M. Busacca, and H. Stirts. 1979. Nutritional aspects of development of the sacoglossan, *Elysia cauze*. Pp. 11–24 in *Reproductive Ecology of Marine Invertebrates,* S. E. Stancyk, ed. University of South Carolina Press, Columbia.

Clauss, M. J., and D. L. Venable. 2000. Seed germination in desert annuals: an empirical test of adaptive bet hedging. *Am. Nat.* **155:** 168–186.

Collin, R., O. R. Chaparro, F. Winkler, and D. Veliz. 2007. Molecular phylogenetic and embryological evidence that feeding larvae have been reacquired in a marine gastropod. *Biol. Bull.* **212:** 83–92.

Cooper, W. S., and R. H. Kaplan. 1982. Adaptive "coin-flipping": a decision-theoretic examination of natural selection for random individual variation. *J. Theor. Biol.* **94:** 135–351.

Crean, A. J., and D. J. Marshall. 2009. Coping with environmental uncertainty: dynamic bet hedging as a maternal effect. *Philos. Trans. R. Soc. B* **364:** 1087–1096.

Crnokrak, P., and D. A. Roff. 1995. Fitness differences associated with calling behaviour in the two wing morphs of male sand crickets, *Gryllus firmus*. *Anim. Behav.* **50:** 1475–1481.

Crnokrak, P., and D. A. Roff. 1998. The genetic basis of the trade-off between calling and wing morph in males of the cricket *Gryllus firmus*. *Evolution* **52:** 1111–1118.

Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* **59:** 433–463.

DeFreese, D., and K. Clark. 1983. Analysis of reproductive energetics of Florida Opisthobranchia (Mollusca: Gastropoda). *Int. J. Invertebr. Reprod.* **6:** 1–10.

Denno, R. F., G. K. Roderick, M. A. Peterson, A. F. Huberty, G. D. Hartmut, M. D. Eubanks, J. E. Losey, and G. A. Langellotto. 1996. Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecol. Monogr.* **66:** 389–408.

Doyle, R. W. 1975. Settlement of planktonic larvae—theory of habitat selection in varying environments. *Am. Nat.* **109:** 113–126.

Doyle, R. W. 1976. Analysis of habitat loyalty and habitat preference in settlement behavior of planktonic marine larvae. *Am. Nat.* **110:** 719–730.

Einum, S., and I. A. Fleming. 2004. Environmental unpredictability and offspring size: conservative versus diversified bet-hedging. *Evol. Ecol. Res.* **6:** 443–455.

Ellingson, R. A. 2006. Variable development versus cryptic speciation: phylogeography and evolutionary history of the sea slugs *Alderia* and *Costasiella* (Opisthobranchia: Sacoglossa). M.S. thesis, California State University, Los Angeles.

Ellingson, R. A., and P. J. Krug. 2006. Evolution of poecilogony from planktotrophy: cryptic speciation, phylogeography and larval development in the gastropod genus *Alderia*. *Evolution* **60:** 2293–2310.

Eyster, L. S. 1979. Reproduction and developmental variability in the opisthobranch *Tenellia pallida*. *Mar. Biol.* **51:** 133–140.

Giard, A. 1905. La poecilogony. *Compte-Rendu des Séances du Sixième Congrès International de Zoologie Berne* 1904, 617–646.

Gibson, G. D. 1995. Why be choosy? Temporal changes in larval sensitivity to several naturally-occurring metamorphic inducers in the opisthobranch *Haminaea callidegenita. J. Exp. Mar. Biol. Ecol.* **194:** 9–24.

Gibson, G. D., and F.-S. Chia. 1989a. Description of a new species of *Haminoea*, *H. callidegenita* (Mollusca: Opisthobranchia), with a comparison with two other *Haminoea* species found in the northeast Pacific. *Can. J. Zool*. **67:** 914–922.

Gibson, G. D., and F.-S. Chia. 1989b. Developmental variability (pelagic and benthic) in *Haminaea callidegenita* (Opisthobranchia: Cephalaspidea) is influenced by egg mass jelly. *Biol. Bull.* **176:** 103–110.

Gibson, G. D., and F.-S. Chia. 1995. Developmental variability in the poecilogonous opisthobranch *Haminaea callidegenita*: life-history traits and effects of environmental parameters. *Mar. Ecol. Prog. Ser*. **121:** 139–155.

Gillespie, J. H. 1974. Natural selection for within-generation variance in offspring number. *Genetics* **76:** 601–606.

Gillespie, J. H. 1976. Natural selection for variances in offspring numbers: a new evolutionary principle. *Am. Nat.* **111:** 1010–1014.

Gosliner, T. M., and D. W. Behrens. 2006. Anatomy of an invasion: systematics and distribution of the introduced opisthobranch snail, *Haminoea japonica* Pilsbry, 1895 (Gastropoda: Opisthobranchia: Haminoeidae). *Proc. Calif. Acad. Sci*. **57:** 1003–1010.

Hadfield, M. G., and S. E. Miller. 1987. On developmental patterns of opisthobranchs. *Am. Malacol. Bull.* **5:** 197–214.

Hadfield, M. G., and M. F. Strathmann. 1996. Variability, flexibility and plasticity in life histories of marine invertebrates. *Oceanol. Acta* **19:** 323–334.

Hedgecock, D., J. Lin, S. DeCola, C. D. Haudenschild, E. Meyer, D. T. Manahan, and B. Bowen. 2007. Transcriptomic analysis of growth heterosis in larval Pacific oysters (*Crassostrea gigas*). *Proc. Natl. Acad. Sci. USA* **104:** 2312–2318.

Hidalgo, E. 2007. Caribbean phylogeography: population structure in sea slugs with dispersing and non-dispersing larvae. M.S. thesis, California State University, Los Angeles.

Hoagland, K. E., and R. Robertson. 1988. An assessment of poecilogony in marine invertebrates: phenomenon or fantasy? *Biol. Bull*. **174:** 109–125.

Hopper, K. R., J. A. Rosenheim, T. Prout, and S. J. Oppenheim. 2003. Within-generation bet-hedging: a seductive explanation? *Oikos* **101:** 219–222.

Imbert, E. 1999. The effects of achene dimorphism on the dispersal in time and space in *Crepis sancta* (Asteraceae). *Can. J. Bot*. **77:** 508–513.

Jensen, K. R. 1997. Evolution of the Sacoglossa (Mollusca, Opisthobranchia) and the ecological associations with the food plants. *Evol. Ecol.* **11:** 301–335.

Jensen, K. R. 2001. Review of reproduction in the Sacoglossa (Mollusca, Opisthobranchia). *Boll. Malacol.* **37:** 81–98.

Kaplan, R. H., and P. C. Phillips. 2006. Ecological and developmental context of natural selection: maternal effects and thermally induced plasticity in the frog *Bombina orientalis*. *Evolution* **60:** 142–156.

Kempf, S. C., and C. D. Todd. 1989. Feeding potential in the lecithotrophic larvae of *Adalaria proxima* and *Tritonia hombergi*: an evolutionary perspective. *J. Mar. Biol. Assoc. UK* **69:** 659–682.

Krug, P. J. 1998. Poecilogony in an estuarine opisthobranch: planktotrophy, lecithotrophy, and mixed clutches in a population of the ascoglossan *Alderia modesta. Mar. Biol*. **132:** 483–494.

Krug, P. J. 2001. Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Alderia modesta*. *Mar. Ecol. Prog. Ser*. **213:** 177–192.

Krug, P. J. 2007. Poecilogony and larval ecology in the gastropod genus *Alderia*. *Am. Malacol. Bull.* **23:** 99–111.

Krug, P. J., and R. K. Zimmer. 2000. Developmental dimorphism and expression of chemosensory-mediated behavior: habitat selection by a specialist marine herbivore. *J. Exp. Biol*. **203:** 1741–1754.

Krug, P. J., and R. K. Zimmer. 2004. Developmental dimorphism: consequences for larval behavior and dispersal potential in a marine gastropod. *Biol. Bull.* **207:** 233–246.

Krug, P. J., R. A. Ellingson, R. A. Burton, and Á. Valdés. 2007. A new poecilogonous species of sea slug (Opisthobranchia: Sacoglossa) from California: comparison with the planktotrophic congener *Alderia modesta* (Lovén, 1844). *J. Molluscan Stud.* **73:** 29–38.

Laaksonen, T. 2004. Hatching asynchrony as a bet-hedging strategy—an offspring diversity hypothesis. *Oikos* **104:** 616–620.

Langellotto, G. A., and R. F. Denno. 2001. Benefits of dispersal in patchy environments: mate location by males of a wing-dimorphic insect. *Ecology* **82:** 1870–1878.

Levin, L. A. 1984. Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of North America. *Biol. Bull*. **166:** 494–508.

Levin, L. A., and T. S. Bridges. 1994. Control and consequences of alternative developmental modes in a poecilogonous polychaete. *Am. Zool.* **34:** 323–332.

Levin, L. A., and T. S. Bridges. 1995. Pattern and diversity in reproduction and development. Pp. 1–48 *in Ecology of Marine Invertebrate Larvae,* L. McEdward, ed. CRC Press, Boca Raton, FL.

Levin, L. A., and E. Creed. 1986. Effect of temperature and food availability on reproductive responses of *Streblospio benedicti* (Polychaeta: Spionidae) with planktotrophic or lecithotrophic development. *Mar. Biol.* **92:** 103–113.

Levin, L. A., and D. V. Huggett. 1990. Implications of alternative developmental reproductive modes for seasonality and demography in an estuarine polychaete. *Ecology* **71:** 2191–2208.

Levin, L. A., J. Zhu, and E. Creed. 1991. The genetic basis of life-history characters in a polychaete exhibiting planktotrophy and lecithotrophy. *Evolution* **45:** 380–397.

Marcus, E., and E. Marcus. 1967. Tropical American opisthobranchs. *Stud. Trop. Oceanogr.* **6:** 1–256.

Marin, A., and J. Ros. 1993. Ultrastructural and ecological aspects of the development of chloroplast retention in the sacoglossan gastropod *Elysia timida*. *J. Molluscan Stud.* **59:** 95–104.

Marshall, D. J., and T. F. Bolton. 2007. Effects of egg size on the development time of non-feeding larvae. *Biol. Bull.* **212:** 6–11.

Marshall, D. J., and M. J. Keough. 2003. Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. *Mar. Ecol. Prog. Ser.* **255:** 145–153.

Marshall, D. J., and M. J. Keough. 2008. The evolutionary ecology of offspring size in marine invertebrates. *Adv. Mar. Biol.* **53:** 1–60.

Marshall, D. J., and T. Uller. 2007. When is a maternal effect adaptive? *Oikos* **116:** 1957–1963.

Marshall, D. J., T. F. Bolton, and M. J. Keough. 2003. Offspring size affects the post-metamorphic performance of a colonial marine invertebrate. *Ecology* **84:** 3131–3137.

Marshall, D. J., C. N. Cook, and R. B. Emlet. 2006. Offspring size effects mediate competitive interactions in a colonial marine invertebrate. *Ecology* **87:** 214–225.

Marshall, D. J., R. Bonduriansky, and L. F. Bussière. 2008. Offspring size variation within broods as a bet-hedging strategy in unpredictable environments. *Ecology* **89:** 2506–2517.

Mathias, A., E. Kisdi, and I. Olivieri. 2001. Divergent evolution of dispersal in a heterogenous landscape. *Evolution* **55:** 246–259.

Menu, F., J.-P. Roebuck, and M. Viala. 2000. Bet-hedging diapause strategies in stochastic environments. *Am. Nat*. **155:** 724–734.

Meyers, L. A., and J. J. Bull. 2002. Fighting change with change: adaptive variation in an uncertain world. *Trends Ecol. Evol.* **17:** 551–557.

Miles, C., and K. B. Clark. 2002. Comparison of biochemical composition and developmental mode in two populations of *Costasiella* [Opisthobranchia: Ascoglossa (= Sacoglossa)]. *J. Molluscan Stud.* **68:** 101–109.

Miller, S. E. 1993. Larval period and its influence on post-larval life history: comparison of lecithotrophy and facultative planktotrophy in the aeolid nudibranch *Phestilla sibogae*. *Mar. Biol.* **117:** 635–645.

Mole, S., and A. J. Zera. 1993. Differential allocation of resources underlies the dispersal-reproduction trade-off in the wing dimorphic cricket, *Gryllus rubens*. *Oecologia* **93:** 121–127.

Moore, M., and D. T. Manahan. 2007. Variation among females in egg lipid content and developmental success of echinoderms from McMurdo Sound, Antarctica. *Polar Biol.* **30:** 1245–1252.

Morse, D. H., and J. Schmitt. 1985. Diaspora size, shape, and fall behaviour in wind-dispersed plant species. *Oecologia* **67:** 372–379.

Nuttall, T. R. 1989. A new *Elysia* (Opisthobranchia: Ascoglossa) from the Florida Keys. *Veliger* **32:** 302–307.

Ortea, J., L. Moro, and J. Espinosa. 1998. Nuevos datos sobre el genero *Elysia* Risso, 1818 (Opisthobranchia: Sacoglossa) en el Atlantico. *Rev. Acad. Canaria Cienc.* **9:** 141–155.

Ortea, J., M. Gutierrez, L. M. Abad, and J. Espinosa. 2005. *Elysia papillosa* Verrill, 1901 y *Elysia patina* Marcus, 1980 (Mollusca: Sacoglossa: Elysiidae) dos nombres para cuatro especies. *Vieraea Santa Cruz de Tenerife* **33:** 495–514.

Pace, D. A., and D. T. Manahan. 2007. Efficiencies and costs of larval growth in different food environments (Asteroidea: *Asterina miniata*). *J. Exp. Mar. Biol. Ecol.* **353:** 89–106.

Pace, D. A., A. G. Marsh, P. K. Leong, A. J. Green, D. Hedgecock, and D. T. Manahan. 2006. Physiological bases of genetically determined variation in growth of marine invertebrate larvae: A study of growth heterosis in the bivalve *Crassostrea gigas*. *J. Exp. Mar. Biol. Ecol.* **335:** 188–209.

Parker, G. A., and M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *Am. Nat.* **128:** 573–592.

Pawlik, J. R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanogr. Mar. Biol. Annu. Rev.* **30:** 273–335.

Payne, A. M., and M. A. Maun. 1981. Dispersal and floating ability of dimorphic fruit segments of *Cakile edentula* var. *lacustris*. *Can. J. Bot*. **59:** 2595–2602.

Pernet, B., and L. McArthur. 2006. Feeding by larvae of two different development modes in *Streblospio benedicti* (Polychaeta: Spionidae). *Mar. Biol.* **149:** 803–811.

Philippi., T., and J. Seger. 1989. Hedging one's evolutionary bets revisited. *Trends Ecol. Evol.* **4:** 41–44.

Raimondi, P. T., and M. J. Keough. 1990. Behavioural variability in marine larvae. *Aust. J. Ecol.* **15:** 427–437.

Roff, D. A. 1994. Habitat persistence and the evolution of wing dimorphism in insects. *Am. Nat*. **144:** 772–798.

Roff, D. A., and D. J. Fairbairn. 1991. Wing dimorphism and the evolution of migratory polymorphisms among the Insecta. *Am. Zool*. **31:** 243–251.

Schulze, S. R., S. A. Rice, J. L. Simon, and S. A. Karl. 2000. Evolution of poecilogony and the biogeography of North American populations of the polychaete *Streblospio*. *Evolution* **54:** 1247–1259.

Seger, J., and H. J. Brockmann. 1987. What is bet-hedging? *Oxf. Surv. Evol. Biol.* **4:** 182–211.

Simons, A. M., and M. O. Johnston. 2006. Environmental and genetic sources of diversification in the timing of seed germination: implications for the evolution of bet hedging. *Evolution* **60:** 2280–2292.

Sisson, C. G. 2002. Dichotomous life history patterns for the nudibranch *Dendronotus frondosus* (Ascanius, 1774) in the Gulf of Maine. *Veliger* **45:** 290–298.

Smolensky, N., M. Romero, and P. J. Krug. 2009. Costs of mating and self-fertilization in a simultaneous hermaphrodite with hypodermic insemination, the opisthobranch *Alderia willowi. Biol. Bull.* **216:** 188–199.

Spight, T. M. 1975. Factors extending gastropod embryonic development and their selective cost. *Oecologia* **21:** 1–16.

Spight, T. M. 1976. Ecology of hatching size in marine snails. *Oecologia* **24:** 283–294.

Strathmann, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annu. Rev. Ecol. Syst*. **16:** 339–361.

Strathmann, R. R. 1990. Why life histories evolve differently in the sea. *Am. Zool*. **30:** 197–207.

Strathmann, R. R. 1995. Peculiar constraints on life-histories imposed by protective or nutritive devices for embryos. *Am. Zool*. **35:** 426–433.

Strathmann, R. R., J. M. Staver, and J. R. Hoffman. 2002. Risk and the evolution of cell-cycle duration of embryos. *Evolution* **56:** 708–720.

Telenius, A., and P. Torstensson. 1989. The seed dimorphism of *Spergularia marina* in relation to dispersal by wind and water. *Oecologia* **80:** 206–210.

Thompson, T. E. 1959. Feeding in nudibranch larvae. *J. Mar. Biol. Assoc. UK* **38:** 239–248.

Thompson, T. E. 1967. Direct development in a nudibranch, *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. *J. Mar. Biol. Assoc. UK* **47:** 1–22.

Thompson, T. E. 1977. Jamaican opisthobranch molluscs I. *J. Molluscan Stud.* **43:** 93–140.

Toonen, R. J., and J. R. Pawlik. 2001a. Foundations of gregariousness: a dispersal polymorphism among the planktonic larvae of a marine invertebrate. *Evolution* **55:** 2439–2454.

Toonen, R. J., and J. R. Pawlik. 2001b. Settlement of the gregarious tube worm *Hydroides dianthus* (Polychaeta : Serpulidae). II. Testing the desperate larva hypothesis. *Mar. Ecol. Prog. Ser.* **224:** 115–131.

Trowbridge, C. D. 1992. Phenology and demography of a marine specialist herbivore: *Placida dendritica* (Gastropoda: Opisthobranchia) on the central coast of Oregon. *Mar. Biol.* **114:** 443–452.

Trowbridge, C. D. 1993. Feeding ecology of the sacoglossan opisthobranch *Aplysiopsis enteromorphae* (Cockerell & Eliot): patterns of distribution and impact on tidepool-dwelling green algae. *J. Exp. Mar. Biol. Ecol.* **114:** 233–257.

Trowbridge, C. D. 2002. Local elimination of *Codium fragile* ssp. *tomentosoides*: indirect evidence of sacoglossan herbivory? *J. Mar. Biol. Assoc. UK* **82:** 1029–1030.

Venable, D. L. 1985. The evolutionary ecology of seed heteromorphism. *Am. Nat*. **126:** 577–595.

Venable, D. L. 2007. Bet hedging in a guild of desert annuals. *Ecology* **88:** 1086–1090.

Verrill, A. E. 1901. Addition to the fauna of the Bermudas by the Yale expedition of 1901, with notes on other species. *Trans. Conn. Acad. Arts Sci.* **11:** 15–62.

West, H. H., J. F. Harrigan, and S. K. Pierce. 1984. Hybridization of two populations of a marine opisthobranch with different developmental patterns. *Veliger* **26:** 199–206.

Zera, A. J., and R. F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects. *Annu. Rev. Entomol*. **42:** 207–230.