

UC Santa Barbara

UC Santa Barbara Previously Published Works

Title

Developmental mode in benthic opisthobranch molluscs from the northeast Pacific Ocean: feeding in a sea of plenty

Permalink

<https://escholarship.org/uc/item/3dk0h3gj>

Journal

Canadian Journal of Zoology, 82(12)

Author

Goddard, Jeffrey HR

Publication Date

2004

Peer reviewed

Developmental mode in benthic opisthobranch molluscs from the northeast Pacific Ocean: feeding in a sea of plenty

Jeffrey H.R. Goddard

Abstract: Mode of development was determined for 130 of the nearly 250 species of shallow-water, benthic opisthobranchs known from the northeast Pacific Ocean. Excluding four introduced or cryptogenic species, 91% of the species have planktotrophic development, 5% have lecithotrophic development, and 5% have direct development. Of the 12 native species with non-feeding (i.e., lecithotrophic or direct) modes of development, 5 occur largely or entirely south of Point Conception, California, where surface waters are warmer, lower in nutrients, and less productive than those to the north; 4 are known from habitats, mainly estuaries, that are small and sparsely distributed along the Pacific coast of North America; and 1 is Arctic and circumboreal in distribution. The nudibranchs *Doto amyra* Marcus, 1961 and *Phidiana hiltoni* (O'Donoghue, 1927) were the only species with non-feeding development that were widespread along the outer coast. This pattern of distribution of developmental mode is consistent with the prediction that planktotrophy should be maintained at high prevalence in regions safe for larval feeding and growth and should tend to be selected against where the risks of larval mortality (from low- or poor-quality food, predation, and transport away from favorable adult habitat) are higher. However, direct development, which includes the most derived mode of non-feeding development, was also correlated with small adult size, reflecting an association common in marine invertebrates. Planktotrophic development also predominates in decapod Crustacea from the northeast Pacific, but is less common in echinoderms and prosobranch gastropods from this region owing to the presence of lineages constrained by phylogeny to non-feeding modes of development.

Résumé : Nous avons déterminé les modes de développement chez 130 des presque 250 espèces d'opisthobranches benthiques d'eaux peu profondes connues du nord-est de l'océan Pacifique. Après l'élimination de quatre espèces introduites ou cryptogéniques, 91 % des espèces possèdent un développement planctotrophe, 5 % un développement lécithotrophe et 5 % un développement direct. Des 12 espèces indigènes qui possèdent un des deux derniers modes de développement sans alimentation, cinq se retrouvent exclusivement ou presque au sud de Point Conception en Californie où les eaux superficielles sont plus chaudes, moins riches en nutriments et moins productives que celles plus au nord; quatre des espèces vivent dans des habitats restreints et clairsemés, surtout dans les estuaires, de la côte pacifique de l'Amérique du Nord; une des espèces a une répartition arctique et circumboréale. Les nudibranches *Doto amyra* Marcus, 1961 et *Phidiana hiltoni* (O'Donoghue, 1927) sont les seules espèces à développement sans alimentation qui sont communes au large de la côte. Ce pattern de répartition en fonction du mode de développement est en accord avec la prédiction qui veut que la planctotrophie devrait s'établir en forte fréquence dans les régions sûres pour l'alimentation et la croissance des larves; elle devrait être sélectionnée négativement là où les risques de mortalité larvaire (à cause d'une nourriture rare ou de pauvre qualité, de la prédation et de l'entraînement loin des habitats favorables aux adultes) sont plus élevés. Cependant, le développement direct, qui comprend le mode le plus évolué de développement sans alimentation, est en corrélation avec une taille adulte réduite, une relation commune chez les invertébrés marins. Le développement planctotrophe prédomine aussi chez les crustacés décapodes du nord-est du Pacifique, mais il est moins répandu chez les échinodermes et les gastéropodes prosobranches de la région à cause de la présence de lignées restreintes phylogénétiquement à des modes de développement sans alimentation.

[Traduit par la Rédaction]

Introduction

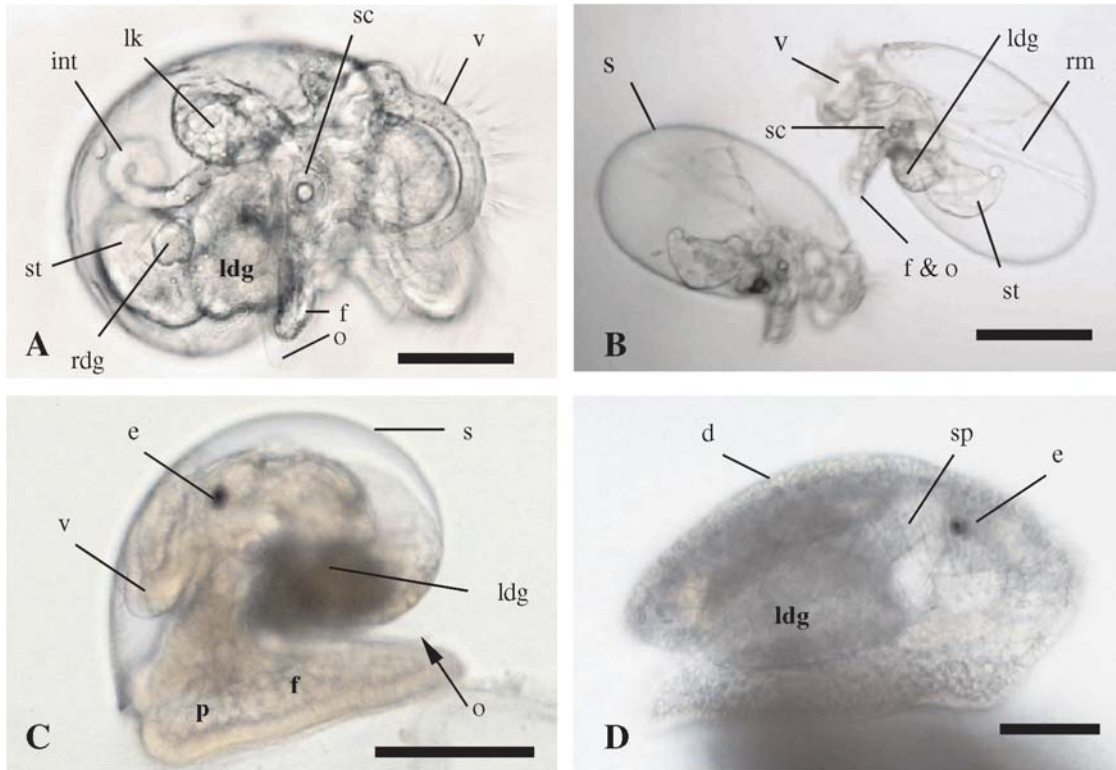
The northeast Pacific Ocean is characterized by moderate temperatures; slow-moving boundary currents; seasonal, localized upwelling; and high primary production (Briggs 1974; Hickey 1979; Briggs et al. 1987; Strub et al. 1987). Rocky shores, punctuated by small bays and estuaries, are

widespread throughout this region and support a high diversity of benthic organisms (Austin 1985; Ricketts et al. 1985; Foster et al. 1991). Larval mortality due to planktonic food shortages and transport away from suitable settlement sites should be lower here than in regions with low productivity, strong currents, and less extensive adult habitat. A larva hatched in northern California and accidentally transported

Received 27 August 2004. Accepted 12 January 2005. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 1 March 2005.

J.H.R. Goddard. Marine Science Institute, University of California, Santa Barbara, CA 93106, USA (e-mail: goddard@lifesci.ucsb.edu).

Fig. 1. Representative hatching larvae and juveniles of nudibranch molluscs from the northeast Pacific Ocean. (A) Hatching planktotrophic larva of *Chromodoris macfarlandi*, right lateral view. This larva has a typical coiled shell (type 1 of Thompson 1961) that will grow during the larval period. (B) Hatching planktotrophic larvae of *Eubrancheus rupium*, right and left lateral views. These larvae have typical egg-shaped, inflated shells (type 2 of Thompson 1961) that are fully formed at hatching. (C) Hatching lecithotrophic larva of *Phidiana lascrusensis*, left lateral view. Although this species is from the eastern tropical Pacific, its larvae are virtually identical to those of *Phidiana hiltoni* from the northeast Pacific (author's personal observations). (D) Hatching juvenile of *Dendrodoris* sp. 3 of Behrens (1991). All panels are photomicrographs of live specimens; scale bars = 50 μ m (A) and 100 μ m (B–D). d, dorsum; e, eyespot; f, foot; int, intestine; ldg, left digestive gland; lk, larval kidney; o, operculum; p, propodium; rdg, right digestive gland; rm, retractor muscle; s, shell; sc, statocyst; sp, spicules; st, stomach; v, velum.



north to Alaska or south to Baja California is likely to encounter benthic habitats resembling those of its natal origin, and indeed, the ranges of numerous species span this distance (Morris et al. 1980; Austin 1985; Ricketts et al. 1985). In this expansive and relatively uniform environment, the high fecundities associated with feeding larval development, or planktotrophy, should more than offset the risks associated with a longer planktonic period (see below). Planktotrophy is also considered the ancestral mode of development of most marine invertebrates (Strathmann 1978). Therefore, we might predict this mode of development to predominate in the early life histories of benthic opisthobranch gastropods. My purpose here is to document and summarize the now fairly extensive data for this taxon in the northeast Pacific Ocean, and lay the foundation for further biogeographic comparisons. Opisthobranchs are rich in this region (Behrens 1991, 2004) and are well suited to studies of developmental mode because in captivity they readily deposit transparent egg masses that are easily reared to hatching.

Development in opisthobranchs can be divided into three

major types (Thompson 1967; Bonar 1978; Todd 1983; Hadfield and Switzer-Dunlap 1984). (1) Planktotrophy is a developmental mode in which newly hatched veliger larvae must feed and grow in the plankton for weeks or months to achieve metamorphic competence (Figs. 1a and 1b). Parental investment per offspring is lowest in this mode, and these larvae develop rapidly from small eggs. At hatching, the larvae are relatively transparent owing to the lack of significant yolk reserves; they also hatch without a propodium and usually without eyespots. (2) Lecithotrophy is a mode in which more advanced veliger larvae develop more slowly from larger eggs and do not need to feed and grow in the plankton to achieve metamorphic competence. These larvae (Fig. 1c) hatch with eyespots, a well-developed foot with a propodium, and all the yolk reserves necessary to fuel metamorphosis into a juvenile slug. They can usually crawl or swim upon hatching and have a precompetent phase lasting a few hours to days. (3) In the direct mode, juveniles, rather than larvae, hatch from the egg coverings (Fig. 1d). As emphasized by Bonar (1978), the direct mode ranges from capsular metamorphic, in which development proceeds through an embryonic veliger stage complete with velum, shell, and operculum, to ametamorphic, in which the characteristic veliger structures are vestigial or absent altogether. Lecitho-

trophic and direct modes of development are sometimes referred to as non-feeding modes, owing to their lack of dependence on external food supplies. However, in the absence of suitable settlement cues, the lecithotrophic larvae of some species can feed in the plankton and delay metamorphosis for long periods, a condition termed facultative planktotrophy (Chia 1974; Kempf and Hadfield 1985; Emler 1986). Extended competent periods are also known for some species with planktotrophic development (e.g., Kempf 1981) and may be necessary to allow return to favorable habitats from which the larvae may have been carried away during the obligate precompetent period (Jackson and Strathmann 1981).

In opisthobranchs, as in most other marine invertebrates, planktotrophy is considered the ancestral mode of development, and once lost, larval feeding structures are rarely, if ever, regained (Strathmann 1978, 1993; Hadfield and Switzer-Dunlap 1984; Todd 1991; Charlotte et al. 2003). Body plans and adult size can also limit the developmental options available to a particular taxon (Strathmann and Strathmann 1982; Strathmann 1985, 1986). Phylogenetic constraints on mode of development can therefore be severe and must be considered in any biogeographic comparison. Because planktotrophic larvae develop from smaller eggs than either lecithotrophic larvae or directly developing juveniles, fecundities associated with this mode of development can be huge and, at least in good years with low larval mortality rates, this probably helps maximize recruitment potential and overall fitness (Vance 1973; Hadfield and Switzer-Dunlap 1984; Strathmann 1985). Worldwide, approximately two thirds of benthic opisthobranch species have a planktotrophic larval stage (Table 3 in Hadfield and Miller 1987), and mode of development in this taxon does not follow any simple correlation with latitude (Goddard 1992; see also Clark and Goetzfried 1978; Hadfield and Switzer-Dunlap 1984; Gonsalves-Jackson 2001), as previously thought for many shallow-water invertebrate taxa (Thorson 1950; Mileikovsky 1971).

Methods

From 1999 to 2002 I collected opisthobranchs intertidally from localities between Punta Rosarito, Baja California (28°33.75'N, 114°09.03'W), and Cayucos, California (35°26.50'N, 120°53.27'W). I obtained additional specimens, collected subtidally in the Santa Barbara area, from collectors at the Marine Science Institute (MSI) at the University of California, Santa Barbara. I held adults in either glass jars or PVC containers with 80- μ m nylon mesh bottoms on a flow-through seawater table at ambient ocean temperatures (11–19 °C, depending on season) in the laboratory at MSI until they laid egg masses. I examined the newly laid egg masses using a compound microscope equipped with an ocular micrometer. If cleavage had not progressed too far and zygotes were still present, I measured the diameter of a random sample of at least 10 zygotes (avoiding elliptical and oblong eggs sometimes observed in egg masses in the process of being laid). I also examined the newly laid egg masses for provisions of extra-zygotic nutrient reserves (indicated by granular or optically refractile, globular material, located either inside or outside the egg capsules) that might influence development (Clark and Jensen 1981; Boucher

1983; Thompson and Salghetti-Drioli 1984; Goddard 1991). I then transferred the egg masses, or samples of large egg masses, to separate vials, changed the water in all vials and jars at least once daily, and examined the egg masses daily until the veligers hatched. I then examined the hatching veligers and assigned developmental type based on the morphological criteria described by Thompson (1967, 1976), Bonar (1978), and Hadfield and Switzer-Dunlap (1984), noting especially the presence or absence of a propodium and eyespots, as well as the size and yolk content of the digestive glands. I measured the longest dimension of the shells of a random sample of at least 10 veligers lying on their sides. To facilitate these measurements, I sometimes immobilized active veligers with a few drops of either 70% ethanol or 4% glutaraldehyde. Measurements of both eggs and shells were accurate to approximately 2.5 μ m. Larval shells were described as type 1 or 2 according to Thompson (1961, 1976). Egg-shaped, inflated, type 2 shells are restricted to and occur in all members of the nudibranch families Dendronotidae, Hancockidae, Tergipididae, Eubranichidae, Calmidae, and Fionidae (Thompson 1976; Hadfield and Switzer-Dunlap 1984; Goddard 2001b). These families were represented in this study by species of the genera *Dendronotus*, *Catriona*, *Cuthona*, *Eubranchus*, and *Fiona*. I did not attempt to rear veliger larvae beyond hatching.

I made a few determinations of developmental mode without obtaining all of the data outlined above. I used a compound microscope to examine the hatching larvae of the cephalaspidean *Haminoea virescens* and the arminian nudibranch *Dirona picta* and determined their mode of development based on morphology, but was unable to measure the size of their shells. For the sacoglossan *Stiliger* sp., I assigned mode of development based on my measurements of egg and egg capsule size and observation of its egg masses, combined with comparisons of egg size, capsule size, and mode of development of sacoglossans from both the northeast Pacific Ocean (Strathmann 1987; this study) and Florida (Clark and Jensen 1981). For the dorid nudibranch *Palio dubia*, I determined mode of development based on my qualitative observations (made in the field using a hand lens) of the small size of its embryos, combined with Thompson and Brown's (1984) report of its egg size in Britain.

I also surveyed and compiled the literature containing data on mode of development of opisthobranchs from the northeast Pacific Ocean. When an author did not explicitly state the mode of development, I assigned it when possible by applying the morphological criteria mentioned above to published figures and descriptions of newly hatched offspring. For eight species of nudibranchs I assigned mode of development based on reports of egg diameter, embryonic period, and comparisons with congeners as described in Goddard (1992, pp. 38–41). For *Thordisa rubescens*, I relied on Behrens and Henderson's (1981) detailed description of its egg mass to estimate egg diameter and assign mode of development. In all nine of these cases, egg diameters or embryonic periods were small or short enough, respectively, to confidently assign planktotrophic development (Tables 2 and 3 in Goddard 1992). Developmental mode was assigned to three other species based on data reported for those species in other parts of the world.

When calculating the percentage of each of the major

modes of development in the northeast Pacific Ocean, I used all of the above determinations but excluded introduced species and cryptogenic species (*sensu* Carlton 1996). In all other data analyses and summaries, I also excluded data reported from other parts of the world. Errors are reported as ± 1 SE. To simplify presentation of the data, I report egg diameters and shell sizes as means or, when measurements were taken from more than one egg mass or more than one study, grand means. When mean egg or shell sizes obtained from different egg masses (or from different literature sources) differed by more than about 10%, I report a range of means. However, for two species of dorid nudibranchs (*Geitodoris heathi* and *Palio zosterae*), the published values for shell size at hatching differed so much that I report each value separately for each species. For the rare cases of variable developmental mode, or poecilogony, I report egg and shell sizes for each mode. To examine the relationship between egg size and shell size at hatching in all species combined, I conducted a linear regression analysis using, with two exceptions, the grand means for each value for each mode of development for each species. The exceptions were for the two dorids mentioned above, for which I used the mean values for shell size (145 and 101 μm , respectively) that I had obtained in my own studies.

Finally, although I am interested here primarily in mode of development, it should be noted that (i) coefficients of variation in egg diameter from individual egg masses typically ranged from about 1% to 6%, with most around 2%–3% (Goddard 1992, pp. 50–51; also see Table 2 in Goddard 1984), and (ii) considerable variation in egg size has been documented between populations of some opisthobranchs, especially those with non-feeding development and restricted gene flow (Todd et al. 2001).

Results

Mode of development was determined for 130 of the nearly 250 benthic, shallow-water species reported by Behrens (2004) from the northeast Pacific Ocean (Table 1). Determinations for 126 of these were based on data collected from the northeast Pacific Ocean. Of the remaining 4 species, the mode of development of one (*Runcina macfarlandi*) was assumed based on Thompson and Brodie's (1988) diagnosis of the genus, and the developmental types of three (*Adalaria proxima*, *Lomanotus vermiformis*, and *Spurilla neapolitana*) were assumed based on data reported from other parts of the world. Three of the species included in Table 1 (*Anteaeolidiella indica*, *Philine auriformis*, and *Tenellia adspersa*) are introduced (Cohen and Carlton 1995; Gosliner 1995; Ruiz et al. 2000), and one (*Haminoea callidegenita*) is likely introduced (S.V. Millen, personal communication 2003) and therefore cryptogenic. The egg diameter reported by Millen (1989) for *Cuthona viridis* is too large to allow determination of its mode of development without additional data (see Fig. 2 and Hadfield and Miller 1987).

Excluding the introduced and cryptogenic species, 91% (115 of 126) of northeast Pacific opisthobranchs have planktotrophic development, 5% are lecithotrophic, and 5% have either capsular metamorphic or ametamorphic development (Table 2). Planktotrophy is significantly more prevalent

in the northeast Pacific Ocean, and the non-feeding modes of development less prevalent, compared with the proportions reported by Hadfield and Miller (1987) for opisthobranchs worldwide (Table 2; 2×3 contingency table analysis, log-likelihood ratio, $\chi^2 = 27.5$, $p < 0.0001$). In this analysis, I did not remove species from Hadfield and Miller's (1987) compilation that are also included here in Table 1; therefore, this result is conservative.

Egg sizes of native northeast Pacific opisthobranchs ranged from a mean diameter of 57 μm in the sacoglossan *Placida dendritica* to 184 μm in *Dendrodoris* sp. 3 of Behrens (1991), with overall mean and modal diameters of 90.7 ± 2.4 μm ($n = 91$) and 95 μm , respectively (Table 1, Fig. 2). Mean egg diameter was 86.2 ± 1.7 μm ($n = 84$) for the species with planktotrophic development, 134.0 ± 14.6 μm ($n = 3$) for those with lecithotrophic development, and 161.2 ± 11.4 μm ($n = 3$) for those with direct modes of development (Fig. 2). Among the planktotrophic species, mean egg size was significantly larger for the species with egg-shaped, inflated larval shells (type 2 of Thompson 1961) than for those with more typical, coiled, type 1 shells (103.6 ± 3.0 μm versus 81.4 ± 1.6 μm , respectively; Wilcoxon's two-sample test, normal approximation, $Z = 5.045$, $p < 0.0001$). With the exception of the sacoglossan *Alderia modesta*, which in southern California produces lecithotrophic larvae from eggs 105 μm in diameter, egg sizes of species with planktotrophic development did not overlap those of species with non-feeding modes of development (Fig. 2).

Extra-zygotic nutrient reserves were observed during this study in the egg masses of two species, the sacoglossan *Stiliger* sp. and the anaspidean *Phyllaplysia taylori*. In *Stiliger* sp. the reserves were in the form of slightly refractile, granular material inside the egg capsules, which averaged 120 μm long by 85 μm wide, and in *P. taylori* they consisted of a clear, refractile material filling an intracapsular body averaging 46 μm in diameter. Bridges (1975) previously noted the presence of these spherical bodies inside the egg capsules of *P. taylori*. The only other species listed in Table 1 known to possess extra-zygotic nutrient reserves is the aeolid nudibranch *Cuthona lagunae*, whose egg capsules contain unusually large, yolk-filled polar bodies (Goddard 1991).

Egg size was a good predictor of shell size at hatching for species with type 1 shells, explaining 90% of the variation in this variable (Fig. 3). In contrast, egg size explained only 38% of the variation in length of type 2 shells, which were also larger than type 1 shells developing from similarly sized eggs (Fig. 3).

Five of the 12 native species with non-feeding modes of development are known mainly or entirely from regions south of Point Conception, California, a well-known boundary separating the Oregonian and Californian biogeographic provinces (Briggs 1974; Burton 1998; Wares et al. 2001) (Table 3). A sixth species, the sacoglossan *Alderia modesta*, occurs in bays from Alaska to Baja California but is poecilogonous (having planktotrophy and lecithotrophy) only south of Point Conception (Krug 1998). Of the remaining six species in Table 3 regularly found north of Point Conception, two occur only in bay and estuarine habitats, one is found only in high intertidal pools on the outer coast, and one is Arctic and circumboreal in distribution and found in the

Table 1. Egg size, shell size at hatching, and mode of development of benthic opisthobranchs from the northeast Pacific Ocean.

| Species | Egg diameter (µm) | Shell size at hatching (µm) | Developmental mode | Distribution | Source of development data |
|--|----------------------|-----------------------------|--------------------|--------------|--|
| Cephalaspidea | | | | | |
| <i>Acteocina inculta</i> (Gould, 1856) | 149 | 270 | CM | N, S | This study |
| <i>Aglaja ocelligera</i> (Bergh, 1894) | — | 155 | P | N, S | Strathmann 1987 |
| <i>Diaphana californica</i> Dall, 1919 | 73 | 123 | P | N, S | Goddard 1984 |
| <i>Gastropteron pacificum</i> Bergh, 1894 | 95 | 158 | P | N, S | Hurst 1967; Strathmann 1987 |
| <i>Haminoea callidegenita</i> Gibson and Chia, 1989 | 220 | 360 | L, CM | N | Gibson and Chia 1989a |
| <i>Haminoea virescens</i> (Sowerby, 1833) | — | — | P | N, S | This study |
| <i>Haminoea vesicula</i> (Gould, 1855) | 90 | 123–139 ^a | P | N, S | Hurst 1967; Strathmann 1987; Gibson and Chia 1989b |
| <i>Melanochlamys diomedea</i> (Bergh, 1894) | 98 | 180 | P | 1° N | Hurst 1967; Strathmann 1987 |
| <i>Navanax inermis</i> (Cooper, 1863) | — | 146 | P | 1° S | This study |
| <i>Philine alba</i> Mattox, 1958 | — | 135 | P | N, S | This study |
| <i>Philine auriformis</i> Suter, 1909 | — | 125 | P | N | Gosliner 1995 |
| <i>Rictaxis punctocaelatus</i> (Carpenter, 1864) | — | 137 | P | N, S | Goddard 2001b |
| <i>Runcina macfarlandi</i> Gosliner, 1991 | — | — | AM ^b | N | Thompson and Brodie 1988 |
| Anaspidea | | | | | |
| <i>Aplysia californica</i> Cooper, 1863 | 81 | 125–135 | P | N, S | Kriegstein et al. 1974; Kriegstein 1977; this study |
| <i>Aplysia vaccaria</i> Winkler, 1955 | — | 152 | P | 1° S | This study |
| <i>Phyllaplysia taylori</i> Dall, 1900 | 144–157 ^c | 250–300 | CM | N, S | Bertsch and Hirschberg 1973; Bridges 1975; Goddard 2001b |
| Notaspidea | | | | | |
| <i>Berthella californica</i> (Dall, 1900) | 93 | 153 | P | N, S | Goddard 1984 |
| <i>Berthellina ilisima</i> (= <i>B. engeli</i>) Marcus and Marcus, 1967 | — | 144 | P | S | This study |
| <i>Berthella strongi</i> (MacFarland, 1966) | — | 131 | P | N, S | This study |
| <i>Pleurobranchaea californica</i> MacFarland, 1966 | — | 215 | P | N, S | Chivers 1967; Goddard 2001b |
| Sacoglossa | | | | | |
| <i>Alderia modesta</i> (Lovén, 1844) | 68–80 | 90–116 | P | N, S | Hand and Steinberg 1955; Strathmann 1987; Krug 1998 |
| | 105 | 186 | L | S | Krug 1998 |
| <i>Aplysiopsis enteromorphae</i> (Cockerell and Eliot, 1905) | 66–70 | 109–113 | P | N, S | Hurst 1967; Goddard 1984; Strathmann 1987 |
| <i>Elysia hedgpethi</i> Marcus, 1961 | 68 | 100–105 | P | N, S | Greene 1968; Strathmann 1987; Goddard 2001b |
| <i>Hermaea vancouverensis</i> (O'Donoghue, 1924) | 63 | 114 | P | N | Goddard 2001b |
| <i>Olea hansineensis</i> Agersborg, 1923 | — | 111 | P | 1° N | Hurst 1967 |
| <i>Placida dendritica</i> (Alder and Hancock, 1843) | 57 | 82–112 | P | N, S | Greene 1968; Goddard 2001b |
| <i>Stiliger fuscovittatus</i> Lance, 1962 | 95 | 150 | P | N, S | Strathmann 1987 |
| <i>Stiliger</i> sp. of Goddard (2000) | 60 | — | P | S | Goddard 2000; this study |
| Nudibranchia: Doridina | | | | | |
| <i>Acanthodoris brunnea</i> MacFarland, 1905 | 80 | 130–150 | P | N, S | Strathmann 1987 |
| <i>Acanthodoris hudsoni</i> MacFarland, 1905 | 67–70 | 127 | P | N, S | Goddard 1987; Strathmann 1987 |
| <i>Acanthodoris nanaimoensis</i> O'Donoghue, 1921 | — | 133 | P | N | Hurst 1967 |
| <i>Acanthodoris pilosa</i> (Abildgaard, 1789) | 70 | 119 | P | N | Hurst 1967; Strathmann 1987 |
| <i>Acanthodoris rhodoceras</i> Cockerell and Eliot, 1905 | — | 112 | P | N, S | Goddard 2001b |
| <i>Adalaria jannae</i> Millen, 1987 | 65 | 109 | P | N | Millen 1987 |

Table 1 (continued).

| Species | Egg diameter (µm) | Shell size at hatching (µm) | Developmental mode | Distribution | Source of development data |
|--|-------------------|-----------------------------|--------------------|--------------|--|
| <i>Adalaria proxima</i> Alder and Hancock, 1854 | (180) | (290) | (L) | N | Thompson 1976 |
| <i>Adalaria</i> sp. 1 of Behrens (1991) | 83 | 140 | P | N | Goddard 1984 |
| <i>Aegires albopunctatus</i> MacFarland, 1905 | 98–120 | 154 | P | N, S | Strathmann 1987; Goddard 2001a |
| <i>Aldisa cooperi</i> Robilliard and Baba, 1972 | 110 | — | P | N | Millen and Gosliner 1985 |
| <i>Aldisa sanguinea</i> (Cooper, 1863) | 90–100 | 163 | P | N, S | Millen and Gosliner 1985; Goddard 1992 |
| <i>Aldisa tara</i> Millen in Millen and Gosliner, 1985 | 110 | — | P | N | Millen and Gosliner 1985 |
| <i>Ancula gibbosa</i> (= <i>A. pacifica</i>) (Risso, 1818) | 59 | 104 | P | N, S | Goddard 1984 |
| <i>Baptodoris mimetica</i> Gosliner, 1991 | 90 | 127 | P | N, S | This study |
| <i>Cadlina flavomaculata</i> MacFarland, 1905 | 80 | 140 | P | N, S | This study |
| <i>Cadlina luteomarginata</i> MacFarland, 1966 | 90–94 | — | P | N, S | Dehnel and Kong 1979; Goddard 1992 |
| <i>Cadlina modesta</i> MacFarland, 1966 | 92 | 157 | P | N, S | Goddard 1984 |
| <i>Cadlina sparsa</i> (Odhner, 1921) | 82 | 131 | P | 1° S | This study |
| <i>Chromodoris macfarlandi</i> Cockerell, 1902 | 95 | 169 | P | 1° S | This study |
| <i>Corambe pacifica</i> MacFarland and O'Donoghue, 1929 | 70 | 130 | P | N, S | Yoshioka 1986 |
| <i>Corambe</i> (= <i>Doridella</i>) <i>steinbergae</i> (Lance, 1962) | 75–85 | 142 | P | N, S | Bickell and Chia 1979 |
| <i>Crimora coneja</i> Marcus, 1961 | 73 | 116–119 | P | N, S | Goddard 1984, 1992 |
| <i>Dendrodoris nigromaculata</i> (Cockerell in Cockerell and Eliot, 1905) | — | n/a | CM | S | Lance 1982 |
| <i>Dendrodoris</i> sp. 3 of Behrens (1991) | 184 | n/a | CM | 1° S | This study |
| <i>Diaphorodoris lirulatocauda</i> Millen, 1985 | 63 | 115 | P | N, S | Goddard 1984 |
| <i>Diaulula</i> (= <i>Discodoris</i>) <i>aurila</i> (Marcus and Marcus, 1967) | 88 | 140 | P | S | This study |
| <i>Diaulula sandiegensis</i> (Cooper, 1863) | 83 | 130–153 | P | N, S | Hurst 1967; Strathmann 1987; Goddard 1992 |
| <i>Doriopsilla albopunctata</i> (Cooper, 1863) | 108 | 195 | P | N, S | This study |
| <i>Doriopsilla gemmela</i> Gosliner, Schaefer and Millen, 1999 | — | — | L | 1° S | Gosliner et al. 1999 |
| <i>Doriopsilla spaldingi</i> Valdés and Behrens, 1998 | — | — | D ^d | 1° S | Valdes and Behrens 1998; Behrens 1998 |
| <i>Doris</i> (= <i>Archidoris</i>) <i>montereyensis</i> Cooper, 1863 | 81–90 | 154–169 | P | N, S | McGowan and Pratt 1954; Hurst 1967; Goddard 1992 |
| <i>Doris</i> (= <i>Archidoris</i>) <i>odhneri</i> (MacFarland, 1966) | 96 | 186–189 | P | N, S | Hurst 1967; Goddard 1992 |
| <i>Geitodoris heathi</i> (MacFarland, 1905) | 73–79 | 102, 145 | P | N, S | Goddard 1984, 1992; Strathmann 1987 |
| <i>Hallaxa chani</i> Gosliner and Williams, 1975 | 82 | 131–152 | P | N | Goddard 1984, 1992 |
| <i>Limacia</i> (= <i>Laila</i>) <i>cockerelli</i> (MacFarland, 1905) | 95 | 142 | P | N, S | Goddard 1984 |
| <i>Okenia</i> (= <i>Hopkinsia</i>) <i>rosacea</i> (MacFarland, 1905) | 81.5 | 141 | P | N, S | Goddard 1992 |
| <i>Onchidoris bilamellata</i> (L., 1767) | 100 | 147–165 | P | N, S | Hurst 1967; Strathmann 1987; Chia and Koss 1988 |
| <i>Onchidoris muricata</i> (Müller, 1776) | 76 | 128–137 ^e | P | N | Goddard 1984, 1992; Millen 1985 |
| <i>Palio dubia</i> (M. Sars, 1829) | (79) | — | P | N | Thompson and Brown 1984; this study |
| <i>Palio zosterarum</i> (O'Donoghue, 1924) | 65–70 | 101, 150 | P | N | Strathmann 1987; Goddard 1992 |
| cf. <i>Peltodoris</i> (= <i>Anisodoris</i>) <i>lentiginosa</i> (Millen, 1982) | 90 | 154 | P | N | Millen 1982 |

Table 1 (continued).

| Species | Egg diameter (µm) | Shell size at hatching (µm) | Developmental mode | Distribution | Source of development data |
|--|-------------------|-----------------------------|--------------------|--------------|---|
| <i>Peltodoris</i> (= <i>Anisodoris</i>) <i>nobilis</i> (MacFarland, 1905) | 83 | 153 | P | N, S | Goddard 1984 |
| <i>Polycera atra</i> MacFarland, 1905 | 68–71 | 122 | P | N, S | Goddard 1992 |
| <i>Polycera hedgpethi</i> Marcus, 1964 | <85 | 131 | P | N, S | This study |
| <i>Polycera tricolor</i> Robilliard, 1971 | — | — | P | N, S | Robilliard 1971 |
| <i>Rostanga pulchra</i> MacFarland, 1905 | 73–80 | 148–161 | P | N, S | Hurst 1967; Anderson 1971; Chia and Koss 1978 |
| <i>Taringa aivica</i> Marcus and Marcus, 1967 | — | 180 | P | S | This study |
| <i>Thordisa rubescens</i> Behrens and Henderson, 1981 | — | — | P | S | Behrens and Henderson 1981 |
| <i>Triopha catalinae</i> (Cooper, 1863) | 75–87 | 131–134 | P | N, S | Hurst 1967; Goddard 1984, 1992; Strathmann 1987 |
| <i>Triopha maculata</i> MacFarland, 1905 | — | — | P | N, S | Mulliner 1972 |
| Nudibranchia: Dendronotina | | | | | |
| <i>Dendronotus albopunctatus</i> Robilliard, 1972 | 108 | — | P | N | Robilliard 1972 |
| <i>Dendronotus dalli</i> Bergh, 1879 | — | — | P | N | Robilliard 1970 |
| <i>Dendronotus diversicolor</i> Robilliard, 1970 | 96 | — | P | N, S | Robilliard 1970; Strathmann 1987 |
| <i>Dendronotus frondosus</i> (Ascanius, 1774) | 85–90 | 230–245 | P | N, S | Strathmann 1987; Goddard 1992 |
| <i>Dendronotus iris</i> (Cooper, 1863) | 110 | 268–280 | P | N, S | Hurst 1967; Strathmann 1987 |
| <i>Dendronotus rufus</i> O'Donoghue, 1921 | — | — | P | N | Robilliard 1970 |
| <i>Dendronotus subramosus</i> MacFarland, 1966 | — | — | P | N, S | Goddard 1992 |
| <i>Doto amyra</i> Marcus, 1961 | 152 | 239 | L | N, S | Goddard 1984, 1996 |
| <i>Doto kya</i> Marcus, 1961 | 78 | 133 | P | N, S | Goddard 1996; this study |
| <i>Doto lancei</i> Marcus and Marcus, 1967 | — | 112 | P | S | Goddard 1996; this study |
| <i>Doto</i> form A of Goddard (1996) | 75 | 120 | P | N, S | Goddard 1996; this study |
| <i>Doto</i> form B of Goddard (1996) | 70 | 122 | P | N | Goddard 1996 |
| <i>Lomanotus vermiformis</i> Eliot, 1908 | (106) | — | (L) | S | Clark and Goetzfried 1978 |
| <i>Melibe leonina</i> (Gould, 1852) | 86–90 | 140–152 | P | N, S | Hurst 1967; Bickell and Kempf 1983; Strathmann 1987; Goddard 1992 |
| <i>Tritonia diomedea</i> Bergh, 1894 | 87 | 145 | P | N, S | Hurst 1967; Kempf and Willows 1977; Strathmann 1987 |
| <i>Tritonia festiva</i> (Stearns, 1873) | 79 | 131 | P | N, S | Goddard 1992 |
| <i>Tritonia myrakeenae</i> Bertsch and Moqueira, 1986 | <80 | 126 | P | S | This study |
| Nudibranchia: Arminina | | | | | |
| <i>Armina californica</i> (Cooper, 1863) | 95–102 | 160 | P | N, S | Hurst 1967; Strathmann 1987 |
| <i>Dirona albolineata</i> MacFarland in Cockerell and Eliot, 1905 | 70 | 113–129 | P | N, S | Hurst 1967; Strathmann 1987; Goddard 1992 |
| <i>Dirona pellucia</i> (= <i>D. albolineata</i>) Volodchenko, 1941 | — | 139 | P | N | Hurst 1967 |
| <i>Dirona picta</i> MacFarland in Cockerell and Eliot, 1905 | 80 ^f | — | P | N, S | Marcus and Marcus 1967; this study |
| <i>Janolus barbansensis</i> (Cooper, 1863) | — | 189 | P | N, S | This study |
| <i>Janolus fuscus</i> O'Donoghue, 1924 | 81 | 138 | P | N | Goddard 1992 |
| Nudibranchia: Aeolidina | | | | | |
| <i>Aeolidia papillosa</i> (L., 1761) | 74 | 116–138 | P | N, S | Hurst 1967; Williams 1980; Strathmann 1987 |
| <i>Aeolidiella chromosoma</i> Cockerell and Eliot, 1905 | — | 127 | P | 1° S | This study |
| <i>Aeolidiella oliviae</i> MacFarland, 1966 | 92 | 153–171 | P | N, S | This study |
| <i>Anteaeolidiella</i> (= <i>Aeolidiella</i>) <i>indica</i> (Bergh, 1888) | — | — | L | S | Mulliner 1972 |

Table 1 (concluded).

| Species | Egg diameter (µm) | Shell size at hatching (µm) | Developmental mode | Distribution | Source of development data |
|--|-------------------|-----------------------------|--------------------|--------------|---|
| <i>Catriona columbiana</i> (O'Donoghue, 1922) | 100–109 | 274–302 | P | N, S | Goddard 1984, 2001b |
| <i>Catriona rickettsi</i> Behrens, 1984 | 98–103 | 291 | P | N, S | Goddard 2001b |
| <i>Cumanotus fernaldi</i> Thompson and Brown, 1984 | 73 | 119–130 | P | N, S | Hurst 1967; Goddard 1992 |
| <i>Cuthona abronia</i> (MacFarland, 1966) | 95 | 224 | P | N, S | Goddard 1991 |
| <i>Cuthona albocrusta</i> (MacFarland, 1966) | 97 | 270–281 | P | N, S | Hurst 1967; Goddard 1991 |
| <i>Cuthona cocoachroma</i> Williams and Gosliner, 1979 | 95 | 257–277 | P | N | Goddard 1984, 1991 |
| <i>Cuthona divae</i> (Marcus, 1961) | 107 | 249 | P | N, S | Goddard 1984 |
| <i>Cuthona fulgens</i> (MacFarland, 1966) | 94 | 252 | P | N | Goddard 1991 |
| <i>Cuthona lagunae</i> (O'Donoghue, 1926) | 98 | 262 | P | N, S | Goddard 1991 |
| <i>Cuthona punicea</i> Millen, 1985 | 128 | — | P | N | Millen 1986 |
| <i>Cuthona pustulata</i> (Alder and Hancock, 1854) | 120 | — | P | N | Gosliner and Millen 1984 |
| <i>Cuthona rolleri</i> Behrens and Gosliner, 1988 | 121 | 283 | P | N | This study |
| <i>Cuthona viridis</i> (Forbes, 1840) | 134 | — | — | N | Millen 1989 |
| <i>Emarcusia morroensis</i> Roller, 1972 | — | — | P | N, S | Roller 1972 |
| <i>Eubranchus rupium</i> (= <i>E. olivaceus</i>) (Möller, 1842) | 85 | 244 | P | N, S | Hurst 1967; Goddard 1992 |
| <i>Eubranchus rustys</i> (Marcus, 1961) | 93 | 240 | P | N, S | Goddard 1984 |
| <i>Fiona pinnata</i> (Eschscholtz, 1831) | 100–150 | 280 | P | N, S | Holleman 1972; Schmekel and Portmann 1982; Strathmann 1987; Goddard 2001b |
| <i>Flabellina iodinea</i> (Cooper, 1862) | — | 153 | P | N, S | Engel 1976; this study |
| <i>Flabellina japonica</i> (Volodchenko, 1941) | — | — | P | N | S. Millen, personal communication 2001 |
| <i>Flabellina trilineata</i> (O'Donoghue, 1921) | 60–65 | 100–110 | P | N, S | Bridges and Blake 1972; Strathmann 1987; Goddard 1992 |
| <i>Flabellina trophina</i> (= <i>F. fusca</i>) (Bergh, 1894) | — | 133 | P | N | Hurst 1967 |
| <i>Flabellina verrucosa</i> (Johnson, 1832) | — | 117 | P | N | Strathmann 1987 |
| <i>Hermisenda crassicornis</i> (Eschscholtz, 1831) | 65 | 102–119 | P | N, S | Hurst 1967; Harrigan and Alkon 1978; Williams 1980; Goddard 1992 |
| <i>Phidiana hiltoni</i> (O'Donoghue, 1927) | 145 | 236 | L | N, S | This study |
| <i>Spurilla neapolitana</i> (delle Chiaje, 1823) | (83–100) | — | (P) | S | Eyster and Eckelbarger 1979; Eyster 1980; DeFreese and Clark 1983 |
| <i>Tenellia adpersa</i> (Nordmann, 1845) | (72) (103) | 228 219 | P L | N N | Eyster 1979; Goddard 2001b Eyster 1979; Goddard 1992 |

Note: Developmental mode: P, planktotrophic; L, lecithotrophic; CM, capsular metamorphic; AM, ametamorphic; D, direct (capsular metamorphic or ametamorphic not specified) (see text). Distributions are north (N) or south (S) of Point Conception, California, and are based on Behrens (1991, 2004), sources listed below, and personal observations; 1° means most of the population occurs north or south of Point Conception. Values are generally means based on at least 10 measurements; n/a, not applicable. Values and developmental mode determined from specimens collected outside the northeast Pacific are in parentheses.

^aStrathmann (1987) reported an anomalously low value of 90 µm and also considered the development data reported by Hurst (1967) for *Haminoea virescens* to probably represent *H. vesicula*, which I have followed here.

^bDevelopment has not been examined for *Runcina macfarlandi*; however, ametamorphic development is considered diagnostic of the genus (Thompson and Brodie 1988).

^cThe egg capsules of *Phyllaplysia taylora* also contain a nutritive body averaging 45–49 µm in diameter (Bridges 1975; author's personal observations).

^dDirect development for this species is based on the statement by Valdés and Behrens (1998, p. 308) that "the larvae exhibit direct or lecithotrophic development (J. Lance, personal communication)" and the statement by Behrens (1998) that "the larvae exhibit lecithotrophic or direct development; a crawling subadult emerges directly from a large egg, rather than the characteristic swimming veliger larvae of most nudibranchs".

^eHurst's (1967) anomalously high value of 186 µm reported for this species may have actually applied to the morphologically similar *Adalaria proxima*, whose eggs are this large in the north Atlantic Ocean (Thompson 1976; Todd et al. 2001).

^fMarcus and Marcus (1967) did not specify whether this value was obtained from living or preserved material.

Fig. 2. Egg size distribution, by mode of development, in native benthic opisthobranchs from the northeastern Pacific Ocean. Egg size data reported from other parts of the world are not included, and *Haminoea callidegenita* is omitted owing to the possibility that it is introduced (see text).

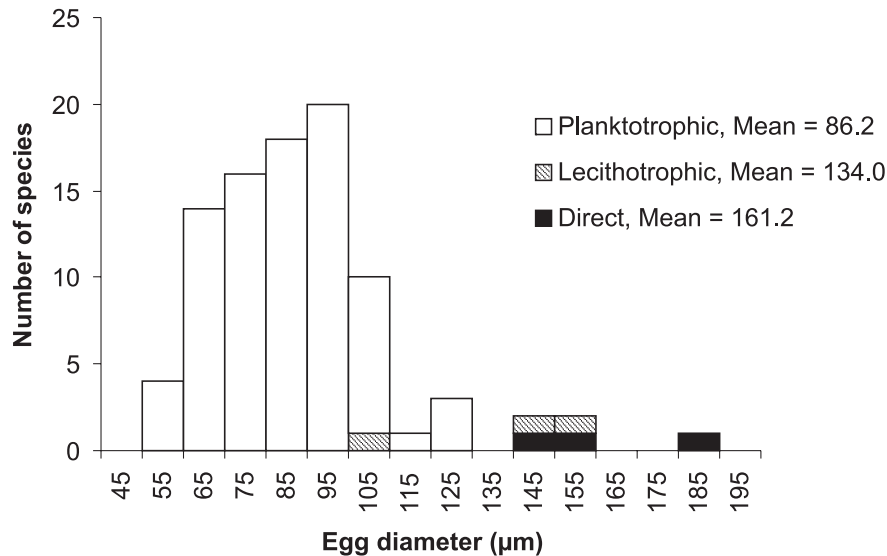


Table 2. Percentages of native benthic opisthobranchs from the northeast Pacific Ocean with each of the three major types of development, compared with worldwide percentages extracted from Table 3 of Hadfield and Miller (1987).

| Mode of development | Percentage of species (no. of species) | |
|---------------------|--|---|
| | Northeast Pacific Ocean (this study) | Worldwide (from Hadfield and Miller 1987) |
| Planktotrophic | 91 (115) | 67 (164) |
| Lecithotrophic | 5 (6) | 15 (37) |
| Direct | 5 (6) | 18 (43) |
| Total | 101 (126) ^a | 100 (244) |

^aPercentages in the northeast Pacific add to 101, and the total number of species to 126, because *Alderia modesta*, which has variable development, is counted twice.

northeast Pacific as far south as British Columbia (Table 3). Only the nudibranchs *Doto amyra* and *Phidiana hiltoni* are widespread on the outer coast. All three of the introduced species with non-feeding development occur exclusively or primarily in bays, and one of these is known only south of Point Conception (Table 3).

Discussion

Ninety-one percent of 126 native, benthic opisthobranchs from the northeast Pacific Ocean have planktotrophic larval development. The relatively few native species with non-feeding modes of development (*i*) occur largely south of Point Conception, California, where surface waters are warmer, lower in nutrients, and less productive than those to the north (Daily et al. 1993; Blanchette et al. 2002) or (*ii*) are known from habitats, such as estuaries, that are small and sparsely distributed along the Pacific coast of North America. Considering only those species known mainly from regions north of Point Conception (see Table 1), 94% have planktotrophic development and 6% have non-feeding

development. These patterns of distribution of developmental mode are consistent with the prediction that planktotrophy should be maintained at high prevalence in regions safe for larval feeding and growth and should tend to be selected against where the risks of larval mortality from food limitation and transport away from favorable adult habitat are higher. These patterns are further reinforced by the findings that (*i*) the 3 estuarine species with non-feeding development (Table 3) represent half of the native opisthobranch species from the northeast Pacific that are strictly estuarine in distribution and (*ii*) the 5 species known primarily from regions south of Point Conception represent 26% of the 19 native opisthobranch species included in Table 1 that share this geographic range (McDonald 1983; Behrens 1991, 2004; author's personal observations). However, the developmental mode of more species from the Californian and Panamic biogeographic provinces needs to be determined to see how this latter proportion holds up.

Planktotrophy is nonetheless still prevalent in estuaries and habitats south of Point Conception, and the above arguments based on relative risk of larval mortality obviously do not apply uniformly to all species found in these habitats. Other kinds of adaptations for reducing larval mortality are possible, and there is no reason to expect shifts in early life-history traits such as egg size and mode of development to occur in all or even a majority of species in habitats where larval mortality is generally greater. For example, vertical migration, combined with sensory adaptations to distinguish water masses, can promote local retention of larvae, reducing mortality resulting from advection away from suitable settlement sites (Cronin 1982; Chen et al. 1997; Sponaugle et al. 2002). Predation can also be an important source of larval mortality in some regions (Rumrill 1990; but see Johnson and Shanks 2003), and organisms with sufficient larval variation in morphological, behavioral, or chemical traits are not limited to reducing or omitting a planktonic larval stage in their life cycle to avoid these threats.

Fig. 3. Relationship between egg size and shell size at hatching, by shell type, in benthic opisthobranchs from the northeastern Pacific Ocean. As in Figure 2, data reported from other regions are not included. *Alderia modesta*, which has variable development and produces two sizes of both eggs and larvae in southern California (Krug 1998), is included twice in the plot for type 1 shells.

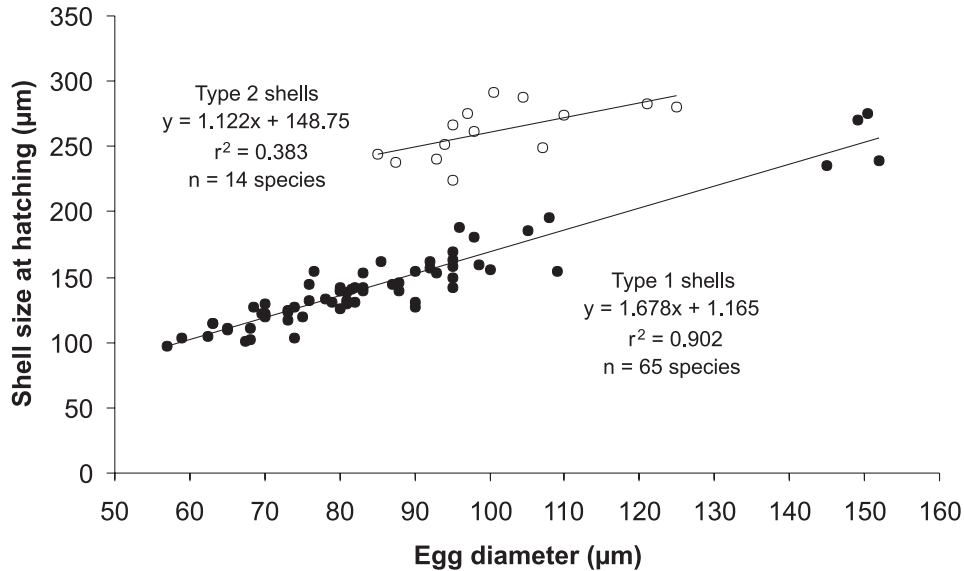


Table 3. Habitats of benthic opisthobranchs with lecithotrophic or direct modes of development in the northeast Pacific Ocean.

| Species | Mode of development | Habitat |
|--|--------------------------------------|---|
| <i>Acteocina inculata</i> | Capsular metamorphic | Bays |
| <i>Haminoea callidegenita</i> * | Lecithotrophic, capsular metamorphic | Bays and lagoons |
| <i>Runcina macfarlandi</i> | Ametamorphic | High intertidal pools, outer coast |
| <i>Phyllaplysia taylori</i> | Capsular metamorphic | Bays |
| <i>Alderia modesta</i> | Planktotrophic, lecithotrophic | Bays; lecithotrophic development is known only from the south |
| <i>Adalaria proxima</i> | (Lecithotrophic) | Outer coast, circumboreal |
| <i>Dendrodoris nigromaculata</i> | Ametamorphic | Outer coast, south |
| <i>Dendrodoris</i> sp. 3 of Behrens (1991) | Ametamorphic | Outer coast, 1° south |
| <i>Doriopsilla gemmela</i> | Lecithotrophic | Outer coast, 1° south |
| <i>Doriopsilla spaldingi</i> | Direct | Outer coast, 1° south |
| <i>Doto amyra</i> | Lecithotrophic | Outer coast |
| <i>Lomanotus vermiformis</i> | (Lecithotrophic) | Outer coast, south |
| <i>Anteaeolidiella indica</i> * | Lecithotrophic | Mainly bays, south |
| <i>Phidiana hiltoni</i> | Lecithotrophic | Outer coast |
| <i>Tenellia adspersa</i> * | Planktotrophic, lecithotrophic | Bays |

Note: South, found only south of Point Conception, California; 1° south, most of distribution lies south of Point Conception. Developmental modes determined from specimens from outside the northeast Pacific are in parentheses. An asterisk (*) indicates an introduced or cryptogenic species (see text). Range and habitat information are from Behrens (1991, 2004), sources listed in Table 1, and personal observations.

Non-feeding modes of development can have selective advantages other than reduction of larval mortality, and this reduction does not necessarily underlie all examples of this type of development observed in the northeast Pacific or elsewhere. For example, ametamorphic development can produce larger juveniles than planktotrophic or lecithotrophic development (Hadfield and Miller 1987) and may therefore effectively reduce juvenile mortality stemming from benthic predation or prey-induced size constraints. In some species, overall fitness may be little affected by mode of development (e.g., Levin and Huggett 1990), leaving other mechanisms of evolution, such as founder effects and genetic drift, to influence egg size and mode of development (see Todd et al. 2001).

Once lost, larval feeding structures are rarely regained, and whole lineages can become constrained to non-feeding modes of development that may offer no selective advantage in new or changed environments. In the northeast Pacific Ocean this constraint appears to have had little effect on the overall pattern of development. Non-feeding modes of development are rare and are spread among unrelated lineages (nine families in four orders), most of which contain sympatric species with planktotrophic development. The genus *Runcina*, represented in the northeast Pacific by *R. macfarlandi*, is apparently constrained to direct development, and northeast and eastern Pacific species of *Phidiana* and *Dendrodoris* may be limited to non-feeding modes as well (Table 1 and unpublished observations).

Table 4. Number of species of Echinodermata with planktotrophic versus non-feeding modes of development in the north-east Pacific Ocean.

| Class | Mode of development | |
|---------------|---------------------|-------------|
| | Planktotrophic | Non-feeding |
| Asteroidea | 10 | 14 |
| Crinoidea | 0 | 1 |
| Echinoidea | 7 | 1 |
| Holothuroidea | 3 | 11 |
| Ophiuroidea | 6 | 2 |
| Total | 26 | 29 |

Note: Data compiled from Strathmann (1987), McEdward and Miner (2001), and Miller (2001). Non-feeding development in echinoderms includes lecithotrophic and direct modes analogous to those in opisthobranchs or, more strictly speaking, all examples of lecithotrophic nutrition and direct morphogenesis as outlined by McEdward and Miner (2001).

Small adult size is often associated with increased brooding and direct development in related, co-occurring marine invertebrates (Strathmann and Strathmann 1982) and might underlie the pattern observed in northeast Pacific opisthobranchs, irrespective of the above biogeographic considerations. Except for *Doriopsilla spaldingi*, the directly developing species listed in Table 3 do tend to be smaller than their relatives in the northeast Pacific that have a pelagic larval stage (Table 1; also see adult sizes reported in Behrens 1991, 2004). However, the species in Table 3 with lecithotrophic development are not smaller than congeneric and confamilial species with planktotrophic development from the northeast Pacific (Behrens 1991, 2004; Goddard 1996).

Egg size was a good predictor of shell size at hatching for species with type 1 shells, but not for those with type 2 shells. This is not surprising given the close fit of the spiral, type 1 shell to the body and the lack of examples of extra-zygotic yolk supplies (which might result in hatching larvae larger than those predicted based on egg size alone). In contrast, type 2 shells are more elongate and spacious than type 1 shells at hatching (Fig. 1) and, in most cases, will grow little, if at all, after hatching; instead, the body grows during larval development to fill the shell (Hadfield and Switzer-Dunlap 1984). Consequently, shell size at hatching in these species generally indicates what the size of the body will be after larval development has been completed, rather than reflecting the size of the body at hatching (which is necessarily dependent on egg size). This was also apparent in the fact that type 2 shells were larger than type 1 shells developing from similarly sized eggs (Fig. 3).

The prediction that planktotrophy should be the predominate mode of development in the northeast Pacific should apply to taxa other than just opisthobranchs. At first glance, this does not appear to be the case for the Echinodermata, another taxon whose development has been well studied in this region as well as worldwide (Emlet et al. 1987; Emlet 1990; Strathmann 1987; McEdward and Miner 2001; Miller 2001). Extracting from these compilations data on developmental mode of northeast Pacific echinoderms, particularly those from regions north of Point Conception, we can see that more than half of the 55 species studied have non-feeding modes of development (Table 4). However, based on

the classification and phylogenies in McEdward and Miner (2001), it becomes clear that phylogeny has constrained developmental mode in these species of Echinodermata to a much greater extent than in opisthobranchs from this region. Twenty-five of the 29 species in Table 4 with non-feeding development are from higher taxa (including one class, a number of orders and families, and one genus) composed entirely of species with non-feeding modes of development. Without these species, the proportions of echinoderms with planktotrophic and non-feeding development in the northeast Pacific are 87% and 13%, respectively, much closer to the 94% and 6% observed for native opisthobranchs from regions north of Point Conception. Why echinoderm taxa limited to non-feeding development have been relatively more successful at colonizing or radiating in the northeast Pacific compared with their counterparts in the Opisthobranchia is beyond the scope of this paper. However, it should be noted that the two groups differ significantly in life histories and trophic roles. Opisthobranchs are generally small, subannual to biennial, semelparous, and predatory (Thompson 1976; Todd et al. 2001), whereas echinoderms are relatively large, long-lived, and iteroparous, with many suspension and deposit-feeding representatives (e.g., Chia and Walker 1991; Pearse and Cameron 1991). The extant classes of echinoderms also originated much earlier than even the earliest known opisthobranchs (Clarkson 1998), perhaps increasing the probability that feeding larvae have been lost in more lineages by chance alone.

The overall pattern of development in prosobranch gastropods from the northeast Pacific (see Table 11.1 in Strathmann 1987) appears to be similar to that in echinoderms from this region. Many species have non-feeding modes of development, but the majority of these are from taxa, such as the Vetigastropoda, Patellogastropoda, Trochidae, and Muricidae, constrained to these modes. Like the echinoderms, prosobranchs are longer lived than opisthobranchs, are iteroparous, and also originated earlier.

Virtually all decapod Crustacea from the northeast Pacific Ocean hatch as feeding zoea larvae and have long larval durations (Strathmann 1987; Jensen 1995; Puls 2001). One conspicuous exception is *Sclerocrangon boreas* (Phipps, 1774), a circumboreal crangonid shrimp with direct development that is rarely found south of Alaska (Jensen 1995). However, owing to their body plans, decapods and other crustaceans may not be as vulnerable to the same sources of planktonic mortality as other taxa. Crustacean larvae attain larger sizes and are more powerful swimmers (owing to their use of muscle-powered limbs rather than cilia) than those of other taxa. They also possess well-developed sensory organs and an exoskeleton ideally suited for the production of strong and lightweight spines to defend against predators. These traits may better enable them to overcome and counter sources of planktonic mortality, especially advection away from favorable settlement sites, and take advantage of planktonic food supplies (e.g., Shanks 1995; Sponaugle et al. 2002). Potential effects of food limitation notwithstanding, biogeographic patterns of developmental mode in this taxon may therefore be less variable than in other taxa, such as Mollusca and Echinodermata.

Planktotrophy is significantly more prevalent in opisthobranchs from the northeast Pacific Ocean than in opistho-

branches worldwide (Table 2), especially considering that many of the older data in Table 1 were included in Hadfield and Miller's (1987) global compilation and summary. Assuming that there has not been a historical bias toward reporting examples of lecithotrophic and direct development in opisthobranchs, other regions of the world must therefore have significantly higher proportions of species with the non-feeding modes of development than observed in the northeast Pacific. A few published compilations support this conclusion. Clark and Goetzfried (1978) reported that 41% and 16% of 32 species of nudibranchs and sacoglossan opisthobranchs from southeast Florida had lecithotrophic and direct development, respectively, and compared these proportions to the 11% and 0% of 18 species and 16% and 10% of 20 species they calculated for southern New England and Britain, respectively. Small sample sizes notwithstanding, they attributed the high incidence of direct development in Florida to the prevalence of what they perceived as "stable" adult food supplies, "reducing the need for a pelagic dispersal stage". Clark and Goetzfried concluded that "direct development...is selected in areas of high climatic or trophic stability". Hadfield and Switzer-Dunlap (1984) pointed out that there are many known examples of opisthobranchs with planktotrophic development that prey as adults on long-lived, persistent prey, such as corals and sponges, in both tropical and temperate regions, and they did not consider Clark and Goetzfried's (1978) conclusion to be broadly supported. Clark and Goetzfried (1978) also ignored the potential advantages, under the environmental conditions they described as "stable", of the increases in fecundity, recruitment, and fitness possible with planktotrophy.

An alternative explanation for the high proportions of species with lecithotrophic and direct development in Florida is that the non-feeding modes have been selected for by less productive subtropical and tropical waters unfavorable to larval feeding and growth and by an increased risk of advection away from favorable settlement sites owing to (i) the fast Florida current and (ii) steep latitudinal gradients in substratum type and surface temperatures on the east coast of North America (Tcherneria 1980; Berger 1989; Pickard and Emory 1990). In stark contrast to the situation at similar latitudes in the northeast Pacific, a larva hatched on a coral reef in Florida and accidentally transported north into New England is not likely to encounter benthic habitats resembling those of its natal origin and, without entering much colder nearshore countercurrents, has little chance of returning home.

More recently, Gonsalves-Jackson (2001) reported in an abstract that 100% of 39 opisthobranchs from the Pacific coast of Panama have "planktonic" development, compared with 83% of 29 species from the Atlantic side. She pointed out that coastal waters on the Pacific side have higher primary productivity and "presumably can more reliably support planktonic larval feeding", and she also alluded to differences between the two regions in substratum type. Her conclusions are consistent with the predictions made above concerning planktonic food supplies and the risk of larval mortality, but are limited by her lack of discrimination between planktotrophic and lecithotrophic modes of larval development. Without more information on the nutrition of the planktonic larvae, we cannot yet rule out that the lecithotrophic form of non-feeding development is actually more

prevalent on the Pacific side of the isthmus than both non-feeding modes combined on the Atlantic side.

Acknowledgements

I thank Shane Anderson and Dave Farrar of MSI for collecting opisthobranchs subtidally in the Santa Barbara area and Lise Schickel Goddard for assistance with collecting and record keeping in the field. I also thank Sandra Millen, Angel Valdés, and Dave Behrens for alerting me to recent changes in taxonomic nomenclature. Chris Todd and three anonymous reviewers made useful suggestions on the manuscript. Much of the work presented here began as part of my dissertation research at the University of Oregon, and I would like to thank again Peter Frank, my major professor, for his support and mentorship during that period.

References

- Anderson, E.S. 1971. The association of the nudibranch *Rostanga pulchra* MacFarland, 1905 with the sponges *Ophlitaspongia pennata*, *Esperiopsis originalis*, and *Plocamia karykina*. Ph.D. thesis, University of California, Santa Cruz, Calif.
- Austin, W.C. 1985. An annotated checklist of marine invertebrates in the cold temperate northeast Pacific. Khoyatan Marine Laboratory, Cowichan Bay, B.C.
- Behrens, D.W. 1991. Pacific coast nudibranchs. Sea Challengers, Monterey, Calif.
- Behrens, D. 1998. *Doriopsilla spaldingi* Valdés & Behrens, 1998 [online]. Available from <http://slugsite.us/bow/nudwk134.htm> [cited 30 December 2004].
- Behrens, D.W. 2004. Pacific coast nudibranchs. Suppl. II. New species to the Pacific coast and new information on the oldies. Proc. Calif. Acad. Sci. **55**: 11–54.
- Behrens, D.W., and Henderson, R. 1981. Two new cryptobranch dorid nudibranchs from California. Veliger, **24**: 120–128.
- Berger, W.H. 1989. Global maps of ocean productivity. In Productivity of the oceans: present and past. Edited by W.H. Berger, V.S. Smetacek, and G. Wefer. John Wiley & Sons, New York. pp. 429–455.
- Bertsch, H., and Hirschberg, J. 1973. Notes on the veliger of the opisthobranch *Phyllaplysia taylori*. Tabulata, **6**: 3–5.
- Bickell, L.R., and Chia, F.S. 1979. Organogenesis and histogenesis in the planktotrophic veliger of *Doridella steinbergae* (Opisthobranchia: Nudibranchia). Mar. Biol. (Berl.), **52**: 291–313.
- Bickell, L.R., and Kempf, S.C. 1983. Larval and metamorphic morphogenesis in the nudibranch *Melibe leonina* (Mollusca: Opisthobranchia). Biol. Bull. (Woods Hole), **165**: 119–138.
- Blanchette, C.A., Miner, B.G., and Gaines, S.D. 2002. Geographic variability in form, size and survival of *Egretta menziesii* around Point Conception, California. Mar. Ecol. Prog. Ser. **239**: 69–82.
- Bonar, D.B. 1978. Morphogenesis at metamorphosis in opisthobranch molluscs. In Settlement and metamorphosis of marine invertebrate larvae. Edited by F.S. Chia and M.E. Rice. Elsevier, New York. pp. 177–196.
- Boucher, L.M. 1983. Extra-capsular yolk bodies in the egg masses of some tropical Opisthobranchia. J. Molluscan Stud. **49**: 232–241.
- Bridges, C.B. 1975. Larval development of *Phyllaplysia taylori* Dall, with a discussion of development in the Anaspidea (Opisthobranchiata: Anaspidea). Ophelia No. **14**: 161–184.

- Bridges, C., and Blake, J.A. 1972. Embryology and larval development of *Coryphella trilineata* O'Donoghue, 1921 (Gastropoda: Nudibranchia). *Veliger*, **14**: 293–297.
- Briggs, J.C. 1974. Marine zoogeography. McGraw-Hill, New York.
- Briggs, K.T., Tyler, W.B., Lewis, D.B., and Carlson, D.R. 1987. Bird communities at sea off California: 1975 to 1983. *Stud. Avian Biol.* No. **11**.
- Burton, R.S. 1998. Intraspecific phylogeography across the Point Conception biogeographic boundary. *Evolution*, **52**: 734–745.
- Carlton, J.T. 1996. Biological invasions and cryptogenic species. *Ecology*, **77**: 1653–1655.
- Charlotte, J.H., Emler, R.B., and Littlewood, D.T.J. 2003. Phylogeny and evolution of developmental mode in temnopleurid echinoids. *Mol. Phylogenet. Evol.* **28**: 99–118.
- Chen, Y.H., Shaw, P.T., and Wolcott, T.G. 1997. Enhancing estuarine retention of planktonic larvae by tidal currents. *Estuar. Coast. Shelf Sci.* **45**: 525–533.
- Chia, F.-S. 1974. Classification and adaptive significance of developmental patterns in marine invertebrates. *Thalassia Jugosl.* **10**: 121–130.
- Chia, F.-S., and Koss, R. 1978. Development and metamorphosis of the planktotrophic larvae of *Rostanga pulchra* (Mollusca: Nudibranchia). *Mar. Biol. (Berl.)*, **46**: 109–119.
- Chia, F.-S., and Koss, R. 1988. Induction of settlement and metamorphosis of the veliger larvae of the nudibranch, *Onchidoris bilamellata*. *Int. J. Invertebr. Reprod. Dev.* **14**: 53–70.
- Chia, F.-S., and Walker, C.W. 1991. Echinodermata: Asteroidea. In *Reproduction of marine invertebrates*. Vol. VI. Echinoderms and lophophorates. Edited by A.C. Giese, J.S. Pearse, and V.B. Pearse. Boxwood Press, Pacific Grove, Calif. pp. 301–353.
- Chivers, D.D. 1967. Observations on *Pleurobranchaea californica* MacFarland, 1966 (Opisthobranchia, Notaspidea). *Proc. Calif. Acad. Sci.* **32**: 515–521.
- Clark, K.B., and Goetzfried, A. 1978. Zoogeographic influences on development patterns of North Atlantic Ascoglossa and Nudibranchia, with a discussion of factors affecting egg size and number. *J. Molluscan Stud.* **44**: 283–294.
- Clark, K.B., and Jensen, K.R. 1981. A comparison of egg size, capsule size, and development patterns in the order Asoglossa (Sacoglossa) (Mollusca: Opisthobranchia). *Int. J. Invertebr. Reprod.* **3**: 57–64.
- Clarkson, E.N.K. 1998. Invertebrate paleontology and evolution. Blackwell Science, Oxford.
- Cohen, A.N., and Carlton, J.T. 1995. Nonindigenous species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and delta. US Fish and Wildlife Service, Washington, D.C., and Connecticut Sea Grant College Program, Groton, Conn.
- Cronin, T.W. 1982. Estuarine retention of larvae of the crab *Rhithropanopeus harrisi*. *Estuar. Coast. Shelf Sci.* **15**: 207–220.
- Daily, M.D., Anderson, J.W., Reish, D.J., and Gorsline, D.S. 1993. The southern California bight: background and setting. In *Ecology of the southern California bight*. Edited by M.D. Dailey, D.J. Reish, and J.W. Anderson. University of California Press, Berkeley, Calif. pp. 1–18.
- DeFreese, D.E., and Clark, K.B. 1983. Analysis of reproductive energetics of Florida Opisthobranchia (Mollusca: Gastropoda). *Int. J. Invertebr. Reprod.* **6**: 1–10.
- Dehnel, P.A., and Kong, D.C. 1979. The effect of temperature on developmental rates in the nudibranch *Cadlina luteomarginata*. *Can. J. Zool.* **57**: 1835–1844.
- Emler, R.B. 1986. Facultative planktotrophy in the tropical echinoid *Clypeaster rosaceus* (Linnaeus) and a comparison with obligate planktotrophy in *Clypeaster subdepressus* (Gray) (Clypeasteroidea: Echinoidea). *J. Exp. Mar. Biol. Ecol.* **95**: 183–202.
- Emler, R.B. 1990. World patterns of developmental mode in echinoid echinoderms. In *Advances in invertebrate reproduction 5*. Edited by M. Hoshi and O. Yamashita. Elsevier, New York. pp. 329–335.
- Emler, R.B., McEdward, L.R., and Strathmann, R.R. 1987. Echinoderm larval ecology viewed from the egg. In *Echinoderm studies II*. Edited by M. Jangoux and J.M. Lawrence. AA Balkema, Rotterdam. pp. 55–136.
- Engel, C.P. 1976. The biology and life history of the nudibranch *Flabellinopsis iodinea* (Cooper, 1863). Ph.D. thesis, University of California, Santa Barbara, Calif.
- Eyster, L.S. 1979. Reproduction and developmental variability in the opisthobranch *Tenellia pallida*. *Mar. Biol. (Berl.)*, **51**: 133–140.
- Eyster, L.S. 1980. Distribution and reproduction of shell-less opisthobranchs from South Carolina. *Bull. Mar. Sci.* **30**: 580–599.
- Eyster, L.S., and Eckelbarger, K.J. 1979. Reproduction in the aeolid nudibranch *Spurilla neapolitana*. *West. Soc. Malacol. Annu. Rep.* **12**: 9–10.
- Foster, M.S., De Vogelaere, A.P., Oliver, J.S., Pearse, J.S., and Harrold, C. 1991. Open coast intertidal and shallow subtidal ecosystems of the northeast Pacific. In *Ecosystems of the world*. Vol. 24. Intertidal and littoral ecosystems. Edited by A.C. Mathieson and P.H. Nienhuis. Elsevier, Amsterdam. pp. 235–272.
- Gibson, G.D., and Chia, F.-S. 1989a. Embryology and larval development of *Haminoea vesicula* Gould (Opisthobranchia: Cephalaspidea). *Veliger*, **32**: 409–412.
- Gibson, G.D., and Chia, F.-S. 1989b. Developmental variability (pelagic and benthic) in *Haminaea callidegenita* (Opisthobranchia: Cephalaspidea) is influenced by egg mass jelly. *Biol. Bull. (Woods Hole)*, **176**: 103–110.
- Goddard, J.H.R. 1984. The opisthobranchs of Cape Arago, Oregon, with notes on their biology and a summary of benthic opisthobranchs known from Oregon. *Veliger*, **27**: 143–163.
- Goddard, J.H.R. 1987. Observations on the opisthobranch mollusks of Punta Gorda, California, with notes on the distribution and biology of *Crimora coneja*. *Veliger*, **29**: 267–273.
- Goddard, J.H.R. 1991. Unusually large polar bodies in an aeolid nudibranch: a novel mechanism for producing extra-embryonic yolk reserves. *J. Molluscan Stud.* **57**(4)(Suppl.): 143–152.
- Goddard, J.H.R. 1992. Patterns of development in nudibranch molluscs from the northeast Pacific Ocean, with regional comparisons. Ph.D. thesis, University of Oregon, Eugene, Ore.
- Goddard, J.H.R. 1996. Lecithotrophic development in *Doto amyra* (Nudibranchia: Dendronotacea), with a review of developmental mode in the genus. *Veliger*, **39**: 43–54.
- Goddard, J. 2000. *Stiliger* sp. from Baja California, Mexico [online]. Available from <http://www.seaslugforum.net/display.cfm?id=2620> [cited 28 December 2004].
- Goddard, J.H.R. 2001a. The early veliger larvae of *Aegires albopunctatus* (Nudibranchia: Notodorididae), with morphological comparisons to members of the Notaspidea. *Veliger*, **44**: 398–400.
- Goddard, J.H.R. 2001b. Mollusca: Gastropoda. In *An identification guide to the larval marine invertebrates of the Pacific Northwest*. Edited by A.L. Shanks. Oregon State University Press, Corvallis, Ore. pp. 86–128.
- Gonsalves-Jackson, D.C. 2001. Developmental strategies in opisthobranch mollusks across the Isthmus of Panama. *Am. Zool.* **41**: 1457–1458.
- Gosliner, T.M. 1995. Introduction and spread of *Philine auriformis*

- (Gastropoda: Opisthobranchia) from New Zealand to San Francisco Bay and Bodega Harbor. *Mar. Biol. (Berl.)*, **122**: 249–255.
- Gosliner, T.M., and Millen, S.V. 1984. Records of *Cuthona pustulata* from the Canadian Pacific. *Veliger*, **26**: 183–187.
- Gosliner, T.M., Schaefer, M.C., and Millen, S.V. 1999. A new species of *Doriopsilla* (Nudibranchia: Dendroborididae) from the Pacific Coast of North America, including a comparison with *Doriopsilla albopunctata* (Cooper, 1863). *Veliger*, **42**: 201–210.
- Greene, R.W. 1968. The egg masses and veligers of southern California sacoglossan opisthobranchs. *Veliger*, **11**: 100–104.
- Hadfield, M.G., and Miller, S.E. 1987. On developmental patterns of opisthobranchs. *Am. Malacol. Bull.* **5**: 197–214.
- Hadfield, M.G., and Switzer-Dunlap, M. 1984. Opisthobranchs. In *The mollusca*. Vol. 7. Reproduction. *Edited by* A.S. Tompa, N.H. Verdonk, and J.A.M. van den Biggelaar. Academic Press, New York. pp. 209–350.
- Hand, C., and Steinberg, J. 1955. On the occurrence of the nudibranch *Alderia modesta* (Lovén, 1844) on the central California coast. *Nautilus*, **69**: 22–28.
- Harrigan, J.F., and Alkon, D.L. 1978. Larval rearing, metamorphosis, growth and reproduction of the eolid nudibranch *Hermisenda crassicornis* (Eschscholtz, 1831) (Gastropoda: Opisthobranchia). *Biol. Bull. (Woods Hole)*, **154**: 430–439.
- Hickey, B.M. 1979. The California current system — hypotheses and facts. *Prog. Oceanogr.* **8**: 191–279.
- Holleman, J.J. 1972. Observations on growth, feeding, reproduction, and development in the opisthobranch *Fiona pinnata* (Eschscholtz). *Veliger*, **15**: 142–146.
- Hurst, A. 1967. The egg masses and veligers of thirty northeast Pacific opisthobranchs. *Veliger*, **9**: 255–288.
- Jackson, G.A., and Strathmann, R.R. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. *Am. Nat.* **118**: 16–26.
- Jensen, G.C. 1995. Pacific coast crabs and shrimps. Sea Challengers, Monterey, Calif.
- Johnson, K.B., and Shanks, A.L. 2003. Low rates of predation on planktonic marine invertebrate larvae. *Mar. Ecol. Prog. Ser.* **248**: 125–139.
- Kempf, S.C. 1981. Long-lived larvae of the gastropod *Aplysia juliana*: do they disperse and metamorphose or just slowly fade away? *Mar. Ecol. Prog. Ser.* **6**: 61–65.
- Kempf, S.C., and Hadfield, M.G. 1985. Planktotrophy by the lecithotrophic larvae of a nudibranch, *Phestilla sibogae*. *Biol. Bull. (Woods Hole)*, **169**: 119–130.
- Kempf, S.C., and Willows, A.O. 1977. Laboratory culture of the nudibranch *Tritonia diomedea* Bergh (Tritonidae: Opisthobranchia) and some aspects of its behavioral development. *J. Exp. Mar. Biol. Ecol.* **30**: 261–276.
- Kriegstein, A.R. 1977. Stages in the post-hatching development of *Aplysia californica*. *J. Exp. Zool.* **199**: 275–288.
- Kriegstein, A.R., Castellucci, V., and Kandel, E.R. 1974. Metamorphosis of *Aplysia californica* in laboratory culture. *Proc. Natl. Acad. Sci. U.S.A.* **71**: 3654–3658.
- Krug, P.J. 1998. Poecilogony in an estuarine opisthobranch: planktotrophy, lecithotrophy, and mixed clutches in a population of the sacoglossan, *Alderia modesta*. *Mar. Biol. (Berl.)*, **132**: 483–494.
- Lance, J.R. 1982. *Dendrodoris nigromaculata*. Opisthobranch Newsletter, **14**: 29. [Illustration only.] Newsletter available from S.J. Long, 12537 9th NW, Seattle, WA 98177, USA.
- Levin, L.A., and Huggett, D.V. 1990. Implications of alternate reproductive modes for seasonality and demography in an estuarine polychaetes. *Ecology*, **71**: 2191–2208.
- Marcus, Er., and Marcus, Ev. 1967. American opisthobranch mollusks. *Stud. Trop. Oceanogr. (Miami)*, **6**: 1–256.
- McDonald, G.R. 1983. A review of the nudibranchs of the California coast. *Malacologia*, **24**: 114–276.
- McEdward, L.R., and Miner, B.G. 2001. Larval and life-cycle patterns in echinoderms. *Can. J. Zool.* **79**: 1125–1170.
- McGowan, J.A., and Pratt, I. 1954. The reproductive system and early embryology of the nudibranch *Archidoris montereyensis* (Cooper). *Bull. Mus. Comp. Zool. Harv. Univ.* **111**: 261–276.
- Mileikovsky, S.A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol. (Berl.)*, **10**: 193–213.
- Millen, S.V. 1982. A new species of dorid nudibranch (Opisthobranchia: Mollusca) belonging to the genus *Anisodoris*. *Can. J. Zool.* **60**: 2694–2705.
- Millen, S.V. 1985. The nudibranch genera *Onchidoris* and *Diaphorodoris* (Mollusca, Opisthobranchia) in the northeastern Pacific. *Veliger*, **28**: 80–93.
- Millen, S.V. 1986. Northern, primitive tergipedid nudibranchs, with a description of a new species from the Canadian Pacific. *Can. J. Zool.* **64**: 1356–1362.
- Millen, S.V. 1987. The nudibranch genus *Adalaria*, with a description of a new species from the northeastern Pacific. *Can. J. Zool.* **65**: 2696–2702.
- Millen, S.V. 1989. Opisthobranch range extensions in Alaska with the first records of *Cuthona viridis* (Forbes, 1840) from the Pacific. *Veliger*, **32**: 64–68.
- Millen, S.V., and Gosliner, T.M. 1985. Four new species of dorid nudibranchs belonging to the genus *Aldisa* (Mollusca: Opisthobranchia), with a revision of the genus. *Zool. J. Linn. Soc.* **84**: 195–233.
- Miller, B.A. 2001. Echinodermata. In *An identification guide to the larval marine invertebrates of the Pacific Northwest*. *Edited by* A.L. Shanks. Oregon State University Press, Corvallis, Ore. pp. 270–290.
- Morris, R.H., Abbott, D.P., and Haderlie, E.C. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, Calif.
- Mulliner, D.K. 1972. Breeding habits and life cycles of three species of nudibranchs from the eastern Pacific. *Festinus*, **3**: 1–5.
- Pearse, J.S., and Cameron, R.A. 1991. Echinodermata: Echinoidea. In *Reproduction of marine invertebrates*. Vol. VI. Echinoderms and lophophorates. *Edited by* A.C. Giese, J.S. Pearse, and V.B. Pearse. Boxwood Press, Pacific Grove, Calif. pp. 513–662.
- Pickard, G.L., and Emery, W.J. 1990. Descriptive physical oceanography. Pergamon Press, Oxford.
- Puls, A.L. 2001. Arthropoda: Decapoda. In *An identification guide to the larval marine invertebrates of the Pacific Northwest*. *Edited by* A.L. Shanks. Oregon State University Press, Corvallis, Ore. pp. 179–250.
- Ricketts, E.F., Calvin, J., and Hedgpeth, J.W. 1985. Between Pacific tides. 5th ed. *Revised by* D.W. Phillips. Stanford University Press, Stanford, Calif.
- Robilliard, G.A. 1970. The systematics and some aspects of the ecology of the genus *Dendronotus*. *Veliger*, **12**: 433–479.
- Robilliard, G.A. 1971. A new species of *Polycera* (Opisthobranchia: Mollusca) from the northeastern Pacific, with notes on other species. *Synopsis*, **4**: 235–243.
- Robilliard, G.A. 1972. A new species of *Dendronotus* from the northeastern Pacific, with notes on *Dendronotus nanus* and *Dendronotus robustus* (Mollusca: Opisthobranchia). *Can. J. Zool.* **50**: 421–432.
- Roller, R.A. 1972. Three new species of eolid nudibranchs from the west coast of North America. *Veliger*, **14**: 416–423.

- Ruiz, G.M., Fofonoff, P.W., Carlton, J.T., Wonham, M.J., and Hines, A.H. 2000. Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annu. Rev. Ecol. Syst.* **31**: 481–531.
- Rumrill, S.S. 1990. Natural mortality of invertebrate larvae. *Ophelia* No. **32**: 163–198.
- Schmekel, L., and Portmann, A. 1982. *Opisthobranchia des Mittelmeeres, Nudibranchia und Saccoglossa*. Springer-Verlag, Berlin.
- Shanks, A.L. 1995. Oriented swimming by megalopae of several eastern north Pacific crab species and its potential role in their onshore migration. *J. Exp. Mar. Biol. Ecol.* **186**: 1–16.
- Sponaugle, S., Cowen, R.K., Shanks, A., Morgan, S.G., Leis, J.M., Pineda, J.S. et al. 2002. Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. *Bull. Mar. Sci.* **70**(1)(Suppl.): 341–375.
- Strathmann, M.F. 1987. *Reproduction and development of marine invertebrates of the northern Pacific coast*. University of Washington Press, Seattle, Wash.
- Strathmann, R.R. 1978. The evolution and loss of feeding larval stages of marine invertebrates. *Evolution*, **32**: 894–906.
- 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. 1986. What controls the type of larval development? Summary statement for the evolution session. *Bull. Mar. Sci.* **39**: 616–622.
- Strathmann, R.R. 1993. Hypotheses on the origins of marine larvae. *Annu. Rev. Ecol. Syst.* **24**: 89–117.
- Strathmann, R., and Strathmann, M. 1982. The relationship between adult size and brooding in marine invertebrates. *Am. Nat.* **119**: 91–101.
- Strub, P.T., Allen, J.S., Huyer, A., and Smith, R.L. 1987. Seasonal cycles of currents, temperatures, winds and sea level over the northeast Pacific continental shelf: 35N to 48N. *J. Geophys. Res.* **92**: 1507–1526.
- Tcherneria, P. 1980. *Descriptive regional oceanography*. Pergamon Press, Oxford.
- Thompson, T.E. 1961. The importance of the larval shell in the classification of the Saccoglossa and Acoela (Gastropoda, Opisthobranchia). *Proc. Malacol. Soc. Lond.* **34**: 233–238.
- Thompson, T.E. 1967. Direct development in a nudibranch, *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. *J. Mar. Biol. Assoc. U.K.* **47**: 1–22.
- Thompson, T.E. 1976. *Biology of opisthobranch molluscs*. Vol. I. Ray Society, London.
- Thompson, T.E., and Brodie, G. 1988. Eastern Mediterranean Opisthobranchia: Runcinidae (Runcinacea), with a review of runcinid classification and a description of a new species from Fiji. *J. Molluscan Stud.* **54**: 339–346.
- Thompson, T.E., and Brown, G.H. 1984. *Biology of opisthobranch molluscs*. Vol. II. Ray Society, London.
- Thompson, T.E., and Salghetti-Drioli, U. 1984. Unusual features of the development of the sacoglossan *Elysia hopei* in the Mediterranean Sea. *J. Molluscan Stud.* **50**: 61–63.
- Thorson, G. 1950. Reproduction and larval ecology of marine bottom invertebrates. *Biol. Rev. Camb. Philos. Soc.* **25**: 1–45.
- Todd, C.D. 1983. Reproductive and trophic ecology of nudibranch molluscs. *In The mollusca*. Vol. 6. Ecology. Edited by W.D. Russel-Hunter. Academic Press, New York. pp. 225–259.
- Todd, C.D. 1991. Larval strategies of nudibranch molluscs: similar means to the same end? *Malacologia*, **32**: 273–289.
- Todd, C.D., Lambert, W.J., and Davies, J. 2001. Some perspectives on the biology and ecology of nudibranch molluscs: generalizations and variations on the theme that prove the rule. *Boll. Malacol.* **37**: 105–120.
- Valdés, A., and Behrens, D.W. 1998. A new species of *Doriopsilla* (Mollusca, Nudibranchia, Dendrodorididae) from the Pacific coast of North America. *Proc. Calif. Acad. Sci.* **50**: 307–314.
- Vance, R.R. 1973. On reproductive strategies in marine benthic invertebrates. *Am. Nat.* **107**: 339–352.
- Wares, J.P., Gaines, S.D., and Cunningham, C.W. 2001. A comparative study of asymmetric migration events across a marine biogeographic boundary. *Evolution*, **55**: 295–306.
- Williams, L.G. 1980. Development and feeding of larvae of the nudibranch gastropods *Hermisenda crassicornis* and *Aeolidia papillosa*. *Malacologia*, **20**: 99–116.
- Yoshioka, P.M. 1986. Life history patterns of the dorid nudibranchs *Doridella steinbergae* and *Corambe pacifica*. *Mar. Ecol. Prog. Ser.* **31**: 179–184.