PATTERNS OF DEVELOPMENT IN NUDIBRANCH MOLLUSCS FROM THE NORTHEAST PACIFIC OCEAN, WITH REGIONAL COMPARISONS

by

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Biogeographic patterns of developmental mode in marine invertebrates have been examined with respect to latitude, depth, and general habitat type. Regional comparisons, which might reveal the influence of specific ecological mechanisms on mode of development, are few. The present study was undertaken to: 1) characterize early development, especially its mode, in nudibranch molluscs from the cold temperate waters of the northeast Pacific Ocean; 2) compare the development of these species to that of nudibranchs from other geographic regions; and 3) attempt to explain the observed patterns on the basis of regional differences in hydrography, geology, and primary production. Observations of egg size, embryonic development and hatching larvae were made for 30 species and were supplemented with data from the literature. All data for other regions were obtained from the literature.

Developmental mode was determined for 69 NE Pacific species, over half the known fauna. Sixty-seven (97%) have planktotrophic development and two (*Doto amyra* and the introduced *Tenellia adspersa*) produce short-term lecithotrophic larvae. No evidence for nurse-eggs was obtained in this study, and only the egg capsules of the aeolid *Cuthona lagunae* were found to contain extra-zygotic yolk reserves. These took the novel form of unusually large, yolk-filled polar bodies that were ingested by the embryonic veligers. Planktotrophic species with egg-shaped, inflated larval shells develop from larger eggs than those of species with typical spiral shells. The former, however, have shorter embryonic periods, owing, in part, to their smaller egg masses; many also hatch with eyespots.

World-wide I conclude that planktotrophy, at least among nudibranchs, is most common in regions with relatively slow currents, high standing stocks of phytoplankton, and large expanses of habitat suitable for the adults. This is documented by evidence from the NE Pacific, NE U.S., Britain, NW Red Sea, and NW Mediterranean. Nonfeeding modes of development tend to predominate in areas with fast boundary currents, oligotrophic waters, rapid changes in physical aspects of the adult environment, or in areas formerly in contact with polar waters (e.g., SE U.S., Marshall Is., New South Wales). Latitude and its correlates do not sufficiently account for the observed regional differences in mode of development.

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DEDICATION

To my parents, Janet and George Goddard,
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TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES

Chapter II

Chapter III

LIST OF FIGURES

Figure Page

Chapter I

Chapter II

LIST OF FIGURES

Chapter III

CHAPTER I

PATTERNS OF DEVELOPMENT IN NUDIBRANCH MOLLUSCS FROM THE NORTHEAST PACIFIC OCEAN, WITH REGIONAL COMPARISONS

Introduction

Development in marine invertebrates can be divided into three general types based on the presence or absence of a larval stage and on whether or not the larvae require particulate foods to complete development: (1) planktotrophic, in which larvae must feed and grow in the plankton before metamorphosing; (2) lecithotrophic, in which the larvae can metamorphose without prior feeding; and (3) "direct", in which juveniles, rather than larvae, hatch from egg capsules or brood chambers (Thorson, 1950; Mileikovsky, 1971; Grahame & Branch, 1985). Planktotrophic larvae may be pelagic or demersal (inhabiting the boundary layer just above the bottom); lecithotrophic larvae may be pelagic, demersal, or benthic (Mileikovsky, 1971; Shimek, 1986; Bosch & Pearse, 1990). The minimum pelagic period (time between hatching and onset of metamorphic competence) necessarily is longest for planktotrophic larvae. However, in the absence of the appropriate settlement cues, many planktotrophic and lecithotrophic larvae can feed and swim for long periods without losing their ability to metamorphose (e.g., Kempf & Hadfield, 1985; also see Jackson & Strathmann, 1981; Scheltema, 1986b). Feeding by he latter has been termed "facultative planktotrophy" (Chia, 1974; Kempf & Hadfield, 1985; Emlet, 1986).

As discussed by Perron & Carrier (1981), Hadfield & Switzer-Dunlap (1984), and others, for many taxa these developmental types really form an evolutionary continuum ranging from long-term planktotrophy to ametamorphic direct development. Moreover, considerable intraspecific variability and flexibility exists in developmental mode (Hines, 1986b).

Planktotrophy is considered the ancestral mode of development in most classes of marine invertebrates, and, once lost, feeding structures are generally not regained (Strathmann, 1978).

Given the physical properties, community composition, and food-rich nature of coastal waters in general (Raymont, 1980; Strathmann, 1990; Mann & Lazier, 1991) it is not surprising that most shallow water marine invertebrates possess a pelagic, feeding larval stage as an integral part of their life cycles (Thorson, 1950; Mileikovsky, 1971; Barnes et al., 1988; Strathmann, 1978, 1985, 1990). Feeding larvae require less parental investment per offspring to complete development and thus allow high fecundities (Vance, 1973; Strathmann, 1987). And while subject to pelagic predators and competitors, pelagic larvae escape the more diverse - and probably more concentrated - sources of mortality found in or adjacent to the benthos (e.g., small predators, filter and deposit-feeders, accidental ingestion by benthic grazers, exposure to surface-borne allelochemicals). Indeed, with respect to predation, the water column may be safer than the benthos for minute and relatively unprotected forms (Strathmann, 1982, 1985). For species sedentary as adults pelagic larvae are usually the principal means of dispersal to new habitats (but see Highsmith, 1985; Johannesson, 1988; Scheltema, 1986b, pp. 310-312; Martel & Chia, 1991a & b) and can be an effective means of spreading the risk associated with variable habitats (Strathmann, 1974, 1985; Palmer & Strathmann, 1981). In some taxa planktotrophic development is associated with wider geographic ranges and lower extinction rates than exist in comparable groups with nonfeeding and benthic modes of development (Shuto, 1974; Hansen, 1980; Jablonski & Lutz, 1980, 1983; Jablonski, 1986; Scheltema, 1986b).

The selective advantages of planktotrophy must be strong indeed to keep a feeding larval stage in the life cycles of organisms pelagic or planktonic as adults (Strathmann, 1985) and to produce the vertical migrations at the beginning and end of the larval stage of deep-sea invertebrates with surface feeding larvae (see review by

Gage & Taylor, 1991, chapter 13).

Planktotrophy, however, carries its own risks. Behavioral and morphological adaptations notwithstanding (see reviews by Crisp, 1974; Scheltema, 1986b; Young & Chia, 1987), currents may sweep larvae away from habitats favorable for subsequent phases of the life cycle (Jackson & Strathmann, 1981). Long stays in the plankton mean prolonged exposure to pelagic predators (Thorson, 1950), an especially serious problem if early developmental stages are subject to higher rates of predation than later stages (e.g. Pennington & Chia, 1984; Pennington et al., 1986). The abundance of planktonic food resources varies on a number of spatial and temporal scales (Raymont, 1980; Mann & Lazier, 1991), and feeding larvae may experience food shortages, reduced growth rates (leading to prolonged exposure to predators), and starvation, especially in typically oligotrophic polar and oceanic waters (Pauley et al., 1985; and see review by Olson & Olson, 1989). Finally, in some taxa planktotrophic development appears to constrain size at metamorphosis, with likely effects on juvenile survivorship (Strathmann, 1977; Hadfield & Miller, 1987).

Other things being equal, planktotrophy should predominate among closely related invertebrates inhabiting waters with high densities of planktonic food, low rates of predation on larvae, and current regimes conducive to settlement in favorable benthic habitats. As these conditions tend toward the opposite, selection could favor some or all of the following: (1) changes in the timing of reproduction; (2) larval traits that counter the environmental changes but which do not alter the basic mode of development (e.g., larger spines to protect against increased levels of predation or behaviors promoting contact with favorable habitats at favorable times); or (3) reduced dependence on planktonic food resources or reductions in the planktonic period itself. Thus, among closely related species, we might expect regional shifts in the life-history traits associated with early development (e.g., parental investment per offspring, fecundity, length of embryonic and larval periods, size at hatching and metamorphosis). If these shifts are large enough, differences in the relative proportions of the different types of development could result.

Patterns of developmental mode in closely related marine invertebrates have been examined with respect to latitude (Thorson, 1950; Ocklemann, 1965; Mileikovsky, 1971; Picken, 1979; White, 1984; Highsmith, 1985; Emlet et al.,1987; Bosch & Pearse, 1990; Emlet, 1990; Shick, 1991; and others), depth (see reviews by Mileikovsky, 1971; Gage & Taylor, 1991), and general habitat type (Spight, 1977; Nelson, 1980; Van Dolah & Bird, 1980; Hines, 1986a). However, comparisons of developmental mode by geographic region (other than latitudinal zones) are few (Emlet, 1990; R. R. Strathmann, personal communication, 1991). As stated by Emlet (1990), "such analyses would indicate the relative importance of ... regional, presumably ecological, conditions that influence the distribution of developmental modes."

Knudsen (1950) found nonpelagic development more common than pelagic development in 34 species of prosobranch molluscs from the Atlantic coast of central Africa and contrasted his results with studies from other tropical areas. Acknowledging the limitations of his sample size, Knudsen suggested that low primary production and strong offshore transport of surface waters might favor nonpelagic development in this region.

Thorson (1950, pp. 18-19) mentioned Knudsen's (1950) results and suggested that non-pelagic development might be unusually common in regions with narrow continental shelves and strong offshore transport of surface waters. He also noted (p. 14) that little was known about the significance of "starvation for the total waste of pelagic larvae". However, Thorson (1950) concluded that both of these factors were less important sources of larval mortality than predation and that the latter, in conjunction with the effects of latitudinal gradients in temperature and availability of planktonic food, was the primary environmental factor shaping mode of development. This conclusion reflects Thorson's well known empirical generalization - dubbed by Mileikovsky (1971) "Thorson's rule" - that planktotrophy predominates in shallow, tropical waters and is gradually replaced by nonpelagic, nonfeeding modes of development over increasing latitude and depth.

Ostergaard (1950) reported pelagic development in 40 of 41 species of gastropods from Hawaii and noted that this proportion was higher than for the tropical areas mentioned by Thorson (1940). Ostergaard concurred with Thorson about the influence of latitude and its correlates on developmental mode but felt that the higher proportion of pelagic development in Hawaii reflected the historical origins of the Hawaiian fauna via long-distance transport of larvae from Micronesia (also see Rosewater, 1975; Vermeij, et al., 1983; Scheltema & Williams, 1983; Scheltema, 1986a).

Natarajan (1957), working on gastropods in southern India, also found a higher incidence of pelagic development than had been reported in other tropical areas. However, he felt his results were consistent with Thorson's (1950) generalizations.

In stark contrast to Thorson's rule, Clark & Goetzfried (1978) found a significantly higher incidence of nonfeeding development in opisthobranch molluscs from south Florida than known in opisthobranchs from southern New England and the British Isles. They argued (p. 288) that "increased climatic and trophic stability" in Florida reduces "the need for a long distance dispersal mechanism" and thus, feeding modes of development. However, their hypothesis does not explain the occurrence of planktotrophy among many species of opisthobranchs feeding on "species with stable, persistent prey, such as corals, bryozoans, and sponges, in both tropical and temperate locales" (Hadfield & Switzer-Dunlap, 1984, p. 317). Moreover, Strathmann (1982, 1985, 1987) argues persuasively that long distance dispersal is better considered an accidental by-product of planktotrophy, rather than a factor selecting for it.

Wilson (1985) and Emlet (1990) noted high incidences of nonfeeding development in cowries (Cypraeidae) and echinoids, respectively, from southern Australia compared to temperate and tropical waters in general[1]. Emlet (1990) also found an abundance of nonfeeding development in echinoids from the Pacific coast of southern Japan. The patterns in Australia were attributed by both authors to historical environmental conditions and therefore found to be consistent with the general latitudinal patterns described by Thorson (1950). No explanation was offered by Emlet (1990) for the patterns of development observed in

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[1] R. B. Emlet, in a seminar presented at the University of Oregon, Eugene, on 11 November 1991, noted similar patterns for Asteroidea, Holothuroidea, chitons (Polyplacophora), and sponge crabs (Dromiidae) from southern Australia.

Japan.

In at least one case potentially significant regional differences in developmental type may have been overlooked or discounted because they did not fit the latitudinal patterns described by Thorson (1950). Mileikovsky, in his comprehensive and influential 1971 review, included in his Table 1 Knudsen's (1950) percentage of species with nonpelagic development, but mistakenly identified Knudsen's study area as the "Southwest coast of Africa". Mileikovsky then attributed the anomalously high proportion of benthic development to the "influence of the cold Guinea current". That current is among the warmest known (c.f. Pickard & Emery, 1990). Risbec's (1932, 1935) data (erroneously attributed to Thorson (1950)) suggesting a high incidence of nonpelagic development in prosobranchs from New Caledonia are footnoted by Mileikovsky (1971, Table 1) as being "insufficient". In addition, Mileikovsky notes the high number of directly developing prosobranchs found in southern Florida and the Bahamas by D'Asaro (1970) but does not discuss them as being inconsistent with Thorson's generalizations about latitude. No mention is made by Mileikovsky (or, for that matter, Thorson) that Lebour's (1945) data showing a high proportion of pelagic development among prosobranchs from Bermuda were biased owing to her sampling methods (the development of 28 of 43 species was determined by observations of veligers collected from the plankton) (Radwin & Chamberlin, 1973). Given the paucity of data from tropical regions available to Mileikovsky (1971) (see his Tables 1-3), these considerations seriously undermine, at least for tropical waters, his conclusion that "Thorson's rule (decrease in number of species with pelagic development from the Equator to the Poles, and from shallow waters to greater depths) is well substantiated by new data" (also see Radwin & Chamberlin, 1973).

On a smaller geographic scale, Emery (1972), using Lewis' (1960) data on the larval development of a variety of intertidal invertebrates from Barbados, noted that a lower proportion of species on the side of the island exposed to the north equatorial current had long periods of pelagic development compared to those on the downstream or "eddy side" of the island. Emery concluded this was evidence for lack of recruitment of larvae from other land masses (Africa and South America) and implied that long-term pelagic larvae released on the exposed side of the island would be permanently swept away from Barbados, while those released on the lee side of the island would be entrained in nearshore eddies and thus be more likely to recruit back to the island.

Emery's results are interesting but are based on a heterogenous data set (39 species belonging to 9 classes and 5 phyla) subject to taxon-specific differences in length of pelagic period and distribution around the island (e.g., chitons, with their short pelagic phase, were, by Lewis' description, virtually absent from the lee side of the island). Moreover, the two sides of the island differ with respect to other factors, such as exposure to wind and waves, that affect species distributions. Gastropods comprised half of the species examined by Lewis (1960). If Emery's analysis of the data is restricted to this group the differences in proportion of species with short or long pelagic periods from the two sides of the island completely disappear.

Many more accounts of developmental mode exist for specific localities or regions. However, most of these do not make comparisons to other regions (e.g., Lebour, 1945; D'Asaro, 1970, 1986; Bandel, 1976a & b; Clark & Jensen, 1981; Goddard, 1984; Perron, 1986).

The coastal waters of the northeast Pacific Ocean are characterized by high (but seasonal) primary production, generally slow-moving currents, and a relatively uniform hydrographic climate, especially when compared to the western boundaries of oceans at similar latitudes (Ricketts et al., 1985; Tchneria, 1980; Pickard & Emery, 1990; Mann & Lazier, 1991). Mean monthly sea surface temperatures vary only about 7°C between Point Conception, California (34°30' N latitude) and the central Washington coast (47°N) (Lynn, 1967; Landry et al., 1989); over the same latitudes on the east coast of the United States they vary almost 30° C (Franz, 1970; Gosner, 1971; Pickard & Emery, 1990). The northwest coastline itself is a finely alternating series of rocky and sandy shores punctuated by generally small estuaries (Ricketts et al., 1985: Schultz, 1990). Thus, larvae transported hundreds and possibly even thousands of kilometers north or south from their point of origin would probably still encounter habitat and conditions suitable for the benthic phase of their life cycle. Larvae transported offshore might return to shallow waters through a variety of mechanisms, including: (1) deep compensatory currents (see Efford, 1970; Scheltema, 1986b); (2) onshore flow of surface waters between periods of upwelling (Bolin & Abbott, 1963); (3) rotation of mesoscale rings or eddies (Flierl & Wroblewski, 1985; Lobel & Robinson, 1988); (4) episodic shoreward wind forcing; and (5) shoreward moving surface slicks associated with tidally generated internal waves (Shanks & Wright, 1987; Mann & Lazier, 1991). Conditions in these waters would, therefore, seem to favor planktotrophic development over nonfeeding modes of development, and we might expect the former to predominate in those taxa not yet constrained by history and other factors to the latter.

Three studies have previously examined aspects of early development in many species of nudibranch molluscs from the northeast Pacific. However, only one (see below) explicitly classified the species by developmental mode (i.e., planktotrophic, lecithotrophic, direct).

Hurst (1967) described morphological aspects of the egg masses and veliger larvae of opisthobranchs (including 25 species of nudibranchs) from the San Juan archipelago. She considered the larvae "poorly equipped for planktonic life" and was uncertain (see p. 286) if the larvae of any of the species studied would feed and grow in the plankton. Hurst was more interested in describing characters that could be used to identify larvae collected in the field and did not attempt to distingush between different modes of development.

Goddard (1984) examined the early development of 18 species from Cape Arago, Oregon and reported planktotrophic development for 17 species and short-term lecithotrophic development for one. He did not discuss these proportions but did note what seemed to be a high proportion of planktotrophic species hatching with larval eyespots. Because the appearance during ontogeny of eyespots and a propodium usually indicate metamorphic competence (Bonar, 1978), Goddard (1984) suggested that these species might have a shorter obligatory planktonic period than the planktotrophic species hatching without eyespots. His data suggest a high incidence of planktotrophic development in the northeast Pacific, but the number of species examined constitutes only 14 % of the 130 species of nudibranchs currently known from the west coast of North America north of Point Conception, California (see Behrens, 1991).

M. F. Strathmann (1987) included many of her own numerous observations and summarized many of the data available on the development of northeast Pacific opisthobranchs. Although she pointed out (p. 268) that one nudibranch species hatched "as advanced crawling veligers" (the term lecithotrophy was not used), Strathmann did not explicitly classify most of the remaining species by developmental type (with the exception of the species with "intracapsular" veligers, the "veliger type" heading in her Table 12.1 refers to shell type, which is not correlated with developmental type).

The present study was undertaken to: (1) characterize early development - especially mode of development and variability in mode of development - in nudibranch molluscs from the coastal, cold temperate waters of the northeast Pacific Ocean; (2) compare the development of these species as a group to that of nudibranchs from other parts of the world; and (3) bearing in mind the relative costs and advantages of pelagic and nonpelagic modes of development, attempt to explain the observed patterns in developmental mode on the basis of regional differences in hydrography, geography, and primary production. Finally, what predictions can we make about patterns of development in nudibranchs from other areas, and how do the results obtained in the present study apply to other taxa? These topics are addressed in the present chapter. Chapters 2 and 3 describe in more detail two of the more unusual examples of development found during the present study.

Opisthobranch molluscs are well suited for the proposed analysis owing to their diversity throughout the world's oceans (Thompson, 1976) and the ease with which developmental types can be determined (Bonar, 1978; Clark & Goetzfried, 1978). As with most other marine invertebrate taxa (Strathmann, 1978), planktotrophy is considered the ancestral mode of development in opisthobranchs. Nonfeeding development has evolved repeatedly in the subclass and, with the exception of some lecithotrophic larvae (the so-called "facultative planktotrophs"), is considered irreversible (Hadfield & Miller, 1987).

Methods

With the exception of six species (see below), adult nudibranchs were collected from the protected, low, rocky intertidal zone at Cape Arago, Oregon (Figure 1; also see Goddard, 1984 for a description of this area). Cumanotus beaumonti was collected from Coos Bay, Oregon; Doto spp. A and B from Drake's Estero, Marin County, Calif.; Hermissenda crassicornis from Port Orford, Oregon; Melibe leonina from Yaquina Bay, Oregon; and Tenellia adspersa from upper Coos Bay. After collection nudibranchs were

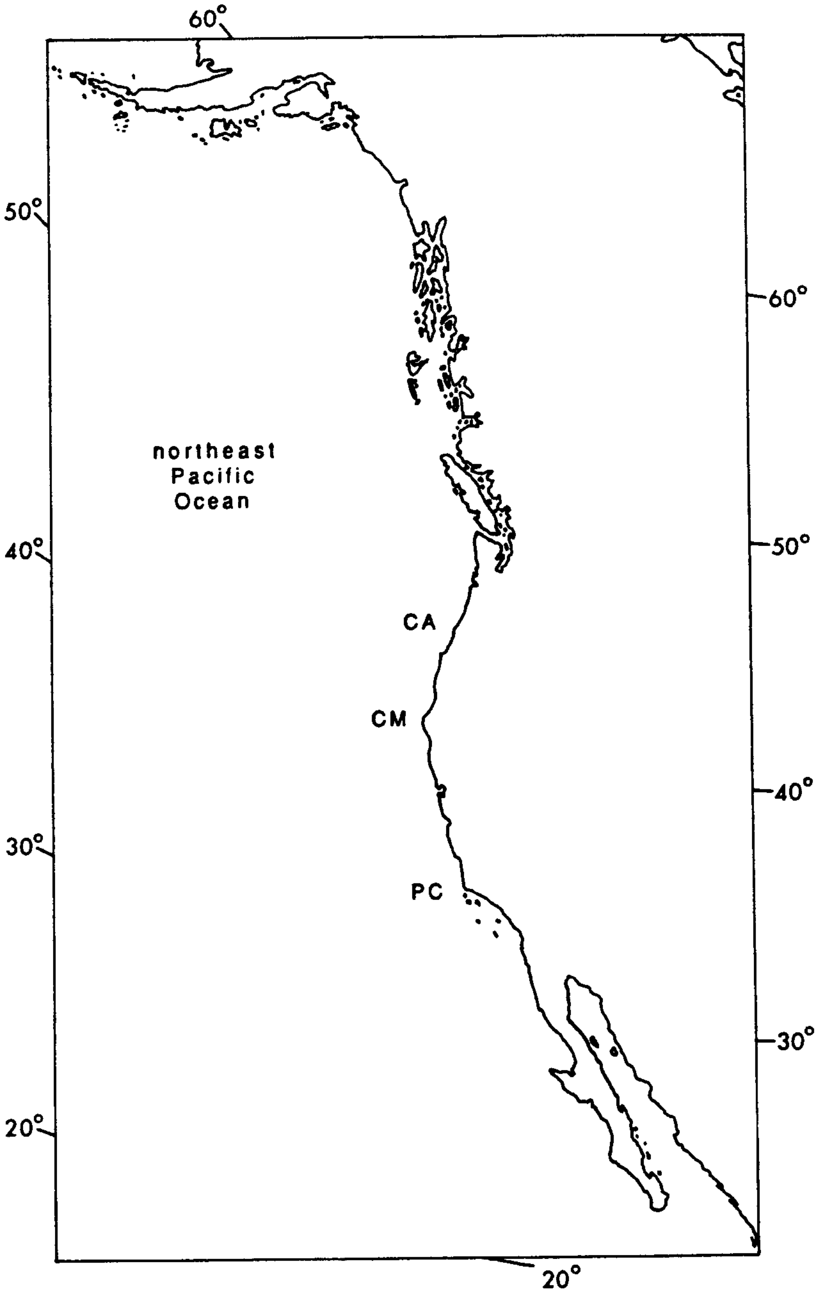

Figure 1. Map of the northeast Pacific Ocean and west coast of North America showing locations of Point Conception, Calif. (PC); Cape Mendocino, Calif. (CM); and Cape Arago, Oregon (CA).

separated by species into wide-mouthed jars or beakers of unfiltered seawater and held in a seawater bath within 1.5° C of local (Cape Arago) sea-surface temperatures. Egg masses deposited on the sides of the containers by smaller species were removed intact, examined with a compound microscope equipped with an ocular micrometer, and then transferred to separate vials of unfiltered seawater and held in the above water bath. Large egg masses were treated as above, but only small sections (from the middle of the egg mass) were used for observation. Seawater in all containers was changed once or twice daily until the veliger larvae hatched, and all containers were exposed to indirect natural lighting in the laboratory. Temperature of the water bath was measured daily to the nearest one half degree C; embryonic period (time from egg-laying to hatching of the larvae) was measured to the nearest day.

Newly hatched veligers were observed alive and their developmental type determined directly based on size, behavior, extent of their yolk reserves, and the presence or absence of propodium and eyespots (see Thompson, 1967, 1976; Bonar, 1978; Todd, 1981; and Hadfield & Switzer-Dunlap, 1984). Estimates of egg diameter and larval shell-size at hatching were obtained by measuring at least 10 uncleaved eggs or veligers from each of one or more egg masses; these values were then averaged to give means and grand means. Larval shells were measured either as the larvae were hatching from the egg mass or in newly hatched larvae immobilized by the addition of small amounts of Bouin's fixative. The latter were measured immediately after addition of the fixative (before it began to dissolve the shells). The longest dimension of the shell was used as the measure of shell-size.

The literature was searched for information pertinent to mode of development of northeast Pacific nudibranchs, especially data on egg size, shell-size at hatching, embryonic period and, of course, descriptions of hatching larvae and developmental type. Embryonic period alone is of little use in determining mode of development unless it is short (suggesting planktotrophy), long (suggesting direct development), or similar to that of congeners of known developmental type. Measurements of embryonic period are virtually useless without temperature data.

In some cases authors did not describe how they obtained values for the parameters of interest. Unless otherwise stated, I treated values reported for egg diameter and shell-size at hatching as means, or, if a range was given, calculated a midpoint and used that in place of a mean.

Regrettably, developmental data are not reported often in descriptions of new species. However, mode of development can sometimes be determined from published descriptions and figures of egg masses, by allowing either:

(1) estimations of egg and (or) veliger size or (2) examination of the occasional depictions of morphological details of the late embryos.

Hurst (1967) remains one of the most important sources of data on the veligers of northeast Pacific opisthobranchs. However, as pointed out by M. F. Strathmann (1987:274), shell dimensions reported by Hurst were from larvae of unspecified ages. Although the larvae may have grown after hatching, Hurst did not feed them and stated (p. 286) that shell-growth appeared negligible. Measurements of shell-size at hatching obtained by other authors for some of the same species generally closely match those reported by Hurst (see Table 1 of the present study) suggesting that little, if any, growth in the larval shells had occurred prior to her measurements. Thus, unless otherwise stated, I treated Hurst's values for shell-length (Hurst, 1967; Table 9) as measures of shell-size at hatching.

After compiling all the new and existing data available on the early development of northeast Pacific nudibranchs (see Table 1), mean egg diameter and mean shell-size at hatching were calculated for each species in the following manner. Mean egg and veliger sizes that I (Goddard, 1984, 1987, 1990, and present study) had obtained at different temperatures (many of these means are actually grand means calculated from measurements from more than one egg mass) were averaged to obtain grand means. These grand means were then averaged with means reported by other authors (see Table 1) to obtain a grand grand mean. The end result for each species was two means, one for egg size and one for veliger size (see Table 6). These means were subsequently used in: (1) calculating the linear regression of shell-size at hatching on egg-diameter shown in Figure 2; (2) for comparison of egg-size between species with different larval shell types; and (3) for an analysis of covariance comparing shell-size at hatching for species with single eggs per egg capsule vs. those with multiple eggs per egg capsule. Where appropriate, descriptions of other statistical analyses are presented with the results.

Ranges were often given for culture temperatures and embryonic period. Midpoints were used in analyses involving these parameters.

Statistical analyses were made using Lotus spreadsheets and (or) programs written by Dr. Peter W. Frank for his biometry classes at the University of Oregon. Statview II was used to calculate multiple regression statistics.

Data on the mode of development of nudibranchs from other regions of the world were obtained from the literature. I sometimes differed with an author's assignment of developmental type, or followed (for a species listed by one author) that of another author. These differences are pointed out where appropriate. In a few cases relevant data are available for a region but no determinations of developmental type were made. Applying the criteria of Thompson (1967), Bonar (1978), Todd (1981), and Hadfield & Switzer-Dunlap (1984) (see above), I assigned a developmental type to as many species from that region as possible. When egg diameter was the only parameter measured I used the egg size distributions compiled by Hadfield & Miller (1987) for the different types of development for nudibranchs world-wide. As shown by Hadfield & Miller (1987), egg diameters under 100 µm virtually always indicate planktotrophic development for nudibranchs; between 100 and 215 µm all types of development are possible; and only direct development is likely with an egg diameter of 215 µm or more. Assignments of developmental mode based on egg diameter are explained further with the results.

Results

Northeast Pacific Ocean

Including the 30 species examined in the present study, data on embryonic and larval development were obtained for 68 species of northeastern Pacific nudibranchs (Table 1). Most of these were collected from Cape Arago, Oregon, the San Juan archipelago, and southern British Columbia (see Figure 1). Ketchikan, Alaska, one of the collection sites for *Cuthona viridis* (see Millen, 1989), was the most northerly collection site; Morro Bay, San Luis Obispo County, California, where Emarcusia morroensis was collected (Roller, 1972), the most southerly.

Data were also obtained for four species (Aeolidiella indica, Corambe pacifica, Triopha maculata, and the yellow porostome dorid) collected from between Point Conception, California and Bahia de Los Angeles, Baja California. Although these waters are better classified as warm temperate (Hedgpeth, 1957; Briggs, 1974; Ricketts et al., 1985) and can be thought of as part of the transition zone between the northeast Pacific and the eastern tropical Pacific, data on the above four species were included in Table 1 to provide contrast with those collected from the northeast Pacific per se (it should be noted, however, that Corambe pacifica and Triopha maculata also occur north of Point Conception). Other than information obtained from descriptions of egg masses (see below), the data for the above four species are, to my knowledge, the only available on the development of nudibranchs from the warm temperate and tropical waters of the eastern Pacific.

Mode of Development

Based on observations of the size and morphology of hatching veliger larvae, mode of development was determined directly for 62 species of northeastern Pacific nudibranchs (Table 1). Only four have non-planktotrophic development:

TABLE 1. Development data for northeastern Pacific nudibranchs. If not stated in the original reference, developmental type was determined using descriptions and figures of hatching veligers and the criteria described by Thompson (1967, 1976), Bonar (1978), Todd (1983), and Hadfield & Switzer-Dunlap (1984); development types determined in this manner are in parentheses. Most values for egg diameter and shell-size at hatching are means, but ranges and some values of unknown derivation are also included (see Methods).

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
DORIDACEA								
Acanthodoris brunnea MacFarland, 1905	80	1	15	11-14	140	-	(P)	27
Acanthodoris hudsoni MacFarland, 1905		1	16	8-11		-	(P)	2
	67	1	9-11	14-16	127	-	P	25
	70						-	27
Acanthodoris nanaimoensis O'Donoghue, 1921		1	9	8-11	133	-	(P)	2
Acanthodoris pilosa (Abildgaard, 1789)	70	1				-	(P)	27

TABLE 1. Continued.

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Adalaria jannae Millen, 1987	65	1-2	11-13	8	109	-	P	26
Adalaria sp.	83	1	11	10-12	140	-	P	20
Aegires albopunctatus MacFarland, 1905	107-120						-	27
Aldisa cooperi Robilliard & Baba, 1972	110	1	19-23	10			"planktonic"	22
Aldisa sanguinea (Cooper, 1863)	100	1					-	22
	90	1	15	12-15	163	-	P	31
Aldisa tara Millen, in Millen & Gosliner, 1985	110	1	31-38	10			P	22

TABLE 1. Continued.

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Ancula pacifica MacFarland, 1905	59	1	9	14-16	104	-	P	20
Anisodoris lentiginosa Millen, 1982	90	4-6	44-46	10	154	-	P	18
Anisodoris nobilis (MacFarland, 1905)	83	up to 20	14	14-17	153	-	P	20
Archidoris montereyensis (Cooper, 1863)	81	1-18	20-25	17		-	(P)	1
		1-3	23-28	8-11	155	-	(P)	2
	81	3-4	14	13-16	154	-	P	31
	90	1-2	21	10-11	169	-	P	31
Archidoris odhneri (MacFarland, 1966)		8-12	22-23	8-11	189	-	(P)	2
	96	3-6	26	10-11	186	-	P	31
Cadlina marginata MacFarland, 1905	90	1	86	5			P	16
	90	1	35	10			P	16
	90	1	25	15			P	16
	94						P	31

TABLE 1. Continued.

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Cadlina modesta MacFarland, 1966	92	1	16-19	12-15	157	-	P	20
Corambe pacifica MacFarland & O'Donoghue, 1929	70	1*	6-7	13-15	130		P	24
Crimora coneja Marcus, 1961	73	1	17-18	10-14	119	-	P	20
		1	10	12-16	116	-	P	31
Diaphorodoris lirulatocauda Millen, 1985	63	1	9-11	12-16	115	-	P	20
Discodoris heathi MacFarland, 1905	77	2-7	15	14-17	145	-	P	20
	73-78	1-2	27-28	12	102		(P)	27
	79	2-4	18	10-11	143	-	P	31

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* Number of eggs per capsule from Anderson (1973).

TABLE 1. **Continued.**

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Discodoris sandiegensis (Cooper,1863)		1-2	22-28	8-11	153	-	(P)	2
					130	-	(P)	27
	83	1-2	17-21	10-11	139	-	P	31
Doridella steinbergae (Lance, 1962)	75-85	1	11-12	9-10	142	-	P	14
	75-85	1	7.5-8	12-15	142	-	P	14
Hallaxa chani Gosliner & Williams, 1975	81	1	15-17	11-15	152	-	P	20
	83	1	12	14-17	131	-	P	31
Laila cockerelli MacFarland, 1905	95	1	17	10-13	142	-	P	20
Onchidoris bilamellata (Linnaeus, 1767)		1-3	12-13	8-11	147	-	(P)	2
	100						-	27
				11	165	-	P	28
Onchidoris muricata (Müller, 1776)		1	7-14	8-11	186	-	(P)	2
	76	1	10-11	7-11	133	-	P	20
	80	1	11	10-11	137	-	P	31

TABLE 1. Continued.

Species[1]	Egg diameter (μm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (μm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Palio zosterae (O'Donoghue, 1924)	70	1			150	-	(P)	27
	65	1	8	15-16	101	-	P	31
Polycera tricolor Robilliard, 1971		1	10	11			-	5
Rostanga pulchra MacFarland, 1905		1-2	30	8-11	161	-	(P)	2
	73	1-2	10-13	15		-	P	4
	80	1-2	16	10-15	148	-	P	12
Triopha catalinae (Cooper, 1863)		1-7	18	8-11	134	-	(P)	2
		1	10	14-18	131	-	P	20,31
	75-87						-	27
Triopha maculata MacFarland, 1905		18*	6				P	10

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* Mean value.

TABLE 1. Continued.

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
yellow porostome							D	10
DENDRONOTACEA								
Dendronotus albopunctatus Robilliard, 1972	108	1	11-13	8-9			-	8
Dendronotus dalli Bergh, 1879		2-9	13-19				-	3
Dendronotus diversicolor Robilliard, 1970		1	8-13				-	3
	96	1					-	27
Dendronotus frondosus (Ascanius, 1774)		1	7-15	8-11		-	(P)	2
		1	13-16				-	3
			6.1-10	14		-	(P)	6
	85-90	1			230	-	(P)	27
	87	1-3	6-9	13-15	245	-	P	31

TABLE 1. Continued.

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Dendronotus iris Cooper, 1863		30-60		8-11	268	-	(P)	2
		31-100	13-17				-	3
	110		10-20	8-11	280	-	P?	27
Dendronotus rufus O'Donoghue, 1921		4-27	13-20				-	3
Dendronotus subramosus MacFarland, 1966			15-18				-	3
Doto amyra Marcus, 1961	154	1	28-29	11-13	240	+	L	20,31
	149	1	19-21	15-17	237	+	L	20,31
Doto kya Marcus, 1961	78	1	7	15-17	133	-	P	20,31
Doto sp. A	76	1	12	11-13	123	-	P	31
Doto sp. B	70	1	11	11-13	122	-	P	31

TABLE 1. Continued.

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Melibe leonina (Gould, 1852)		5-25	8-15	8-11	152	-	(P)	2
			10	12-14	149		P	19*
	90	5-35					-	27
	86	1-5	7-8	12-15	140	-	P	31
Tritonia diomedea Bergh, 1894		30-60	12-16	8-11	146	-	(P)	2
			10-21	11-13	145	-	P	11
	87	30-60	7	20-22		-	-	27
Tritonia festiva (Stearns, 1873)			13	10-12		+	P	31
	79	1-3	10	12-14	131	-,+	P	31
ARMINACEA								
Armina californica (Cooper, 1863)		12-15	17-23	8-11	160	-	(P)	2
	95-102						-	27

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* The data from this reference (#19) were found too late for inclusion in statistical analyses.

TABLE 1. Continued.

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Dirona albolineata Eliot, in Cockerell & Eliot, 1905		8-12		8-11	113	-	(P)	2
	70						-	27
	69	2-5	13	11-13	129	-	P	31
Dirona aurantia Hurst, 1966		1-6	13	8-11	139	-	(P)	2
Janolus fuscus O'Donoghue, 1924	81	50-60	14-16	11-12	138	+	P	31
AEOLIDACEA								
Aeolidia papillosa (Linnaeus, 1761)		3-15	10-24	8-11	138	-	(P)	2
	74		8	14	116	-	P	17
			17-18	11		-	(P)	27
Aeolidiella indica Bergh, 1888							L	10

TABLE 1. Continued.

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Catriona columbiana (O'Donoghue, 1922)		1	13	8-11	230	-	(P)	2
	100	1	10	15-17	274	+	P	20
			19	10		+	-	27
Cumanotus beaumonti (Eliot, 1906)		4-14	10	8-11	119	-	(P)	2
	73	1	9-10	12-16	130	-	P	31
Cuthona abronia (MacFarland, 1966)	95	1	10	12-14	224	+	P	31
Cuthona albocrusta (MacFarland, 1966)		1	20-21	8-11	270	+	(P)	2
	97	1	10	12-14	281	+	P	31
Cuthona cocoachroma Williams & Gosliner, 1979	96	1	6	15-17	257	-	P	20
	95	1	9	12-13	277	-,+	P	31

TABLE 1. Continued.

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Cuthona divae (Marcus, 1961)	107	1	7-8	15-17	249	-	P	20
Cuthona fulgens (MacFarland, 1966)	94	1	9	10-12	252	+	P	31
Cuthona lagunae (O'Donoghue, 1926)	98	1	9-11	12-14	262	+	P	30
Cuthona punicea Millen, 1985	128	1	14-15	10			P	23
Cuthona pustulata (Alder & Hancock, 1854)	120	1-3	18-19	10		-	P	21

TABLE 1. Continued.

Species[1]	Egg diameter (μm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (μm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Cuthona viridis (Forbes, 1840)	134	1					-	29
Emarcusia morroensis Roller, 1972			5				-	9
Eubranchus rustyus (Marcus, 1961)	93	1	6	15-17	240	+	P	20
Eubranchus olivaceus (O'Donoghue, 1922)		1	11	8-11	245	-	(P)	2
	85	1	8	12-13	244	+	P	31
Flabellina fusca (O'Donoghue, 1921)		1-2	7-8	8-11	133	-	(P)	2
Flabellina trilineata (O'Donoghue, 1922)		1	4-6	15-16		-	(P)	7
	60	1	22	10	100-110	-	(P)	27
	65	1	8	13-15	103	-	P	31

TABLE 1. Continued.

Species[1]	Egg diameter (µm)	Eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell size at hatching (µm)	Eyespots at hatching[2]	Dev. type[3]	Ref.[4]
Flabellina verrucosa (Sars, 1829)		1	23	8-11	117	-	(P)	2
Hermissenda crassicornis (Eschscholtz, 1831)		1-4	7-8	8-11	116	-	(P)	2
	65	1-9	5-6	13-15		-	P	13
	65		7	14	102	-	P	17
		1-2	11	12-14	119	-	P	31
Tenellia adspersa (Nordmann, 1845)			4-5	15			-	15
					217	+	L	31

[1] Most species were collected from Cape Arago, Oregon; the San Juan archipelago; and southern British Columbia. With the exceptions of six, all species observed in the present study (reference number 30) were from Cape Arago (see Methods for the other collection localities in this study). For additional locality data see Results and original references.

[2] - = absent, + = present

[3] P = planktotrophic, L = lecithotrophic, D = direct (capsular metamorphic or ametamorphic), - = developmental type was not stated and could not be determined based on the available description (or lack thereof) of the hatching veliger.

TABLE 1. Continued.

[4] 1, McGowan & Pratt (1954); 2, Hurst (1967); 3, Robilliard (1970); 4, Anderson (1971); 5, Robilliard (1971); 6, Williams (1971); 7, Bridges & Blake (1972); 8, Robilliard (1972); 9, Roller (1972); 10, Mulliner (1973); 11, Kempf & Willows (1977); 12, Chia & Koss (1978); 13, Harrigan & Alkon (1978); 14, Bickell & Chia (1979); 15, Cooper (1979); 16, Dehnel & Kong (1979); 17, Williams (1980); 18, Millen (1982); 19, Bickell & Kempf (1983); 20, Goddard (1984); 21, Gosliner & Millen (1984); 22, Millen & Gosliner (1985); 23, Millen (1986); 24, Yoshioka (1986); 25, Goddard (1987); 26, Millen (1987); 27, Strathmann (1987); 28, Chia & Koss (1988); 29, Millen (1989); 30, Goddard (in press); 31, present study.

the yellow porostome from the Gulf of California has ametamorphic (direct) development (Mulliner, 1972), while Aeolidiella indica, Doto amyra, and Tenellia adspersa all have lecithotrophic development (Mulliner, 1972; Goddard, 1984, 1990, present study). Of these four, only the yellow porostome and Doto amyra are native to the northeastern Pacific. The short-term lecithotrophic development of Doto amyra is described in detail in Chapter 2.

Based on egg-size, embryonic period, and the development of sympatric congeners, mode of development can be inferred for 8 of the 10 species in Table 1 whose developmental type was not determined directly. These inferences are described below and listed in Table 2.

Millen & Gosliner (1985) reported a "planktonic" larval stage for Aldisa cooperi, but did not distingush between planktotrophy and lecithotrophy. Given the diameter of its eggs (110 µm) and the egg-size distributions reported by Hadfield & Miller (1987) for the Nudibranchia as a whole, A. cooperi could have lecithotrophic development. However, both of its sympatric congeners produce eggs of similar size and have planktotrophic larvae (Table 1). In addition, the embryonic period of A. cooperi is considerably shorter than that of A. tara at the same temperature. Because lecithotrophic larvae generally take longer to hatch than planktotrophic larvae at the same temperatures (Thompson, 1976; Todd, 1981), the reverse would be expected if A.

Table 2. Northeast Pacific nudibranchs whose hatching larvae have not been examined but whose mode of development can be inferred from other data in Table 1 (e.g., egg-size, embryonic period, and development of sympatric congeners) (see text).

Species	Mode of development[1]
Aldisa cooperi	P
Dendronotus diversicolor	P
Dendronotus dalli	P
Dendronotus rufus	P
Dendronotus subramosus	P
Dendronotus albopunctatus	P
Polycera tricolor	P
Emarcusia morrensis	P
Aegires albopunctatus	P or L
Cuthona viridis	P or L

[1] P = planktotrophic, L = lecithotrophic

cooperi had lecithotrophic development. Therefore, A. cooperi probably has planktotrophic development.

The egg diameter of Dendronotus diversicolor is just under the 100 µm minimum known for nudibranchs with lecithotrophic development (see Hadfield & Miller, 1987) and is also smaller than that of D. iris, a sympatric species with planktotrophic development (Table 1). Robilliard (1970) reported embryonic periods for D. diversicolor and other species of Dendronotus but did not give corresponding temperature data (see Table 1). However, assuming the temperatures of his cultures were similar to those reported by Hurst (1967) (both worked at Friday Harbor, Washington), the embryonic period of D. diversicolor, as well as those of D. dalli, D. rufus, and D. subramosus, are comparable to that of D. frondosus, another sympatric species with planktotrophic development, as well as to that of D. iris (Table 1). Thus, D. diversicolor, D. dalli, D. rufus, and D. subramosus probably all have planktotrophic development. Based on similar comparisons of egg size and embryonic period, D. albopunctatus probably also has planktotrophic development.

At 11° C, embryos of Polycera tricolor develop faster than most of the other dorids in Table 1, strongly suggesting planktotrophic larval development for this species. Finally, although Roller (1972) did not report the temperatures at which his embryos of Emarcusia morroensis developed, a comparison of its embryonic period to those of the other eolids in Table 1 (especially those with type 1 shells) suggests planktotrophic development for this species as well.

Aegires albopunctatus and Cuthona viridis are the only species in Table 1 for which mode of development could not be determined. Based on egg size, Aegires has either planktotrophic or lecithotrophic development (dorids known to have direct development develop from eggs greater than 200 µm in diameter (Hadfield & Miller, 1987: Table 4)). C. viridis, with an egg diameter of 134 µm, could have any of the three types of development. However, as pointed out in chapter 2, no hydroid-feeding aeolid nudibranchs are known to have direct development (no food data are available for Pacific C. viridis, but specimens from British waters are known to prey on hydroids (Thompson & Brown, 1984)).

Using published descriptions and figures of egg masses, developmental mode was inferred for an additional five species (Table 3). All very likely have planktotrophic development. Although Marcus & Marcus (1967) reported an egg diameter for Dirona picta, it was not included in Table 1 because it is not clear whether the value was obtained from measurements of live or preserved material (measurements of the latter might not accurately represent the former).

The above determinations of developmental mode are

Table 3. Northeast Pacific nudibranchs whose mode of development can be inferred from published descriptions and figures of egg masses (see text).

Species	Mode of development[1]	Locality	Reference
<u>Cuthona longi</u> Behrens, 1985	P	Gulf of Calif.	Behrens (1985a)
<u>Cuthona rickettsi</u> Behrens, 1984	P	San Francisco Bay, La Jolla	Behrens (1984)
<u>Dirona picta</u> MacFarland in Cockerell & Eliot, 1905	P	Gulf of Calif.	Marcus & Marcus (1967)
<u>Eubranchus cucullus</u> Behrens, 1985	P	Gulf of Calif.	Behrens (1985b)
<u>Thordisa rubescens</u> Behrens & Henderson, 1981	P	southern Calif.	Behrens & Henderson (1981)

[1] P = planktotrophic

summarized in Table 4, the last row of which gives the proportions of the three modes for species collected north of Point Conception, California. These 69 species constitute 53% of the nudibranch species currently known from the west coast of North America north of Point Conception (see Behrens, 1991). Sixty of the 62 species whose type of development could be determined directly (and thus most reliably) occur north of Point Conception. Fifty-eight of these have planktotrophic development, two lecithotrophic, and none direct.

Table 4. Frequency of the three major types of development among northeastern Pacific nudibranchs. Values are numbers of species.

Method of determination of development type	Type of development[1]			Number of species examined
	pk	lec	dir	
size, morphology, and behavior of hatching veligers (see Table 1)	58	3	1	62
other embryological data in Table 1 (see Table 2 and text)	8	0	0	8
published descriptions & figures of egg masses (see Table 3)	5	0	0	5
total	71	3	1	75
number of species (out of above total) found north of Point Conception, Calif.	67	2	0	69

[1] pk = planktotrophic, lec = lecithotrophic, dir = direct

Finally, mode of development is suggested for those species whose development has been examined outside the Pacific Ocean, but whose distribution includes at least part of the northeast and eastern tropical Pacific. These species include the arctic _Flabellina salmonacea_ and four warm-water species (Table 5). _Cuthona nana_ has not been included in this list owing to its possible synonymy with the northeastern Pacific _C. divae_ (see Thompson & Brown,

Table 5. Nudibranchs found in the northeast Pacific or eastern tropical Pacific whose early development is known only from other regions.

Species	Mode of development[1]	Locality	Reference
Dendrodoris krebsii (Morch, 1863)	D	Florida	Clark & Goetzfried (1978), DeFreese & Clark (1983)
Flabellina salmonacea (Couthouy, 1838)	D	Gulf of Maine	Morse (1971), Kuzirian (1979)
Lomanotus vermiformis Eliot, 1908	L	Florida	Clark & Goetzfried (1978)
Phidiana lynceus Bergh, 1867	L	Florida	Clark & Goetzfried (1978), DeFreese & Clark (1983)
Spurilla neopolitana (Delle Chiaje, 1823)	P,L	Florida	Clark & Goetzfried (1978), Eyster (1980), DeFreese & Clark (1983)

[1] P = planktotrophic, L = lecithotrophic, D = direct.

1984, p. 117). Owing to their geographic isolation, developmental mode could have diverged between Pacific and Atlantic-Caribbean populations of these species and thus can not be reliably determined for Pacific populations using only data from other oceans. However, given the unlikelihood of planktonic development evolving from direct development (Strathmann, 1978), divergence would be unlikely in species possessing only direct development prior to the isolation of previously contiguous populations.

No examples of poecilogony (intra-specific variability in developmental mode) were found in the present study and review.

Egg size

Mean egg diameters, obtained for 59 species, varied from 59 µm in *Ancula pacifica* to 152 µm in *Doto amyra* and had an overall mean of 88 µm (Table 6 and Figure 2). The largest mean egg diameter for a species with planktotrophic development was 128 µm for *Cuthona punicea* (Millen, 1986). This could rise to 134 µm if the larvae of *C. viridis* are found to be planktotrophic. Egg diameter was not available for the yellow porostome, the only species with direct development.

Planktotrophic species with type 2 shells (see below) developed from eggs averaging 100.9 µm in diameter (SD =

Table 6. Egg diameter and shell-size at hatching for 59 species of northeast Pacific nudibranchs. Values are means or grand means calculated from data in Table 1 (see Methods). An asterisk (*) next to a value for egg diameter indicates multiple embryos (per egg capsule) are known for that species.

Species	Egg diameter (µm)	Shell-size at hatching (µm)
species with type 1 larval shells		
Ancula _pacifica_	59	104
Flabellina _trilineata_	62	104
Diaphorodoris _lirulatocauda_	63	115
Adalaria _jannae_	65*	109
Hermissenda _crassicornis_	65*	112
Palio _zosterae_	67	126
Acanthodoris _hudsoni_	68	127
Dirona _albolineata_	69*	121
Corambe _pacifica_	70	130
Doto sp. A of present study	70	122
Acanthodoris _pilosa_	70	---
Cumanotus _beaumonti_	73*	124
Crimora _coneja_	73	118
Aeolidia _papillosa_	74*	127
Doto sp. B of present study	76	123
Rostanga _pulchra_	76*	154
Discodoris _heathi_	77*	123
Onchidoris _muricata_	78	135

Table 6. Continued.

Species	Egg diameter (µm)	Shell-size at hatching (µm)
Doto kya	78	133
Tritonia festiva	79*	131
Doridella steinbergae	80	142
Acanthodoris brunnea	80	140
Triopha catalinae	81*	132
Janolus fuscus	81*	138
Hallaxa chani	82	142
Discodoris sandiegensis	83*	141
Archidoris montereyensis	83*	158
Adalaria sp.	83	140
Anisodoris nobilis	83*	153
Tritonia diomedea	87*	145
Melibe leonina	88*	146
Anisodoris lentiginosa	90*	154
Cadlina marginata	92	---
Cadlina modesta	92	157
Aldisa sanguinea	95	163
Laila cockerelli	95	142
Archidoris odhneri	96*	187
Armina californica	98*	160
Onchidoris bilamellata	100*	156
Aldisa cooperi	110	---

Table 6. Continued.

Species	Egg diameter (µm)	Shell-size at hatching (µm)
Aldisa tara	110	---
Aegires albopunctatus	113	---
Doto amyra	152	239
species with type 2 larval shells		
Eubranchus olivaceus	85	244
Dendronotus frondosus	87*	237
Eubranchus rustyus	93	240
Cuthona fulgens	94	252
Cuthona abronia	95	224
Cuthona cocoachroma	95	267
Dendronotus diversicolor	96	---
Cuthona albocrusta	97	275
Cuthona lagunae	98	262
Catriona columbiana	100	252
Cuthona divae	107	249
Dendronotus albopunctatus	108	---
Dendronotus iris	110*	274
Cuthona pustulata	120*	---
Cuthona punicea	128	---
Cuthona viridis	134	---

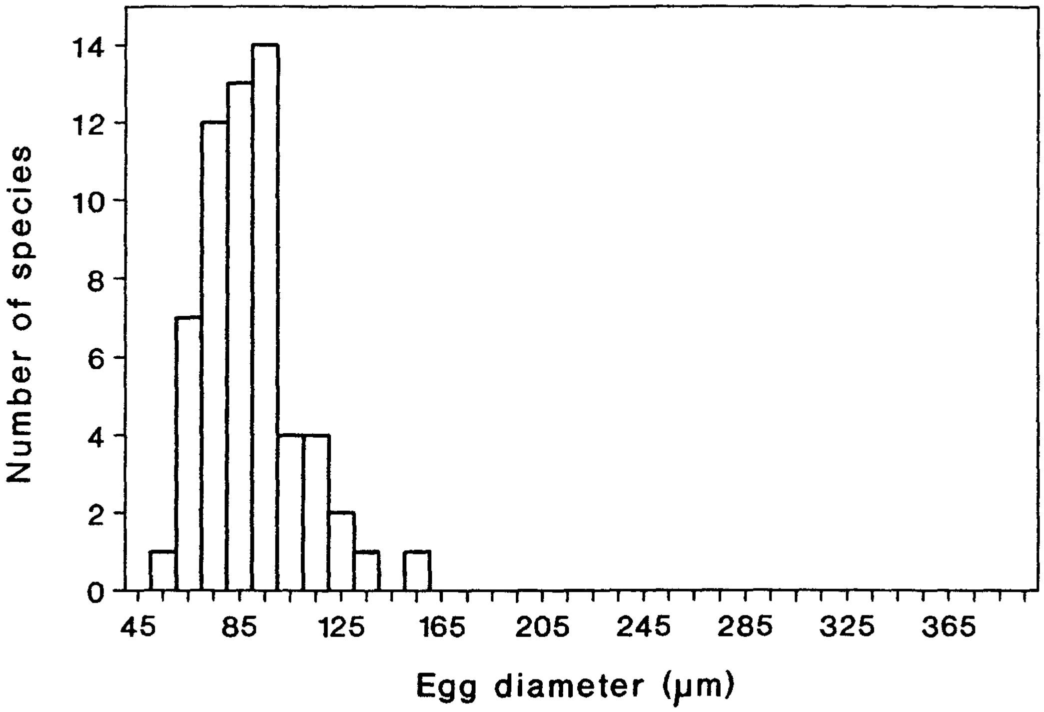

Figure 2. Egg size distribution for 59 species of NE Pacific nudibranchs. Data from Table 6.

11.8 µm, n = 15); those with type 1 shells from eggs averaging 80.5 µm in diameter (SD = 12.4 µm, n = 41). These means are significantly different ($t = 5.5$, $p < 0.001$).

The largest range in the diameter of individual eggs for a species (all egg masses and localities combined) was 36 µm for Cuthona punicea (see Millen, 1985), followed by 23.7 µm for C. lagunae (personal observations), 22.6 µm for Doto amyra (personal observations), and at least 19 µm for Aldisa sanguinea (personal observations combined with the value from Millen & Gosliner, 1985). Coefficients of

Table 7. Largest known ranges in mean diameter of eggs of northeast Pacific nudibranchs. Each mean is based on measurements from a different egg mass.

Species	Number of egg masses examined	Egg diameter (µm) 1. low 2. high $\bar{X}$	(s)	n	Range in mean egg diameter (µm)	Source
Aldisa sanguinea	4	86.9 100	(1.6) --	10 --	13.1	Millen & Gosliner (1985), present study
Doto amyra	8	145.1 157.6	(3.1) (3.3)	10 20	12.5	present study
Archidoris montereyensis	2	81.0 90.4	(2.3) (2.4)	10 10	9.4	present study
Cuthona lagunae	4	93.9 102.3	(1.6) (5.6)	10 15	8.4	present study

variation in the diameter of eggs from individual egg masses varied from 0.6 % for an egg mass laid by Diaphorodoris lirulatocauda to 5.5 % for C. lagunae; most were 2 to 3 % (personal observations of the egg masses of 37 species). The largest ranges in the mean diameter of eggs from individual egg masses were 13.1 µm for A. sanguinea and 12.5 µm for Doto amyra (Table 7).

Extra-Zygotic Yolk

A single - and novel - example of extra-zygotic yolk (EZY) was found. Averaging over 18 µm in diameter, the polar bodies of the aeolid Cuthona lagunae together contained approximately 2 % of the yolk remaining in the eggs and were ingested by the late embryos. Owing to their unusual size, yolk content, and apparent function as yolk reserves, the polar bodies of C. lagunae are described and discussed separately in Chapter 3.

Size and Type of Shell at Hatching

At hatching, aeolids of the genera Catriona, Cuthona, Eubranchus, and Tenellia and dendronotaceans of the genus Dendronotus possessed egg-shaped, inflated shells (type 2 of Thompson, 1961); all other species (except for the directly developing yellow porostome, which, according to Mulliner (1972), does not develop a shell) had typical spiral shells (type 1 of Thompson, 1961).

Mean shell-size at hatching for species with type 1 shells varied from 104 µm for Ancula pacifica and Flabellina trilineata to 187 µm for the planktotrophic Archidoris odhneri and 239 µm for the lecithotrophic Doto amyra (Tables 1 and 6, Figure 3). For species with type 2 shells mean shell size at hatching varied from 217 µm for Tenellia adspersa to 275 µm for Cuthona albocrusta. Coefficients of variation in shell-size at hatching for larvae from individual egg masses varied from 1.0 % in an egg mass laid by Cuthona lagunae to 6.0 % for one laid by Adalaria sp.; like those for egg diamater, most were 2 to 3 % (personal observations).

Egg diameter is a good predictor of shell size at hatching for species with type 1 shells ($r^2 = 0.88$, $p < 0.001$)*, but not for species with type 2 shells ($r^2 = 0.24$, $p = 0.12$)* (Figure 3). Excluding Doto amyra (the only species in Figure 3 with lecithotrophic development) the regression equation for species with type 1 shells becomes $y = 1.50x + 18.01$ ($r^2 = 0.77$, $p < 0.001$)*.

Nurse-Eggs

Despite the prevalence of species laying multiple eggs per egg capsule (see Table 1, column 3 and Table 6), direct evidence that some of these eggs are serving as nurse-eggs

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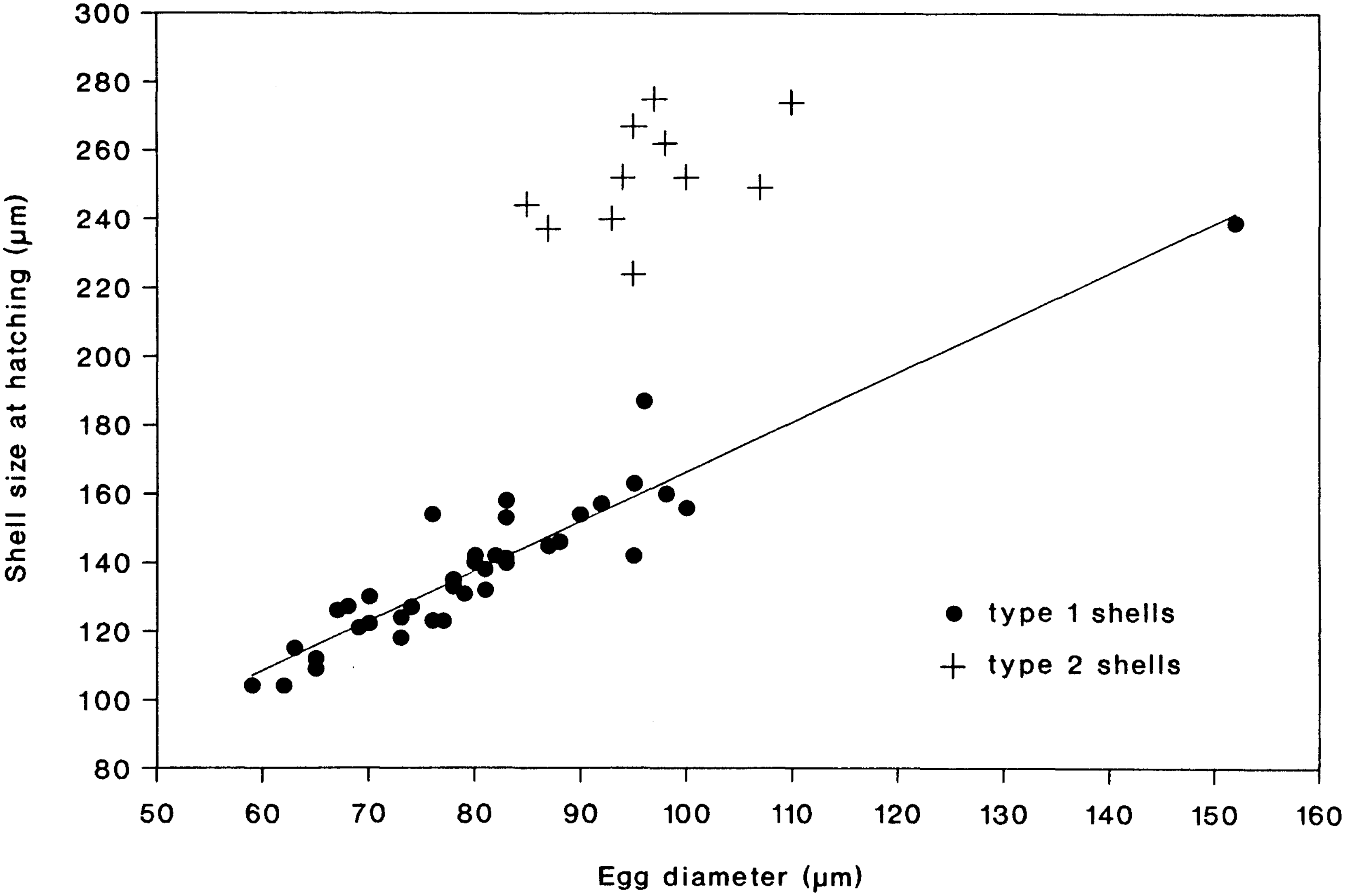
* Owing to the nonindependence of the data points (e.g., see Felsenstein, 1985), as well as biases of collection, these probability levels must be viewed with caution.

Figure 3. Relation between mean egg size and mean shell size at hatching for 49 species of northeast Pacific nudibranchs (38 species with type 1 shells, 11 with type 2 shells). Data from Table 6. For species with type 1 shells, $y = 1.45x + 21.82$, $r^2 = 0.88$.



300
280
260
240
220
200
180
160
140
120
100
80
Shell size at hatching (µm)
50
60
70
80
90
100
110
120
130
140
150
160
Egg diameter (µm)
● type 1 shells
+ type 2 shells

was not obtained in the present study, and no accounts of this phenomenon were found in the literature.

Given the high correlation between egg diameter (and thus yolk supply) and shell-size at hatching, at least for species with type 1 shells (see above), shell size at hatching should be larger for embryos assimilating the extra yolk in nurse-eggs. Thus, if nurse-eggs are common, one would expect (after adjusting for interspecific differences in egg size) shell size at hatching to be larger for species with multiple eggs per capsule than for those with eggs encapsulated singly. Analyses of covariance (with mean egg diameter as the covariate) did not reveal statistically significant differences in mean shell-size at hatching between species with type 1 shells and a single egg per capsule (n = 19) and: 1) those with one or more eggs per capsule (n = 19); or 2) those only with multiple eggs per capsule (n = 6). Nurse-eggs, therefore, appear to be either uncommon or nonexistent among the species in Table 1. This result is also suggested by examining the relative distribution of the two types of points for the species with type 1 shells in Figure 4. If nurse-eggs were common, the points for species with multiple eggs would generally lie above those for species with single eggs. They clearly do not.

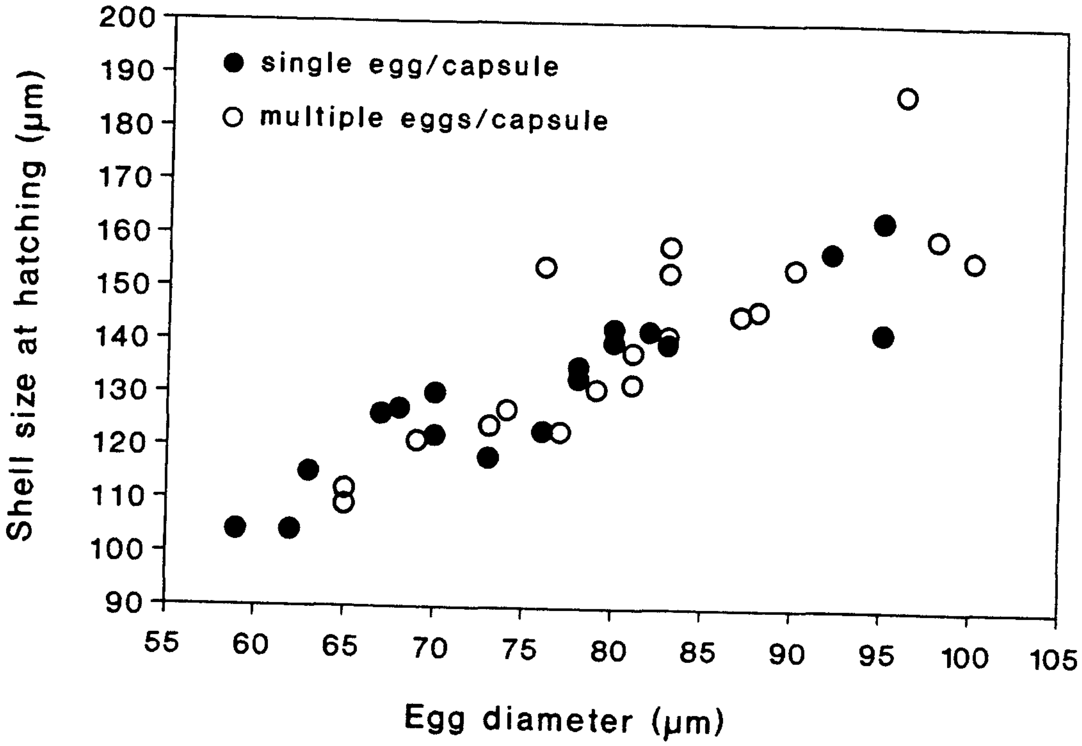


Figure 4. Relation between egg size and shell size at hatching for 37 species of NE Pacific nudibranchs with single or multiple embryos per egg capsule (n = 19 and 18 species, respectively). Data from Table 6.

Embryonic Period

Measurements of embryonic period were obtained for 66 species (Table 1). Using one value of embryonic period per species (that obtained at the temperature closest to 11° C), mean embryonic period for these species was 14.8 days. Planktotrophic species with type 2 shells (n = 17) appeared to develop faster than the 47 species with type 1 shells (X = 13.0 and 15.3 days, respectively), despite developing from significantly larger eggs (see section 2 above). However, given the wide range of egg-diameters and culture temperatures for these species, as well as the influence of these variables on embryonic period, a more detailed analysis (described below) is needed to determine if the planktotrophic species with type 2 shells actually develop faster than those with type 1 shells.

Complete data on egg-size (D), embryonic period (P), and temperature (T) were available for 54 species in Table 1. In order to compare the embryonic periods of different larval types, as well as examine the relationship between P, D, and T, these data were treated as follows. A single value for each variable was used for each species. If more than one value was available, that obtained at the temperature closest to 11 C was used (e.g., out of the measurements available for <u>Archidoris</u> <u>montereyensis</u> (see Table 1), values of 90 µm (D), 21 days (P), and 10.5° C (T) were used). Midpoints were used in place of ranges, and, if values for P and T were obtained from a source that did not report D, an average D, calculated using data from the other sources for that species, was substituted. Following (with slight modifications) Thompson & Jarman (1986), the relationship between P, D, and T was assumed to be of the form $P = aD^b10^{c/T}$, where P = embryonic period in days, D = egg diameter in microns, T = temperature in degrees Celsius, and a, b, and c are constants. Aside from its similarity to exponential equations relating metabolic rate and temperature (e.g., Hill, 1976), in its logarithmic form ($\log(P) = \log(a) + b(\log(D)) + c/T$) this equation can be fitted to the data using ordinary multiple regressions methods.

Mean embryonic period, egg diameter, and temperatures for the 54 species are given in Table 8. While mean P for these species is similar to that obtained above for all 66 species, the disparity in P between species with different larval shell types appears to have increased. However, variances are large, and the two embryonic periods are not quite significantly different ($t_s = 1.769$, $0.1 > p > 0.05$; Wilcoxon two-sample test; Sokal & Rohlf, 1981). Nevertheless, based on mean D alone (mean temperatures for the two groups are virtually identical), one would expect species with type 2 shells to have a longer embryonic period than those with type 1 shells. The opposite trend

Table 8. Embryonic period, egg diameter, and rearing temperature for northeast Pacific nudibranchs divided by larval shell type (see Thompson, 1961) and egg mass size ("small" or "large"; see text). Values are means (± one standard deviation) based on one value per variable per species (see text for further explanation).

Larval shell type	Embryonic period (days)	Egg diameter (µm)	Rearing temp. (° C)	Number of species
1 and 2	15.5 ± 7.5	86.9 ± 17.6	11.4 ± 2.1	54**
1	16.2 ± 7.8	80.4 ± 12.5	11.4 ± 2.0	40*
2	12.4 ± 4.7	100.7 ± 12.4	11.5 ± 2.4	13*
1, from small egg masses	11.4 ± 4.0	71.6 ± 7.6	11.8 ± 2.4	17*
1, from large egg masses	19.7 ± 8.2	87.6 ± 11.0	11.1 ± 1.6	23*

** Includes one species (Doto amyra) with lecithotrophic development.

* Includes only species with planktotrophic development.

observed in Table 8 suggests either a fundamental difference in the inherent developmental processes of the two groups or that another factor affecting their embryonic development has been overlooked.

One difference between the two groups that might affect rate of development is the size of their egg masses. Excepting the dendronotids, all of the species with type 2 shells have small adult size and lay minute egg masses with relatively high surface to volume ratios (Hurst, 1967; personal observations). The egg masses of dendronotids are larger but are laid in long strings and thus also have high surface to volume ratios (personal observations). Other things being equal, processes limiting metabolic rate and thus embryonic period (e.g., diffusion of gases and waste products) are less likely to be hindered in small egg masses and those with high surface to volume ratios, especially in the relatively stagnant conditions often occurring in culture vessels (see Chaffee & Strathmann, 1984). Therefore, we might expect species with minute egg masses generally to have shorter embryonic periods than those with large ones and that this might explain the apparent difference in P between species with type 1 and type 2 shells. This hypothesis is supported at least partially by the results shown in the last two rows of Table 8, where mean P, D, and T are calculated separately for species with type 1 shells and small egg masses and those with large egg masses. Embryonic periods of the latter differed significantly from those with type 2 shells ($t_s = 3.052$, $p < 0.01$, Wilcoxon two-sample test), while those of the former did not ($t_s = 0.294$, $p > 0.5$); they also differed from each other ($t_s = 4.118$, $p < 0.001$). Average culture temperatures for all of these groups were similar.

The hypothesis that egg mass size affects embryonic period is also supported by comparing the amount of variance in P explained by multiple regression on D, T, larval shell type, and egg mass size (Table 9). The increased amount of variance in P explained by the addition of a categorical, two-valued variable for shell type is at least matched when that variable is replaced by one for egg mass size and only slightly altered when shell type and egg mass size are included together. Virtually identical results are obtained if the data at all temperatures are included in the analysis (Table 9, bottom half). F-tests for all of the regressions in Table 9 give probabilities of 0.0004 or less. However, they are not included owing to violations of the assumptions of analysis of variance (random sampling, independence of data points, etc.).

Although the mean embryonic period of species with type 2 larval shells is similar to that of the species with type 1 shells and small egg masses, mean egg diameter of the former is still larger (Table 9). Thus, independent of egg

Table 9. Relation between embryonic period and egg diameter, rearing temperature, larval shell type, and egg mass size for 54 species of NE Pacific nudibranchs. Multiple regression equations for data extracted from Table 1 (see Text).

Regression equation[1]	R^2
a) one point per species (n = 54)	
$y = 0.722x_1 + 4.669x_2 - 0.665$	0.26
$y = 1.286x_1 + 4.358x_2 - 0.229x_3 - 1.672$	0.48
$y = 0.639x_1 + 4.078x_2 + 0.184x_4 - 0.531$	0.50
$y = 0.994x_1 + 4.092x_2 - 0.133x_3 + 0.124x_4 - 1.159$	0.55
b) one or more points per species (n = 90)	
$y = 0.781x_1 + 6.168x_2 - 0.920$	0.46
$y = 1.345x_1 + 5.730x_2 - 0.233x_3 - 1.916$	0.62
$y = 0.719x_1 + 5.597x_2 + 0.169x_4 - 0.822$	0.61
$y = 1.126x_1 + 5.520x_2 - 0.158x_3 + 0.104x_4 - 1.537$	0.66

[1] y = log(embryonic period in days)
x_1 = log(egg diameter in microns)
x_2 = 1/(temperature in °C)
x_3 = larval shell type (a 2-valued, categorical variable)
x_4 = egg mass size (a 2-valued, categorical variable).

mass size, species with type 2 shells may indeed develop faster than those with type 1 shells given the same amount of yolk.

Using the first regression equation in Table 9, and setting egg diameter = 86.9 µm (the mean for this data set; see Table 8), increasing the temperature from 9.3 to 13.5°C ($\bar{X}$ T ± 1 standard deviation; see Table 8) decreases the embryonic period by 5.2 days (from 17.3 to 12.1 days). Similarly, decreasing egg diameter from 104.5 to 69.3 µm ($\bar{X}$ D ± 1 SD), while holding temperature at 11.4°C, decreases the embryonic period by 4.1 days (from 15.9 to 11.8°C). For this data set, then, temperature appears to influence embryonic period slightly more than egg diameter.

Egg Size and Mode of Development in Nudibranchs from other Regions

Data pertaining to mode of development in nudibranchs from outside the northeast Pacific were obtained for seven regions, including the northwest Red Sea the northwest Mediterrean, two areas in the Pacific Ocean, and three in the Atlantic (Table 10). Proportions of the three types of development were calculated for each region and are shown in Table 10, along with those for the northeast Pacific. The number of species examined in the northeast Pacific, British Isles, both parts of the eastern United States, and the Gulf of Naples constitutes between 43 and 53% of the respective nudibranch faunas (see Behrens,1991; Thompson & Brown, 1984; Franz, 1970; Gosner, 1971; Eyster, 1980; Schmekel & Portmann, 1982). Given the diversity of nudibranchs in the Indo-Pacific and the southern Australian region (e.g. Willan & Coleman, 1984; Gosliner, 1987), the number of species whose development is known in the Marshall Islands, the Red Sea, and New South Wales is probably small compared to the number of species present, and the proportions given in Table 10 for these areas should be viewed with caution.

The northeast Pacific and the Marshall Islands are notable in their apparent absence of directly developing nudibranchs (Table 10). However, lecithotrophic development is virtually absent from the northeast Pacific and abundant in the latter. Direct development is by far most common in New South Wales and may be more common in the southeastern United States than in other parts of the Atlantic. The proportion of lecithotrophic development is similar in the Mediterrean, Red Sea, New South Wales, and the British Isles but is low in the northeast Pacific and significantly higher in the Marshall Islands and the southeast U. S., comprising nearly half the species in the latter region.

Planktotrophy is the most common mode of development in seven of the eight areas in Table 10. However, reflecting the above proportions of the other two modes, these regions can be divided into four groups based on their frequencies

TABLE 10. Proportions of planktotrophic, lecithotrophic, and direct modes of development in nudibranchs of known developmental type from the northeast Pacific Ocean and seven other geographic regions.

	Percentage of species with following type of development:[1]				
Region	pk	lec	dir	Number of species examined	Sources
northeast Pacific[2]	97	3	0	69	present study (see Table 4)
British Is.	83	13	4	47	Thompson & Brown, 1984; Todd, 1981, 1983
east coast of U.S. north of Cape Hatteras	77	14	9	22	Clark, 1975; Clark & Goetzfried, 1978; Kuzirian, 1979; Thompson & Brown, 1984
east coast of U.S. south of Cape Hatteras[3]	40	47	13	30	Clark & Goetzfried, 1978; Eyster, 1979, 1980, 1981; DeFreese & Clark, 1983; Carrol & Kempf, 1990
Marshall Islands (central Pacific)[4]	56	44	0	32	Johnson & Boucher, 1983; Boucher, 1986
Gulf of Naples (northwest Mediterranean Sea)	81	15	4	52	Schmekel & Portmann, 1982

TABLE 10. Continued.

Region	Percentage of species with following type of development:[1] pk	lec	dir	Number of species examined	Sources
northwest Red Sea	86	9	5	22	Soliman, 1991
New South Wales, Australia	64	9	27	22	Rose, 1985

[1] pk = planktotrophic, lec = lecithotrophic, dir = direct

[2] northeast Pacific north of Pt. Conception, Calif.

[3] Clark & Goetzfried (1978) reported an egg diameter of 120 um for Hypselodoris edenticulata but did not determine its mode of development. Eyster (1980) reported "pelagic" development and egg diameters of 149 and 161 um for Anisodoris prea and Learchis poica, respectively, but did not distingush between planktotrophy and lecithotrophy for these species. Based on the egg-size distributions reported by Hadfield & Miller (1987) for different development types for nudibranchs worldwide, I assumed each of these three species has lecithotrophic development.

Eyster (1979, 1980) reported both "pelagic (planktotrophic?)" and capsular metamorphic (direct) development in Tenellia adspersa (= T. pallida) from South Carolina. Most capsular metamorphic individuals hatched with their shells, and some could swim (Eyster, 1979, p.137). I therefore categorized, as did Todd (1981, 1983), the development of these Tenellia as lecithotrophic.

In two cases accounts of developmental mode of the (supposedly) same species differed. I followed Eyster's (1980, 1981) determination of lecithotrophy for

Table 10. Continued.

[3] (continued) *Armina trigrina* and Eyster's (1980) and DeFreese and Clark's (1983) reports of planktotrophy for *Spurilla neopolitana*.

[4] Proportions shown for this area are estimates based primarily on egg-size data. Johnson & Boucher (1983) reported egg-sizes for 31 species, stated that 25 of these have "pelagic" larvae, but did not distingush between planktotrophy and pelagic lecithotrophy. Based on Hadfield & Miller's (1987) results (see above), I used an egg diameter of 125 um to divide the above 25 species into those with planktotophic larvae and those with lecithotrophic development. Based on egg-sizes alone, I assumed three of the remaining six species (*Thorunna clitonata*, *T. norba*, and *Gymnodoris ceylonica*) have planktotrophic larvae, and two (*Dendrodoris elongata* and *Gymnodoris citrina*) lecithotrophic. The last species, *Gymnodoris striata*, was later found to produce unusual lecithotrophic larvae (see Boucher, 1986).

[5] Schmekel & Portmann (1982) described direct development in one species (*Cuthona granosa*), lecithotrophic development in 4 species, and "pelagic" development for 37 others. Of the latter, egg diameters were given for 31. I used an egg diameter of 125 um to divide these 31 species into those with planktotrophic development and those with lecithotrophic development (the remaining 6 species with pelagic larvae were not included in this table). In addition, Schmekel & Portmann reported egg diameters for another 16 species. Of these, I assumed *Hypselodoris messinensis*, with an egg diameter of 200 um, to have direct development; *Peltodoris atromaculata*, with an egg diameter of 180 um, to have lecithotrophic larvae; and the rest, all with eggs 110 um or less in diameter, to have planktotrophic development.

of planktotrophic development: (1) the northeast Pacific, where development is almost exclusively planktotrophic; (2) Britain, northeast U. S., Red Sea, and Gulf of Naples, where planktotrophy predominates at about 80%; (3) Marshall Islands and New South Wales, with frequencies of about 60%; and (4) southeast U. S., where about 40% of the species have planktotrophic development.

Egg size distributions for the different regions (except the Gulf of Naples) are shown in Figures 5 and 6. Even though the sources of data are the same, the sample sizes in these figures do not always match those in Table 10 because egg sizes were not available for every species whose mode of development is known. Modal and mean egg diameters for these distributions are given in Table 11.

The distributions for the northeast Pacific, British Isles, northeast U. S., and Gulf of Naples (not shown) are all similar except for the lack of large egg diameters (reflecting the lack of non-planktotrophic species) in the northeast Pacific. The distribution for the southeast U. S. is flattened (platykurtic) compared to the above four, and, reflecting the larger egg sizes associated with lecithotrophic and direct development, the mode and mean are shifted to the right. The distributions for the Red Sea, Marshall Islands, and New South Wales are not as smooth as those for the other areas, owing to the smaller samples sizes for these three regions. Moreover, in

Figure 5. Egg size distribution in nudibranchs from the NE Pacific, British Is., and two other regions (n = number of species whose egg diameter is known). See Table 10 for sources of data. Note different vertical scales.

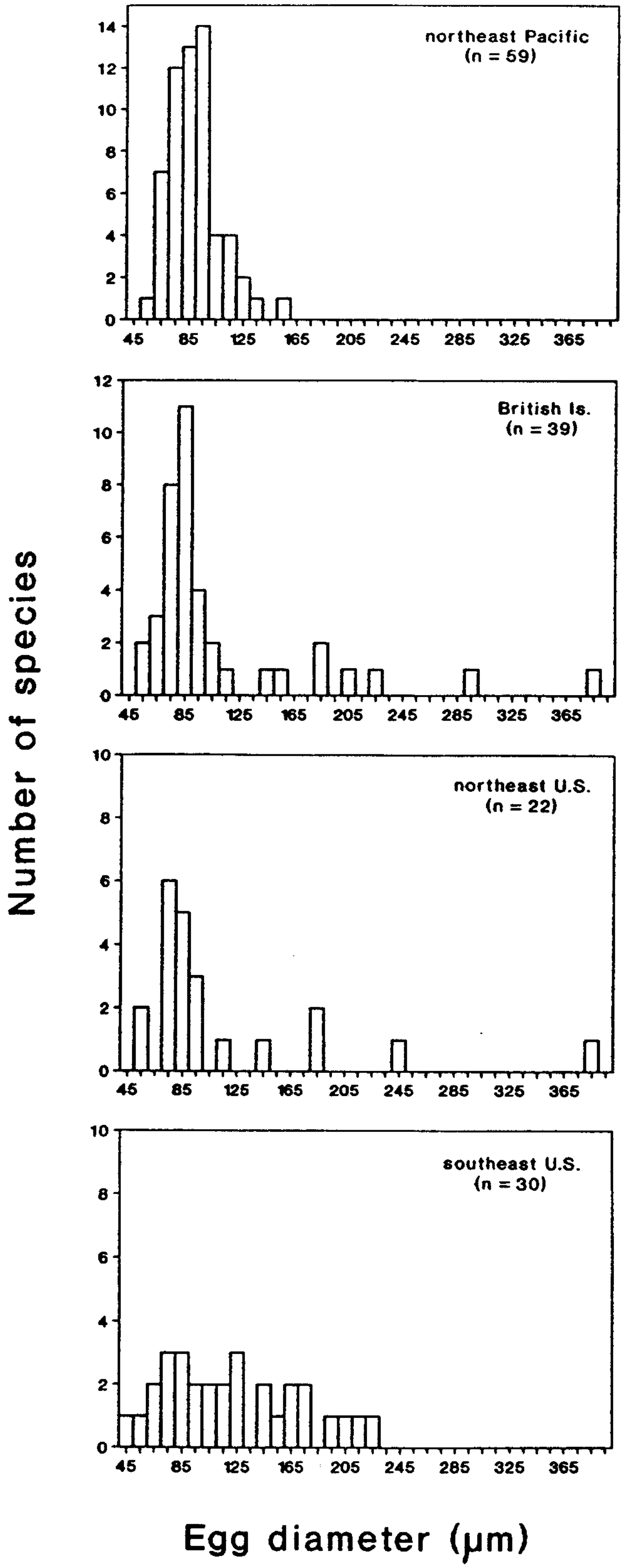
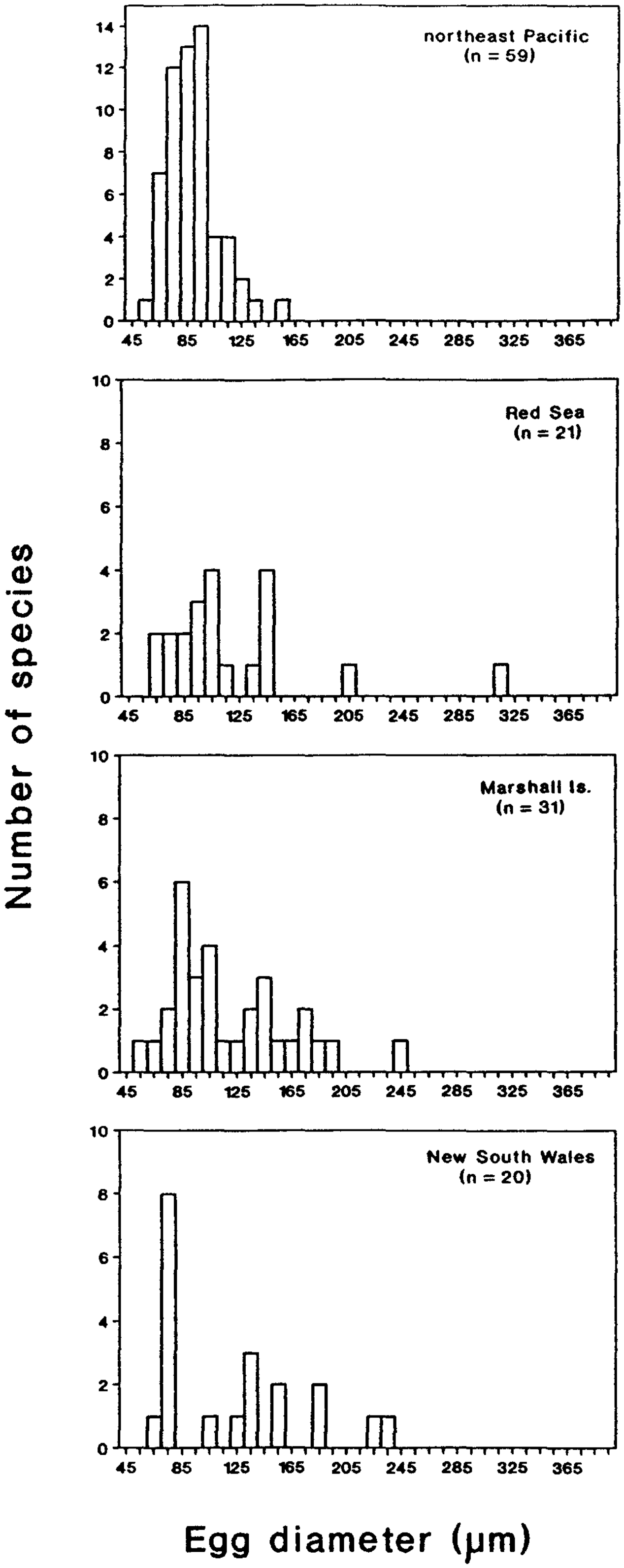

northeast Pacific
(n = 59)
British Is.
(n = 39)
northeast U.S.
(n = 22)
southeast U.S.
(n = 30)
0
2
4
6
8
10
12
14
45
85
125
165
205
245
285
325
365
Number of species
Egg diameter (µm)

Figure 6. Egg size distribution in nudibranchs from the NE Pacific, NW Red Sea, and two other regions (n = number of species whose egg diameter is known). See Table 10 for sources of data. Note different vertical scales.


northeast Pacific
(n = 59)
0
2
4
6
8
10
12
14
45
85
125
165
205
245
285
325
365
Red Sea
(n = 21)
0
2
4
6
8
10
Marshall Is.
(n = 31)
New South Wales
(n = 20)
Number of species
Egg diameter (µm)

contrast to the unimodal distributions of the other five regions, some of these distributions could be bimodal (Figure 6).

Table 11. Modal and mean egg diameters for the egg size distributions shown in Figures 5 and 6, as well as for the Gulf of Naples. Sources of data in Table 10.

Region	Mode (µm)	Mean (µm)	SD (µm)	Number of species
northeast Pacific	95	88.4	18.3	59
British Isles	85	108.8	66.1	39
northeast U. S.	75	113.4	74.1	22
southeast U. S.	80, 125	122.0	49.1	30
Red Sea	105, 145	116.7	54.9	21
Marshall Islands	85	118.3	42.8	31
New South Wales	75	121.9	52.4	20
Gulf of Naples	85	98.8	37.9	51

Reflecting the proportions of the different modes of development in the various regions, mean egg diameter is smallest in the northeast Pacific and largest in the regions with many lecithotrophic and directly developing species. In this regard, however, the Red Sea species are anomalous. Their mean egg diameter is closest to that of the Marshall Island species, but the proportions of the developmental modes are most similar to those for the British Isles.

Discussion

Northeast Pacific Ocean

Mode of Development

In this study mode of development was determined, directly or indirectly, for 69 species of nudibranchs found in the nearshore, cold-temperate waters north of Point Conception, California. 67 (97%) of these have planktotrophic development; Doto amyra, from the outer coast, and the estuarine Tenellia adspersa have lecithotrophic development (the latter species is considered introduced by Carlton (1979)); and no species are known with direct development (Tables 1-4; chapter 2). Aegires albopunctatus and Cuthona viridis may also have lecithotrophic development (Table 2), and, based on data from the north Atlantic (see Table 5), it is likely that Flabellina salmonacea, an arctic-boreal species (Millen, 1983; Platts, 1985), has direct development. Including the latter three species changes the percentages of the different types of development in the northeast Pacific to 93, 5, and 2.

Although the above 72 species constitute over 50% of the nudibranch species known to occur in the northeast Pacific (see Behrens, 1991), most of these are from the central and northern portions of this region. More observations are needed on the development of species whose ranges extend northward only to California (e.g., non-Cadlina members of the Chromodoridae; most of the northeast Pacific species of Facelinidae; see Behrens, 1991). In addition, more observations (preferably of hatching veliger larvae) are neeeded to confirm the types of development inferred in the present study for the fifteen species listed in Tables 2 and 3. These biases and qualifications aside, the proportion of planktotrophic development in the northeast Pacific appears to be considerably higher than the 66 to approximately 80% reported by Hadfield and Miller (1987, pp. 201-203) for nudibranchs worldwide, as well as the 77% for nudibranchs worldwide estimated by combining the data (including those for the northeast Pacific) in Table 10 (see below).

There is obviously no correlation between mode of development of northeast Pacific species and taxonomic affinity. Nor is there a correlation with the type of adult prey - the species listed in Table 1 consume a wide variety of generally sessile prey, ranging (with some notable exceptions) from sponges, bryozoans, and ascidians for most of the dorids to various cnidarians and bryozoans for members of the other three suborders (Thompson, 1976; Todd, 1981, 1983; McDonald & Nybakken, 1978; Goddard, 1984, and unpublished observations).

Assuming Dendrodoris krebsii, Flabellina salmonacea, Lomanotus vermiformis, Phidiana lynceus, and Spurilla neopolitana fom the Pacific have the same type of development as their Atlantic counterparts, the data in Table 5 suggest an increase in the incidence of non-planktotrophic development as one moves southward from the northeast Pacific into the eastern tropical Pacific. However, given the concurrent increase in species diversity, as well as the lack of data on the development of other tropical and subtropical eastern Pacific species, these data do not permit a firm conclusion. Similarly, consideration of the development of Flabellina salmonacea, the only species in Table 5 with a primarily arctic distribution (Franz, 1970; Kuzirian, 1979; Millen, 1983; Platts, 1985), might suggest an increase in non-planktotrophic development moving into the Bering Sea and Arctic Ocean. But, again, the data are too few, and most of the arctic-boreal species in Table 1 (e.g., Onchidoris bilamellata, Aeolidia papillosa, and Dendronotus frondosus) have planktotrophic development.

Three species examined in the present study were found to have different types of development in the northeast Pacific than is known in populations of the same species in the north Atlantic:

1) In Britain Dendronotus frondosus lays eggs 220 µm in diameter that hatch into lecithotrophic larvae (Thompson &

Brown, 1984); in the northeast U.S. D. frondosus apparently have planktotrophic development from eggs averaging 113 µm in diameter (Clark, 1975). In contrast, data from five studies at three different localities in the northeast Pacific all indicate planktotrophic development (Table 1), and the values for egg size obtained by M. Strathmann (1987) in the San Juan Islands are remarkably similar to those obtained in the present study. As noted by M. Stathmann (1987) for this species, "the loss of the shell within 2 days of hatching, reported by Williams (1971) as metamorphosis, may be abnormal." I concur. The hatching veligers depicted by Williams lack eyespots, propodium, and significant yolk reserves and are thus clearly planktotrophic and would require more than a few days to attain metamorphic competence. While it is possible that Williams' observations indicate D. frondosus loses its shell prior to metamorphosis (leaving the larvae completely unprotected from predators and osmotic stress), a more likely explanation would be that shell-loss resulted from unfavorable culture conditions or inherently abnormal development. I know of no other reports of nudibranch larvae losing their shells so early in development.

2) Eyster (1979) found pelagic (planktotrophic?) and nonpelagic lecithotrophy within the same populations of Tenellia adspersa in South Carolina, and Rasmussen (1944) reported pelagic and nonpelagic lecithotrophy in

geographically separated populations of the same species in northern Europe (there is, however, some question about the specific identity of Eyster's specimens; see Hoagland & Robertson, 1988). In the present study Tenellia adspersa from Coos Bay, Oregon produced pelagic lecithotrophic veligers, but the time to settling was not determined precisely (it was under 5 days at 20 C°(personal observations)). Cooper (1979) reared T. adspersa from Elkhorn Slough, California through its life cycle but did not state if they hatched as juveniles or larvae. More observations are, therefore, needed on the development of this species before adequate comparisons can be made with Atlantic populations.

3) Cuthona pustulata from British Columbia were reported by Gosliner & Millen (1984) to lay eggs 120 µm in diameter that develop into planktotrophic larvae. In contrast, Thompson & Brown (1984) reported eggs 180 µm in diameter and noted (p. 125) that "the finding of clusters of as many as 30 juveniles (2-3 mm) on tufts of Halecium might suggest non-pelagic development."

Given the rarity of true cases of poecilogony (variable mode of development within a species) in marine invertebrates (Hoagland & Robertson, 1988, Bouchet, 1989), more work on the systematics of Atlantic and Pacific representatives of the above three species is needed before we can rule out the possibility that the above geographic differences in mode of development actually represent species-specific differences (e.g., see Hirano & Hirano, 1991).

Although reports of shell size at hatching varied considerably for some species, those for egg size did not (see Table 1 and below), and no examples of poecilogony are known from the northeast Pacific. However, further observations on the development of Tenellia adspersa from the northeast Pacific may reveal poecilogony.

Although data on the length of the larval phase were not obtained or compiled for the planktotrophic species during the present study, some of the planktotrophic species with larger eggs may have shorter planktonic periods than those developing from smaller eggs. For example, Gosliner & Millen (1984) reported that veligers of Cuthona pustulata developed eyes after three days and appeared competent for metamorphosis after an additional 11 days (however, none of these larvae metamorphosed). This is about half (or less) of the minimum planktonic period observed for other planktotrophic, northeast Pacific species of nudibranchs cultured in the laboratory (Kempf & Willows, 1977; Chia & Koss, 1978; Harrigan & Alkon, 1978; Bickell & Chia, 1979; Bickell & Kempf, 1983; Millen, 1985, p. 85).

Most planktotrophic opisthobranch larvae lack eyespots at hatching (Thompson, 1967; Todd, 1981; Hadfield &

Switzer-Dunlap, 1984; present study, Table 1), and as stated by Bonar (1978, p. 187) "the eyes ... usually develop rather late in embryogenesis, and along with the appearance of an enlarged propodium signal the approach of metamorphic competence." However, in the nine species of Tergipedidae (species of *Cuthona* and *Catriona*) in Table 1 known to be planktotrophic, at least six hatch with eyespots. So do *Eubranchus olivaceus*, *E. rustyus* and the dendronotacean *Tritonia festiva*[1]. Eyespots have also been noted in the hatching larvae of *Cuthona foliata* (Forbes & Goodsir, 1839) from Britain (Todd & Havenhand, 1985), and, in the words of Todd (1991, p. 3), are "not, therefore, indicative always of a lecithotrophic strategy."

Eyespots in planktotrophic species may, however, be correlated with shorter precompetent periods (Goddard, 1984, p. 155). Except for *Tritonia festiva*, the above species with eyespots at hatching develop from eggs that are generally larger than those laid by other

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[1] In contrast to Goddard (1984) and M. Strathmann (1987), Hurst (1967) did not observe eyespots in hatching *Catriona columbiana*. However, the larvae observed by Hurst were considerably smaller than those observed by the former authors and probably hatched early compared to the other species. Three species in Table 1 (*Tritonia festiva*, *Cuthona cocoachroma*, and *Eubranchus olivaceus*) appear to hatch around the time eyespots are forming. Owing to intraspecific variability in both hatching time (e.g., Harris et al., 1980) and state of development at hatching (e.g., Williams, 1980; personal observations), some larvae of these species will have eyespots at hatching; others will not.

planktotrophic species (Table 1; and see below). Over a wide enough size range, increasing egg size is correlated with decreased dependence on planktonic food and a reduced pelagic phase. As described above, Cuthona pustulata appears to fit this pattern (although this species does not develop eyes until a few days after hatching). Eyespots are also correlated with the possession of type 2 shells, and, as discussed below, it is possible that the extra yolk in the eggs of these species may be required for shell-building rather than for reducing the precompetent period. If this is so, the presence of eyespots so early in the development of these species, but not in other planktotrophic species, is puzzling. Being ectodermal in origin, perhaps eyespots appear at a certain stage of development of the mantle, independent of the development of other embryonic features (and the mantle must be larger in species with type 2 shells to accommodate shell-secretion).

Egg Size, Shell Type, and Shell Size at Hatching

Based on the available data, intra-specific variation in the egg size of northeast Pacific nudibranchs is rather limited. This is consistent with the apparent lack of intra-specific variability in mode of development of these species. The largest range in individual egg size known for these species is 36 um for Cuthona punicea (Millen, 1985), and the largest known range in the mean diameter of eggs from individual egg masses is 13.1 µm for Aldisa sanguinea (Millen & Gosliner, 1985; personal observations). Coefficients of variation in the size of eggs from individual egg masses averaged 2-3 % (personal observations).

Adult diet, which has been shown by Qian and Chia (1991) significantly to affect egg size and fecundity in the polychaete worm Capitella sp., may have caused the differences in mean egg size shown in Table 7 for two egg masses of Archidoris montereyensis (these means are significantly different; $t_s = 8.94$; $p < 0.001$). The smaller eggs were laid by an individual of A. montereyensis collected from South Slough, Coos Bay, Oregon, where the diet of A. montereyensis is restricted to Halichondria panicea, while the larger eggs were deposited by an individual that had been preying on Myxilla incrustans and Axocielita sp. in exposed surge channels at Cape Arago, Oregon (personal observations). Given the unlikelihood of genetic isolation of the South Slough and Cape Arago populations (the two locales are separated by only a few kilometers, and A. montereyensis, judging from the morphology of its veliger larvae, probably has a long planktonic period), the difference in egg size between the two egg masses may well reflect environmental differences. Diet is the most obvious factor, and its potential effects on egg size (and fecundity) in A. montereyensis warrant further study.

Planktotrophic larvae with egg-shaped, type 2 shells develop from larger eggs than those with more typical, spiral, type 1 shells, suggesting either: (1) the cost of making type 2 shells is greater, or (2) species with type 2 shells, for reasons unrelated to shell type, have shorter precompetent periods and decreased dependence on planktonic food and thus require larger initial yolk reserves to attain metamorphic competence. If type 2 shells are more costly to make than type 1 shells (more mantle tissue is probably needed to secrete type 2 shells), then they likely confer some advantages; possibilities include: (a) increased protection against predators (at least during the early part of the pelagic period) owing to larger effective size at hatching (type 2 shells do not grow during larval life (see c below) but are considerably longer than type 1 shells at hatching (Figure 3)); (b) Type 2 shells, with their fusiform shape, might reduce drag and increase swimming efficiency (M. Strathmann, personal communication); (c) unlike type 1 shells, type 2 shells do not grow during larval life (Todd, 1981; Hadfield & Switzer-Dunlap, 1984). Freed from shell building, planktotrophic larvae with type 2 shells may be able to grow faster and attain metamorphic competence sooner after hatching than planktotrophic larvae with type 1 shells. This would effectively reduce the length of the pelagic period, and, presumably, larval mortality. This last possibility could be distingushed from (2) above (in which the precompetent period also is reduced) by examining the yolk reserves in hatching larvae. If type 2 shells do not cost more to make than type 1 shells, then larvae with type 2 shells developing from larger eggs will have greater yolk reserves at hatching than larvae with type 1 shells developing from smaller eggs. But, how much yolk makes the difference? How different in size or composition do the eggs have to be?

Excepting some of the species of Dendronotus, all of the species with type 2 shells in Table 1 are predators of hydroids (McDonald & Nybakken, 1978; Goddard, 1984, and unpublished observations; Thompson & Brown, 1984). Assuming a pelagic larval stage is adaptive in the life histories of organisms preying on hydroids (see chapter 2), fecundities of these predators must be high enough to counter high larval mortality rates in the plankton (Thorson, 1950; also see review by Rumrill, 1990). However, the body plan of hydroids (thin tubes with high ratios of nutritionally poor perisarc to nutritive coenosarc) probably severely constrains the adult size of their nudibranch predators (Thompson, 1976; Goddard, unpublished). This in turn constrains fecundity, especially for species with subannual life cycles (like aeolid nudibranchs). In this context, type 2 shells may be a response to selection for increased survivorship of planktotrophic larvae in the face of restricted fecundities (the large polar bodies of the hydroid-feeding Cuthona lagunae, if not an adaptation for speeding embryonic development (see chapter 3), may represent a similar sort of adaptation). However, this begs the questions of why type 2 shells are not more widespread among nudibranchs if they are advantageous compared to type 1 shells. As discussed above, there may be an increased cost to producing type 2 shells, and this cost may be outweighed by the advantages only at low fecundities and low rates of larval survivorship.

Type 2 shells (Table 1) are restricted to, and found in all members of, the aeolid families Eubranchidae and Tergipedidae and the dendronotid family Dendronotidae. This suggests the evolution of type 2 shells has occurred a number of times and is irreversible. Given the above arguments concerning adult size, fecundity, and type 2 shells, this might explain the occurrence of these shells in the Dendronotidae, many of which are large as adults.

Reports of shell size at hatching for Discodoris heathi, Onchidoris muricata, Palio zosterae, and Catriona columbiana varied considerably between different authors (Table 1). Hurst's (1967) value of 186 µm for O. muricata is at least 50 um greater than values obtained by both Goddard (1984, and present study) and Millen (1985) for this species and may indicate that considerable larval feeding and growth occurred before Hurst measured shell length in this species (M. Strathmann, 1987). Discrepancies in shell size at hatching for the other species could have resulted from a number of factors, including: errors of measurement; small sample sizes; larvae hatching at different stages of development owing to differences in culture conditions or genetic makeup; and possibly even the examination of different species. M. Strathmann's (1987) value of shell size at hatching for Discodoris heathi is anomalously low considering that the embryonic period she reported for this species is considerably longer than those given by other authors (rearing temperatures were similar) (Table 1).

The correlation between shell size at hatching and egg diameter for species with type 1 shells was quite strong (Figure 3), and it will be interesting to see how closely the shell sizes of species with larger eggs (e.g., Aegires albopunctatus and Aldisa spp.) fit the trend shown in Figure 3.

Although the correlation between egg size and energetic content of eggs can be surprisingly poor in intra-specific comparisons (e.g., McEdward & Coulter, 1987), McEdward & Chia (1991) recently reported a strong correlation between these variables among different species of echinoderms. This is the kind of relationship that underlies the trend toward larger shell size at hatching with increasing egg size shown in Figure 3.

Nurse-Eggs and Extra-Zygotic Yolk

Direct evidence for nurse-eggs was not obtained in the present study, but counts of number of eggs per capsule were crude, and no counts were made of hatching larvae - a comparison of these two numbers (or direct observation of ingestion of extra-zygotic yolk) is required to demonstrate directly the use of nurse-eggs.

Analysis of covariance did not reveal significant differences in mean shell size at hatching between species with a single egg per egg capsule and those with multiple eggs per capsule, further indicating that nurse-eggs are uncommon or nonexistent among the species in Table 1. However, this result does not exclude the possibility that particular species utilize nurse eggs or that nurse-eggs exist but affect aspects of the hatching larvae other than shell size (e.g., size of yolk reserves). No evidence for the latter was observed. With regard to the former, it may be significant that three of the four species represented by the points lying farthest above the regression line in Figure 3 (*Archidoris montereyensis*, *A. odhneri*, and *Anisodoris nobilis*) all commonly lay multiple eggs per capsule (see references in Table 1) (the fourth species, *Rostanga pulchra*, usually lays one egg per capsule (Hurst, 1967; Anderson, 1971; Chia & Koss, 1978). However, if nurse-eggs occur in the egg capsules of these three species we might expect (owing to differences between embryos in their access to, and assimilation of, extra-embryonic yolk) increased variation in the shell size of their hatching larvae. Coefficients of variation in shell size at hatching of larvae from individual egg masses for these three species varied from 1.7 to 3.1 %, values virtually identical to those for the other species represented in Figures 3 and 4 (personal observations).

The available evidence, therefore, suggests nurse-eggs are not utilized by any species in Table 1. However, a more systematic and quantitative approach (examining many more egg masses) to this question is needed. Even if nurse-eggs per se do not exist in these species, it would seem advantageous for embryos to consume any nutritive particles available, including the remains of aborted or abnormally developed siblings, which can be common in some egg masses (personal observations; also see Rumrill, 1990, pp. 164-165).

With the exception of the unusually large polar bodies of <u>Cuthona lagunae</u>, no examples of extra-zygotic yolk (EZY) were found in the present study. EZY in opisthobranchs occurs primarily in warm waters in the nudibranch family Chromodorididae and the sacoglossan family Elysiidae (Boucher, 1983; Thompson & Salghetti-Drioli, 1984).

As discussed in chapter 3, use of EZY is thought to accelerate early development (less yolk to cleave) and thus reduce mortality caused by exposure of embryos to predators and physical stresses. EZY may thus be more abundant in warm waters as an adaptive response to high benthic predation pressure at low latitudes (see discussion in Highsmith, 1985).

Although the formation of large, yolk-filled polar bodies seems an inexpensive way of providing EZY (no need for modification of the adult reproductive system), this use of polar bodies appears to be very rare, not only in the Nudibranchia, but also in the animal kingdom as a whole (see chapter 3). This may be because the changes in development required to produce large polar bodies, occurring so early in development, could disrupt other processes upon which the rest of development depends.

Embryonic Period

As suggested by the data in Table 1, intra-specific variability in hatching times can be considerable (and this variability is probably underestimated since embryonic periods are often reported as averages). Intra-specific differences in embryonic period can result from individual differences in the rate of development or from variation in the stage of development at hatching (e.g., Williams, 1980). A prolonged period of fertilization and egg laying (e.g., Millen, 1985), could also contribute to the variation.

As shown by Chaffee & Strathmann (1984) and Strathmann & Chaffee (1984) egg mass size and morphology significantly affect rates of development of the enclosed embryos. In the present study egg mass size appears to explain much of the difference in embryonic period observed between planktotrophic species with type 1 and type 2 larval shells (see Tables 8 & 9). However, egg masses were only divided into two size classes, and embryonic periods were often recorded only to the nearest day (or represent an average). A more quantitative analysis is, therefore, required to determine if the embryonic period of species with type 2 shells is in fact similar (per unit of yolk) to species with type 1 shells.

Embryonic periods reported for Aldisa tara and Anisodoris lentiginosa are unusually long compared to other planktotrophic species in Table 1 with type 1 shells reared at similar temperatures. The advantages of such long hatching times are obscure, and they warrant further study.

Regional Comparisons of Developmental Mode

Based on their results from the north Atlantic Clark & Goetzfried (1978) concluded (in contrast to Thorson's rule) that lecithotrophic and direct modes of development should be more common in opisthobranchs from polar and tropical waters than in those from temperate waters. Clark &

Goetzfried argued that climatic and trophic stability reduces the need for long distance dispersal and results in selection for nonfeeding modes of development. A primary measure of climatic stability was temperature, and in their words, "maximum trophic instability is found in areas of wide temperature variation". Clark & Goetzfried also concluded that nonfeeding development should be more common in maritime climates ("areas of low annual temperature variation") than in waters exposed to continental climates.

Arranged by latitude the data on mode of development obtained in the present study generally support Clark & Goetzfried's prediction (Table 11). The data from the lowest latitudes (limited to the Marshall Islands), however, suggest the trend at low latitudes is toward lecithotrophic rather than direct development. Data from polar waters are limited but also suggest an increase in nonfeeding development, though not to the extent seen in tropical waters. Thirty-three species are recorded by Platts (1985) as occurring in arctic waters (locations 1, 2, 3, and 5 in her Figure 1). Using developmental data in Thompson & Brown (1984) and Kuzirian (1979), mode of development can be determined for 17 of these; 12 (70%) have planktotrophic development, 3 (18%) lecithotrophic, and 2 (12%) direct.

While the data in Table 12 suggest a trend toward nonfeeding development in tropical waters, grouping the

Table 12. Latitudinal distribution of nudibranch developmental types (northern and southern hemispheres combined). Data from Table 10.

Latitude	Percentage of species with following type of development:[1] pk	lec	dir	Number of species examined	Regions represented
46-60°	83	13	4	47	British Is.
31-45°	85	9	6	165	NE Pacific, NE U.S., NW Medit. Sea, New South Wales
16-30°	60	31	10	52	NW Red Sea, SE U.S.
0-15°	56	44	0	32	Marshall Is.

[1] pk = planktotrophic, lec = lecithotrophic, dir = direct

regional data by latitude obscures significant differences between regions at similar latitudes (Table 10; Figure 7). For example, planktotrophic development appears far more common in the northwest Red Sea than on the southeast coast of the United States or in New South Wales, and is considerably more common in the northeast Pacific than in the Gulf of Naples or on the northeast coast of the United States. By Clark & Goetzfried's reasoning nonfeeding development should be much more common in the Red Sea. In addition, the data for the northeast Pacific clearly refute Clark & Goetzfried's prediction that maritime climates should have relatively high levels of nonfeeding

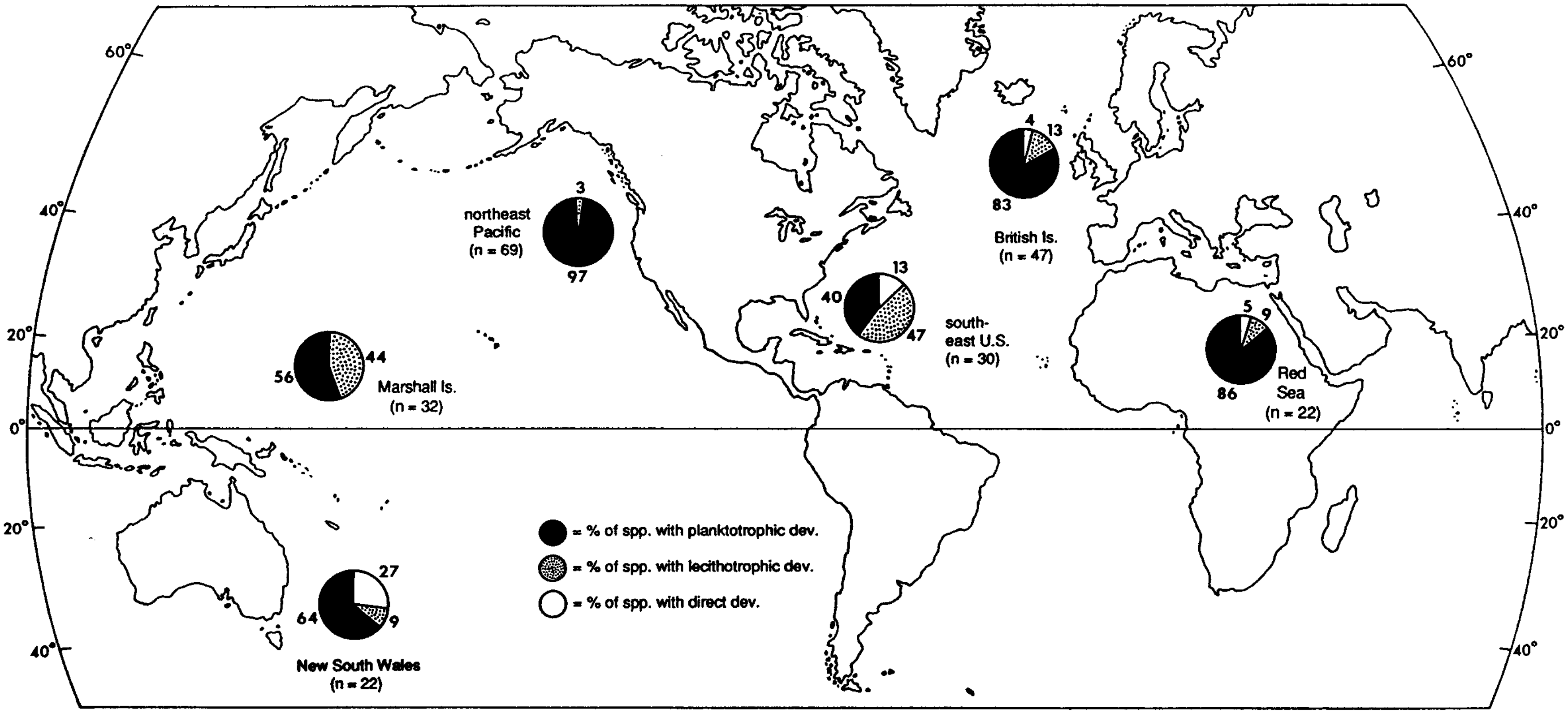

Figure 7. Map of world showing regional differences in proportions of nudibranchs with planktotrophic, lecithotrophic, and direct modes of development. Values adjacent to pie charts are percentages; n = number of species whose development is known. Data from Table 10. Van der Grinten projection, adapted from A. Cooper (ed.) The Times atlas of the oceans (1983).

development. Sea-surface temperatures vary less in the nearshore waters of the northeast Pacific than in all the other regions listed in Table 10 except the Marshall Islands (see Introduction; Tchneria, 1980; Pickard & Emery, 1990) but the northeast Pacific has the highest incidence of planktotrophic development.

Clearly then, latitude and its correlates (temperature, daylength, and length of phytoplankton growing season) do not adequately account for the regional differences in mode of development observed in the present study, and other factors need to be considered. As alluded to in the introduction, important environmental factors affecting mode of development appear to include: (1) the nature of the current regime and potential for transport of larvae away from habitats favorable for the benthic phases of the life cycle; (2) extent of habitat and environmental conditions suitable for juveniles and adults; 3) rates of primary production and size of standing crops of phytoplankton consumed by the larvae; (4) abundance of larval predators; and (5) intensity of predation on the settling and post-metamorphic stages (high levels of this factor could result in selection for juvenile sizes that may only be possible with ametamorphic direct development (see Hadfield & Miller, 1987, pp. 204-205)). With respect to the consequences for successful settlement, factors 1 and 2 are interrelated: from a larval point of view, a small area with weak currents may be equivalent to a much larger one with strong currents. Regional differences in mode of development are discussed below with respect to the first three of these factors. Not enough is known about regional differences in the last two to permit adequate comparisons (see review by Rumrill, 1990).

Diets of nudibranch larvae in the wild are unknown, making it difficult to relate estimates of phytoplankton production to larval food availability. In laboratory cultures nudibranch larvae grow fastest on various mixtures of phytoflagellates and diatoms with cells ranging from 4 to 10 µm in diameter and at cell densities "two to three orders of magnitude greater than those larvae might encounter in nature" (Hadfield & Switzer-Dunlap, 1984). In the present study late embryos of the aeolid Cuthona lagunae ingested large, yolk-filled polar bodies up to 18 µm in diameter (see chapter 3), raising the possibility that some nudibranch larvae consume relatively large cells in the wild. Despite this lack of knowledge of larval diets in the field, as well as the probable underestimation of the contribution by nanoplankton to overall phytoplankton production (see discussions in Raymont, 1980; Berger, 1989), available estimates of primary productivity should provide at least a crude measure of the food available for nudibranch larvae in different regions.

Estimates of average annual primary productivity and velocity of major surface currents are compiled in Table 13 for each of the regions listed in Table 10. The values given for these two factors mask important variability over a wide range of temporal and spatial scales (e.g., see Monin's (1986) discussion of the east Australian current and Mann & Lazier's (1991) summary of seasonal patterns of phytoplankton production in temperate waters). In addition, the currents listed are primarily oceanic, and thus may not have much affect on larval distributions of coastal species unless significant exchange occurs between coastal and oceanic waters. These weaknesses aside, the magnitude of the regional differences in these two factors seem large enough to allow speculation concerning their consequences for larval survivorship and mode of development.

Larval development of nudibranchs from the coastal waters of the northeast Pacific Ocean is almost exclusively planktotrophic, and this mode of development predominates at about 80% in the British Isles, the northeast United States, the Gulf of Naples, and the northwest Red Sea. Surface currents in the coastal and oceanic waters of all of these areas are slow and diffuse (Table 13). Thus long-lived, feeding larvae released in these waters probably have a good chance of encountering favorable benthic habitat upon attaining metamorphic competence, especially in the northeast Pacific, with its vast stretch of relatively uniform habitat and environmental conditions

Table 13. Major surface currents and average annual primary productivity of the waters in or adjacent to the regions listed in Table 10.

Region	Average annual 1° productivity of coastal waters[1] ($gCm^{-2}yr^{-1}$)	Major surface currents name	velocity[2] (cm/sec)
northeast Pacific	350	California Alaska Davidson[3]	5-20 5-15 5-15
British Is.	130	N. Atlantic	20
northeast U.S.	350	(Gulf Stream	100-250)[4]
southeast U.S.	130	Florida	75-250
Marshall Is.	25	N. equatorial	20-30
northwest Mediterranean Sea	130	--	--
northwest Red Sea	80	--	--
New South Wales	70	E. Australian	0-200

[1] Values are midpoints of ranges (or combined ranges) in Figure 6 of Berger (1989).

[2] Values from Tchneria, 1980; Pickard & Emery, 1990; Monin, 1986; Griggs, 1974; Hickey, 1979; Boland & Church, 1981.

[3] Nov. to Feb. only; flows over continental shelf.

[4] The Gulf Stream lies considerably offshore of the NE U.S. continental shelf and slope.

(see Introduction), and in the enclosed and relatively homogenous Red Sea, with its extensive rocky shores and coral reefs (see Jones et al., 1987 and Head, 1987). Excepting the northwest Red Sea, the productivity of the waters in each of these areas is moderate to high (Table 13) and probably can support high numbers of planktotrophic larvae. Data on productivity in the Red Sea are sketchy, but production appears to increase significantly as one moves south toward the Straits of Bab Al Mandab and the Gulf of Aden (see review by Weikert, 1987).

Assuming the proportions of the different modes of development shown in Table 10 for the Red Sea are accurate, it may be significant that mean egg size of the Red Sea species is larger than the means for the other regions with a high incidence of planktotrophic development (Table 11). If nudibranch larvae in the Red Sea are limited by planktonic food supplies they would probably require greater initial yolk reserves to reach metamorphic competence. In addition, two of these species provision their embryonic offspring with extra-capsular yolk supplies (see review by Boucher, 1983). Of the species included in Table 10, only species from the oligotrophic waters around the Marshall Islands and two species from New South Wales are known to employ this tactic (see below).

Despite the apparently low overall productivity of the northern Red Sea, larvae may be able to take advantage of higher productivites in coastal waters, where nutrient inputs from seagrass meadows and mangroves could be considerable (see Jones et al., 1987). Data on the diets, distribution, and longevity of planktotrophic nudibranch larvae in the northwest Red Sea and the potential for food limitation are needed to reconcile the apparently high incidence of planktotrophic development with the apparently low productivity of the waters. In this regard a comparison of egg sizes (and developmental mode) of the same species from the more productive southern Red Sea or Gulf of Aden would also be useful.

The coastal waters of the northeast United States are very productive, but of the above five regions, have the lowest percentage of species with planktotrophic development. This can be attributed to: (1) the steeper environmental gradients (especially temperature) on the east coast and thus an increased chance of larvae being swept away from favorable adult habitat; and (2) a directly developing arctic faunal component (*Flabellina salmonacea* and *Cadlina laevis*) that, owing to the low diversity of nudibranchs on the east coast, constitutes a higher relative proportion of the fauna. Although Thorson's (1950) generalization of a gradual increase in the proportion of direct development as one moves from the equator to the poles is questionable for many higher taxa of marine invertebrates (see Introduction), his conclusion that nonfeeding modes of development predominate in polar waters (which are typically oligotrophic, very cold, and subject variable surface salinities) has been substantiated by numerous studies (e.g., Picken, 1979; White, 1984; Bosch & Pearse, 1990; but see Shimek, 1986). Data on the development of polar nudibranchs are scarce (see above) but suggest an increase in nonfeeding development in this group as well. Thus, we might expect a higher proportion of lecithotrophically and directly developing species in regions with a polar faunal component (also see discussion of New South Wales below). The virtual absence of nonfeeding development in nudibranchs from the northeast Pacific in part reflects its comparative isolation from arctic waters.

Species with lecithotrophic and direct modes of development predominate off the southeast coast of the United States and constitute about 40% of the fauna in both the Marshall Islands and New South Wales (Table 10, Figure 7). Direct development is absent from the Marshall Islands, most common in New South Wales, and intermediate in frequency (at 13%) in the southeast United States.

Primary production off the southeast United States is comparable to that around the British Isles and probably could support long-lived, feeding nudibranch larvae, but two factors appear to select against planktotrophy in these waters. First, the swift, northward flowing Florida current lies close to shore. Larvae caught in this current likely would be transported long distances in a short time. Secondly, environmental conditions, including the temperature regime and physical nature of the benthos, change markedly north of southern Florida (salt marshes and (or) soft substrates predominate from central Florida to Cape Cod, and average sea-surface temperatures decline rapidly north of Cape Hatteras (Gosner, 1971)). Long-term larvae originating from a coral reef in southern Florida and caught in the Florida current would not encounter significant amounts of hard substrata (which the prey of most nudibranchs require) until they reached either: (1) New England and the Gulf of Maine, with their markedly different different environmental conditions; (2) Bermuda; or (3) entered seasonal, southward flowing shelf currents and managed to reach southern Florida (with regard to this last possibility, see summary in Bowden, 1983, chapter 9). Despite these apparently adverse conditions for long-term larvae, some 40% of the nudibranch species off the southeast U.S. have planktotrophic development. Some of these are probably associated as adults with more widespread habitats (e.g., fouling communities, oyster reefs, or salt marshes); others may possess larval behaviors that promote retention in, or return to, the area in which they hatched. Finally, in southern Florida some species may consist of populations that persist only through larval recruitment from other populations located in the Caribbean or Gulf of Mexico. This last possibility raises the question of whether mode of development in any species in southern Florida reflects adaptation to local or distant conditions. While conditions in southern Florida might select for nonfeeding modes of development, gene flow (in the form of larval recruitment) from other areas might preclude local adaptation, and force us to explain mode of development in a species on the basis of selective factors acting in another area. Determination of the level of endemism in Florida nudibranchs, combined with intra- and inter-specific comparisons of developmental mode elsewhere in the Caribbean and tropical west Atlantic are needed to resolve these questions. Measures of gene flow between populations in this larger region (e.g., Mitton et al., 1989; Todd et al., 1991) would also be useful.

Nearshore waters off New South Wales, Australia are apparently less productive than those off the southeast U.S. coast, but like the latter, are close to a swift western boundary current (Table 13). However, as summarized by Boland & Church (1981) and Koshlyakov (1986), the east Australian current is episodic in occurrence and often forms long-lived eddies and loops of varying length . Larvae entrained in the former might periodically encounter suitable adult habitat as the eddies rotate (see Lobel & Robinson, 1988), but, owing to the general south to southeastward drift of the eddies (see Koshlyakov, 1986, Figure 4.3.1), are probably more likely to be transported slowly offshore. Owing to the generally oligotrophic waters and lack of land masses in the south central Pacific, larvae that do not reach Tasmania or New Zealand are likely lost.

Although the number of species whose development is known in New South Wales is small compared to the size of the fauna, this region appears to have a higher proportion of species with planktotrophic development than the southeast United States, possibly reflecting the episodic nature of the east Australian current. That is, conditions for planktotrophic development are favorable when the current is weak or nonexistent, and this happens frequently enough to allow the persistence of species with this mode of development. As in Florida, some of these species may also be able to take advantage of other mechanisms, such as depth regulation and the use of counter-currents, to prevent being swept away from favorable habitat, even when the east Australian current is close to shore and at full-strength.

New South Wales is unique among the regions listed in Table 10 in its high proportion of species with direct development. Because three families are represented by these six species, no phylogenetic biases appear to influence the pattern of development in New South Wales. Similar patterns have been noted for cowries and echinoid echinoderms from southern Australia (Wilson, 1985; Emlet, 1990, respectively). In both of the latter cases the high incidence of nonfeeding development was attributed to marked cooling of the surrounding ocean waters during the late Tertiary (see summary in Quilty, 1984) and therefore found to be consistent with the general increase in nonfeeding development in polar waters. In this regard, Australia's former proximity to Antarctica may also be important. Even though climatic conditions in Antarctica and Australia during much of the Mesozoic and early Cenozoic appear to have been mild (reviewed by Quilty, 1984), phytoplankton production would probably have been strongly seasonal owing to the high latitude. A short phytoplankton growing season (combined with cold or cool water temperatures) is thought to be one of the major factors selecting for nonfeeding development in polar invertebrates (Thorson, 1950; Clarke, 1982; White, 1984).

The high proportion of nonfeeding development in nudibranchs from the Marshall Islands can be attributed to the very low productivity of the surrounding waters (Table 13) - planktonic food is simply not abundant enough to fuel the timely growth of large numbers of planktotrophic larvae. The dependence of nudibranch larvae in this region on parentally supplied yolk is further indicated by the number of species that provision their egg masses with extra-capsular yolk supplies. Of the 32 species whose egg masses were observed, 8 (25%) produce extra-capsular yolk (Johnson & Boucher, 1983; Boucher, 1986). Of the other regions considered in the present study, only a few species from the Red Sea and two species from New South Wales are known to produce extra-capsular yolk reserves for their embryos (see Boucher, 1983). It is probably no coincidence that productivities in the latter two areas are also low.

But why the apparent lack of direct development in the Marshall Islands? While the ocean area with environmental conditions suitable for these species is large (most of the Indo-Pacific), individual habitats, especially in the central Pacific, are relatively small and separated by large expanses of deep water (Scheltema, 1986a). Individuals with a larval stage would be able to spread among island habitats (and locate new patches of prey) much more effectively than those with direct development, especially if opportunities for dispersal by rafting of juveniles and adults are limited (see Highsmith, 1985). The low productivities of the waters in much of this area, however, preclude planktotrophy for many, if not most, species. Owing to the distances between some of the island groups, as well as the generally slow current speeds (Scheltema, 1986a), I would also predict a high incidence of facultative planktotrophy and potentially very long competent periods in species with lecithotrophic development. Representatives of many other groups of invertebrates have long-lived, teleplanic larvae in the central Pacific (Scheltema, 1986a).

Even if originally colonized by species with long-term pelagic larvae, extremely isolated islands, if old enough, may have higher incidences of direct development (and increased levels of endemism) owing to selection for local retention of offspring (e.g., see Rosewater, 1975; Clark, 1984) Other mechanisms that might result in retention of offspring in the vicinity of isolated islands include: (1) timing the release of pelagic larvae to take advantage of seasonal eddies, gyres, and convection currents associated with some islands (e.g., Boden, 1952; Emery, 1972; Lobel & Robinson, 1988), and (2) vertical movements by larvae to take advantage of nearshore currents, tidal current oscillations, or reduced current flow near the bottttom (e.g., Bowden & Kampa, 1953; Hadfield, 1978). The evolution of these adaptations in specific populations depends, of course, on the existence of adequate variability in the appropriate life history traits and on the frequency and degree of gene flow from regions with different environmental conditions.

Conclusions

Based on the above evidence, I conclude that, world-wide, planktotrophy among shallow water nudibranchs is most common in regions with relatively slow currents, high standing stocks of phytoplankton, and large expanses of habitat favorable for the adults. Nonfeeding modes of development tend to predominate in regions with fast boundary currents, relatively oligotrophic waters, rapid changes in physical aspects of the adult environment, or in areas once in contact with polar waters. In addition to an increase in the incidence of nonfeeding development, nudibranchs from oligotrophic waters are more likely to provision their egg masses with supplies of extra-zygotic yolk that are consumed by the developing embryos or newly hatched larvae. In general, planktotrophy should be more common in nudibranchs from the eastern boundaries of oceans than in the western areas owing to the slower currents and maritime climates of the former. Planktotrophy also should be more common in temperate waters than in polar waters, with their short phytoplankton growing seasons, or in frequently stratified, oligotrophic tropical waters.

Given the above general patterns, I would predict a high incidence of planktotrophy off the Pacific coasts of Central America and most of South America, with their extensive rocky shores and strong upwelling (southern

Chile, however, probably has an antarctic faunal component with nonfeeding development) and off NW and SW Africa, with their strong upwelling and very productive waters (see Berger, 1989). Patterns of development off NW and SW Africa, however, will also depend on the strength of the offshore transport of surface waters and on the extent of the habitat suitable for particular nudibranchs (like the east coast of the United States, these areas are parts of an old, trailing edge coast dominated subtidally by soft substrates (Schultz, 1990), rather than the hard substrates required by most nudibranchs and their prey).

Examples of areas where nonfeeding development should be more common include: (1) the Pacific coast of southern Japan, which is close to the swift Kuroshiro current and an area of wide temperature fluctuation; (2) off eastern Brazil, south of the equator (low productivity, limited hard substrate, and close to the Brazil current); (3) in the eastern Mediterranean Sea (low productivity); (4) off southern Australia and Tasmania (historically cold waters); and (5) in the center of the major subtropical ocean gyres, with their low productivity (see maps in Pickard & Emery, 1990; Berger, 1989). Nonfeeding modes of development may also be more common on old isolated islands than on young ones, owing to selection for adaptations preventing loss of individuals from favorable habitat. These predictions should be considered tentative, since they are based on only cursory evaluations of hydrography, geology, and productivity in the respective areas.

The above arguments should not be expected to explain all cases of development in nudibranchs, but only general regional patterns. Mode of development in any one species is undoubtedly shaped by many factors acting on a wide variety of scales, and other aspects of the ecology of a species can result in selection for a particular mode of development, regardless of the prevailing environmental conditions considered above. For example, ametamorphic direct development, which can produce larger juvenile sizes than the other modes of development (Hadfield & Miller, 1987), may be an effective way of overcoming defenses or size constraints imposed by the prey of the juveniles. In some species overall fitness may be little affected by mode of development (e.g. Levin & Huggett, 1990), leaving other mechanisms of evolution to shape developmental mode. Finally, as mentioned in chapter 2, selection has many aspects of the larval stage to work with, not just the size of their yolk reserves and degree of dependence on planktonic food for growth.

Improvements in the approach taken in the present study include: (1) consideration of the seasonality of reproduction, primary production, and of the various hydrographic factors; reproduction in many species is undoubtedly timed to take advantage of seasonally favorable conditions; (2) determination of larval diets in the wild, and evaluation of the potential for food limitation in different regions; some larvae may utilize bacteria and detritus as their primary food sources, especially in oligotrophic waters (e.g., Rivkin et al., 1986); (3) increased knowledge of larval behavior, especially with regard to retention in, or advection from, an area, (4) better understanding of the exchange between coastal and oceanic waters, (5) determination of historical differences in marine climate and hydrography, and (6) measures of predation on pelagic larvae and on the early benthic stages. This last factor will probably prove important in determining the selective advantages of pelagic lecithotrophic development vs. benthic nonfeeding development, which, as pointed out by Bosch & Pearse (1987, p. 45) are poorly understood. Why should nonfeeding development in the Marshall Islands be entirely lecithotrophic, and primarily direct in New South Wales and perhaps polar waters?

The conclusions drawn in the present study should apply to some groups of marine invertebrates, but not necessarily others, owing to differences in: (1) life histories (e.g., short-lived, species like nudibranchs vs. long-lived iteroparous species); (2) trophic level and degree of dietary specialization; (3) phylogenetic constraints; and (4) habitat requirements. For example, the amount of habitat favorable for some suspension-feeding, subtidal, infaunal bivalves may be immense, greatly reducing the chances of larvae being swept away from favorable adult habitat.

Regional variability in the mode of development of tropical prosobranch molluscs (e.g., Knudsen, 1950; Natarajan, 1957; Bandel, 1976a, b; D'Asaro, 1970, 1986) and the different types of larval development known in, for example, corals (reviewed by Fadlallah, 1983) suggest that regional environmental differences (other than just latitude and its correlates) probably influence patterns of development in these and other groups. Emlet's (1990) finding that nonfeeding development is common in echinoid echinoderms from southern Japan is consistent with the predictions made above for nudibranchs and certainly warrants further investigation. Constraints of time and space preclude further consideration in the present study of global patterns of development in other taxa, and, for now, I leave it to other workers to examine the data for their respective groups with respect to the environmental factors considered above.

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CHAPTER II

LECITHOTROPHIC DEVELOPMENT IN DOTO AMYRA NUDIBRANCHIA: DENDRONOTACEA), WITH A REVIEW OF DEVELOPMENT IN THE GENUS

Introduction

Development in opisthobranchs can be divided into three general types based on the presence or absence of a larval stage and on whether or not the larvae require particulate foods to complete development: (1) planktotrophic, in which the veliger larvae must feed and grow in the plankton before metamorphosing; (2) lecithotrophic, in which the larvae can metamorphose without prior feeding; and (3) "direct", in which juveniles, rather than larvae, hatch from the egg capsules (Thompson, 1967; 1976; Bonar, 1978; Hadfield & Switzer-Dunlap, 1984). Direct development entails development of an embryonic veliger, followed by capsular metamorphosis, or may be ametamorphic. The latter two types of development have been described for only a few opisthobranchs from the cold temperate waters north of Point Conception, California. Bridges (1975) described capsular metamorphic development in the anaspidean *Phyllaplysia taylori* Dall 1900. Embryos of the cephalaspidean *Haminoea callidegenita* Gibson & Chia, 1989 hatch from their egg capsules as either non-feeding lecithotrophic veliger larvae or as benthic post-larvae in the last stages of metamorphosis (both apparently from eggs and egg capsules of the same size and without extra-zygotic yolk) (Gibson & Chia, 1989). Goddard (1984) briefly described lecithotrophic development in the small dendronotacean nudibranch Doto amyra Marcus, 1961, and Goddard (1990) observed lecithotrophic development in the aeolid nudibranch Tenellia adspersa (Nordman, 1845), an introduced species whose mode of development appears to vary both between and within populations in the North Atlantic (Rasmussen, 1944; Eyster, 1979; but see Hoagland & Robertson, 1988 and Bouchet, 1989).

Larval development of the cephalaspidean Aglaja inermis (Cooper, 1862) (which ranges as far north as Monterey Bay, but is more common south of Point Conception) has not been described, but a photograph in Morris et al. (1980) of its egg mass shows embryonic veligers with large eyespots and possibly a propodium, suggesting lecithotrophic development in this species as well (see Thompson, 1967; Bonar, 1978).

This paper describes in greater detail aspects of the larval development, metamorphosis, and post-larval growth of Doto amyra, the only one of the above species known primarily from the open coast, and the only one which is a native nudibranch (see Chapter 1 for an analysis of patterns of development in northeastern Pacific nudibranchs as a whole). D. amyra occurs from northern Baja California to Vancouver Island (McDonald, 1983; Millen, 1983) and preys suctorially on the coenosarc of hydroids such as Abietinaria sp. and Sertularia furcata (Goddard, 1977; 1984).

Based on personal observations of adults, larvae, and prey of specimens of Doto from central California to central Oregon, as well as on information provided by other workers, D. amyra as presently accepted by Beeman & Williams (1980), Behrens (1980), McDonald & Nybakken (1980); and McDonald (1983) may include two, and as many as four, distinct species. Aspects of the external morphology, color, and larval development of these varieties are described below in an appendix in order to distingush which specimens I regard as D. amyra.

Consideration of the evolution and adaptive significance of lecithotrophic development in Doto amyra (see discussion) led to an examination of the data available on development in other members of the genus. These data, not previously examined as a whole, are summarized and analyzed in a separate section, and patterns of development in the genus are compared to some of those recently described by Hadfield & Miller (1987) for the Nudibranchia as a whole.

Methods

Adults and egg masses of Doto amyra were collected, along with their hydroid substrate and prey Abietinaria sp. (A. anguina of Ricketts et al., 1985) from semi-protected, low intertidal pools at Middle Cove, Cape Arago during spring and summer of 1983 and 1985 (see Goddard, 1984 for a description of this area). Nudibranchs and hydroids were maintained together in small wide-mouth jars of unfiltered seawater held in seawater baths at either 12-15°C (spring 1983), 15-17°C (summer 1983), or 11-13°C (1985). Water in these jars was changed once or twice daily. Small pieces (~1 cm long) of hydroid colonies on which egg masses had been laid were cut off and maintained in separate vials of unfiltered seawater. A few newly deposited egg masses were completely removed from the hydroids and held separately. Water in all vials was changed once or twice daily until the veliger larvae hatched and every two or three days thereafter. All adults, egg masses, and larvae were exposed to indirect natural lighting in the laboratory. Observations of development, measurements of size, and photomicrographs were made using live material, a Zeiss compound microscope equipped with a calibrated ocular micrometer, and bright field optics.

Observations

Egg Masses and Eggs

At Cape Arago Doto amyra (Figure 1) laid their egg masses primarily on the stolons and basal portions of the hydrocaulus of Abietinaria sp. The egg masses (Figure 2) are short, inflated ribbons laid on edge and broadly rounded at the ends. They are attached to the substratum by a translucent white, tough, gelatinous sheet shorter than the egg mass itself. Longer ribbons usually fold or curve back on themselves a few times; smaller masses are kidney- or crescent-shaped. The pale yellow eggs number one per capsule and give the egg masses their color. Egg masses observed in this study were up to 6 mm long and 1.8 mm high, with a mean of 79 eggs per mm^2 of ribbon (SD = 8, 4 samples from two egg masses). One typical egg mass 2 mm long and 1.7 mm high contained 240 eggs. The mean diameter of zygotes in eight egg masses varied from 145.1 µm in one egg mass to 157.6 µm in another, with a grand mean of 151.8 µm (Table 1).

Larvae

Veliger larvae hatched after an embryonic period of 19 to 21 days at 15-17°C, and 28-29 days at 11-13°C (Table 1; Figures 3 and 4). They had large eyespots, a large foot with a well developed propodium, and a relatively small

Figure 1. _Doto_ _amyra_. Live specimen, 12 mm long, from Middle Cove, Cape Arago, Oregon (June, 1985).