

Worldwide patterns in mode of development in calyptraeid gastropods

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ABSTRACT: The mode of development in marine invertebrates is believed to have consequences for dispersal, gene flow, geographic range, and speciation and extinction rates. The factors responsible for among-species differences in mode of development are not well understood and patterns of variation in mode of development have not been documented for many groups. I present a compiled data set of developmental characters for 78 species of calyptraeid gastropods: 53 *Crepidula*, 9 *Calyptrea*, 11 *Crucibulum* and 5 other species. Analysis of this data set shows that egg- and hatching-size distributions are strongly positively skewed. As expected, egg size correlates with hatching size and time to hatching in species without nurse eggs. Egg size is not significantly different between species with planktotrophic development and species with direct development with nurse eggs. Hatching size of direct developers with and without nurse eggs do not differ. Developmental characters do not vary with adult body size among species. There are strong latitudinal effects in mode of development, the frequency of planktotrophic species decreases with increasing latitude while the proportion of direct developers increases. There is also a striking latitudinal pattern in the occurrence of nurse eggs; almost all species with nurse eggs occur in the southern hemisphere. These latitudinal patterns do not appear to be explained by sea surface temperature. Comparisons with other gastropods for which similar compilations are available show a striking difference between heterobranchs (opisthobranchs and pulmonates) and caenogastropods in developmental characteristics.

KEY WORDS: Larvae · Invertebrate development · *Crepidula* · *Crucibulum* · *Calyptrea*

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INTRODUCTION

Studies of a variety of marine invertebrates have shown that the type of embryonic and larval development (direct or indirect, brooded, encapsulated or planktonic) has far reaching evolutionary consequences. Species with planktonic developmental stages are thought to have higher rates of dispersal and, therefore, higher rates of gene flow than species with direct development (e.g. Berger 1973, 1977, Hedgecock 1982, McMillian et al. 1992, Duffy 1993, Hunt 1993, Hoskin 1997, Collin 2001). Mollusc and echinoderm species with planktonic planktotrophic larvae also inhabit larger geographic ranges than

similar species with direct development (Scheltema 1989, Kohn & Perron 1994, but also see Ó Foighil 1989, Emler 1995). These features are thought to result in lower rates of speciation and lower rates of extinction for species with planktonic feeding larvae than for species with direct, non-feeding development (e.g. Hansen 1978, 1980, 1982, Strathmann 1985, Jablonski 1986a,b, 1987).

It is not clear what evolutionary factors lead to differences in mode of development among species. However, patterns in mode of development appear to exist with latitude, habitat depth and body size (Thorson 1946, 1950, Ockelmann 1965, Mileikovsky 1971, Strathmann & Strathmann 1982). Latitudinal patterns have

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been demonstrated for bivalve and gastropod faunas from the North Atlantic (Thorson 1950, Ockelmann 1965) and the South American coast (Gallardo & Pencheszadah 2001); however, they have received little attention in other geographic regions. Geographic patterns of ascoglossan and nudibranch egg size have been examined (Clark & Goetzfried 1978), but geographic patterns of developmental characters have not been closely examined for other, more exclusive monophyletic groups of molluscs. Differences in brooding and body size for sympatric pairs of species were reviewed by Strathmann & Strathmann (1982), but again, the available data are limited. Despite the fact that these patterns have been demonstrated only for geographically and taxonomically limited groups, they have provided the impetus for the development of various theories of the evolution of mode of development. For example, it has been proposed that seasonal productivity limits development at high latitudes to non-feeding development (e.g. Thorson 1950), and that allometric constraints limit small animals to be brooders or produce embryos with non-feeding development (reviewed in Strathmann & Strathmann 1982).

Basic comparative data on the reproductive characteristics of monophyletic groups of marine invertebrates are essential both to document patterns and to compare them with the patterns predicted by life history modeling. Reviews and analyses of variation among species in reproductive and developmental characters are common for echinoderms (e.g. Mortensen 1921, Emlet et al. 1987, Emlet 1990, 1995, Pearse 1994, Sewell & Young 1997). Developmental data compilations for echinoids include 204 species (24% of all known echinoids and 45% of extant regular echinoids; Emlet 1995), and egg-size data sets for other echinoderms include 149 species of asteroids, 132 species of ophiuroids and 184 species of holothuroids (Sewell & Young 1997). Such data compilations have been successfully used to test Orton's and Thorson's 'Laws' (trends with depth and latitude; see Pearse 1994), Vance's prediction of a bimodal distribution of egg size (Sewell & Young 1997), and the ideas that the size of a species' biogeographic range, body size and habitat depth are associated with mode of development (Emlet 1995). In addition, comparative analyses have used data from these compilations in combination with explicit phylogenies to investigate the patterns of evolution of mode of development (Wray 1996, Cunningham 1999). Because other invertebrate phyla show distinct types of development that are not present in echinoderms, and because variation in mode of development often appears to be distributed differently among taxa in these groups, it is important to examine patterns in other invertebrate taxa. Unfortunately, the

necessary data compilations are not widely available for most groups of marine invertebrates.

The few existing compilations of data on gastropod development usually focus on a specific taxon and often cover a small percentage of extant species. Perhaps because they contain complete data for few taxa, most reviews of gastropod development (e.g. 38 species of cephalaspids, Schaefer 1996; 53 species of muricids, Spight 1976; 30 species of calyptraeids, Hoagland 1986; have not been analyzed in as much detail as have the echinoid data. However, in-depth analysis of development for 62 species of Indo-Pacific *Conus* (~15% of valid extant species; Kohn & Perron 1994) showed that the mode and duration of development correlate with egg size and that these characteristics are associated with the size of a species geographic range. Subsequently the same data were used by Duda & Palumbi (1999) to test the hypotheses that speciation rate is associated with mode of development. A large data set for opisthobranch molluscs (Hadfield & Switzer-Dunlap 1984) shows that the egg size distribution of 260 species is not, as predicted by Vance (1973a,b), bimodal and that duration of development, size at hatching and mode of development all correlate with egg size. The results from these 2 analyses both show significant associations between developmental variables and egg size. However, the limited variation in mode of development and geographic range of these groups constrain the generalizations that can be made from these 2 studies alone. For example, neither group includes species with nurse eggs (where embryos developing from small eggs consume other eggs or embryos), a strategy common among caenogastropods (Spight 1976, Rivest 1983), and *Conus* is an entirely tropical or sub-tropical genus.

Fifteen years ago, Hoagland (1986) published a review of development and reproduction of 30 species in the caenogastropod family Calyptraeidae (both egg size and hatching size for only 12 species). The present paper builds on these data by reviewing information in more recently published papers and including previously unpublished observations. I use this data set to examine patterns of variation in mode of development as it relates to egg size, hatching size, female body size and latitude. Specifically, I ask the following questions: Are the egg size and hatching size distributions right skewed and/or bimodal? How are egg size, hatching size and mode of development related? Is there a relationship between body size and hatching size? Is there a relationship between latitude or habitat temperature and mode of development? This analysis provides a data set and analyses similar to those already available for *Conus* (Kohn & Perron 1994) and for opisthobranchs (Hadfield & Switzer-Dunlap 1984). Because all calyptraeid species are protandrous hermaphrodites that

brood for the early portion of development and nurse eggs occur in numerous species (characteristics that are not present in these other groups), this study significantly increases the coverage of differing types of development among compilations of data on invertebrate development.

MATERIALS AND METHODS

Data. To document patterns of development, I compiled a data set of developmental characters for 78 calyptraeid species (Tables 1 & 2). In addition to developmental data (egg size, hatching size, size at settlement and presence/absence of nurse eggs), this data set includes latitude and female body size (Table 1). Time to hatching, time to settlement and temperature were also recorded where available (Table 2).

Unless noted otherwise, the methods outlined in Collin (2000a) were used to measure and count embryos and to raise larvae (except that larvae were fed *Isochrysis galbana* and *Dunaliella* sp. in Panama City, Panama, and *Chaetoceros gracilis* and *Belerochia polymorpha* in La Paz, Mexico). To supplement my observations, I also compiled all available published information. Methods used to obtain data in these published studies can be found in the relevant references.

In some cases, several different values are reported by different authors for the same species. Because different modes of development (poecilogony) have not been reported for any species of calyptraeids (many of which have been examined in detail; Hoagland 1984, 1986, Véliz 1998, Collin 2000b, 2001) it is likely that large differences are the result of observations from different cryptic species. In many published reports of development, adult morphology is not described in enough detail to verify the species identification and no voucher specimens are available for study. When significant differences in development are reported, I list each individual observation separately, as a separate entry. In several cases, there are known cryptic species that have not yet been formally described. I have listed these distinct unnamed species in the same way. For species with direct development and lecithotrophic development, settling size is the same as hatching size and is used this way in subsequent analyses.

Because calyptraeids are protandrous hermaphrodites with variable size at sex change and indeterminate and variable growth, it is difficult to characterize female body size in a satisfactory way. However, it is clear that females of some species are larger than those of other species. I coded female size as the average shell length of the 5 largest females that I collected from the same population as the developmental data.

For species that I have not observed in the field, I either used data from publications on their reproduction or the 5 largest shells for that species from the geographically closest locality in the collections of The Field Museum, Chicago, Illinois.

Analyses. The developmental data (Table 1) were not collected or reported in a uniform way. Analyses were conducted using the mean value for each character. If the mean was not reported, I used the midpoint of the reported range. For all analyses except examination of latitudinal effects, only a single value of each variable was used for each species. Again the mean or midpoint of the reported ranges was used when several trustworthy values are reported. When there was a question about the validity of a value (e.g. inconsistent values used by a single author, illustrations of abnormal embryos, etc.) it was excluded.

All analyses were conducted using each species as an independent data point. Phylogenetic generalized least-squared analyses (Martins & Hansen 1997, Pagel 1997) showed that the phylogenetic variance (λ) is not significantly different from 0 for the continuous variables examined here (Collin 2002a, Collin unpubl.). This means that there is no detectable phylogenetic effect and therefore, the data from each species should be treated as independent.

Relationships between egg size, hatching size, settling size, time to hatching and time to settlement were examined using correlation analysis. Differences between species with different modes of development were examined using *t*-tests or 1-way ANOVAs.

There is considerable variation not only in the known latitudinal ranges for these species, but also the confidence with which the range is known. For example, distinctive intertidal species probably have better documented ranges than do indistinct, uncommon or subtidal species. In some cases, there are clusters of cryptic species that are indistinguishable on the basis of shell characters (e.g. Gallardo 1977b, Véliz 1998, Collin 2000b, Véliz et al. 2001). In addition, our knowledge varies with region: range data are well known in North America and Chile, but occurrences are poorly documented in much of tropical America and Africa.

Latitudinal trends in the prevalence of the different modes of development were examined by counting the number of species with each type of development in every 10° of latitude. Species that occur in more than 1 bin of 10° are counted more than once. In a few cases, the geographic range of well-known species was inferred. I made the conservative assumptions that: (1) Species distributions were continuous (i.e. that if a single species with known development is well recorded from 2 localities it probably occurs inbetween these localities); and (2) well-known species with dis-

Table 1. Compilation of developmental characters of calyptraeids. ?: cases where authors' conclusion seems to be at odds with their reported observations, pt: planktotrophic, dd: direct development, pv: hatching as a non-feeding pediveliger larvae

Species ^a	Location	Latitude	Shell length (mm)	Egg size (µm) ^b	Hatching size (µm) ^b	Settling size (µm) ^b	Nurse eggs	Mode of development	Source
<i>Crepidula</i> Lamarck, 1822									
<i>cf. aculeata</i>	La Paz, Mexico	24° 07' N	16	488 (18, 41.6)	–	–	No	dd	Pers. obs.
<i>aculeata</i>	Mote, FL	27° 30' N	27.2	–	–	–	No	dd	Pers. obs.
	Key Biscayne, FL	25° 45' N	25 (18)	380 (360–390)	840	–	No	dd	Hoagland (1986)
<i>cf. aculeata</i>	Cape Town, South Africa	33° 50' S	24	–	–	–	Cleaved	dd	Pers. obs.
	San Antonio Oeste, Argentina	40° 43' S	18	197.6 (18, 7.29)	–	–	Cleaved	dd	Pers. obs.
<i>cf. aculeata</i>	Naos, Panama	8° 55' N	25	–	345 (22, 11)	810 (13, 103)	No	pt	Pers. obs.
	Panama	~8° N	30 (25)	180	360	–	No	pt	Hoagland (1986)
	Hawaii	21° 20' N	29	–	300–330	–	No	pt	Taylor (1975)
	Hawaii	21° 20' N	–	–	320	700+	No	pt	Bell (1993)
	Zorritos, Peru	3° 45' S	28	–	–	–	No	pt	Pers. obs.
<i>cf. aculeata</i>	Onomichi, Japan	34° 15' N	22	–	1000	–	No	dd	Ishiki (1936)
	Japan	–	–	200	1200	–	–	dd	Amio (1963)
<i>cf. aculeata</i>	Sydney, Australia	33° 50' S	21.3	530–560	–	–	No	dd	Pers. obs.
<i>adunca</i>	Friday Harbor, WA	48° 30' N	16	262–315	1500–2700	–	No	dd	Collin (2000a)
	Friday Harbor, WA	48° 30' N	–	240	1000–2000	–	No	dd	Strathmann (1987)
	Southern California	~33° N	–	410 (400–420)	–	–	No	dd	Coe (1949)
	Pacific Grove	–	–	–	1190	–	No	dd	Putnam (1964)
<i>aplysioides</i>	La Restinga, Venezuela	10° 45' N	18	300	600	–	No	dd	Miloslavich & Penchaszadeh (1997)
<i>argentina</i>	Mar del Plata, Argentina	38° 0' S	33	170 (±10)	190–230(?)	–	No	pt	Simone et al. (2000)
<i>arenata</i>	Southern California	~33°	–	160	–	–	No	pt	Coe (1949)
<i>atrasolea</i>	Sanibel, FL	26° 28' N	21.6	335 (±20)	1002	–	No	dd	Pers. obs.
	Fort Pierce, FL	28° 30' N	16.9	–	900	–	No	dd	Hoagland (1986)
<i>capensis</i>	Cape Town, South Africa	33° 50' S	25	–	–	–	Uncleaved	dd	Pers. obs.
<i>cerithicola</i>	Point Charmé, Panama	8° 30' N	12	–	234 (12, 17)	–	No	pt	Pers. obs.
<i>cerithicola</i> ^c	Panama	~8° N	27 (19)	170 (160–180)	800 (670–920)	–	Yes	dd	Hoagland (1986)
	Bay of Panama	8° 55' N	25	–	–	–	Cleaved	dd	Pers. obs.
<i>complanata</i>	Langabaaan Lagoon, South Africa	34° 15' S	30	438 (55, 22.4)	1064 (38, 118.8)	–	No	dd	Pers. obs.
<i>convexa</i>	New England	~40° N	17 (13)	300 (280–320)	1000 (900–1080)	–	No	dd	Hoagland (1986)
	Woods Hole, MA	41° 30' N	–	280	–	–	No	dd	Conklin (1897)
	Woods Hole, MA	41° 30' N	–	280	–	–	No	dd	Coe (1949)
	Delaware Bay, NJ	39° 15' N	20	320	950 ± 9	–	No	dd	Hendler & Franz (1971)
	New England	~40° N	19	–	973	–	No	dd	Ament (1979)
	Breezey Point, NY	40° 45' N	16 (22)	262 (? , 1.6)	920 ± 7	–	No	dd	Aitken-Ander (1987)
<i>cf. convexa</i>	E Panama	~9° N	8 (6.4)	300 (260–400)	800	–	Yes? (1) ^d	dd	Hoagland (1986)
	Bocas del Toro, Panama	9° 20' N	10	286 (11, 5.8)	515 (10, 30)	–	No	pv	Pers. obs.
<i>coquimbensis</i>	Coquimbo, Chile ^e	29° 58' S	32	228 (? , 16.7)	1142 (? , 95)	–	Cleaved	dd	Véliz (1998)
<i>costata</i>	Leigh, New Zealand	36° 15' S	43	256 (13, 3.4)	447 (31, 21.1)	?	No	pt	Pers. obs.
	Auckland, New Zealand	~36° S	–	–	–	–	No	pt	Pilkington (1974)
	Leigh, New Zealand	36° 15' S	–	–	–	1500–2000	–	pt	O'Keefe (1973)
<i>depressa</i>	Sanibel, FL	26° 28' N	29.9	–	255	–	No	pt	Collin (2000b)
<i>dilatata</i>	Puerto Montt, Chile	41° 31' S	53	240 (195–263)	900–1370	–	Uncleaved	dd	Gallardo (1977)
	Chiloé, Chile	41° 52' S	37.8	–	1075–1600	–	Uncleaved	dd	Chaparro & Paschke (1990)
	Coquimbo, Chile	29° 58' S	37	220.4 (? , 20)	1239 (? , 302)	–	Uncleaved	dd	Véliz (1998)
	Puerto Madryn, Argentina	42° 46' S	33.6	239 (55, 24.0)	1375 (43, 210)	–	Uncleaved	dd	Pers. obs.

Table 1 (continued)

Species ^a	Location	Latitude	Shell length (mm)	Egg size (µm) ^p	Hatching size (µm) ^b	Settling size (µm) ^b	Nurse eggs	Mode of development	Source
<i>explanata</i>	Friday Harbor, WA	48° 30' N	25	–	–	–	No	dd	Pers. obs.
<i>fecunda</i>	Puerto Montt, Chile ^e	41° 31' S	70	212 (204–238)	500–560	–	No	pt	Gallardo (1977b)
	Coquimbo, Chile ^e	29° 58' S	56.2	191 (? , 8)	294 (? , 30)	–	No	pt	Véliz (1998)
	Chiloé, Chile	41° 52' S	58	–	400–500	–	No	pt	Chaparro et al. (2002)
	Lima, Peru	12° 5' S	50	275.4 (9, ?)	–	–	No	pt	Pers. obs.
<i>fimbriata</i>	Friday Harbor, WA	48° 30' N	24	–	1570 (7, 56)	–	No	dd	Pers. obs.
<i>fornicata</i>	New England	~40° N	55 (38)	170 (160–180)	–	–	No	pt	Hoagland (1977, 1986)
	Woods Hole, MA	41° 30' N	–	165–180	–	–	No	pt	Coe (1949)
	New England	~40° N	52	–	–	988	No	pt	Ament (1979)
	New England	~41° N	–	–	445–489	941–1003	No	pt	Pechenik et al. (1996)
<i>incurva</i>	Venado, Panama	8° 55' N	16	150 (12, 3.5)	270 (80, 26)	772 (7, 121)	No	pt	Pers. obs.
	La Paz, Mexico	24° 07' N	13	171 (15, 5.4)	287 (22, 17.5)	–	No	pt	Pers. obs.
	Panama	~8° N	19 (13)	160	200	–	No	pt	Hoagland (1986)
<i>cf. incurva</i>	Zorritos, Peru	3° 45' S	18	–	–	–	No	pt	Pers. obs.
<i>lessoni</i>	Venado, Panama	8° 55' N	36	213 (37, 20)	321 (25, 14)	830 (33, 183)	No	pt	Pers. obs.
	Panama	~8° N	30 (21)	260	320	–	No	pt	Hoagland (1986)
	Zorritos, Peru	3° 45' S	22	–	–	–	No	pt	Pers. obs.
<i>lingulata</i>	Friday Harbor, WA	48° 30' N	26	150	275–363	745 (? , 82.4)	No	pt	Collin (2000a)
	Santa Barbara, CA	34° 28' N	20	150.8 (22, 2.2)	271 (60, 12.7)	–	No	pt	Pers. obs.
	Southern California	~33° N	–	150	–	–	No	pt	Coe (1949)
	Balboa Island, CA	–	18 (15)	150	–	–	No	pt	Hoagland (1986)
<i>maculosa</i>	Florida	–	18	440	–	–	No	dd	Hoagland & Coe (1982)
	Panacea, FL	30° 00' N	23	–	–	–	No	dd	Pers. obs.
<i>marginalis</i>	Venado, Panama	8° 55' N	23.5	–	296 (33, 19)	–	No	pt	Pers. obs.
	Naos, Panama	8° 55' N	25	151 (7, 2)	382 (10, 13.2)	973 (19, 93)	No	pt	Pers. obs.
	Costa Rica	10° 11' N	–	143–168	204–229	–	No	pt	Cruz & Giusti (1990)
	Puerto Pizarro, Peru	3° 30' S	31.5	–	–	–	No	pt	Pers. obs.
<i>monoxyla</i>	Leigh, New Zealand Turbinid	36° 15' S	21.1	156 (100, 16.3)	2779 (12, 257)	–	Uncleaved	dd	Pers. obs.
	Leigh, New Zealand Hermit crab	36° 15' S	28	160 (17, 15.5)	2900 (5, 100)	–	Uncleaved	dd	Pers. obs.
	Leigh, New Zealand Turbinid	36° 15' S	20	–	2500–3000	–	–	dd	O'Keefe (1973)
	Leigh, New Zealand Turbinid	36° 15' S	–	–	2000–3250	–	Yes	dd	Pilkington (1974)
<i>naticarum</i>	Santa Barbara, CA	34° 28' N	28.5	164 (8, 7.1)	275 (76, 18.5)	–	No	pt	Pers. obs.
<i>cf. navicula</i>	Grand Bahama Island	26° 30' N	–	–	–	–	No	dd	Hoagland (1986)
<i>navicula</i>	Morrococoy, Venezuela	10° 45' N	7	350	550–1170	–	–	pv	Miloslavich & Penchaszadeh (1987)
<i>nivea</i>	Southern California	~33° N	–	130–140	–	–	–	pt	Coe (1949)
<i>norrisarum</i>	Santa Barbara, CA	34° 28' N	39.9	498 (104, 21.6)	1243 (116, 141.7)	–	No	dd	Pers. obs.
	Southern California	~33° N	–	500	–	–	–	dd	Coe (1949)
<i>nummaria</i>	Alaska	–	24	~400	–	–	–	dd	Dehnel (1955)
	Long Marine Lab, CA	–	–	–	–	–	–	dd	J. Pearse pers. comm.
<i>onyx</i>	Santa Barbara, CA	34° 28' N	35.8	–	297 (112, 16.5)	–	No	pt	Pers. obs.
	La Paz, Mexico	24° 07' N	29	150–160	294 (7, 11.4)	–	No	pt	Pers. obs.
	Balboa Island, CA	–	33 (50)	172 (160–180)	–	–	No	pt	Hoagland (1977, 1986)
	Southern California	~33° N	–	172	–	–	–	pt	Coe (1949)
<i>cf. onyx</i>	Santa Barbara, CA	34° 28' N	18	–	–	–	Cleaved	dd	Pers. obs.
<i>'onyx'</i>	San Antonio Oeste, Argentina	40° 53' S	32	–	–	–	No	pt	Pers. obs.
<i>perforans</i>	Southern California	~33° N	–	500	–	–	No	dd	Coe (1949)
<i>cf. perforans</i>	Santa Barbara, CA	34° 28' N	–	135 (12, 6.8)	239 (58, 17)	–	No	pt	Pers. obs.
<i>philippiana</i>	Mehuín, Chile	39° 25' S	28	140–160	3000	–	Uncleaved	dd	Gallardo (1977a)

(Table continued on next page)

Table 1 (continued)

Species ^a	Location	Latitude	Shell length (mm)	Egg size (µm) ^b	Hatching size (µm) ^b	Settling size (µm) ^b	Nurse eggs	Mode of development	Source
<i>plana</i>	New England	~40° N	–	136	–	–	No	pt	Conklin (1897)
	New England	~40° N	25 (47)	136 (130–140)	–	–	No	pt	Hoagland (1986)
	Woods Hole, MA	41° 30' N	–	130–140	–	–	No	pt	Coe (1949)
	New England	~40° N	41	–	–	965	No	pt	Ament (1979)
	New England	~40° N	–	–	~300	1098–1133	–	pt	Pechenik et al. (1996)
<i>porcellana</i>	West Africa	9° 28' N	25.5	400	1000	–	No	dd	Knudsen (1950)
<i>protea</i>	Brasil	24° 30' S	32	~150	–	–	No	pt	Hoagland (1983a)
<i>striolata</i>	Panama & Costa Rica	~8° N	16 (29)	160 (140–180)	400 (240–440)	–	No	pt	Hoagland (1986)
<i>unguiformis</i>	Northern Latium, Italy	41° 30' N	38	–	–	–	No	dd	Pers. obs.
' <i>ustulatulina</i> '	Florida	–	24 (12)	~300	840	–	No	pv	Hoagland (1986)
	Key Largo, FL	25° 10' N	9.4	300–340	744	–	No	pv	Pers. obs.
	Mote, FL	27° 30' N	11.6	–	–	–	No	pv, dd	Pers. obs.
<i>williamsi</i>	Santa Barbara, CA	34° 28' N	37	403 (11, 13.3)	1470 (15, 103.2)	–	No	dd	Pers. obs.
	Southern California	~33° N	–	450	–	–	–	dd	Coe (1949)
sp. wf	Puerto Pizarro, Peru	3° 30' S	28	–	–	–	No	pt	Pers. obs.
sp. B	Kodiak Island, AK	–	17	–	–	–	No	dd	Pers. obs.
sp. C	La Paz, Mexico	24° 07' N	19	345 (78, 27.9)	976 (48, 88.8)	–	No	pv	Pers. obs.
sp. D	La Paz, Mexico	24° 07' N	19	158 (12, 4.0)	318 (19, 24.6)	1014 (22, 92.2)	No	pt	Pers. obs.
Crucibulum									
<i>auricula</i>	Venezuela	10° 42' N	23	218 (99, 16)	728 (10, 70)	–	Cleaved	dd	Miloslavich & Penchaszadeh (2001b)
<i>marensis</i>	Golfo Triste, Venezuela	0° 45' N	–	–	1020–1160	–	No?	dd	Penchaszadeh (1985)
<i>personatum</i>	Costa Rica & Panama	8° N	28	–	320	–	No	pt	Hoagland (1986)
	Venado, Panama	8° 55' N	24	–	326 (14, 32)	948 (19, 115)	No	pt	Pers. obs.
<i>quirquinae</i>	Bahía Tongoy, Chile. Scallops	31° 45' S	60	325 (309, 21)	458 (132, 14)	–	No	pt	Véliz et al. (2001)
	Bahía Tongoy, Chile. Turitellids	31° 45' S	22	309 (79, 16)	468 (143, 46)	–	No	pt	Véliz et al. (2001)
<i>radiatum</i>	Venado, Panama	8° 55' N	25	169 (18, 11)	366 (18, 19.7)	–	No	pt	Pers. obs.
<i>scutellatum</i>	Panama & Costa Rica	~8° N	30/57	–	–	–	No	pt	Hoagland (1986)
cf. <i>scutellatum</i>	Red Sea	~25° N	–	–	700	–	Maybe	p	Thorson (1940)
<i>spinosum</i>	Venado, Panama	8° 55' N	25	–	325 (10, 10)	–	No	pt	Pers. obs.
	Panama & Costa Rica	~8° N	19 (36)	–	280 (240–360)	–	No	pt	Hoagland (1986)
	Southern California	~33° N	–	170–190	250–300	–	Maybe	pt	Coe (1938, 1949)
	Honolulu Bay, HI	21° 20' N	38	–	330	700	No	pt	Bell (1993)
cf. <i>spinosum</i>	Santa Maria, Peru	12° 20' S	55	–	388 (13, ?)	–	No	pt	Pers. obs.
<i>umbrella</i>	Panama & Costa Rica	~8° N	30/55	–	440 (380–480)	–	No	pt	Hoagland (1986)
sp. A	La Paz, Mexico	24° 07' N	25.9	230 (34, 5.8)	934 (21, 106.3)	–	Cleaved	pv	Pers. obs.
sp. B	Coquimbo, Chile ^e	29° 58' S	18	292 (187, 17)	1067 (69, 103)	–	Cleaved	dd	Véliz et al. (2001)
Calyptraea									
<i>chinensis</i>	UK	51° 30' N	21	480	–	–	No	dd	Wyatt (1960)
cf. <i>chinensis</i>	West Africa	5° 59' N	22	480	700	–	No	dd	Knudsen (1950)
<i>conica</i> ^f	Panama & Costa Rica	~8° N	30 (33)	200	360 (320–380)	–	–	pt	Hoagland (1986)
	Point Charmé, Panama	8° 55' N	28	177 (11, 5.8)	–	–	No	pt	Pers. obs.
<i>extinctorum</i>	Hong Kong	22° 15' N	20.7	200–215	–	–	–	–	Knudsen (1994)
<i>fastigata</i>	Friday Harbor, WA	48° 30' N	21.3	?	1400 (12, 153)	–	No	dd	Pers. obs.
<i>lichen</i> ^f	Venado, Panama	8° 55' N	13	–	–	–	No	pt	Pers. obs.
<i>mamillaris</i>	Point Charmé, Panama	8° 30' N	15	–	340 (7, 32)	–	No	pt	Pers. obs.
	Costa Rica	~8° N	16 (20)	200	360 (320–380)	–	No	pt	Hoagland (1986)
<i>morbida</i>	Taiwan	22° 40' N	–	–	–	–	–	pt	Chen & Soong (2000)
<i>pellucida</i>	Red Sea	~25° N	–	120	220–227	–	No	pt	Thorson (1940)

Table 1 (continued)

Species ^a	Location	Latitude	Shell length (mm)	Egg size (µm) ^b	Hatching size (µm) ^b	Settling size (µm) ^b	Nurse eggs	Mode of development	Source
<i>Siphopatella</i>									
<i>walshi</i>	Hong Kong	22° 15' N	35	240–260	–	–	No?	pt?	Knudsen (1994)
	Onomichi, Japan	34° 15' N	22	190	–	–	No	pt	Ishiki (1939)
	Japan	–	–	–	350	–	–	pt	Amio (1963)
	Red Sea	~25° N	–	–	350	–	No?	pt	Thorson (1940)
<i>Sigapatella</i>									
<i>novaezelandiae</i>	Otago, New Zealand	45° 50' S	26	–	1050–1200	–	Yes	dd	Pilkington (1974)
<i>Trochita</i>									
<i>calyptraeformis</i>	Coquimbo, Chile ^e	29° 58' S	85.9	460 (250, 14)	1150 (180, 46)	–	No	dd	Cañete & Ambler (1992)
<i>Zegalarus</i>									
<i>tenuis</i>	Leigh, New Zealand	36° 15' S	21.1	–	249 (71, 12.9)	–	No	pt	Pers. obs.
	Portabello, New Zealand	45° 50' S	–	–	–	–	No	pt	Pilkington (1974)
^a A taxonomic revision of various calyptraeids is currently in preparation by the author and voucher material is deposited at the Field Museum of Natural History, Chicago ^b Mean (range) or (sample size, SD) ^c Examination of Hoagland's vouchers (Hoagland 1986) shows that her <i>Crepidula cerithicola</i> is not the same as the organisms here identified as <i>C. cerithicola</i> on the basis of the original descriptions and type material ^d Only a single nurse egg was observed in each capsule ^e Cases where I have independently verified species identification and mode of development ^f Species identifications follows Broderip (1834), and not Keen (1971)									

tinctive morphologies, for which there was no suggestion of cryptic species, are single species with a single mode of development throughout their reported ranges. Data from less well-known species or species that are known to belong to cryptic species complexes were used only for the latitudes at which development has been observed. I also examined latitudinal effects on egg and hatching size by plotting the data for the latitude at which they were actually observed. Because there are numerous similar observations for some species at a single latitude, I plotted only 1 observation per species per 10°. The results did not differ qualitatively when each species was used coded only for its range mid-point.

Associations between developmental variables and ocean temperature were examined using data from remote sensing. Annual average sea surface temperature (SST), the months with the lowest and highest average temperatures, and the range of average monthly temperatures were obtained for each locality from the National Oceanographic Data Center (NODC) World Ocean Atlas from the National Oceanic and Atmospheric Administration-Cooperative Institute for Research in Environmental Science (NOAA-CIRES) Climate Diagnostics Center, Boulder, Colorado (available at www.cdc.noaa.gov). Relationships between egg and hatching size and the maximum and range of SST were tested using linear regression and analysis of variance.

RESULTS

Data were compiled for 78 species of calyptraeids: 53 *Crepidula*, 9 *Calyptraea*, 11 *Crucibulum* and 5 other species. This represents more than 85% of currently recognized *Crepidula* species, but only 15 to 20% of *Calyptraea* and *Crucibulum* species. There are 5 basic types of development observed in the calyptraeids (Tables 3 & 4). Small eggs can develop into small planktotrophic larvae, large eggs can develop into pediveligers that swim for a few hours before settling, or they can develop directly into juveniles. In addition, small eggs can develop into pediveligers or juveniles by ingesting nurse eggs (eggs or embryos that do not develop normally). Planktotrophic and direct development (with and without nurse eggs) are the 2 most common modes of development, and lecithotrophic development with a short-lived pediveliger stage is uncommon. In many cases, different types of development occur in morphologically similar sympatric species.

Egg size, hatching size and mode of development

Egg- and hatching-size distribution are strongly skewed and have modal values near the minimum of the observed ranges (145 to 170 µm category for egg size and 220 to 420 µm category for hatching size;

Figs. 1 & 2). There is a significant difference between species with planktotrophic development (pt) and species with direct development (dd) (with and without nurse eggs) in egg size (mean_{pt} = 189 μ m, SD_{pt} = 66.6 μ m, n_{pt} = 26; mean_{dd} = 336 μ m, SD_{dd} = 131.5 μ m, n_{dd} = 25; *t*-test, *p* < 0.005), hatching size (mean_{pt} = 343 μ m, SD_{pt} = 98.0 μ m, n_{pt} = 26; mean_{dd} = 1295 μ m, SD_{dd} = 599.6 μ m, n_{dd} = 22; *t*-test, *p* < 0.005) and size

at settlement (mean_{pt} = 974 μ m, SD_{pt} = 272 μ m, n_{pt} = 10; mean_{dd} = 1295 μ m, SD_{dd} = 599.6 μ m, n_{dd} = 22; *t*-test, separate variances *p* < 0.05, pooled variances *p* = 0.12). Direct developing species have larger eggs, larger hatchlings and a larger size when the juveniles are first present in the benthic environment (i.e. settling size in planktotrophs and hatching a larger size in direct developers). Species with lecithotrophic development

Table 2. Duration of development in calyptraeid gastropods. Abbreviations as in Table 1

Species	Location	Days to hatching	Temperature (°C)	Days from hatching to settlement	Temperature (°C)	Mode of development	Source
<i>Crepidula</i>		8–9	28–30	14–18	21–22.5	pt	Pers. obs.
<i>cf. aculeata</i>	Panama						
<i>cf. aculeata</i>	Japan	28–35				dd	Ishiki (1936)
<i>adunca</i>		~120	12	0	12	dd	Collin (2000a)
<i>cerithicola</i>		–	–	19–23	21–22.5	pt	Pers. obs.
<i>convexa</i>		2 wk?		0	–	dd	Hendler & Franz (1971)
		30	18.5	0	–	dd	Ament (1978, 1979)
		14	24	0	–	dd	Ament (1978, 1979)
		29.5 ± 1.8	19	0	–	dd	Aitken-Ander (1987)
<i>onyx</i>	Mexico	12–15	20–21.5	–	20–21.5	pt	Pers. obs.
<i>onyx</i>	Santa Barbara	~20	15–18	23	15–18	pt	Pers. obs.
<i>cf. perforans</i>		~22	15–18	16–20	15–18	pt	Pers. obs.
<i>fornicata</i>		17	18.5	12–14	18.5	pt	Ament (1978, 1979)
				11.5 ± 2	20	pt	Pechenik et al. (1996)
<i>incurva</i>	Panama	5–6	28–30	11–23	21–22.5	pt	Pers. obs.
<i>lessoni</i>		6	28–30	12–22	21–22.5	pt	Pers. obs.
<i>lingulata</i>		24–33	12	29–45	12	pt	Collin (2000)
<i>marginalis</i>	Costa Rica	8–10	25–28	?	25–28	pt	Cruz & Giusti (1990)
		6–7	25–28	14–25	21–22.5	pt	Pers. obs.
<i>plana</i>		17	18.5	12–14	18.5	pt	Ament (1978, 1979)
				18–21	23–25	pt	Pechenik et al. (1996)
mex sp. A		21	20–21.5	hours	20–21.5	pv	Pers. obs.
mex sp. B		9–10	20–21.5	10	20–21.5	pt	Pers. obs.
<i>monoxyla</i>		73	14–16	0	14–16	dd	O'Keefe (1973)
<i>Crucibulum</i>							
<i>cf. personatum</i>		31	20–21.5	1–4 h	20–21.5	pv	Pers. obs.
<i>radiatum</i>		7	28–30	22	21–22.5	pt	Pers. obs.
<i>spinosum</i>	Panama	7–9	28–30	–	21–22.5	pt	Pers. obs.
<i>Trochita</i>							
<i>calyptraeaformis</i>		51	14.6 ± 1.3	0	14.6 ± 1.30	dd	Cañete & Ambler (1992)
<i>Calyptreaea</i>							
<i>chinensis</i>		~30	10–16	0	10–16	dd	Wyatt (1960)
<i>Siphopatella</i>							
<i>walshi</i>		<=21	–	–	–	pt	Ishiki (1936)

Table 3. Observed modes of development in calyptraeids

Mode of development	Number of species	Egg size	Hatching size	Planktonic phase	Feeding larvae
Planktotrophic	39 (50%)	Small	Small	Long	Present
Lecithotrophic	3 (3.8%)	Large	Large	Very short	Absent
Lecithotrophic with nurse eggs	1 (1.2%)	Small	Large	Very short	Absent
Direct without nurse eggs	24 (30%)	Large	Large	Absent	Absent
Direct with nurse eggs	11 (14%)	Small	Large	Absent	Absent

Table 4. Summary of development in other monophyletic groups of marine gastropods

Group (no. of species)	Planktotrophic egg size (μm)	Lecithotrophic egg size (μm)	Direct developer egg size (w/o nurse eggs)	Planktotrophic hatching shell length (μm)	Direct developer hatching shell length (μm)	Source
Caenogastropods						
Calyptraeids (78)	189 (120–256)	321 (286–345)	336 (240–540)	343 (220–500)	1295 (700–3000)	This Study
<i>Conus</i> (62)	125–425	390	470–1000	391 (215–840)	1130 (700–1430)	Kohn & Perron (1994)
Muricids (53)	179 (80–280)	?	240–920 (497)	312 (130–420)	1280 (700–2500)	Spight (1976)
Heterobranchs						
Opisthobranchs (53)	60–115	80–250	205 (113–380)	146.6 (95–279)	268 (195–375)	Hadfield & Switzer-Dunlap (1984)
Nudibranchs (37)	60–115	120–220	113–380	162 (95–279)	239 (195–300)	Hadfield & Switzer-Dunlap (1984)
Cephalaspids (38)	60–100	200	180–380	?	?	Schaefer (1996)

without nurse eggs have an average egg size similar to direct developers (321 μm for all lecithotrophic species without nurse eggs; 298 μm including the single species with nurse eggs) but hatching size was about 25% smaller than direct developers (792 μm for all lecithotrophic species without nurse eggs; 827 μm including the single species with nurse eggs).

Overall, there was no significant correlation between egg and hatching size ($p > 0.05$; Fig. 3), or egg and settlement size ($p > 0.05$; Fig. 4). However, when species with nurse eggs are removed from the analysis, a significant amount of variation in hatching size can be explained by variation in egg size (Fig. 3) (ordinary least squares; $n = 33$; $r^2 = 0.558$; m (slope) = 0.203, $p < 0.0005$). Two outliers in Fig. 3B are *Crepidula aculeata* from Japan and *C. adunca*. The published data for *C. aculeata* from Japan are minimal and somewhat vague (Amio 1963, Ishiki 1936), allowing for the possibility that nurse eggs are present in this species. Eggs of *C. adunca* are more variable in size than any other spe-

cies discussed here. Even eggs from different capsules within a brood of a single female can differ significantly (pers. obs.) and therefore, the hatching size reported here may not correspond to juveniles that developed from eggs of the size reported in Table 1.

Nurse eggs

There is little evidence that direct development with nurse eggs differs from direct development without nurse eggs in any respect other than egg size. There is a significant difference in egg size between direct developers with (ne) and without nurse eggs (nne) ($\text{mean}_{\text{nne}} = 398 \mu\text{m}$; $\text{mean}_{\text{ne}} = 203 \mu\text{m}$; $n_{\text{nne}} = 17$; $n_{\text{ne}} = 8$; t -test, $p < 0.005$). The hatching size of species with nurse eggs tends to be larger than species with direct development from large eggs ($\text{mean}_{\text{dd}} = 1172 \mu\text{m}$;

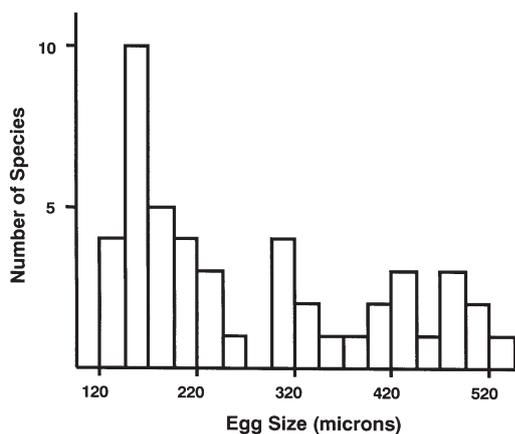


Fig. 1. Egg size for 51 calyptraeid species

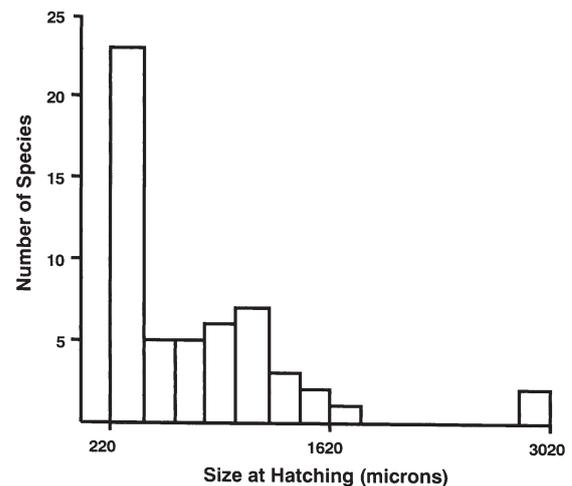


Fig. 2. Hatching size for 48 calyptraeid species

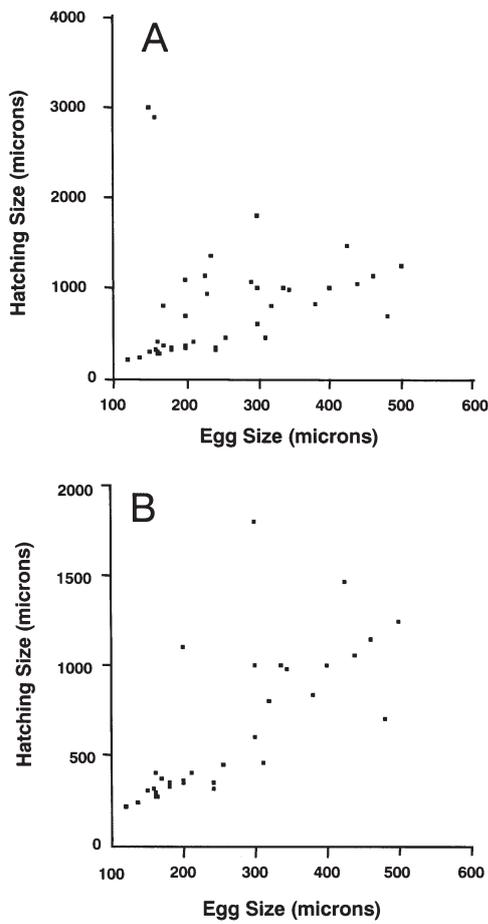


Fig. 3. Relationship between hatching size and egg size. (A) All calyptraeids, (B) all calyptraeids except those with nurse eggs (ordinary least squares; $n = 33$, $r^2 = 0.558$, $m = 0.203$, $p < 0.0005$)

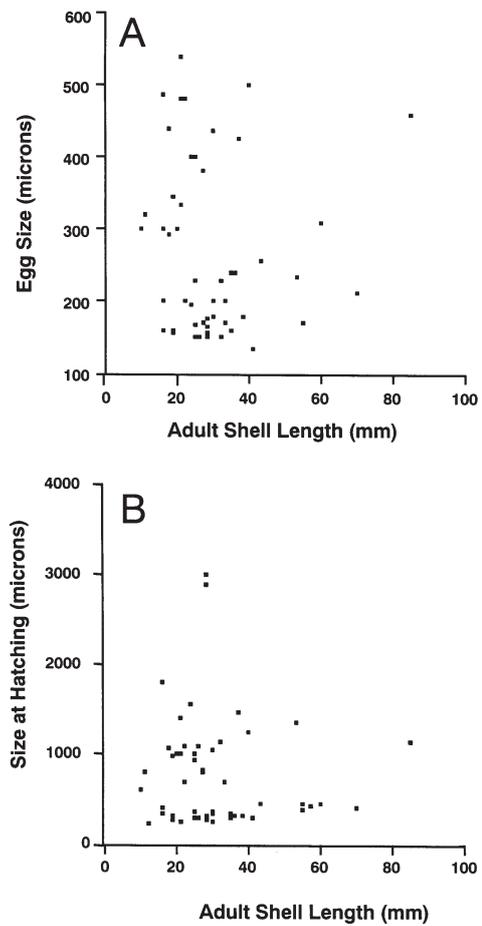


Fig. 5. Relationship between adult shell length and development. (A) Egg size versus adult shell length, (B) size at hatching versus adult shell length

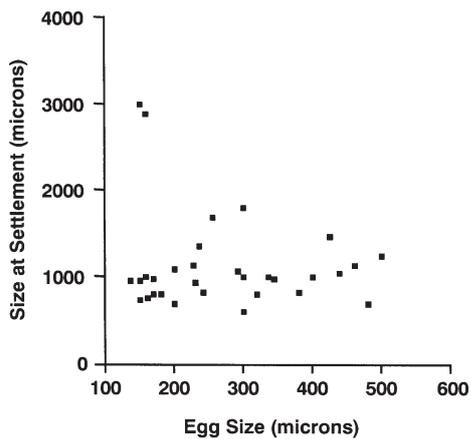


Fig. 4. Relationship between egg size and size at settlement. For direct developers, size at settlement is equal to size at hatching

mean_{ne} = 1509 μ m; $n_{nne} = 14$; $n_{ne} = 8$) but was not significantly different ($p > 0.1$). The 2 species with the largest hatching size (~3 mm), *Crepidula monoxyla* and *C. philippiana*, both have direct development with nurse eggs in which only a single embryo develops in each egg capsule. This large hatching size is about twice that of hatchlings of both direct developing species without nurse eggs, and other direct developing species with nurse eggs in which multiple embryos develop in each capsule. These data offer support for the idea that direct development with nurse eggs allows embryos to attain larger sizes at hatching than embryos developing from large eggs (Spight 1976). From the few data on the standard deviation (SD) of hatching size for direct developers reported in Table 1, it appears that direct developers with nurse eggs produce hatchlings with more variable sizes. However, most of this variation is due to differences in hatching size and not to an effect of nurse eggs per se (i.e. species with larger hatching size have larger SDs in hatching size).

Body size effects

There is no detected effect of female shell length on any of the variables examined here. *T*-tests showed no differences between body size of species with direct development and species with planktotrophic development ($p > 0.1$). Among direct developers, species with and without nurse eggs did not differ in adult body size ($p > 0.1$). Additionally, there is no correlation between maximum shell length and egg or hatching size (Fig. 5).

Latitudinal patterns

In the northern hemisphere, there is a clear latitudinal trend in mode of development (Appendix 1, Fig. 6). The proportion of planktotrophic species decreases with latitude as the proportion of direct developers increases (Fig. 6). In the southern hemisphere, there is a slight indication of a similar pattern; however, the sample sizes are small. The presence of nurse eggs in

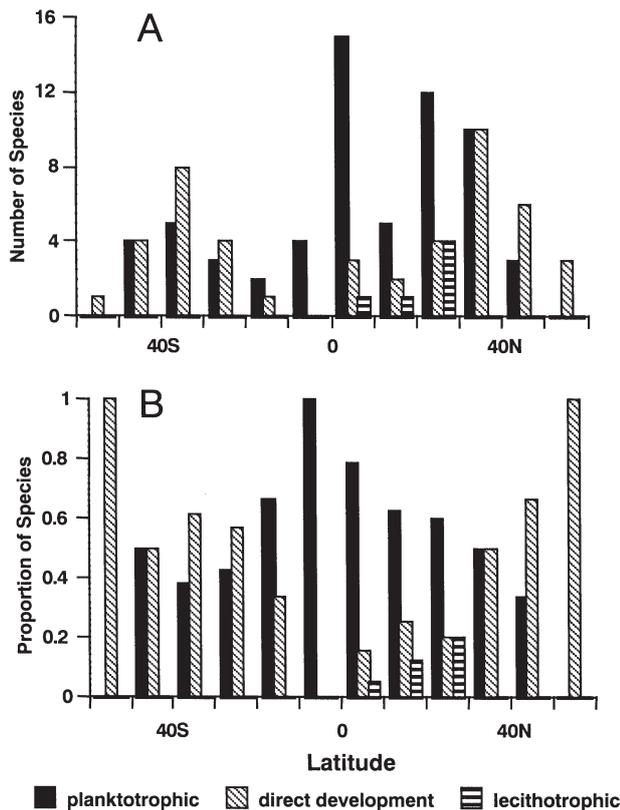


Fig. 6. Relationship between mode of development and latitude for 78 species of calyptraeid gastropods. (A) Number of species with each mode of development, (B) proportion of species with each mode of development in each 10° bin

direct developing species is strongly associated with latitude: most direct developing species in the southern hemisphere develop with nurse eggs, while direct developing species in the northern hemisphere develop without nurse eggs (chi-square = 7.326 with Yates' correction, $p < 0.01$; Table 5, Fig. 7). This pattern is not due to species from any single region, as nurse eggs are common in South America, South Africa and New Zealand. Because species from each region are not particularly closely related to each other (Collin 2002a, unpubl.), the latitudinal difference is likely due to ecological differences rather than phylogenetic effects.

Scatter plots show no discernible latitudinal pattern in egg size, in overall hatching size or size at settlement (Fig. 8). Hatching size of planktotrophic species does not vary with latitude, but the hatching size of direct developing species shows an increase with latitude in the northern hemisphere (Fig. 8B). Again, the limited latitudes for which data are available from the southern hemisphere are too small to show a clear pattern.

Ocean temperature

There was no significant relationship between egg size and the maximum or annual range of SST (data in Appendix 2; ordinary least squares [OLS], $p > 0.2$). There was a significant negative relationship between hatching size and maximum SST ($r^2 = 0.14$; $p < 0.05$), and a significant positive relationship between hatching size and annual range in SST ($r^2 = 0.21$; $p < 0.05$). Since both the maximum and range of SSTs are highly correlated with latitude ($r^2 > 0.6$, $m = -1.99$, $n = 74$, $p < 0.001$; $r^2 > 0.9$, $m = 0.92$, $n = 74$, $p < 0.001$, respectively), it is difficult to statistically untangle the effects of the separate variables. As a result of this correlation, there is no significant effect of latitude or SST when both variables were included (ANOVA, $p > 0.05$), although the model is significant overall. Therefore, it is not clear if the latitudinal patterns in development reported here are causally related to SST or some other

Table 5. Chi-square contingency table comparing the frequency of direct developing species with and without nurse eggs in the northern and southern hemisphere. Chi-square = 7.326 with Yates' correction, $p < 0.01$

	Observed number of species		Expected number of species	
	North	South	North	South
Nurse eggs	4	8	8.108	3.892
No nurse eggs	21	4	16.892	8.108

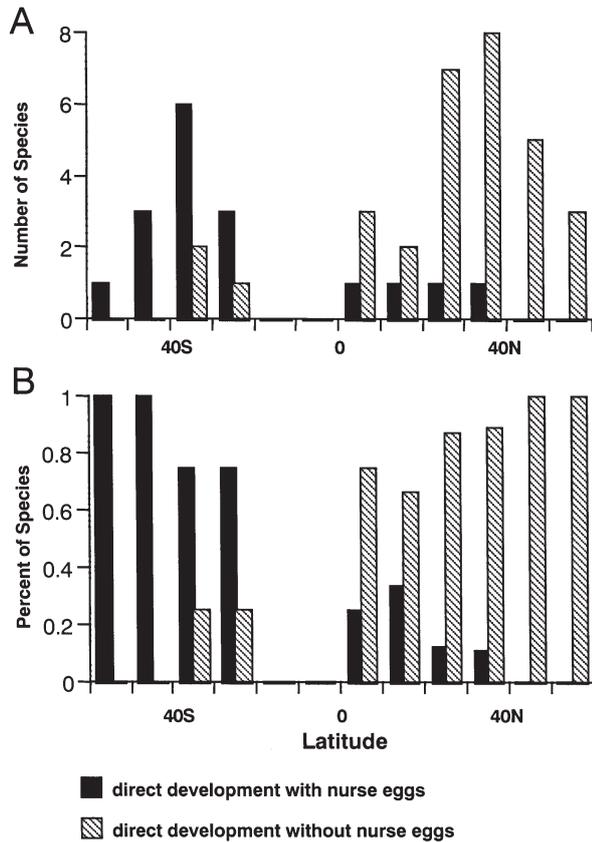


Fig. 7. Relationship between mode of development and latitude for 35 species of calyptraeids with direct development. (A) Number of species with and without nurse eggs, (B) proportion of species with and without nurse eggs in each 10° bin

variable correlated with latitude. These results do not differ when the range in latitude and SST are standardized.

Duration of development

The limited data available on the duration of development (Table 2) strongly support a significant effect of temperature on time to hatching (Fig. 9) and a weak effect on the duration of larval development (Fig. 9). There is no significant effect of egg size on duration of development to hatching when all the species are included. When *Crepidula monoxyla* and *Crucibulum* n. sp. from La Paz (the species with nurse eggs) are excluded, there is a significant effect of egg size (Fig. 9); however, this effect disappears when temperature is taken into account (ANOVA, $p > 0.05$). Because there is a clear difference in duration of development in large and small eggs at the same temperature (e.g. Collin 2000a), it is likely that the absence of a significant effect is due to low power and small sample sizes rather than reflecting a true absence of effect.

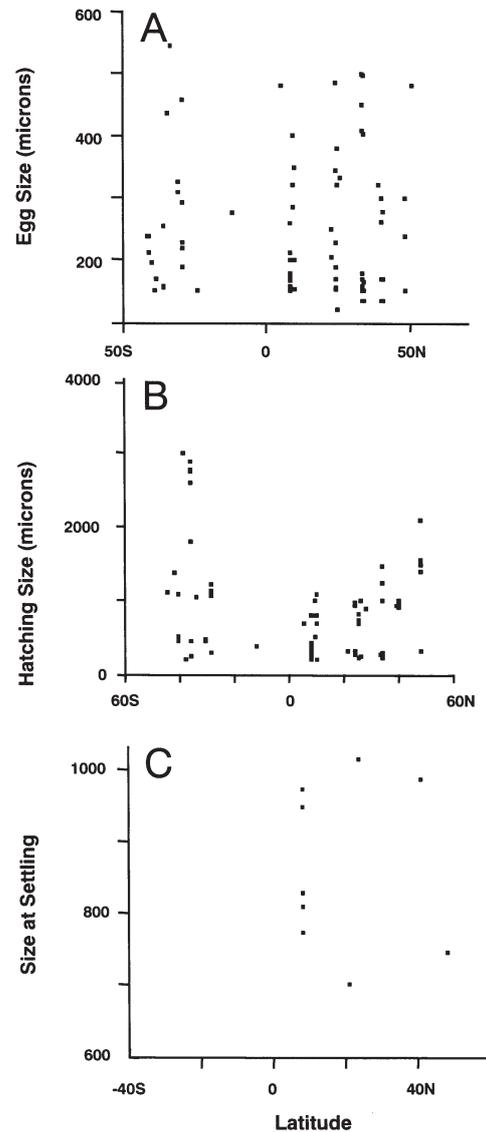


Fig. 8. Developmental variables versus latitude. (A) Egg size versus latitude, (B) hatching size versus latitude, (C) size at settlement versus latitude

DISCUSSION

Egg size, hatching size and mode of development

Analysis of this data set compiled from developmental characters of calyptraeid gastropods produced results similar to those for other gastropods and echinoderms. As has been demonstrated in cephalaspids (Schaefer 1996), opisthobranchs (Hadfield & Switzer-Dunlap 1984), muricids (Perron & Carrier 1981) and *Conus* (Kohn & Perron 1994), egg size distribution is not bimodally distributed. In fact, egg size distributions with a strong peak at or near the mini-

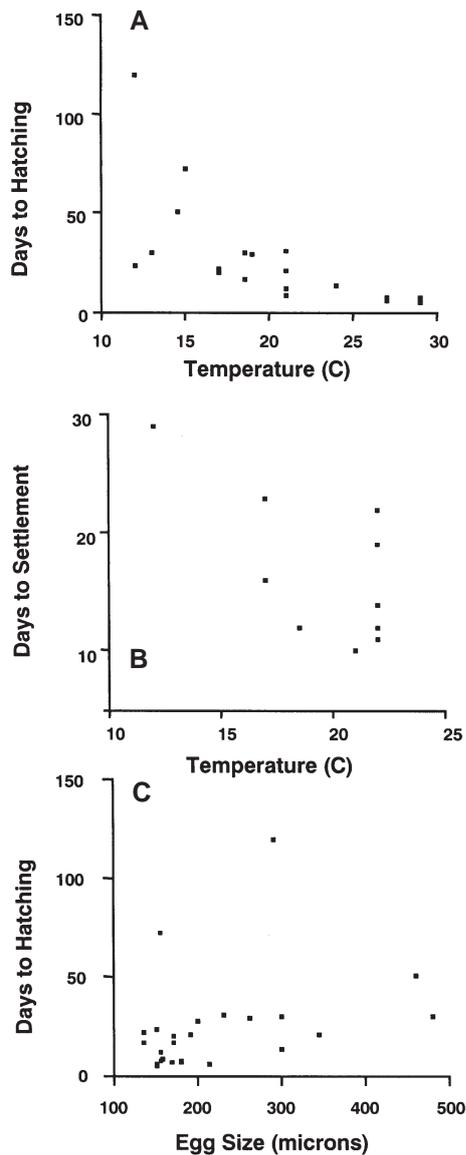


Fig. 9. Patterns of duration of development. (A) Temperature versus days to hatching, (B) temperature versus days to settlement, (C) egg size versus days to hatching

mum egg size and a strong positive skew have been found in all these gastropod groups as well as for bivalves (Ockelmann 1965) and 4 classes of echinoderms (Sewell & Young 1997). This type of distribution is consistent with the idea that smaller egg sizes are generally favored, but that there is some minimum size 'constraint'. However, data from echinoids show that species with small eggs can develop normally when their eggs have been experimentally halved or quartered (McEdward 1996). The similarity between the egg size distributions of groups of free spawners and groups with copulation suggests that

factors associated with fertilization kinetics of free spawners, which have been used to shed light on egg size distributions in echinoids (e.g. Levitan 1993), may not be the cause of the skewed distributions (Podolsky & Strathmann 1996). Likewise models that incorporate the cost of encapsulation to produce a unimodal prediction (Perron & Carrier 1981) cannot explain the similarities of egg size distributions among groups of free spawners (e.g. echinoderms) and groups with encapsulated (e.g. muricids and *Conus*) and brooded (e.g. calyptraeids) development.

More recent models have produced skewed and unimodal predictions of egg size by varying food availability, water temperature, and growth and mortality rates (Christiansen & Fenchel 1979, Strathmann 1985, Levitan 2000). These models hold constant factors other than the single variable of interest. Since all compilations of egg size combine data from species living in a variety of habitats at a variety of water temperatures and food availabilities, it is unclear if data compilations can actually be used to test the predictions of such models. In addition, if different subclades have significantly different distributions of egg size (see below), concatenation of data from several groups could obscure patterns or create artificial patterns.

Previously, the use of egg size as a proxy for reproductive effort has been criticized on the basis that the energy content of eggs might vary independently of egg size (e.g. Sewell & Young 1997, McEdward & Morgan 2001). The good correlation between egg and hatching size in species without nurse eggs documented here suggests that there is a general correlation between egg size and energy content. More detailed information on egg energy content, nutritional value of intracapsular albumin, and the costs associated with producing egg capsules and brooding are necessary before female reproductive effort can be accurately quantified.

The distribution of egg size in relation to mode of development in calyptraeids appears to be similar to other groups of caenogastropods (Table 4), although extensive data are available for few families. There is a noticeable high level phylogenetic effect on egg size and the sizes at which shifts in mode of development occur among gastropods. The minimum egg size in caenogastropod groups is generally much larger than in heterobranch gastropods. The egg sizes that produce planktotrophic development in caenogastropods roughly correspond to egg size of direct developing heterobranchs. Eggs as large as those that produce direct development in caenogastropods rarely occur in heterobranchs (Table 4). Similarly, the hatching size and settling size of caenogastropods are greater than they are for heterobranchs (Table 4).

Nurse eggs

Despite considerable attention in the literature, nurse eggs remain one of the most mysterious aspects of gastropod development. The method and mechanism of nurse egg determination has not been discovered. There is considerable variation in the morphology and consumption of nurse eggs in calyptraeids, suggesting that there is no common mechanism of nurse egg determination in this group. In some species (e.g. *Crepidula dilatata*, *C. monoxyla*), the nurse eggs are uncleaved eggs that are ingested whole by the embryos (Gallardo & Garrido 1987, Véliz 1998, author's pers. obs.). In other species (e.g. *C. capensis*, *C. cf. onyx*, *C. coquimbensis*), initial development of nurse eggs is indistinguishable from development of normal embryos (Véliz 1998, author's pers. obs.). Subsequent to gastrulation, development is arrested and the nurse eggs remain as ciliated yolk-filled balls. In several of these species, the embryos appear to suck the yolk out from within the nurse eggs and the nurse eggs become hollow balls of ciliated epithelium as development progresses; in other species, the embryos consume the entire nurse eggs.

The allocation of embryos and nurse eggs to egg capsules appears to be random in species with numerous developing embryos per capsule (Rivest 1983); however, it has not been investigated in species in which only a single embryo develops in each capsule. Hadfield (1989) found that the number of nurse eggs per capsule varied with female size in the vermetid *Petalococonchus montereyensis*, a species with nurse eggs and a single embryo per capsule, and suggested that this implied that nurse egg identity was assigned prior to encapsulation. An increase in the number of nurse eggs per capsule with female size occurs in all calyptraeid species I have examined in detail (unpubl. data).

The present study does shed light on some aspects of development with nurse eggs and highlights areas that are in need of more work. Three advantages of development with nurse eggs over development from large eggs have been hypothesized: (1) There is greater variance in hatchling size; (2) development may be faster; and (3) larger hatchling sizes can be attained with nurse eggs. The idea that nurse eggs increase variance in hatching size has been proposed as both an advantage (Rivest 1983) and a disadvantage (Strathmann 1995) of nurse eggs. The data presented here are equivocal with respect to the applicability of the first and second hypotheses to calyptraeids, because the small number of species for which there are data severely limits the power to detect small effects. However, *Crepidula monoxyla* and *C. philippiana*, the only species in which a single

embryo hatches from each egg capsule after consuming nurse eggs, have hatchlings that are twice the size of other direct developers. These species also have larger hatchlings than any muricid species (with or without nurse eggs) listed in Spight (1976) or any *Conus* species (none of which have nurse eggs; Kohn & Perron 1994). However, other groups such as melongenids, volutids and buccinids commonly have much larger hatchlings than the largest calyptraeid hatchlings and development in species from these groups often lacks nurse eggs. Calyptraeid species with nurse eggs with multiple embryos per capsule do not hatch at larger sizes than do direct developers without nurse eggs. This is also true for the muricid species listed in Spight (1976). Although a reproductive strategy involving nurse eggs can produce larger hatchlings than appear to be possible without nurse eggs, the majority of calyptraeid (and possibly all gastropod) species with nurse eggs do not use this strategy.

There is a striking biogeographic distribution of calyptraeid species with nurse eggs. It is clear that among direct developing species, development with nurse eggs predominates in the southern hemisphere, while it is rare in the northern hemisphere. These data include species from South America, New Zealand and South Africa; thus, the prevalence of nurse eggs in the southern hemisphere is not the result of factors in a single region. Since I have been unable to demonstrate differences in adult size and hatching size between direct developing species with and without nurse eggs, I am at a loss to explain this latitudinal pattern in prevalence of direct development with nurse eggs. To my knowledge, such a latitudinal pattern in species with nurse eggs has not been demonstrated in any other group.

Adult body size

Correlation analysis between egg size and female shell-length and *t*-test comparisons of shell length of direct developers and planktotrophs did not demonstrate any relationship between body size and mode of development. This is a curious result because it is commonly believed that there is a general relationship between mode of development and body size in marine invertebrates (see review in Strathmann & Strathmann 1982). The lack of such a relationship in calyptraeids does not appear to be due to shape differences between *Crepidula* and the other genera obscuring an effect, and re-analysis of the data for *Crepidula* alone does not produce a significant relationship. Similar results were reported for Indo-Pacific *Conus* species (Kohn & Perron 1994).

The idea that body size affects mode of development in marine invertebrates is based on the prevalence of brooding among small species (Strathmann & Strathmann 1982). Strathmann & Strathmann (1982) explain that such a pattern is only expected for co-occurring similar species. They cite earlier data from calyptraeids in support of the pattern that among species which brood for some period of time, smaller species are more likely to brood for the entire course of development than are larger species. However, data from the current compilation do not appear to support this pattern. Along the east coast of North America, the pattern does appear to hold: the smallest species (*Crepidula convexa*, *C. atrasolea*) have direct development, while the larger species (*C. plana*, *C. fornicata*) have planktotrophic development. However, the large species *C. maculosa* also has direct development. In the north island of New Zealand, the smallest (*Zegalarus tenuis*) and largest species (*C. costata*) have planktotrophic development and the intermediate-sized species (*C. monoxyla*) has direct development. Along the north coast of Chile, 7 species co-occur (*C. fecunda*, *C. dilatata*, *Crepidula* n. sp., *C. coquimbensis*, *Trochita calyptraeiformis*, *Crucibulum quiriquinae* and *Crucibulum* n. sp.). The largest (*T. calyptraeiformis*) has direct development. The large *C. fecunda* has planktotrophic development but the similarly-sized *Crepidula* n. sp. has direct development. The smaller *C. dilatata* and *C. coquimbensis* have direct development as does *Crucibulum* n. sp., whereas the slightly larger *C. quiriquinae* has planktotrophic development. These data show that there is no consistent relationship between small size and brooding in calyptraeids from a single locality.

The idea that body size affects mode of development in marine invertebrates can be theoretically justified by the idea that reproductive output scales with surface area in brooders and volume in species that do not brood (reviewed in Strathmann & Strathmann 1982). Although all species of calyptraeids brood for some period, the relationship between reproductive output scales with female dry weight (an estimate of volume) to a factor of 0.76 in flat species to 1.1 in more convex species and does not appear to differ between direct developers and planktotrophs (Collin 2000a, unpubl. data). This suggests that reproductive output does not scale with surface area (i.e. volume to the $\frac{2}{3}$ power) and, at least in convex species, it appears to scale with body size. This may explain the lack of relationship between size and brooding in calyptraeids; however, the potential for female reproductive output to increase faster than the available brood area has not been explicitly examined. Unfortunately, data are not currently available to address the other hypotheses reviewed by Strathmann & Strathmann (1982).

Latitudinal trends

Previous studies of molluscan faunas in the North Atlantic have demonstrated latitudinal trends in mode of development (Thorson 1950, Ockelmann 1965, Mileikovsky 1971). Direct development is more common among species from higher latitudes than it is in the tropics. Gallardo & Pencheszedah (2001) have shown that this pattern also exists along the Pacific coast of South America but not along the Atlantic coast. However, latitudinal patterns in development have not been examined for the North Pacific or much of the southern hemisphere, and possible differences in the proportion of species from different subclades have not been assessed. My analysis is the first to show a latitudinal trend (in the northern hemisphere at least) in mode of development in a monophyletic group of gastropods with a worldwide distribution. Because most northern hemisphere calyptraeids are not from the North East Atlantic, these results are geographically and taxonomically independent of previous analyses of latitudinal patterns of gastropod development. The possibility that high level phylogenetic effects influence latitudinal patterns of development in addition to influencing egg size (see above), has not been examined in depth. Some evidence for such effects is presented by Gallardo & Pencheszedah (2001) who demonstrate that the very different faunas from the Pacific and Atlantic coasts of South America demonstrate different latitudinal patterns. This pattern has been explained by the difference in substrate type along the 2 coasts (Gallardo & Pencheszedah 2001), which results in differences in the taxonomic composition of the faunas. Clark & Goetzfried (1978) have also pointed out that opisthobranchs often have direct development at low latitudes. Additional analyses of monophyletic groups as opposed to regional faunas are necessary to further explore this possibility.

Explanations of the increase in frequency of direct development at high latitudes are often based on arguments about productivity and phytoplankton availability for feeding larvae (Thorson 1950). If phytoplankton blooms of short duration combined with cold temperatures are driving a trend to reduce the duration of pelagic development at high latitudes, one might also expect to see a latitudinal increase in the hatching size of planktotrophic species. This is not supported by the calyptraeid data which show no latitudinal pattern in size of planktotrophic larvae. The latitudinal increase in hatching size for direct developers could be explained by a latitudinal pattern in selection on juvenile size. However, this hypothesis is not supported by data on planktotrophs, which show no latitudinal trend in settling size.

CONCLUSIONS

Comparisons of the compiled developmental data for calyptraeids with similar data sets for other groups of invertebrates suggest some features common among all invertebrates, some that may be common among all gastropods and other features that maybe group-specific. General similarities include the left-skewed distribution of egg size and hatching size in both echinoderms and gastropods, and the increasing incidence of direct development with increasing latitude, in at least some regions. The absence of an association between female size and mode of development in *Conus* and calyptraeids, 2 groups with entirely different strategies of parental care, suggests that this may be a common feature of gastropod reproduction. Within gastropods there is a high level phylogenetic effect on reproductive characters dividing the caenogastropods from the heterobranchs with respect to egg size and hatching size of planktotrophs and direct developers, as well as egg mass characteristics. Finally, there are family-specific features (for example, all calyptraeids brood). Since general theories seeking to explain variation in mode of development are often based on patterns that have been observed only in a single taxonomic group, and since these theories usually predict patterns that should hold across many groups, understanding the hierarchical levels of variation in development is vital both to the development and testing of such theories. The available data now

include a group of obligate brooding gastropods which contains many species with nurse eggs; features that were not well represented in the groups subject to previous compilations.

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Appendix 1. Latitudinal range of each species as used in this analysis. Each species was recorded from each bin of 10° in latitude. 0N = 0 to 10° N; 10N = 10 to 20° N; 20N = 20 to 30° N; 30N = 30 to 40° N; 40N = 40 to 50° N; 50N = 50° N+

***Crepidula*:** *aculeata* Mexico, 20N; *aculeata* Florida, 20N; *aculeata* South Africa, 30–40S; *aculeata* Panama, 0S–0N; *aculeata* Japan, 30N; *aculeata* Australia, 30S; *adunca*, 30–40N; *argentina*, 30S; *atrasolea*, 20–30N; *arenata*, 20N; *capensis*, 30S; *cerithicola*, 0N; *cerithicola*^a, 0N; *complanata*, 30S; *convexa*, 30–40N; '*ustulatulina*', 10–20N; cf. *convexa* Bocas, 0N; *coquimbensis*, 20S; *costata*, 30–40S; *depressa*, 10–30N; *dilatata*, 20–50S; *explanata*, 40N; *fecunda*, 10–40S; *fimbriata*, 40N; *fornicata*, 20–50N; *incurva*, 0–20N; *lessoni*, 0S–20N; *lingulata*, 30–40N; *maculosa*, 10–20N; *marginalis*, 0S–0N; *monoxyla*, 30–40S; *naticarum*, 30N; *navicula*, 20N; *nivea*, 30N; *norrisarum*, 30N; *nummaria*, 30N–50N; *onyx*, 20N–30N; cf. *onyx*, 30N; '*onyx*', 30–40S; *perforans*, 30N; cf. *perforans*, 30N; *philippiana*, 30S; *plana*, 30–40N; *porcellana*, 0N; *protea*, 20S; *striolata*, 0N; *unguiformis*, 40N; *williamsi*, 30N; n.sp. B, 50N; n. sp. C, 20N; n. sp. D, 20N. ***Crucibulum*:** *spinosum*, 0–10N; cf. *spinosum* Peru, 10S; *scutellatum*, 0S–0N; n. sp. mx, 20N; n. sp. Chile, 20S; *auricula*, 10N; *marensis*, 10N; *umbrella*, 10N; *personatum*, 0–20N; *quirquinae*, 30S; *striatum*, 0N. ***Calyptrea*:** *chinensis*, 30–40N; *fastigata*, 40N; *mamillaris*, 0N; *pellucida*, 20N; *conica*, 0N; *morbida*, 20N; *lichen*, 0N; *extinctorum*, 20N. ***Siphopatella*:** *novazealandea*, 30–40S. ***Trochita*:** *calyptraeformis*, 10–20S. ***Zegalarus*:** *tenuis*, 30–40S

^aExamination of Hoagland's vouchers (Hoagland 1986) shows that her *Crepidula cerithicola* is not the same as the organism here identified as *C. cerithicola* on the basis of the original description and type material

Appendix 2. Sea surface temperatures (SST) for each collecting locality

Locality	Annual average SST (1998/1994)	Highest monthly SST	Lowest monthly SST	Range of monthly SST
La Paz, Mexico	24.5	30.4	19.5	10.9
	24.3	29.3	20.0	9.3
Key Biscayne, FL, USA	26.7	28.9	24.3	4.6
	26.5	29.1	23.8	5.3
San Antonio Oeste, Argentina	15.6	19.7	11.0	8.7
	14.5	19.0	10.3	8.7
Puerto Madryn, Argentina	12.7	17.0	8.6	8.4
	12.3	16.7	8.5	8.2
Naos, Panama	27.0	27.8	25.0	2.8
	27.2	28.0	25.7	2.3
Bocas del Toro, Panama	27.9	28.9	27.0	1.9
	28.3	28.8	27.3	1.5
Keneohe Bay, HI, USA	25.1	26.5	23.7	2.8
	25.1	26.5	23.7	2.8
Cape Town, South Africa	18.2	20.4	15.8	4.6
	18.0	20.0	15.9	4.1
Zorritos, Peru	21.2	24.4	19.3	5.1
	21.5	24.7	19.2	5.5
Sydney, Australia	21.6	24.6	18.8	5.8
	21.3	24.2	18.5	5.7
Friday Harbor, WA, USA	11.1	14.4	8.4	6.0
	11.1	14.8	8.2	6.6
Mar del Plata, Argentina	12.0	17.6	7.4	10.2
	15.5	19.2	12.0	7.2
Sanibel, FL, USA	25.5	28.9	20.9	8.0
	25.5	28.9	21.3	7.6
Fort Pierce, FL, USA	26.3	29.3	23.2	6.1
	26.9	29.4	24.4	5.0
Onemichi, Japan	21.9	27.5	17.1	10.4
	21.7	27.3	17.1	10.2
Woods Hole, MA, USA	9.2	17.0	2.6	14.4
	10.7	18.1	4.4	13.7
Leigh, New Zealand	18.3	21.3	15.8	5.5
	18.5	21.6	16.0	5.6
Coquimbo, Chile	15.8	18.6	13.5	5.1
	16.0	18.7	13.5	5.2
Venezuela	27.1	28.3	25.8	2.5
	26.9	28.3	25.7	2.6
Chiloe, Chile	13.2	15.2	11.1	4.1
	13.1	15.6	11.0	4.6
Lima, Peru	18.9	22.4	15.6	6.8
	19.3	22.9	15.9	7.0
Santa Barbara, CA, USA	15.1	17.1	13.4	3.7
	15.3	17.5	13.6	3.9
West Africa	23.7	28.4	19.5	8.9
	26.5	27.9	25.4	2.5
Sao Paulo, Brazil	23.5	25.5	21.5	4.0
	24.2	26.5	22.3	4.2
Latium, Italy	18.0	24.4	13.3	11.1
	18.2	24.5	13.5	11.0
Kodiak Island, AK, USA	7.1	12.0	3.9	8.1
	7.0	11.6	3.9	7.7
Hong Kong	25.4	28.9	21.2	7.7
	25.5	28.9	21.6	7.3
Plymouth, UK	12.7	16.4	10.5	5.9
	12.6	16.4	10.3	6.1
Red Sea	27.0	30.3	24.0	6.3
	27.0	30.2	24.1	6.1

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