Dispersal and divergence across the greatest ocean region: Do larvae matter?

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Synopsis For marine, benthic animals, duration of planktonic larval stages is expected to correlate with dispersal ability, and thus species ranges, at least where planktonic dispersal is necessary to reach habitats. Yet past analyses of larval duration and species ranges across the insular Pacific show at most a weak correlation. So, do larvae matter in determining species ranges in such an island setting? We analyze an extensive dataset on cowries and find, again, that estimated larval duration does not correlate with species ranges. Several factors can obscure a real correlation, however, including estimation error, intraspecific variation, other factors affecting dispersal, poor taxonomy, and remote endemics. We show that taking these into consideration greatly improves correlation. Further evidence for the importance of larval duration comes from diversity and speciation patterns. Diversity of poor dispersers drops more rapidly eastward across the Pacific and leads to taxonomic differences in community composition across the basin. Geographic scale of differentiation is strongly influenced by larval duration and leads to the most rapid diversification at intermediate dispersal capacities. A major lesson from the phylogenetically corrected cowrie dataset is that without accurate and appropriate taxonomy, clear and important distributional and diversity patterns can become obscured. Inappropriate taxonomic scale can also obscure macroecological patterns: cowrie tribes/subfamilies show substantial variation in the steepness of their diversity cline across the Pacific and in their proportional local abundance, showing the importance of ecological traits in controlling distributions. In contrast such variation was not evident in a study focused at the family level in corals and fishes.

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Introduction

The dispersal ability of organisms impacts their distribution, ecology, and evolution. In most benthic marine species dispersal is largely confined to embryonic and larval stages that remain in the water column from minutes to months, before metamorphosing and settling to the benthos. Considerable attention has been given to how dispersal ability varies with life history strategy. The simplest expectation is that larval dispersal range should correlate with duration of planktonic period; this has been robustly demonstrated across algae, invertebrates, and fishes (Shanks and others 2003; Siegel and others 2003). A further expectation is that dispersal ability and distributional range should be correlated (for example, Thorson 1950; Shuto 1974). Distributional range in turn has numerous ecological and evolutionary consequences (for example, Gaston 1998).

The impact of dispersal on distributional range has been clearly demonstrated in some systems. For example there is strong correlation between larval duration (inferred from larval shells or apical disc plates) and species range size in Cretaceous and Tertiary gastropods along the American Gulf and Atlantic coastal plains (Hansen 1980; Jablonski and Lutz 1983; Jablonski 1986) and in Tertiary echinoids in southern Australia (Jeffery and Emlet 2003). The correlation is strong despite biases of the fossil record, indirect estimate of larval duration, and continental setting, where, if suitable habitat is sufficiently contiguous, organisms with limited dispersal ability can, over time, disperse extensively.

Surprisingly, in insular settings, where long-distance dispersal is essential for establishment of wide ranges, the correlation between larval duration and range is often not significant. This is especially striking in the Indo-west Pacific (IWP), the largest marine biogeographic region, extending from East Africa to the central Pacific, and dominated by islands and reefs reachable only across substantial open ocean barriers. The best data available in this region are from reef fishes, where actual duration of planktonic period can be determined from growth lines in otoliths of

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newly settled juveniles. The first study to utilize this technique found a surprising lack of correlation between larval period and species range among pomacanthid fishes (Thresher and Brothers 1985). Similar lack of correlation emerged from a study of 100 species of Pacific and Atlantic pomacentrid fishes (Wellington and Victor 1989), and much variation noted, (though not tested by regression) among 100 wrasses (Victor 1986). Further work along the largely continental East Pacific similarly failed to find significant correlation between planktonic period and geographic range in labrids and pomacentrids (Victor and Wellington 2000).

The relationship between planktonic period and geographic range has also been investigated in sea urchins and cone snails. In regular echinoids, correlation between planktonic period and geographic range was not significant among 33 species tested (Emlet 1995). By increasing sample size with the addition of taxa for which planktonic period was not known, but mode of development was, Emlet (1995) found that pelagic planktotrophs had significantly greater ranges than pelagic lecithotrophs, a developmental mode usually associated with a shorter planktonic period (but see below). Kohn and Perron (1994) found a significant correlation between planktonic period (estimated from egg size) and geographic range for IWP *Conus*, but this correlation was largely driven by species with direct development, lacking planktonic dispersal stages. The correlation loses significance if analysis is restricted to cones with planktonic propagules ($r^2 = 0.39$, $P \ll 0.0001$ with direct developers included ($N = 61$); $r^2 = 0.05$, $P > 0.1$ with direct developers excluded ($N = 51$), based on Kohn and Perron's (1994) data, kindly provided by A. J. Kohn). Similarly, protoconch shape (correlated with planktonic period) and geographic range are not significantly correlated in IWP cypraeid gastropods (cowries, see below). Lack of correlation between dispersal ability and geographic range is not uncommon (Gaston 1998).

Why is there such poor correlation between planktonic period and geographic range in such insular, dispersal-limited settings? The objectives of this paper are to evaluate the impact of the duration of planktonic period on the biogeography and evolution of IWP marine life. We (1) explore how various factors may obscure an underlying correlation and whether the correlation improves if such factors are taken into consideration, and (2) test some biogeographic and evolutionary predictions based on a presumed correlation. We do this in part on a new dataset derived from a global study of cypraeid gastropods, supplemented with examples from the literature.

Methods

We analyzed the relationship between inferred planktonic period and distributional range for species and also for evolutionary significant units (ESUs) of the gastropod family Cypraeidae (cowries). ESUs are reciprocally monophyletic taxa delineated on the basis of mitochondrial sequences (see Meyer 2003, 2004 for detailed treatment). They provide a finer, more accurate, and objective delineation of genetically connected populations and correspond almost one to one with described species and subspecies. We prefer the term ESU to species because many of these species-level taxa are allopatric, represent various stages of the speciation process, and whether they meet the criteria of the biological species concept is untested. Our use of ESUs prevents over-lumping ranges of populations that are not genetically connected. We performed analyses both on traditional cowrie species, as delineated in recent revisions (Burgess 1985; Lorenz and Hubert 1993; Lorenz 2002), and ESUs based on the most recent phylogenetic analysis (Meyer 2004).

We used protoconch shape as an estimate of larval planktonic period. Cowrie protoconchs are covered over by subsequent shell growth, thus are usually well preserved, but accessible only through sectioning. We used Foin's (1982) quantification of protoconch shell angle and generating parameter, based in turn on Ranson's (1967) extensive illustrations of sectioned cowrie protoconchs. We tested the utility of protoconch as a measure of developmental mode by regressing protoconch shape on egg diameter. Egg diameters were taken from samples collected in association with brooding females and fixed in 70% ethanol, and 10 eggs or early embryos measured per capsule.

Distributional ranges were compiled from a variety of sources (Schilder FA and Schilder M 1938; Burgess 1985; Lorenz and Hubert 1993; Lorenz 2002; F. Lorenz personal communication; C. P. Meyer personal observation) and quantified as the number of 5° × 5° grid cells occupied by a species/ESU. We also used this distributional database to establish species diversity and composition at 253 sites across the IWP and to address species assemblage bias. In particular, we examined whether the relative proportion of major cowrie lineages in local assemblages fall within expected ranges based on random draws from the regional species pool, using the methods developed by Bellwood and Hughes (2001). One thousand bootstrap iterations were performed to determine the 95% confidence interval across a variety of local richness values for each cowrie lineage. IWP cowrie taxa were deconstructed into seven major, monophyletic lineages: (1) *Ipsa* + *Nesiocypraea*: 5 ESUs; (2)

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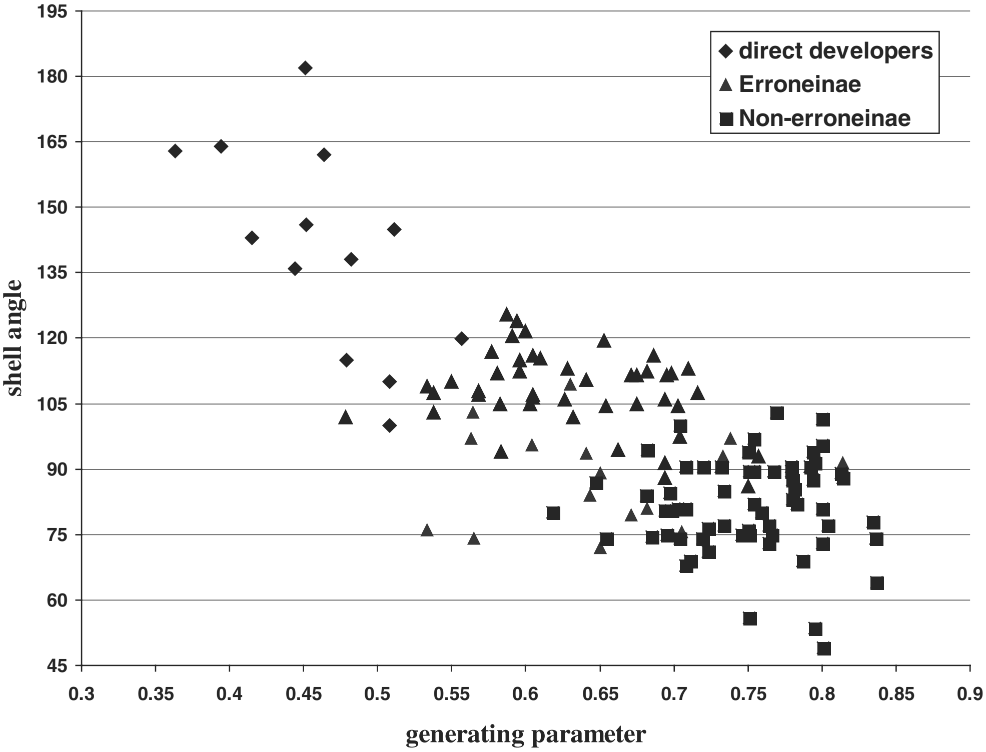

Fig. 1 Correlation between shell angle and generating parameter in cowrie protoconchs. Note restriction of direct developers to upper left, dominance of Erroneinae in middle, and rest of the family toward lower right.

Erosariini: 36 ESUs; (3) Cypraeinae: 24 ESUs; (4) *Barycypraea*: 1 ESU; (5) Luriinae: 25 ESUs; (6) *Pustularia*: 9 ESUs; and (7) Erroneinae: 128 ESUs. Data are presented for the four most diverse lineages: Erosariini, Cypraeinae, Luriinae, and Erroneinae. Diversity clines were also constructed based on distributional data for (1) all IWP taxa, (2) Erroneinae, and (3) non-Erroneinae taxa.

Results and discussion

Geographic range versus larval form in cowries

The protoconch shell angle and generating parameter correlate strongly ($r^2 = 0.54$, $P < 0.0001$, Fig. 1). Low spire and rapid expansion rate (upper left of graph) in protoconchs are characteristic of gastropods with abbreviated planktonic development, while high spires and slow expansion rates (lower right of graph) are found in species with long-lived planktonic larvae (Shuto 1974). Cowries fit the expected pattern: species with direct development cluster at the upper left, while those with planktonic larvae are spread across the middle and lower right of this regression. Given the strong correlation between generating parameter and shell angle, and the relation of both to mode of development, we derived a single numerical proxy (Protoconch Shape Parameter, PSP) for planktonic duration, by taking the ratio of the two. PSP values and egg diameter are inversely correlated ($r^2 = 0.62$, $P < 0.0001$; Fig. 2), indicating that protoconch morphometry is a robust proxy for developmental mode. The correlation between PSP and geographic range is not significant for IWP cowrie species with planktonic development (Table 1, Fig. 3A).

Protoconch shape and mode of development have strong phylogenetic signatures in cowries (Foin 1982; Meyer 2003). Direct development, although it arose independently at least six times, is limited to seven genera, all species of which appear to lack planktonic larvae (Meyer 2003). Among species with pelagic development, members of the subfamily Erroneinae cluster in the middle of the regression, while other cowries with planktonic development fall at the high spire, low expansion rate end of the curve (Fig. 1). Thus direct developers have low, erroneines intermediate, while other cowries have high PSP values. Erroneinae species also have larger and fewer eggs per capsule (0.16–0.34 mm, 20–76 eggs/capsule) than members of other cowrie subfamilies (0.09–0.17 mm, 500–1200 eggs/capsule) (Table 2; Ostergaard 1950; Natarajan 1957; Osorio and others 1992). This implies that species of Erroneinae generally have shorter planktonic periods than other cypraeids with planktonic larvae.

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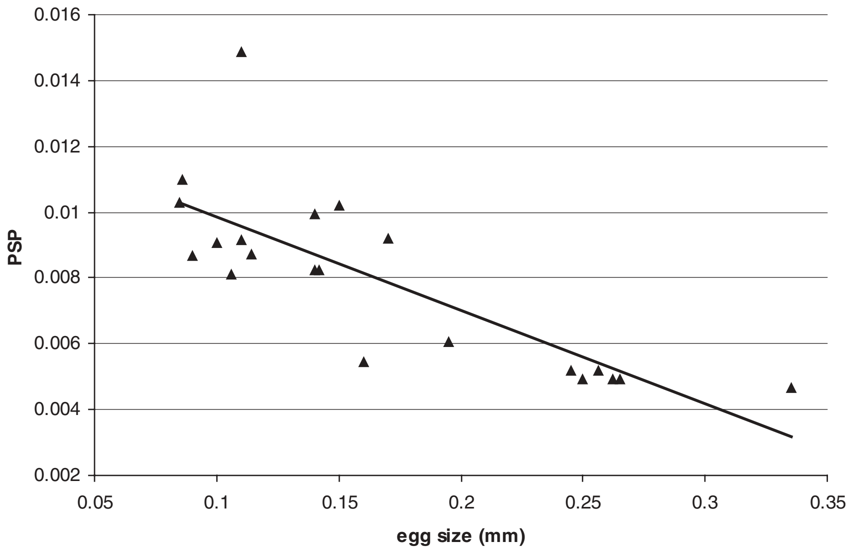

Fig. 2 Correlation between Protoconch Shape Parameter (PSP) and egg size (from Table 2).

Table 1 Correlation between PSP and species range in IWP cowries

Taxa included	r^2	P
IWP species	0.02	0.20
IWP + S temperate species	0.08	0.002
IWP ESUs	0.11	<0.001
IWP + S temperate ESUs	0.15	<0.001
IWP − remote islands ESUs	0.19	<0.001
IWP + S temperate − remote islands ESUs	0.23	<0.001

IWP: cowries that inhabit the IWP region. S temperate: cowries that inhabit the warm temperate-subtropical coasts of South Africa and Australia, adjacent to the tropical IWP. Remote islands: cowries endemic to Hawaii, Marquesas, and Easter Islands are excluded in these analyses.

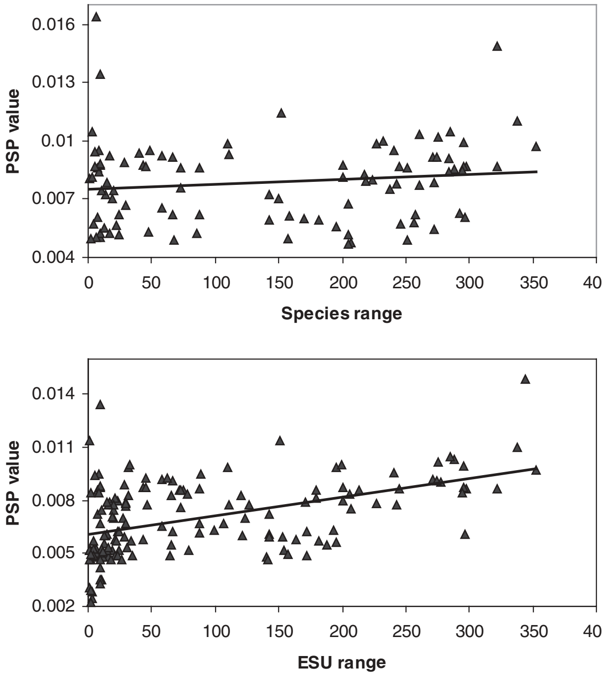

Fig. 3 Correlation between PSP and geographic range (measured as number of 5° × 5° cells occupied) of traditional morphological species (above) versus ESUs (below).

Confounding factors

The poor correlations between estimates of planktonic larval durations and species ranges raise the issue whether larvae matter: whether developmental modes influence species distributions in the IWP? Either they do not, or confounding factors obscure the expected correlation. Several potential factors can be identified and the impact of some of these evaluated with data from cowries.

Estimation error

While fish otoliths provide a direct measure of planktonic period from field-collected recruits, most estimates of planktonic duration are more indirect and can have substantial estimation errors. Next best are laboratory estimates of planktonic period. These are often based on the length of the precompetent period (minimum planktonic period), when larvae are allowed to metamorphose immediately upon reaching competency. These estimates are impacted by culture conditions such as quality of (potentially artificially spawned) eggs, artificial food regimes, culture temperature, availability of settlement cues, etc. More importantly, they exclude the potentially much longer competent period from consideration, and thus underestimate dispersal potential. Conversely, estimates of

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Table 2 Egg size in cowries

	Egg diameter
Non-Erroneinae	
Monetaria annulus	0.09
Monetaria moneta	0.09
Erosaria helvola[a]	0.09
Monetaria caputserpentis	0.10
Monetaria caputdraconis[b]	0.11
Erosaria poraria	0.11
Luria isabella[a]	0.11
Lyncina sulcidentata	0.11
Mauritia arabica	0.14
Lyncina carneola	0.14
Mauritia arabica	0.14
Mauritia mauritiana[a]	0.15
Macrocypraea cervinetta	0.17
Erroneinae	
Purpuradusta fimbriata	0.16
Talostolida teres	0.20
Cribraria cribraria	0.25
Erronea errones	0.25
Cribraria cribraria	0.26
Erronea errones	0.26
Erronea errones[c]	0.27
Bistolida stolida	0.34

Data from this study, except from literature where noted by superscript. Egg diameter (mean of [max diameter + min diameter/2]) in mm.

[a] Ostergaard (1950).

[b] Osorio and colleagues (1992).

[c] Natajaran (1957).

maximum larval life spans, based on larvae sheltered from settlement cues, can be biased in the opposite direction, if larvae survive beyond a stage where they have sufficient energy reserves for successful settlement or juvenile's existence (for example, Lucas and others 1979; Highsmith and Emlet 1986).

Even more removed and thus prone to estimation error are estimates of relative planktonic period based on morphological features of developing stages, such as egg size, and larval shell size or shape. Kohn and Perron (1994) provide an extensive analysis of correlations between minimum planktonic period measured in the laboratory, egg size, and protoconch diameter for the gastropod family Conidae, and show that in cones at least there is tight correlation among these three variables.

Intraspecific variation in planktonic period

Substantial intraspecific variation in planktonic period, especially when combined with limited interspecific variation, could obscure potential correlation between planktonic period and range size. We lack data to evaluate this factor in cowries, but examples from the literature illustrate substantial potential variation. Both precompetent and competent periods are variable, although the latter has potentially much greater impact on dispersal range, because larvae can settle immediately after reaching competency, or delay substantially. Nevertheless duration of precompetent period is also variable, influenced by intrinsic (for example, egg size [Levitan 2000]) and extrinsic (for example, temperature (for example, Thorson 1950; Pechenik 1984; Green and Fisher 2004), food availability (for example, Thorson 1950; Paulay and others 1985; Fenaux and others 1994, and so on) factors.

Variation in duration of competent period is related to capacity to delay settlement among species and realization of that capacity within species. Capacity to delay settlement varies substantially among taxa; it may be substantially limited in some reef fishes, while it may be virtually unlimited in certain gastropods and echinoderms. The extent to which reef fishes can delay metamorphosis is debated, although otolith studies suggest relatively short competent periods. Wellington and Victor (1989) noted limited intraspecific variation in planktonic period in pomacentrids and suggested that most damselfish may not be able to delay metamorphosis substantially. In contrast Victor (1986) found considerable intraspecific variation in larval duration in wrasses. McCormick (1999) found limited variation in planktonic period among recruiting larvae of the surgeonfish *Acanthurus triostegus*, but demonstrated that these recruits could delay metamorphosis for several days if moved away from the reef. Nevertheless larvae that delayed metamorphosis deposited metamorphic bands on their otolith, demonstrating a decoupling of metamorphic morphogenesis of otolith from gross body morphology. Similar delay and decoupling of otolith and body metamorphosis have been demonstrated in the pearl fish *Carapus homei* (Parmentier and others 2004). However larvae in both studies were captured after they recruited onto shallow reefs, thus observed changes in otolith banding may reflect a partial induction of metamorphosis by this encounter. If so, otolith data remain a reliable indication of larval life span. The limited variation in planktonic period determined from otoliths may indicate either a lack of ability to delay, or that most larvae recruit from local larval pools as soon as they are competent, that is, that delay is possible, but too uncommon to be encountered in small samples. Fish larvae may remain in the vicinity of reefs allowing rapid settlement upon reaching competency (Colin 1991; Swearer and others 1999; Leis and others 2003). Examination of late stage larvae

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caught at sea far from appropriate habitat could test whether substantial delay is possible in potential colonists. Fishes that truly have limited capacity for delaying settlement would be model organisms for studying the relationship between planktonic period and dispersal.

In contrast some other taxa appear capable of delaying settlement indefinitely, having virtually immortal larvae. Thus the ranellid gastropod *Cymatium parthenopeum* appears to enter developmental arrest in open ocean: protoconch size does not vary with distance from shore across the Atlantic (Pechenik and others 1984). Most if not all ranellids have such teleplanic larvae (Scheltema 1971; Beu 1998). Miller and Hadfield (1990) showed that extension of competent period to >3 times the duration of precompetent period has no impact on adult life span of the nudibranch *Phestilla sibogae*, implying developmental arrest during delay. Not all marine gastropods are capable of developmental arrest, however, thus the shells of some calyptraeids, cerithiids, and epitoniids keep growing during competency (Pechenik 1986; Robertson 1994). Clonal reproduction in some echinoderm larvae is another example of virtual larval immortality (Bosch and others 1989; Knott and others 2003).

The length of the competent period may be limited by energy reserves in lecithotrophs and mixotrophs. For example in barnacles, the competent, cyprid, larvae do not feed, and delaying settlement is strikingly limited by energy reserves (Lucas and others 1979). McEdward and colleagues (1988) showed that the crinoid *Florometra seratissima* uses 81% of the egg's energy content during larval and pre-feeding, benthic development, imposing severe energetic limits for delaying settlement. Egg size of crinoids is morphologically constrained by pinnule diameter; *Florometra*'s 195 μm eggs, although typical for crinoids, are much smaller than lecithotrophic eggs of other echinoderm classes (Emlet and others 1987). This constraint leads to a striking contrast in delaying capacity among echinoderms. Thus eggs of the lecithotrophic holothurian *Cucumaria curata* are 500 times as energy rich as those of *F. seratissima*, yet use <1% of their energy content through metamorphosis, leaving ample reserves for delay (McEdward and others 1988). Hoegh Guldberg and Emlet (1997) demonstrated a similarly minor loss of energy reserves during development in the lecithotrophic echinoid *Heliocidaris erythrogramma*. Not surprisingly, Birkeland and colleagues (1971) found that the lecithotrophic asteroid *Mediaster aequalis*, with similarly large eggs, can delay settlement for over a year, much longer than the typical planktonic period of planktotrophic echinoderms.

Because lecithotrophic larvae do not need to acquire energy through feeding, the minimum (precompetent) planktonic period of lecithotrophs is typically shorter than that of planktotrophs (Thorson 1961; Emlet and others 1987). However the huge egg size and energy reserves of some lecithotrophs can also provide impressive capacity for delaying settlement. Thus the observation that pelagic lecithotrophs have more limited dispersal capacity than planktotrophs (for example, Jablonski and Lutz 1983; Emlet 1995) is unlikely to hold across all taxa and environments.

Other intrinsic factors influencing dispersal ability

Although the biogeographic literature has focused on larval planktonic period, other intrinsic attributes, such as larval behavior, site and time of gamete/larval release, also influence dispersal capacity. Yamaguchi (1977) noted that sea stars with demersal, positively geotactic larvae have more restricted, continental distributions, while otherwise similar species with negatively geotactic larvae, are widespread, reaching remote, oceanic islands. Shanks and colleagues (2003) noted that species that disperse less than expected given their planktonic period generally have demersal larvae, either because of negative buoyancy or behavior. Extensive studies of the west Australian lobster, *Panulirus cygnus*, have demonstrated the importance of larval behavior in offshore transport and homing (Phillips and others 1979). The importance of sensory and swimming capabilities of other large larvae are becoming clear from numerous studies on reef fishes (Bellwood and Fisher 2001; Leis 2002; Fisher and Bellwood 2003; Simpson and others 2005). The timing and location of spawning (or larval release) also has substantial influence over whether propagules are carried offshore or entrained near islands/reefs (Colin 1991; Appeldoorn and others 1994; Hensley and others 1994).

Larvae are not the only stages capable of dispersal, and for some taxa they are not the primary means of long-distance colonization. Adult fishes and some errant invertebrates are capable of swimming for long distances. Behavior (reluctance to swim far from bottom), however, appears to keep many from traversing open ocean. Thus while tetraodontid and kyphosid fish juveniles and adults are commonly encountered along flotsam at sea, post-larval chaetodontid and pomacanthid fishes, for example, are not (R. F. Myers personal communication). Similar psychological bias appears to limit the dispersal of certain birds among islands, relative to equally well flying relatives (Diamond and others 1976). Sepiid cephalopods have demersal development and are largely confined to

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continents. Nevertheless a few species reach nearby oceanic islands apparently as swimming adults. Thus adults of *Sepia latimanus*, the most widespread IWP sepiid, can be encountered at FADs (Fish Attracting Devices) a few miles off Guam over bathyal depths (G. Davis, personal communication). Rafting also provides effective dispersal, especially for sessile species, their associates, and species of small body size (Highsmith 1985; Jokiel 1990a, 1990b; Thiel 2003), and sessile, clonal invertebrates are often much more widely distributed than expected from larval dispersal capacities (Jackson 1986). The abundance, diversity, and endemism of invertebrates with larval life spans of 0–2 days (for example, direct-developing mollusks, peracarid crustaceans, and ascidians) on remote Pacific islands demonstrate the efficacy of rafting for a wide range of taxa (Sleurs and Preece 1994; Reid and Geller 1997; Eldredge and Evenhuis 2003).

Taxonomic artifacts

The abundance of sibling species in the sea (Knowlton 1993) raises the issue whether taxonomic failures to recognize them impact potential correlation between planktonic period and species range. The Cypraeidae is the best-studied marine family from an integrative taxonomic perspective, as >90% of species-level taxa have been genetically characterized, often from several locations across their ranges (Meyer 2003, 2004). The recognition of resulting reciprocally monophyletic, species-level taxa as ESUs provides an instructive comparison with traditional species defined solely on morphological criteria. While protoconch shape and geographic range are not significantly correlated among traditional IWP species ($r^2 = 0.02$, $P > 0.2$), they are significantly correlated among IWP ESUs ($r^2 = 0.11$, $P < 0.001$; Fig. 3, Table 1), demonstrating that taxonomic artifacts can obscure existing correlation. As noted below, groups with poor dispersal capacities are especially prone to allopatric differentiation and frequently comprised allopatric complexes of sibling species (for example, Kirkendale and Meyer 2004; Meyer and others 2005). Thus artificial lumping of species complexes is most likely in taxa with limited dispersal, increasing their apparent range, and thus decreasing apparent correlation between planktonic period and range size.

Remote island effect

Many reef fishes are little impacted by the factors reviewed above: otoliths provide good estimations of *in situ* planktonic period, there may be limited intraspecific variation in planktonic period, dispersal is frequently limited to larval stages, and fish species are taxonomically relatively well known. Why is the correlation between planktonic period and range so poor in fishes then? One possibility is that remote island endemics confound the signal: they have the smallest geographic ranges, yet their ancestors needed exceptional dispersal capacity to reach their remote home (Victor 1986). Such long-lived larvae are frequently retained in remote endemics, likely partly because of phylogenetic inertia (Thresher 1985; Victor 1986; Wellington and Victor 1992). There is little evidence for evolutionary reduction in planktonic period to facilitate retention on islands, rather there is growing evidence that long-lived larvae can be locally retained around, or home to, reefs and islands (Jones and others 1999; Swearer and others 1999; Robertson 2001; Leis and others 2003; Taylor and Hellberg 2003).

The impact of remote island endemics can be evaluated by excluding them from analysis. Excluding remote endemics (those confined to the Hawaiian, Marquesas, and Easter Islands) raises the coefficient of regression between the protoconch shape and ranges for IWP cowrie ESUs from 0.11 to 0.19 (Table 1). Sister taxa of four of the 10 Hawaiian cowrie endemics have IWP-wide ranges, demonstrating the exceptional dispersal ability needed to reach such remote island groups.

Planktonic versus non-planktonic development

Given the substantial potential for variation in planktonic period noted in above, the poor correlation between planktonic period and species range is less surprising. However these biases have little impact on taxa that lack planktonic propagules. Not surprisingly addition of taxa with direct, non-planktonic development increases the significance of correlation in cowries, as noted earlier for *Conus*. While none of the IWP cowries is known to have direct development (although *Barycypraea teulerei* is suspected), most South African and temperate Australian species are direct developers, and their inclusion substantially increases the correlation between PSP and species range in all comparisons (Table 1).

Evolutionary and biogeographic consequences

Correcting for confounding factors improves the correlation between planktonic period and geographic range. Additional evidence for the importance of larval dispersal on range size comes from evolutionary and biogeographic consequences, which we now examine. Dispersal ability leaves a substantial signature on the distribution of biodiversity and speciation.

(1) Pacific diversity cline

The most striking biogeographic pattern in the IWP is the cline of decreasing species richness from the global

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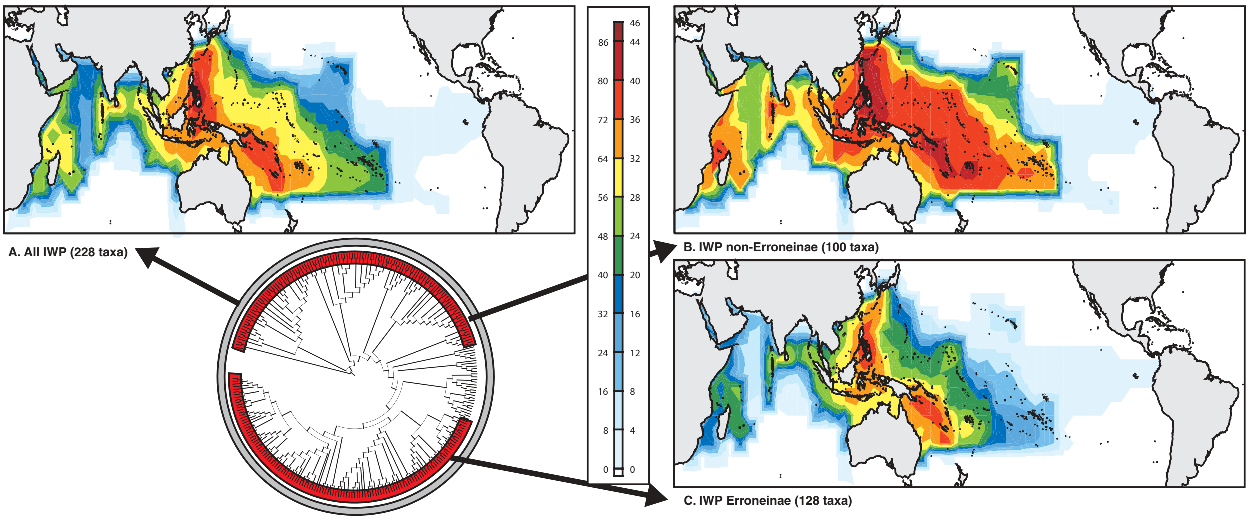

Fig. 4 Deconstructed diversity clines for IWP cowries. (A) The distribution of all IWP taxa (228 ESUs) reflect standard longitudinal and latitudinal diversity clines for IWP groups. (B) Non-Erroneinae IWP taxa (100 ESUs). (C) Erroneinae taxa (128 ESUs). Diversity cline is much steeper for Erroneinae clade than for remaining IWP species. Values to the left in scale bar are for A; values to the right are for B and C.

center of marine diversity in Indo-Malaya eastward across the Pacific basin (Stehli and Wells 1971; Kay 1979) (Fig. 4A). Although this pattern has multiple causes (Paulay 1997), dispersal limitation upstream into the insular Pacific is clearly important. A prediction of the dispersal limitation hypothesis is that groups with better dispersal abilities should be proportionately better represented in the oceanic central Pacific than groups with poorer dispersal abilities. A correlate is that the steepness of the Pacific diversity cline should vary inversely with dispersal ability. Are these predictions supported when developmental mode or planktonic period is used as a measure of dispersal ability?

The Erroneinae, noted above for their putative shorter planktonic periods than other cowries, have a correspondingly steeper diversity cline than other cypraeids (Fig. 4), matching the prediction of the dispersal limitation hypothesis. Kay (1990) also noted this taxonomic pattern in species composition across the Pacific basin, and attributed it to an increase in central Pacific endemics in non-Erroneinae clades.

The predictions of the dispersal limitation hypothesis are also supported by previous observations. Thus groups that lack planktonic propagules (and do not raft effectively), are largely confined to the continental western Pacific, absent from the oceanic central Pacific. These include direct developing gastropods, including members of Conidae (Kohn and Perron 1994), Cypraeidae (Meyer 2003), and all Volutidae (Bouchet and Poppe 1988; Poppe and Goto 1992). Similarly, several major taxa that lack feeding larval stages, such as dendrochirotid holothurians and crinoids, rapidly drop out toward the central Pacific, and are absent from shallow water faunas of eastern Polynesia and Hawaii (Paulay 1997). Kay (1967) noted that "archaeogastropods" are consistently underrepresented in Oceania, where they are proportionately only half as common as in the continental IWP. This bias is consistent with the dispersal limitation hypothesis: larvae of the paraphyletic "Archaeogastropoda", with the exception of neritoids, are lecithotrophic, while planktotrophic larvae prevail among higher gastropods.

(2) Dispersal and community composition

Bellwood and Hughes (2001) demonstrated that the proportional diversity of major reef fish and coral families is relatively constant across the Indo-Pacific, with local diversity of particular families not significantly different from that expected from random assignment of species from the total Indo-Pacific species pool. This implies that community composition at the family level across this vast region can be approximated by random allocation from the regional species pool. Thus Bellwood and Hughes (2001) noted that "ecological traits (for example, body size, longevity, larval type) have surprisingly little impact on distribution patterns of species at a regional scale."

We performed the same analysis on cowries to assess the impact of dispersal on community composition and found that unlike fishes and corals, IWP cowrie communities are not assembled randomly from the regional species pool (Fig. 5). Local diversities of cowrie lineages with short-lived larvae, like the Erroneinae, fall largely below expected values based on their regional diversity, while cowries with long-lived larvae, like the

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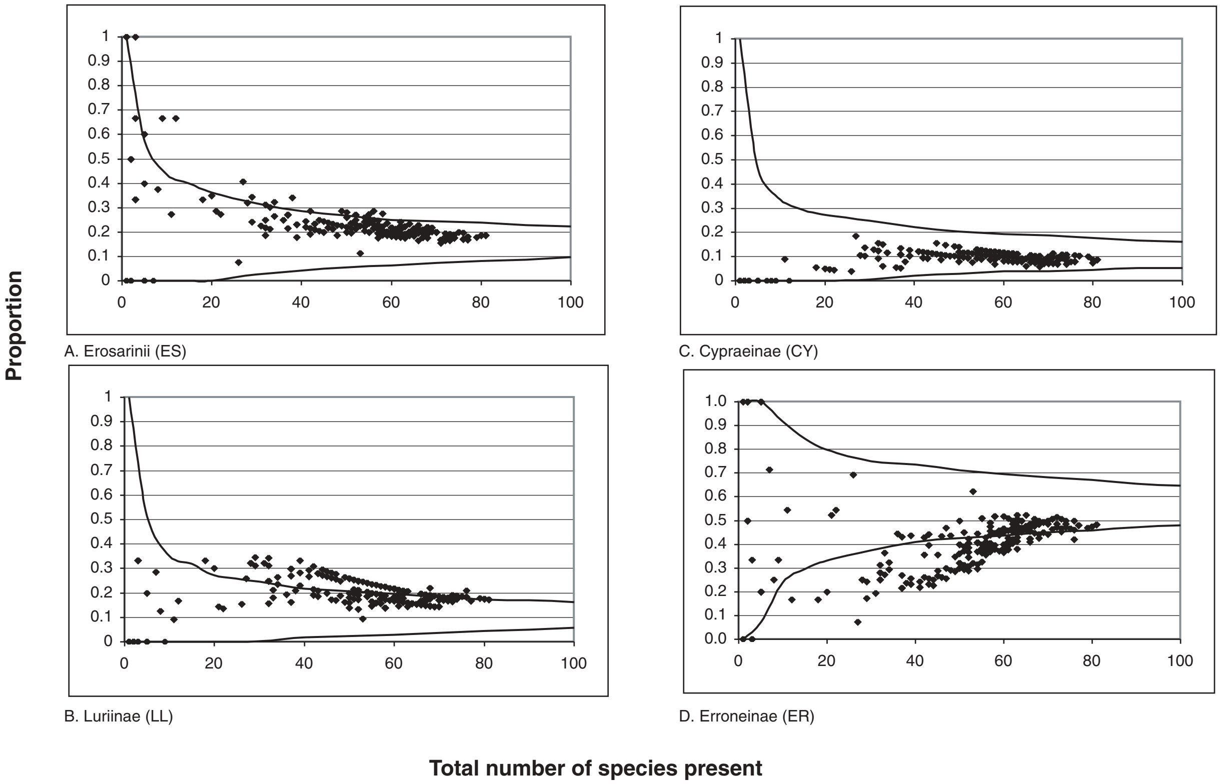

A. Erosarinii (ES)

C. Cypraeinae (CY)

B. Luriinae (LL)

D. Erroneinae (ER)

Fig. 5 Contribution of the four most diverse IWP cowrie clades to diversity at 253 localities across the IWP. Each point represents proportional diversity (*y*-axis) at that site of the clade graphed against total number of cowrie species present (*x*-axis) at that site. Upper and lower black lines represent bootstrapped 95% confidence intervals based on random sampling of species from the total IWP species pool.

Luriinae and Erosariini, have higher local diversities than expected. How and why are cowries different from fishes and corals? Are these differences the result of fundamentally differences among these taxa, or of the different taxonomic levels (subfamilial versus familial) at which comparisons were made?

The disparity in proportional representation of cowrie lineages among local and regional species pools is caused by inter-lineage variation in species range size, likely reflecting differences in dispersal ability. These differences appear to be substantial among cowrie tribes and subfamilies, but minor among coral or fish families. Species-level variation in dispersal/range size could also be greater overall in cowries than corals and fishes, providing more material for inter-taxon differentiation to draw on.

Phylogenetic inertia impacts the evolution of life histories, as of other traits. Phylogenetic inertia in marine invertebrate life histories is clearly apparent at lower taxonomic levels, but tends to disappear at higher taxonomic levels (for example, Lessios 1990; Collin 2003). For differences to be apparent among taxa, comparisons need to be made at the taxonomic level where such differences are manifest, where differences in dispersal capacity have not been averaged out over longer evolutionary time (Lessios 1990). Our data suggest that dispersal limitations substantially impact range size and through it community assembly, but this may be clearly evident only at the appropriate taxonomic scale. The non-random community assembly apparent within cowries could disappear if family level gastropod taxa were the basis of comparisons. Thus inappropriately scaled taxonomic comparisons can obscure significant biogeographical and macroecological pattern.

Although the impact of dispersal ability does not come across in Bellwood and Hughes (2001) family level comparisons, potentially because dispersal ability does not vary substantially at the family level in corals and fishes, in another study they demonstrate more subtle impacts of planktonic dispersal on species ranges (Hughes and others 2002). They find that while the proportion of species with especially wide (pandemic) and narrow (endemic) ranges are remarkably constant across fish families, "the five families that have significantly more pandemics than expected are all broadcast spawners (Acanthuridae, Chaetodontidae, Holocentridae, Lutjanidae, and Serranidae), whereas the three families that have significantly fewer pandemics than expected are benthic spawners with

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an extended period of parental care (Apogonidae, Blennidae, and Pomacentridae)". The latter groups spend part of their development in the benthos and thus have shorter planktonic periods.

3) Speciation

Recent syntheses indicate that speciation is predominantly allopatric in general, as well as in the IWP in particular (Coyne and Orr 2004; Williams and Reid 2004; Meyer and others 2005; Meyer and Paulay manuscript in preparation). Dispersal ability impacts the potential geographic range of species and thus the scale over which allopatric speciation operates.

In IWP gastropods planktonic period is roughly correlated with geographic scale of speciation, and in turn is related to rate of diversification. Diversification of highly dispersive species is limited by opportunities for isolation, while diversification of poorly dispersive species is limited by slow buildup of sympatric diversity. Thus diversification is potentially greatest at intermediate levels of dispersal. Meyer (2003) divided IWP cowrie genera into three groups based on species ranges and diversity. The first group includes genera with 1–3 ESUs, with species generally spread across the entire region with little genetic structuring. Thus they have high dispersal ability and this appears to have limited their diversification. The second group includes genera with 5–26 ESUs, with mostly subbasinal ranges, that have speciated on a basinal/subbasinal scale across the IWP. The third group, the Erroneinae, are the most diverse (128 ESUs), and have speciated on the finest geographic scale. Although the first two groups have similar protoconchs, erroneines have larval shells indicative of more abbreviated planktonic development (Fig. 1). Finally, direct developing cowries are unique in having very limited ranges along the continental coasts of South Africa and temperate Australia and diversifying within the confines of these coasts (Liltved 1989; Meyer 2003; Wilson and Clarkson 2004).

Similar patterns are evident in other groups. Most invertebrates and fishes that have been investigated by phylogeographic studies in the IWP have relatively long-lived planktonic stages, show basinal to regional genetic structuring, and modest intra-clade diversity. Thus planktotrophic echinoids generally speciate over wide geographic scales and have accumulated little species diversity per genus or family across the IWP (Palumbi and others 1997; Lessios and others 1999, 2001, 2003). Littorines with pelagic egg capsules and planktotrophic larvae speciate over basinal scales, and have high local as well as regional diversity (Williams and Reed 2004). In contrast vetigastropods and patellogastropods, with short-lived, lecithotrophic larvae, comprise extensive, fine-scale species complexes diversifying largely on an archipelagic scale (Paulay and Meyer 2002; Meyer and Kirkendale 2004; Meyer and others 2005). In these latter groups local diversity is relatively low, but regional diversity relatively high, as a result of the abundance of allopatric, narrow-range species.

Importance of taxonomy

A major lesson from the cowrie dataset is that without accurate taxonomy and appropriate taxonomic scale, distributional and diversity patterns can become obscured. Inappropriate species delineation is a major reason for the lack of correlation between planktonic larval duration and species range in cowries. Correlation becomes significant by improving species delineations through genetic scrutiny. Similarly, inappropriate taxonomic scale can obscure distributional and macroecological patterns. Egg size, developmental mode, and planktonic duration exhibit substantial phylogenetic inertia. Biogeographic and evolutionary correlates of these developmental attributes, such as community assembly, can be strikingly variable at taxonomic levels impacted by phylogenetic inertia, but less variable at higher taxonomic levels, where differences have averaged out.

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References

Appeldoorn RS, Hensley DA, Shapiro DY, Kioroglou S, Sanderson BG. 1994. Egg dispersal in a Caribbean coral reef fish, *Thalassoma bifasciatum*. II. Dispersal off the reef platform. Bull Mar Sci 54:256–70.

Bellwood DR, Fisher R. 2001. Relative swimming speeds in reef fish larvae. Mar Ecol Prog Ser 211:299–303.

Bellwood DR, Hughes TP. 2001. Regional-scale assembly rules and biodiversity of coral reefs. Science 292:1532–4.

Beu AG. 1998. Indo-West Pacific Ranellidae, Bursidae and Personidae (Mollusca: Gastropoda). A monograph of the New Caledonian fauna and revisions of related taxa. Mém Mus Nat d'Hist Natur 178:1–255.

Birkeland C, Chia FS, Strathmann RR. 1971. Development, substratum selection, delay of metamorphosis, and growth in the sea star *Mediaster aequalis* Stimpson. Biol Bull 141:99–108.

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Bosch I, Rivkin RB, Alexander SP. 1989. Asexual reproduction by oceanic planktotrophic echinoderm larvae. Nature 337:169–70.

Bouchet P, Poppe G. 1988. Deep water volutes from the New Caledonian region, with a discussion on biogeography. Venus 47:15–32.

Burgess CM. 1985. Cowries of the World. Cape Town, S Africa: Gordon Verhoef, Seacomber Publications.

Colin PL. 1991. Reproduction of the Nassau grouper, *Epinephelus striatus* and its relationship to environmental conditions. Environ Biol Fishes 34:357–77.

Collin R. 2003. Worldwide patterns in mode of development in calyptraeid gastropods. Mar Ecol Prog Ser 247:103–22.

Coyne JA, Orr HA. 2004. Speciation. Sunderland, MA: Sinauer.

Diamond JM, Gilpin ME, Mayr E. 1976. Species-distance relation for birds of the Solomon Archipelago, and the paradox of the great speciators. Proc Nat Acad Sci USA 73:2160–4.

Eldredge LG, Evenhuis NL. 2003. Hawaii's biodiversity: a detailed assessment of the numbers of species in the Hawaiian Islands. Bishop Mus Occ Pap 76:1–28.

Emlet RB. 1995. Developmental mode and species geographic range in regular sea urchins (Echinodermata: Echinoidea). Evolution 49:476–89.

Emlet RB, McEdward LR, Strathmann RR. 1987. Echinoderm larval ecology viewed from the egg. In: Jangoux M, Lawrence JM, editors. Echinoderm studies. Volume 2. Rotterdam: Balkema Press. p 55–136.

Fenaux L, Strathmann MF, Strathmann RR. 1994. Five tests of food-limited growth of larvae in coastal waters by comparisons of rates of development and form of echinoplutei. Limnol Oceanogr 39:84–98.

Fisher R, Bellwood DR. 2003. Undisturbed swimming behaviour and nocturnal activity of coral reef fish larvae. Mar Ecol Prog Ser 263:177–88.

Foin TC. 1982. Systematic implications of larval shell parameters for the genus *Cypraea* (Gastropoda: Mesogastropoda). J Molluscan Stud 48:44–54.

Gaston KJ. 1998. Species-range size distributions: products of speciation, extinction and transformation. Philos Trans R Soc Lond B Biol Sci 353:219–30.

Green BS, Fisher R. 2004. Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. J Exp Mar Biol Ecol 299:115–32.

Hansen TA. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. Paleobiology 6:193–207.

Hensley DA, Appeldoorn RS, Shapiro DY, Ray M, Turingan RG. 1994. Egg dispersal in a Caribbean coral reef fish, *Thalassoma bifasciatum*. I. Dispersal over the reef platform. Bull Mar Sci 54:256–70.

Highsmith RC. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. Mar Ecol Prog Ser 25:169–79.

Highsmith RC, Emlet RB. 1986. Delayed metamorphosis: effect on growth and survival of juvenile sand dollars (Echinoidea: Clypeasteroida). Bull Mar Sci 39:347–61.

Hoegh Guldberg O, Emlet RB. 1997. Energy use during the development of a lecithotrophic and a planktotrophic echinoid. Biol Bull 192:27–40.

Hughes TP, Bellwood DR, Connolly SR. 2002. Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. Ecol Lett 5:775–84.

Jablonski D. 1986. Larval ecology and macroevolution in marine invertebrates. Bull Mar Sci 39:565–87.

Jablonski D, Lutz RA. 1983. Larval ecology of marine benthic invertebrates: paleoBiol. implications. Biol Rev 58:21–89.

Jackson JBC. 1986. Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. Bull Mar Sci 39:588–606.

Jeffery CH, Emlet RB. 2003. Macroevolutionary consequences of developmental mode in temnopleurid echinoids from the Tertiary of Southern Australia. Evolution 57: 1031–48.

Jokiel PL. 1990a. Long-distance dispersal by rafting: reemergence of an old hypothesis. Endeavour 14:66–73.

Jokiel PL. 1990b. Transport of reef corals into the Great Barrier Reef. Nature 347:665–7.

Jones GP, Milicich MJ, Emslie MJ, Lunow C. 1999. Self-recruitment in a coral reef population. Nature 402:802–4.

Kay EA. 1967. The composition and relationships of marine molluscan fauna of the Hawaiian Islands. Venus 25:94–104.

Kay EA. 1979. Little worlds of the Pacific An essay on Pacific basin biogeography. Univ Hawaii Harold L Lyon Arbor Lect 99:1–40.

Kay EA. 1990. Cypraeidae of the Indo-Pacific: Cenozoic fossil history and biogeography. Bull Mar Sci 47:23–34.

Kirkendale LA, Meyer CP. 2004. Phylogeography of the *Patelloida profunda* group (Lottidae: Mollusca): Diversification in a dispersal-driven marine system. Mol Ecol 13:2749–62.

Knott KE, Balser EJ, Jaeckle WB, Wray GA. 2003. Identification of asteroid genera with species capable of larval cloning. Biol Bull 204:246–55.

Knowlton N. 1993. Sibling species in the sea. Ann Rev Ecol Syst 24:189–216.

Kohn AJ, Perron FE. 1994. Life history and biogeography patterns in *Conus*. Oxford: Clarendon Press.

Leis JM. 2002. Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. Environ Biol Fishes 65:199–208.

Leis JM, Trnski T, Dufour V, Harmelin Vivien M, Renon JP, Galzin R. 2003. Local completion of the pelagic larval stage of coastal fishes in coral-reef lagoons of the Society and Tuamotu Islands. Coral Reefs 22:271–90.

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Lessios HA. 1990. Adaptation and phylogeny as determinants of egg size in echinoderms from the two sides of the isthmus of Panama. Am Nat 135:1–13.

Lessios HA, Kessing BD, Robertson DR, Paulay G. 1999. Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. Evolution 53:806–17.

Lessios HA, Kessing BD, Pearse JS. 2001. Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. Evolution 55:955–75.

Lessios HA, Kane J, Robertson DR. 2003. Phylogeography of the pantropical sea urchin *Tripneustes*: contrasting patterns of population structure between oceans. Evolution 57:2026–36.

Levitan DR. 2000. Optimal egg size in marine invertebrates: theory and phylogenetic analysis of the critical relationship between egg size and development time in echinoids. Am Nat 156:175–92.

Liltved WR. 1989. Cowries and their Relatives of Southern Africa. Capetown, South Africa: Gordon Verhoef, Seacomber Publications.

Lorenz F. 2002. New worldwide cowries. Hackenheim, Germany: ConchBooks.

Lorenz F, Hubert A. 1993. A guide to worldwide cowries. Wiesbaden, Germany: C. Hemmen.

Lucas MI, Walker G, Holland DL, Crisp DJ. 1979. An energy budget for the free-swimming and metamorphosing larvae of *Balanus balanoides* (Crustacea: Cirripedia). Mar Biol 55:221–9.

McCormick MI. 1999. Delayed metamorphosis of a tropical reef fish (*Acanthurus triostegus*): a field experiment. Mar Ecol Prog Ser 176:25–38.

McEdward LR, Carson SF, Chia F-S. 1988. Energetic content of eggs, larvae, and juveniles of *Florometra serratissima* and the implications for the evolution of crinoid life histories. Int J Invert Repr 13:9–22.

Meyer CP. 2003. Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. Biol J Linn Soc Lond 79:401–59.

Meyer CP. 2004. Toward comprehensiveness: increased molecular sampling within Cypraeidae and its phylogenetic implications. Malacologia 46:127–56.

Meyer CP, Geller JB, Paulay G. 2005. Fine scale endemism on coral reefs: archipelagic differentiation in turbinid gastropods. Evolution 59:113–25.

Miller SE, Hadfield MG. 1990. Developmental arrest during larval life and life-span extension in a marine mollusc. Science 248:356–8.

Natarajan AV. 1957. Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and the Palk Bay. Proc Indian Acad Sci Sect B 46:170–228.

Osorio C, Gallardo C, Atan H. 1992. Egg mass and intracapsular development of *Cypraea caputdraconis* Melvill, 1888, from Easter Island (Gastropoda: Cypraeidae). Veliger 35:316–22.

Ostergaard JM. 1950. Spawning and development of some Hawaiian marine gastropods. Pacific Sci 4:75–115.

Palumbi SR, Grabowsky G, Duda T, Geyer L, Tachino N. 1997. Speciation and population genetic structure in tropical Pacific sea urchins. Evolution 51:1506–17.

Parmentier E, Lecchini D, Lagardere F, Vandewalle P. 2004. Ontogenic and ecological control of metamorphosis onset in a carapid fish, *Carapus homei*: Experimental evidence from vertebra and otolith comparisons. J Exp Zool 301A:617–28.

Paulay G. 1997. Diversity and distribution of reef organisms. In: Birkeland CE, editor. Life and death of coral reefs. New York: Chapman & Hall. p 298–353.

Paulay G, Boring L, Strathmann RR. 1985. Food limited growth and development of larvae: experiments with natural sea water. J Exp Mar Biol Ecol 93:1–10.

Paulay G, Meyer C. 2002. Diversification in the tropical Pacific: comparisons between marine and terrestrial systems and the importance of founder speciation. Integr Compar Biol 42:922–934.

Pechenik JA. 1984. The relationship between temperature, growth rate, and duration of planktonic life for larvae of the gastropod *Crepidula fornicata* (L.). J Exp Mar Biol Ecol 74:241–57.

Pechenik JA. 1986. Field evidence for delayed metamorphosis of larval gastropods: *Crepidula plana* Say, *C. fornicata* (L.), and *Bittium alternatum* (Say). J Exp Mar Biol Ecol 97: 313–9.

Pechenik JA, Scheltema RS, Eyster LS. 1984. Growth stasis and limited shell calcification in larvae of *Cymatium parthenopeum* during trans-Atlantic transport. Science 224:1097–9.

Phillips BF, Brown PA, Rimmer DW, Reid DD. 1979. Distribution and dispersal of the phyllosoma larvae of the western rock lobster, *Panulirus cygnus*, in the south-eastern Indian Ocean. Aust J Mar Freshw Res 30:773–83.

Poppe GT, Goto Y. 1992. Volutes. Ancona: L'Infromatore Piceno.

Ranson G. 1967. Les protoconques ou coquilles larvaires des cyprées. Mém Mus Nat d'Hist Natur Sér A Zool 47:93–126.

Reid DG, Geller JB. 1997. A new ovoviviparous species of *Tectarius* (Gastropoda: Littorinidae) from the tropical Pacific, with a molecular phylogeny of the genus. J Moll Stud 63:207–33.

Robertson DR. 2001. Population maintenance among tropical reef fishes: Inferences from small-island endemics. Proc Nat Acad Sci USA 98:5667–70.

Robertson R. 1994. Protoconch size variation along depth gradients in a planktotrophic *Epitonium*. Nautilus 107:107–12.

Scheltema RS. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of

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shallow-water benthic marine gastropods. Biol Bull 140:284–322.

Schilder FA, Schilder M. 1938. Prodrome of a monograph on living Cypraeidae. Proc Malac Soc Lond 23:119–231.

Shanks AL, Grantham BA, Carr MH. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecol Appl 13:S159–69.

Shuto T. 1974. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. Lethaia 7:239–56.

Siegel DA, Kinlan BP, Gaylord B, Gaines SD. 2003. Lagrangian descriptions of Mar. larval dispersion. Mar Ecol Prog Ser 260:83–96.

Simpson SD, Meekan M, Montgomery J, McCauley R, Jeffs A. 2005. Homeward sound. Science 308:221.

Sleurs WJM, Preece RC. 1994. The Rissoininae (Gastropoda: Rissoidae) of the Pitcairn Islands, with the description of two new species. J Conch 35:67–82.

Stehli FG, Wells JW. 1971. Diversity and age patterns in hermatypic corals. Syst Zool 20:115–26.

Swearer SE, Cadelle JE, Lea DW, Warner RR. 1999. Larval retention and recruitment in an island population of a coral-reef fish. Nature 402:799–802.

Taylor MS, Hellberg ME. 2003. Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. Science 299:107–9.

Thiel M. 2003. Rafting of benthic macrofauna: Important factors determining the temporal succession of the assemblage on detached macroalgae. Hydrobiologia 503:49–57.

Thorson G. 1950. Reproductive and larval ecology of marine invertebrates. Biol Rev 25:1–45.

Thorson G. 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. In: Sears M, editor. Oceanography. Washington, D.C.: American Association for the Advancement of Science. p 455–74.

Thresher RE, Brothers EB. 1985. Reproductive ecology and biogeography of Indo-West Pacific angelfishes (Pisces: Pomacanthidae). Evolution 39:878–87.

Victor BC. 1986. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Mar Biol 90:317–26.

Victor BC, Wellington GM. 2000. Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. Mar Ecol Prog Ser 205:241–8.

Wellington GM, Victor BC. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Mar Biol 101:557–67.

Wellington GM, Victor BC. 1992. Regional differences in duration of the planktonic larval stage of reef fishes in the eastern Pacific Ocean. Mar Biol 113:491–8.

Williams ST, Reid DG. 2004. Speciation and diversity on tropical rocky shores: a gobal phylogeny of snails of the genus *Echinolittorina*. Evolution 58:2227–51.

Wilson B, Clarkson P. 2004. Australia's spectacular cowries: A review and field study of two endemic genera—*Zoila* and *Umbilia*. El Cajon CA: Odyssey Publishing.

Yamaguchi M. 1977. Larval behavior and geographic distribution of coral reef asteroids in the Indo-West Pacific. Micronesica 13:283–96.

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