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Ecology of extreme faunal turnover of tropical American scallops

J. Travis Smith and Jeremy B. C. Jackson

Abstract.—The marine faunas of tropical America underwent substantial evolutionary turnover in the past 3 to 4 million years in response to changing environmental conditions associated with the rise of the Isthmus of Panama, but the ecological signature of changes within major clades is still poorly understood. Here we analyze the paleoecology of faunal turnover within the family Pectinidae (scallops) over the past 12 Myr. The fossil record for the southwest Caribbean (SWC) is remarkably complete over this interval. Diversity increased from a low of 12 species ca. 10–9 Ma to a maximum of 38 species between 4 and3 Ma and then declined to 22 species today. In contrast, there are large gaps in the record from the tropical eastern Pacific (TEP) and diversity remained low throughout the past 10 Myr. Both origination and extinction rates in the SWC peaked between 4 and 3 Ma, and remained high until 2–1 Ma, resulting in a 95% species level turnover between 3.5 and 2 Ma. The TEP record was too incomplete for meaningful estimates of origination and extinction rates. All living species within the SWC originated within the last 4 Myr, as evidenced by a sudden jump in Lyellian percentages per faunule from nearly zero up to 100% during this same interval. However, faunules with Lyellian percentages near zero occurred until 1.8 Ma, so that geographic distributions were extraordinarily heterogeneous until final extinction occurred. There were also striking differences in comparative diversity and abundance among major ecological groups of scallops. Free-swimming scallops constituted the most diverse guild throughout most of the last 10 Myr in the SWC, and were always moderately to very abundant. *Leptopecten* and *Argopecten* were also highly diverse throughout the late Miocene and early Pliocene, but declined to very few species thereafter. In contrast, byssally attaching scallops gradually increased in both diversity and abundance since their first appearance in our samples from 8–9 Ma and are the most diverse group today. Evolutionary turnover of scallops in the SWC was correlated with strong ecological reorganization of benthic communities that occurred in response to declining productivity and increased development of corals reefs.

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Introduction

The isolation of the Atlantic from the Pacific Ocean by the Isthmus of Panama ca. 3.5 Ma (Coates et al. 1992, 2004; Coates and Obando 1996; Bartoli et al. 2005) was associated with large changes in oceanographic conditions, high faunal turnover, and significant reorganization of the benthic communities in the Tropical Western Atlantic (TWA) between about 3.5 and 1.5 Ma (Woodring 1966; Jackson and Johnson 2000; Todd et al. 2002; O'Dea et al. 2007. Early studies were based largely on extinction of gastropods (Woodring 1966; Vermeij 1978; Petuch 1982; Jones and Hasson 1985; Vermeij and Petuch 1986), but more recent analyses have included bivalves (Jackson et al. 1993; Roopnarine 1996; Anderson 2001; Anderson and Roopnarine 2003), reef corals (Budd and Johnson 1999), and bryozoans (Cheetham and Jackson 1996, 2000, all of which exhibit increased evolutionary turnover after 3.5 Ma. Rates of origination and extinction vary greatly among different taxa, resulting in very strong faunal turnover in some taxa such as gastropods, reef corals, and erect bryozoans but not in other groups such as bivalves and encrusting bryozoans (Cheetham and Jackson 1996; Budd and Johnson 1999; Jackson and Johnson 2000; Todd et al. 2002; Johnson et al. 2007). Greater focus on origination also revealed that overall molluscan diversity within the southwest Caribbean (SWC) increased during faunal turnover (Jackson et al. 1993), despite high extinction rates of several "paciphillic" taxa that were

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the primary focus of most earlier analyses (Woodring 1966; Jones and Hasson 1985; Vermeij and Petuch 1986).

Some of the most important ecological changes are apparent only through compilations of relative abundance instead of just lists of taxa (Todd et al. 2002). Predatory gastropods and suspension-feeding bivalves declined significantly in abundance, but not in overall diversity, while reef dwelling gastropods became more abundant (Todd et al. 2002). In contrast, other ecological groups of mollusks remained relatively unchanged in abundance. These differences between ecological patterns based on relative abundance data versus those derived only from taxonomic lists emphasize the importance of using abundance data in addition to diversity (McKinney et al. 1998; Jackson and Erwin 2006). However, abundance data can be highly affected by sampling biases, so samples must be collected in a standardized and systematic fashion (Jackson et al. 1999; Jackson and Erwin 2006).

A major enigmatic feature of the SWC extinction is that much of the peak in rates of faunal turnover, especially for gastropods and reef corals, occurred up to 2 Myr after the final closure of the Isthmus and associated major changes in TWA environments (Budd and Johnson 1999; Jackson and Johnson 2000; O'Dea et al. 2007). High levels of extinction around the end of the Pliocene and early Pleistocene have also been noted in faunas as far north as Florida (Stanley and Campbell 1981; Stanley 1986a; Petuch 1982, 1995; Allmon et al. 1993, 1996) and California (Stanley 1986b; Smith and Roy 2006). However, the relation of extinction patterns in these more northern faunas to the formation of the Isthmus is difficult to define, despite the temporal correlation. Synthesizing the previous work of Petuch (1982), Vermeij and Petuch (1986), Jones and Allmon (1995), and Roopnarine (1996), Allmon (2001) postulated that the major environmental cause of extinction in the TWA was a regional decrease in productivity. This hypothesis is supported by major changes in abundance of different trophic groups in the SWC and by evidence for a regional drop in productivity ca. 4–3 Ma (Todd et al. 2002; O'Dea et al. 2007). However, the relationship between events in the SWC and the North American faunas analyzed by Stanley and Campbell (1981), Stanley (1986a) and Allmon et al. (1993, 1996) is still unclear.

In this paper, we describe basic patterns of diversity, origination, and extinction, as well as apparent causes of faunal turnover, for species of the highly diverse and abundant bivalve family Pectinidae (scallops) in the SWC and TEP over the past 12 Myr. The family Pectinidae is monophyletic (Waller 1978, 1984, 1991, 1993, 2006) yet exhibits a great variety of life habits and ecology that are useful to dissect how changes in the environment have affected the evolutionary expansion or decline of different functional groups. We also examine patterns of origination and extinction at different taxonomic levels as well as the correspondence between diversity and abundance on a sample-by-sample basis. Use of all the available information provides a much more complete and subtle understanding of evolution and environment than that based on taxon counting alone. Analysis of the relationships between environmental change and scallop life-history evolution will be presented in a separate paper.

Materials and Methods

Quantitative samples of fossil scallops from Panama, Costa Rica, and Ecuador were obtained from 226 bulk samples supplemented by the more than 350 collections of specimens gleaned from outcrops by members of the Panama Paleontology Project (PPP) over the past 20 years. Paleontologists have studied all of the sedimentary basins included here since the 1920s so that we have been able to build on their early collections and stratigraphic framework. Samples come from three regions: (1) the TEP, (2) central and eastern Panama (referred to here as "isthmian"), and (3) the Bocas del Toro and Limon regions of northwestern Panama and southeastern Costa Rica (Fig. 1). The most important collections from the TEP are from the Borbon and Manabi basins in Ecuador (Pilsbry and Olsson 1941; Olsson 1964; Hasson and Fischer 1986; Aalto and Miller 1999; Landini et al. 2002; Cantalamessa et al. 2005), the Nicoya Peninsula in Costa Rica, and the Burica Peninsula in Panama

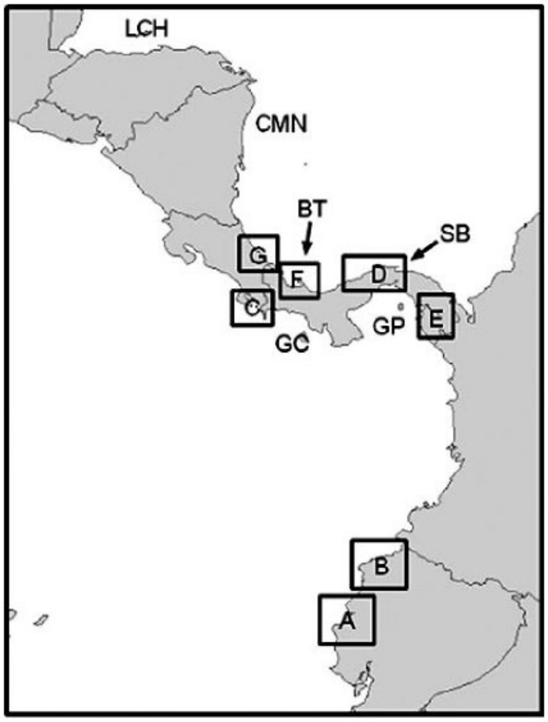

FIGURE 1. Map of sample areas. Boxed areas enclose the generalized sedimentary basins described in the text. A, Manabí. B, Borbon. C, Burica/Nicoya Peninsulas. D, Canal Zone. E, Chucunaque. F, Bocas del Toro. G, Limón. Dredge samples were collected in the region of all five basins sampled for fossils in Panama and Costa Rica, as well as two areas off Nicaragua and Honduras where no fossils were sampled. Abbreviations: GP, Gulf of Panama; GC, Gulf of Chiriquí; SB, western San Blas archipelago; BT, Bocas del Toro province from the Laguna Chiriquí to the Golfo de los Moskitos; LCH, Los Cochinos, Honduras; CMN, Cayos Moskitos, Nicaragua.

(Olsson 1942; Coates et al. 1992). Collections from the isthmian region that have both TEP and SWC affinities include the classic formations from the Canal Zone (Woodring 1957–1982; Collins et al. 1996b; Johnson and Kirby 2006), the north-central Coast of Panama (Coates 1999), and the Darien region of Panama (Coates et al. 2004). The Bocas del Toro and Limon region is the most extensively sampled and includes the Limon Basin in northeastern Costa Rica (Olsson 1922; Collins et al. 1995; McNeill et al. 2000), and the Bocas del Toro Basin in northwestern Panama (Olsson 1922; Collins 1993; Collins et al. 1995; Coates et al. 2003, 2005; Coates 2006). In the analyses that follow, samples from the Isthmian and Bocas del Toro/Limon regions were combined to constitute the SWC regional fauna. Finally, dredge samples of recent scallops were obtained from the TEP and SWC as a baseline for comparison and calculation of Lyellian percentages for samples of fossils (Fig. 1) (Smith et al. 2006).

Bulk samples were first sorted to class (e.g., bivalve, gastropod, coral). Scallops were picked and sorted from the bivalve fraction and identified to species following Waller (1969, 1984, 1991, 1993, 2006). Previously undescribed species were identified using open nomenclature pending more thorough taxonomic comparison with samples from outside the regions sampled. Appendix 1 includes a complete list of all of the species found in this study. Individual samples were combined into faunules (Jackson et al. 1999; O'Dea et al. 2007) to obtain a more representative sample of the composition and diversity of the scallop fauna from different places, environments, and ages through time. A faunule represents a group of samples from a single outcrop or closely adjacent exposures that can be assigned with confidence to the same age and environment. Appendix 2 lists all of the faunules along with their age, environmental conditions, and diversity of scallops used in this study. These groupings do not reflect completely equivalent sampling in terms of range of environment or sampling intensity, but they provide larger sample sizes allowing analysis of patterns within time bins.

Diversity was calculated as species richness (S) and Shannon-Weiner diversity (*H*) (Hayek and Buzas 1997; Foggo et al. 2003). Species richness was calculated from all of the different collections combined. *H* was calculated from only the quantitative data from bulk samples. We calculated stratigraphic ranges for all species collected on the basis of actual occurrence and range-through data and used 1-Myr time bins to assess general trends in diversity. We also calculated extinction and origination rates through time on the basis of numbers of occurrences and per-taxon rates.

We have not calculated confidence intervals for first and last occurrences of species because all of the established methods are based only on occurrences (Strauss and Sadler 1989; Marshall 1994, 1997; Wang and Marshall

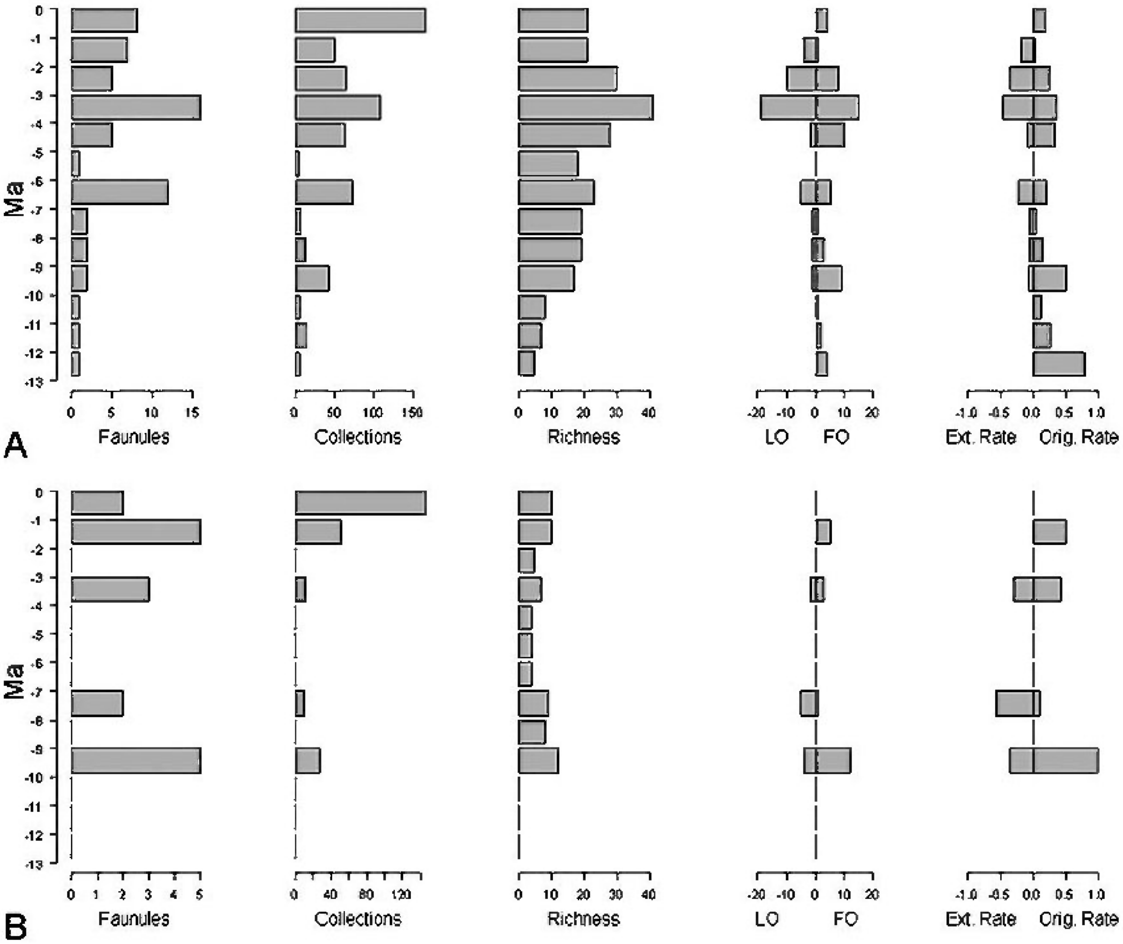

FIGURE 2. Sampling, species diversity, extinction, and origination. Sampling is plotted as the number of faunules and collections. Species values are plotted as numbers of species for richness, first occurrences (FO), and last occurrences (LO), and as per-taxon rates for extinction and origination rates. All data were calculated in 1-Myr time bins. A, Southwest Caribbean (SWC). B, Tropical eastern Pacific (TEP).

2004), even though non-occurrences are of obvious biostratigraphic and evolutionary significance (Hayek and Bura 2001). Most scallop species in our collections are rare, as is typical of faunal samples generally (Hayek and Buzas 1997; Jackson et al. 1999), and more than half of the Caribbean species and >80% of eastern Pacific species occur in just three or fewer faunules. In spite of their rarity, however, the collector's curves for most of the younger stratigraphic intervals suggest that we have sampled most of the available species. Thus, it is unlikely that the absence of species from horizons younger than their last observed occurrence is an artifact. For all of these reasons, and the lack of practical alternative statistical methods that incorporate non-occurrences (Hayek and Bura 2001), we have taken the ranges of species occurrences of species at face value.

Diversity in Space and Time

The fossil record of the past 12 Myr is much more complete for the SWC than for the TEP (Coates et al. 1992) (Fig. 2A,B). Detailed sampling in the Bocas del Toro and Limon Basins has produced a reasonably complete record of scallop macroevolution in this region, especially for the last 5 Myr. We sampled 14 faunules from the late Pliocene and Pleistocene, 16 faunules from the early Pliocene, and seven faunules from the late Miocene. The most important gap in the record is for the Pleistocene younger than 1.4 Ma and the relatively poorly sampled interval from about 4.3 to 7 Ma. The isthmian region includes 15 late Miocene faunules and nothing from younger deposits including the Pleistocene deposits reported by Woodring (1957–1982). In contrast, the record from the TEP includes a huge gap in sampling between 7.3 and 3.6 Ma. Seven faunules were sampled from the late Miocene and seven faunules from the late Pliocene to early Pleistocene.

Scallops were present in more than 95% of all the samples both fossil and recent, indicating that the species within this family utilize a very broad range of environments comparable to bivalves as a whole. There were 82 species of Pectinidae in our collections, 61 from the SWC, 18 from the TEP, and three that occur as fossils in both regions (Appendix 1). Species richness over the past 12 Myr was much more variable in the SWC than the TEP (Fig. 2B). Diversity in the SWC increased from a low of eight species in the late Miocene to a high of 41 species in the middle Pliocene (4–3 Ma) and then declined to 22 species today (Fig. 2A). In contrast, diversity in the TEP was essentially unchanged over the same period, with the apparent decrease between 7 and 4 Ma due to a lack of samples for this interval, so the data are for range-through taxa only. Ten species occurred in the late Miocene and early Pliocene collections and nine to ten species in the Pleistocene to Recent (Fig. 2B).

Collector's curves were constructed for each time bin sampled to test for sampling bias, and compared numbers of species collected to the total known diversity represented by collected and range-through taxa combined. In the SWC (Fig. 3A), the most heavily sampled fossil time bin, as measured by total number of specimens, is the middle Pliocene (4–3 Ma). A remarkable 40 of 41 total known taxa (98%) were recovered from this interval. Excluding the early Pleistocene (2–1 Ma), the next four most heavily sampled time bins (10–9, 5–4, 3–2, and 7–6 Ma) contained 82–92% recovery of species known to have been present. In contrast, the five most poorly sampled bins (6–5, 9–8, 8–7, 12–11, and 11–10 Ma) contained fewer than 50% of the species known to have occurred in the SWC during those age intervals.

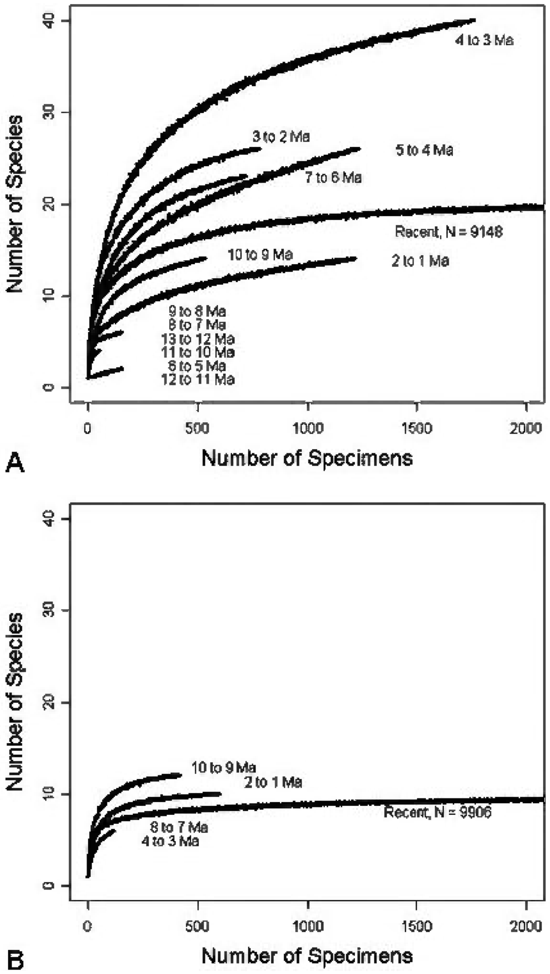

FIGURE 3. Collector's curves. Sampling effort for the time bins sampled in the SWC (A) and TEP (B). The x-axis was truncated at 2000 specimens, far fewer than the sampled level of the Recent time bins, to allow visual appraisal of the fossil time bins.

The records for two additional bins require separate comment. The high recovery (80%) of the oldest bin (13–12 Ma) is an artifact of the first occurrence of all but a single early Miocene species. In contrast, the early Pleistocene (2–1 Ma) bin is relatively well sampled (the third most specimens), but contained only 67% of the species known to have occurred in the TWA during this time. We attribute this low recovery to the small number of faunules sampled (all from Swan Cay and several faunules in the Limon Basin) coupled with the increasing heterogeneity of Caribbean environments at this time (O'Dea et al. 2007). Testing these ideas, however, will require comparably detailed sampling from other regions of the TWA.

Sampling in the TEP was generally good (Fig. 4B) despite the relatively small number of specimens because of the greater homogeneity of TEP environments and relatively low numbers of species throughout the last 12 Myr. The stratigraphic ranges of all species in this study are depicted in Figure 4.

Origination, Extinction, and the Ecology of Faunal Turnover

The peaks in both origination and extinction in the SWC at 4–3 Ma coincide with the maximum diversity of scallop species (Fig. 2A). This is true for both the raw numbers of first and last occurrences and for per-taxon rates. In contrast, there is no obvious peak in origination or extinction in the TEP, although the 3-Myr gap in sampling may obscure a genuine peak in faunal turnover between 4 and 3 Ma (Fig. 2B).

The overall patterns of diversity and evolution of scallops in the SWC correlate closely with those observed for bivalve genera and subgenera from the same region (Todd et al. 2002). There is a significant correlation between numbers of scallop species and of bivalve genera and subgenera (Fig. 5A; $r^2 = 0.739$, $p = 0.0003$) and between rates of extinction for bivalves and for scallops (Fig. 5B, $r^2 = 0.736$, $p = 0.0004$). However, the correlation between rates of origination for the two groups is only marginally significant (Fig. 5C; $r^2 = 0.324$, $p = 0.0536$).

Scallops exhibit a very wide range of life habits, including byssal attachment, free swimming, and cementing and nestling on both level bottoms and hard substrata (Stanley 1970), although the two latter life habits were not observed in our samples from the SWC. Several genera exhibit a mixture of life habits. Most species of scallops begin their juvenile benthic existence attached by byssal threads to small hard substrata, but subsequently detach to become merely sedentary or strongly free-swimming as adults (Stanley 1970; Waller 1984, 1991, 2006). However, species in several genera, particularly those associated with coral reef and seagrass environments, retain byssal attachment as adults. Life habit of most species is readily apparent for fossil as well as living species from their shell morphology (Stanley 1970), although the genus *Leptopecten* does not fit the overall morphological pattern as well as other genera included in Stanley's (1970) study.

We exploited these ecological differences among scallops to examine the ecological patterns associated with faunal turnover. Species were assigned to one of four groups based on differences in life habits and taxonomy: (1) byssally attaching; (2) free swimming; (3) *Argopecten* sensu stricto, excluding the undescribed Pectinid Genus A (Smith et al. 2006), that exhibit a combination of byssally attaching and free-swimming habits; and (4) *Leptopecten* (plus *Pacipecten*) that defy clear-cut ecological separation. These four groups include 63 of the 82 scallop species (77%) of the entire tropical American fauna sampled from the two oceans; the rest were excluded from the ecological analyses.

Byssally attaching scallops include species in the genera *Spathochlamys*, *Demarzipecten*, *Caribachlamys*, *Bractechlamys*, and *Laevichlamys*. *Spathochlamys* occurs in both the TWA and TEP, whereas the other byssally attaching genera are restricted to the Caribbean, where they are overwhelmingly associated with coral reef environments (Waller 1993). Free-swimming species include all those traditionally assigned to the genus *Euvola* (Waller 1991). However, Waller (2006) has emended this group and species are now assigned to two genera, *Leopecten* and *Euvola*. This group also includes species traditionally considered *Amusium*, which Waller (1991) included in the genus *Euvola*. The two taxonomically defined groups are distinct ecologically and are diverse and abundant enough to justify separate analysis. *Argopecten* occurred in all environments sampled whereas *Leptopecten* was more narrowly distributed ecologically in the SWC. Recent *Leptopecten* in the eastern Pacific have been described as r-selected (Morton 1994), a life-history pattern that appears to be unique among tropical American scallops.

The proportional diversity and abundance of the four groups in the SWC varied greatly

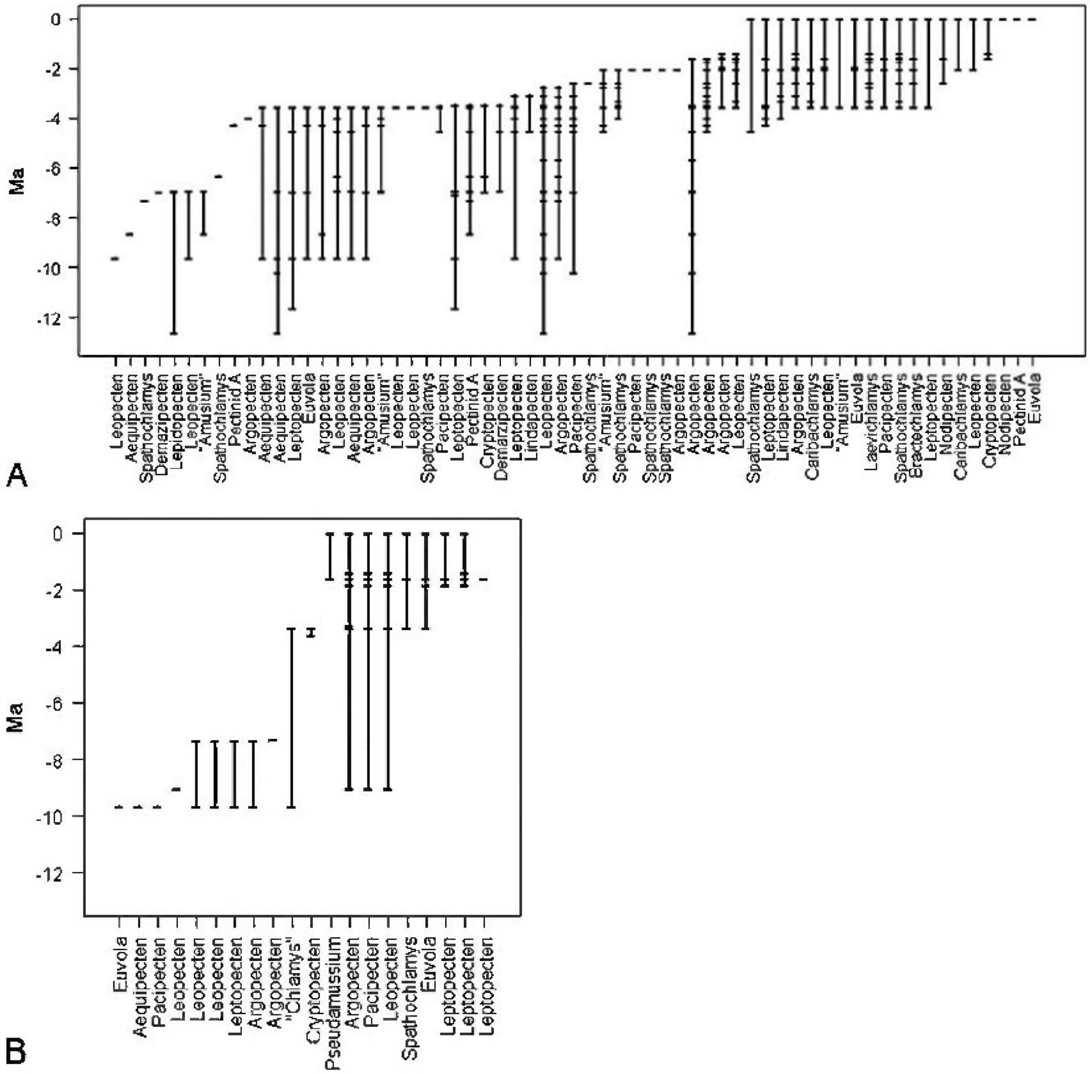

FIGURE 4. Stratigraphic ranges of tropical American scallops in the SWC (A) and TEP (B). Tick marks indicate actual stratigraphic occurrences. Generic names are indicated for each species for comparison with Appendix 1.

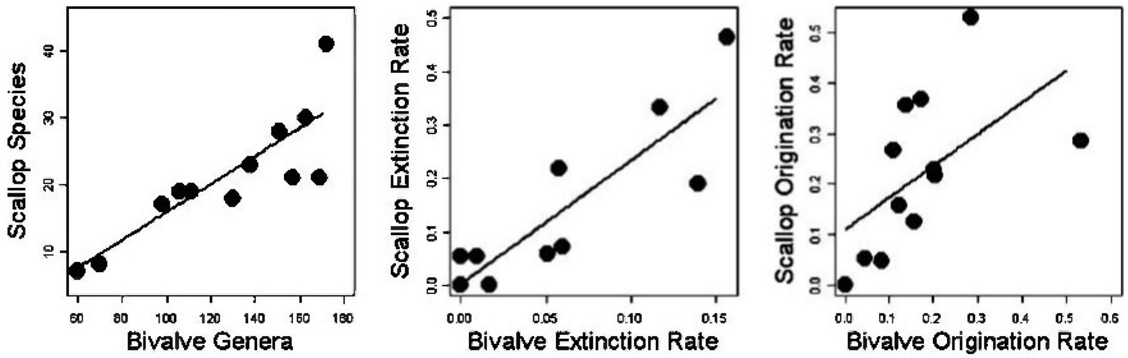

FIGURE 5. Comparison of taxonomic extinction rates in the SWC. Plot compares the extinction rates for all bivalves (data from Todd et al. 2002) with the rates obtained in this study for scallop species. Individual points represent a 1-Myr time bin. There is a significant correlation between the calculated rates (see text).

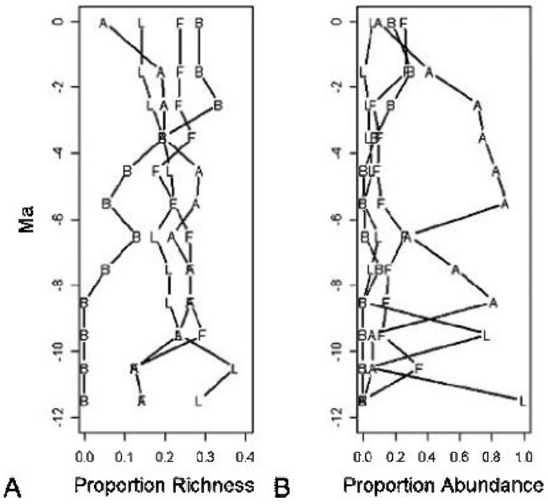

FIGURE 6. Proportions of species richness and abundance in the SWC for byssally attaching (B), free-swimming (F), *Argopecten* (A), and *Leptopecten* (L) in 1-Myr time bins. These data do not include all species in the data set, so proportions do not sum to 1 (see text for explanation of these four ecological/taxonomic groups).

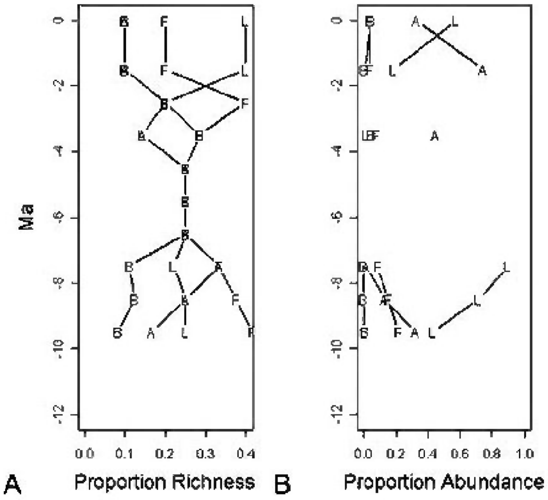

FIGURE 7. Proportions of richness and abundance in the TEP. Data are for the same groups as in Figure 6.

over the last 13 Myr (Fig. 6A,B). We used proportions instead of absolute numbers of species and specimens to reduce the effects of sampling bias. The proportion of species richness through time was based on actual occurrences plus range through data (Fig. 6A). The most notable difference is in the byssally attaching group, which was absent prior to 8 Ma except for one species from the Emperador Limestone (16 to 18 Ma) that was not included in the analysis. The proportion of byssally attaching species increased gradually to about 15% from 8 to 4 Ma, after which diversity increased more rapidly until 2–3 Ma when byssally attaching species became the most diverse group. *Argopecten* diversity increased to about 30% of early Pliocene pectinid faunas, when it was the most diverse scallop genus, and then gradually declined to only a single species. *Leptopecten* was the most diverse group ca. 11–10 Ma but declined thereafter.

Patterns of proportional abundance for the four groups contrast markedly with patterns of proportional diversity (Fig. 6B). Sampling is poorest before 8 Ma (Fig. 3A), so the highly erratic nature of the older portion of this plot is most likely due to sampling bias. Between 8–9 Ma and 1–2 Ma *Argopecten* was overwhelmingly the most abundant group of scallops in the SWC before plummeting in the late Pleistocene to Recent. Byssally attaching species steadily increased in relative abundance after 4 Ma but did not become numerically dominant. Relative abundance of *Leptopecten* and free-swimming scallops varied much less after 8 Ma.

As for origination and extinction, patterns of proportional diversity and abundance in the TEP (Fig. 7A,B) are obscured by the 3 Ma gap in samples. There are no samples prior to 9 Ma, between 7 and 4 Ma, and between 3 and 2 Ma (Fig. 2). Nevertheless, it is obvious that the patterns are strikingly different from those in the SWC because *Leptopecten* or *Argopecten* are overwhelmingly dominant for the two well-sampled fossil horizons in the TEP as well as the Recent (Smith et al. 2006) (Fig. 7B). In contrast, byssally attaching and free-swimming species are both low in diversity and numerically rare. The decline in diversity but not abundance of *Argopecten* in the SWC and TEP is similar to the pattern observed for this genus in California (Stump 1979; Smith and Roy 2006), the Gulf of Mexico, and the Atlantic coast of Florida (Waller 1969).

Origination rates in the SWC declined greatly over time for all groups except *Leptopecten*, which remained low throughout the entire 12 Myr (Fig. 8). Focusing just on the last 5 Myr for which sampling is generally excellent, all four groups exhibit elevated evolu-

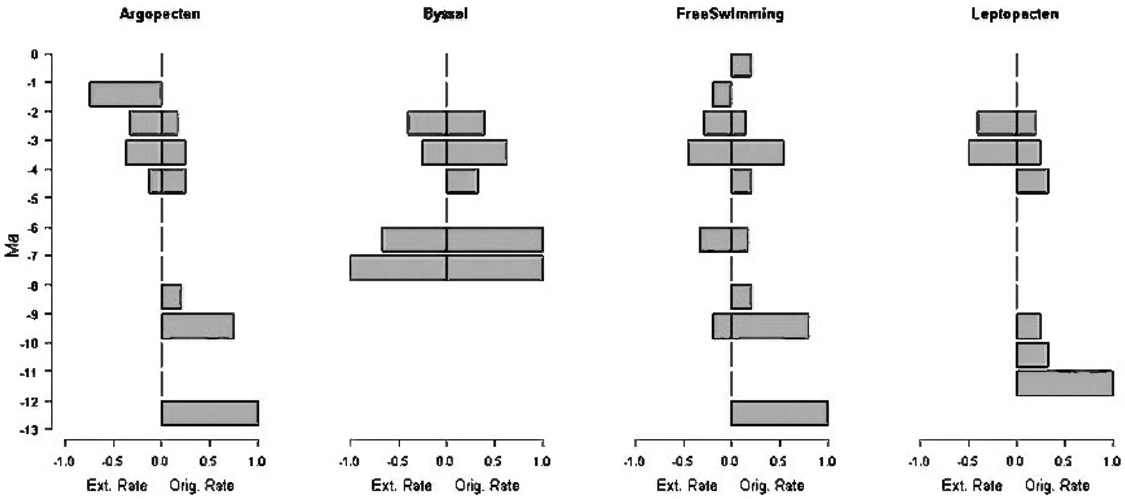

FIGURE 8. Extinction and origination rates for the four ecological groups plotted in 1-Myr time bins.

tionary rates between 4 and 3 Ma, just as for the family as a whole (Fig. 2A). However, the timing of peaks in extinction varies among the groups. *Argopecten* extinction rates peaked between 2 and 1 Ma, whereas rates for byssally attaching species peaked between 3 and 2 Ma, and rates for *Leptopecten* and free-swimming species peaked at 4–3 Ma. Because all of these rates were calculated from the same samples, the differences among groups almost certainly reflect differences in their ecology. The earliest peaks in extinction for all four groups are artifacts of their first occurrence in our collections.

Local versus Regional Diversity and Geographic Heterochrony

Analyses of trends through time using 1-Myr bins ignore the very considerable spatial variability among local communities that we know are important in Recent benthic communities (Jackson 1972, 1973; Jackson et al. 1999; Smith et al. 2006; O'Dea et al. 2007). Therefore we compared patterns over time for faunules versus those based on 1-Myr bins to determine the magnitude of spatial variability in the SWC over time. Diversity of every faunule is invariably less than for the 1-Myr bin that contains the faunule (Appendix 2). This is unsurprising because faunules constitute a much smaller sample than all of the faunules from an entire 1-Myr time bin, so the differences in diversity may entirely reflect the differences in sample size. Thus, as expected, there is a clear relationship between species richness and sampling intensity among faunules with different numbers of specimens (Fig. 9A). However, plots of proportional species richness (proportion of the richness in the time bin) versus numbers of specimens per faunule demonstrate that the relationship breaks down above approximately 100 specimens per faunule (Fig. 9B). This is because each faunule includes a much narrower range of environmental conditions and more closely approximates a local benthic community as recognized in the Recent than do all the samples from all the faunules in an entire 1-Myr time bin.

We used two measures of species diversity in plotting diversity of faunules against time in the SWC: (1) species richness incorporating all the data, and (2) the Shannon Diversity Index *H*, which was based only on quantitative samples. The much higher species richness of Recent faunules (Fig. 10A) is due to some combination of the greater sampling intensity, wider range of bottom conditions encountered in a dredge haul that inevitably encompasses multiple habitats in heterogeneous tropical environments, and differential taphonomic effects of dredge versus bulk samples. However, the differences are much less for Shannon's *H*, for which some of the fossil faunules approach the diversity of the Recent (Fig. 10B). Excluding the Recent, diversity within

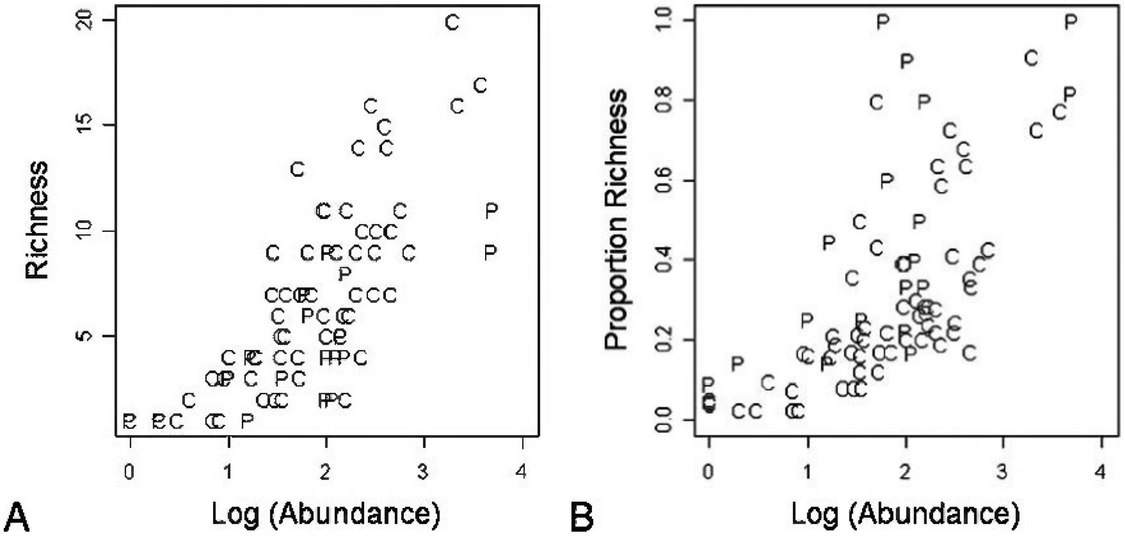

FIGURE 9. Effect of sampling intensity. Sampling effort, plotted as the log of the total abundance in a faunule against the species richness (A) and against the proportion of total diversity recovered (B). C signifies faunules from the SWC, and *p* from the TEP.

faunules increased through time (ANOVA, $F = 10.76$, $p = 0.0022$), but peaked between 4 and 3 Ma, and subsequently declined. These patterns for faunules mirror those for total regional diversity (Fig. 2A).

Petuch (1982) proposed the idea of "geographic heterochrony" whereby relict and modern faunas could coexist temporally through the occupation of different habitats. If this is true, we should see faunules composed primarily or entirely of extant species co-occurring within the same 1-Myr age intervals with faunules dominated by extinct species. To assess this possibility, we calculated Lyellian percentage for all the faunules using species occurrences and occurrences weighted by abundance. There was a striking shift in Lyellian percentages in the SWC between 4 and 2 Ma regardless of whether abundance data were used (Fig. 11A,B, solid circles). However,

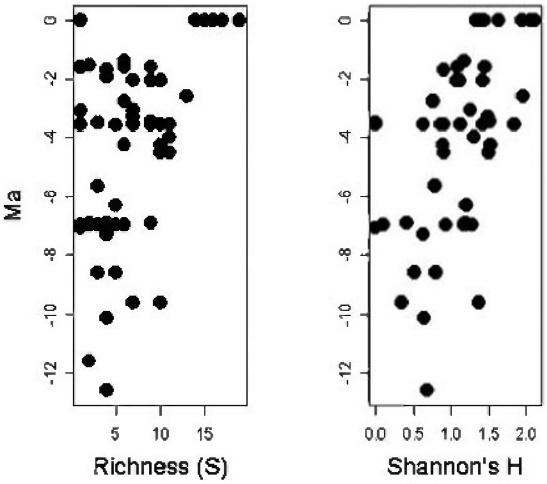

FIGURE 10. Diversity through time in the SWC. Species richness and Shannon's *H* are plotted through time. Values were calculated by faunule. Richness includes all samples and *H* includes only the bulk samples we have obtained (see text).

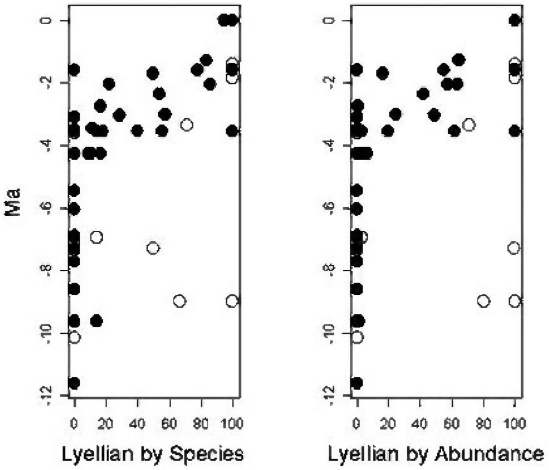

FIGURE 11. Lyellian percentages through time. Data are plotted by faunule, using both species diversity and abundance. Filled circles are SWC, open circles TEP.

faunules with Lyellian percentages close to zero persisted until 1.6 Ma whereas faunules with Lyellian percentages close to 100% occurred as early as 3.5 Ma. Faunules with intermediate Lyellian percentages were also common throughout this time. Thus "geographic heterochrony" was widespread throughout the SWC for 2 Ma. In contrast, the shift from low to high Lyellian percentages occurred between 7 and 10 Ma in the TEP (Fig. 11A,B, open circles), and these differences are especially apparent for calculations weighted by abundance data.

Petuch postulated that relict faunas would occupy marginal environments. To test this idea, we compared the Lyellian percentages for faunules in the SWC during faunal turnover (4.5–1 Ma) to the percent carbonate in the sediment, mean annual range of temperature (MART), and water depth (Appendix 2; data from O'Dea et al. 2007). None of these variables were significantly correlated with Lyellian percentages despite their importance for explaining changes in overall community composition during this time.

Discussion and Conclusions

Patterns of scallop diversity have changed dramatically in the SWC over the past 12 Myr but not in the TEP. Total numbers of scallop species and their origination and extinction rates per million years in the SWC closely track their respective values for the entire bivalve fauna at the generic and subgeneric level (Fig. 6) (Todd et al. 2002). All values peaked between 4 and 3 Ma as the barrier between the TEP and SWC was finally sealed and oceanographic conditions changed from modern TEP conditions to those observed in the SWC today (Haug and Tiedemann 1998; Coates et al. 2004; Bartoli et al. 2005; O'Dea et al. 2007). However, the evolutionary rates for scallops have been shown to be universally higher than for bivalves as a whole (Stanley 1986b), and in this fauna the intensity of faunal turnover was nearly three times greater for scallop species than for bivalve genera as a whole, and none of the extant species in the SWC originated earlier than 4.5 Ma.

The large stratigraphic gaps in the record from the TEP preclude detailed analysis, but it is highly unlikely that richness of species in the TEP ever exceeded their richness today because species richness remained stable and low before and after the sampling gap. Interestingly, several of the species with first occurrences in the late Pliocene of Ecuador have earlier fossil records in the Gulf of California or farther north along the outer coast of Baja California or in California (Stump 1979; Moore 1984; Smith and Roy 2006). This pattern of northern species occurring in Ecuador during this time has been noted for fish and foraminifera (Landini et al. 2002). Moreover, unlike the SWC, three of the species alive today originated before 9 Ma. Such long species durations are always suspect, because detailed morphological analysis commonly reveals cryptic species (Knowlton 1986; Roopnarine and Vermeij 2000). But this is not always the case, as is well documented for bryozoans (Jackson and Cheetham 1994; Cheetham et al. 2007), and the exceptional persistence is not unsuspected in the TEP where conditions do not appear to have changed nearly as much as the SWC over the last 10 Myr.

Three of the four main groups of scallops exhibited opposite patterns of success in the SWC and TEP as reflected in their proportional diversity and abundance (Figs. 6, 7). *Leptopecten* was the most diverse and abundant genus in most samples from the TEP over the past 12 Myr but steadily declined in both diversity and abundance in the SWC. *Argopecten* diversity declined sharply in both oceans over the past 2 Myr as has been observed elsewhere in North America (Waller 1969; Smith and Roy 2006). *Argopecten* abundance remained high in the TEP but plummeted in the SWC in the last 2–3 Myr. The decline of *Argopecten* abundance is all the more striking because the genus represents the most abundant group of scallops in the SWC for the preceding 6 Myr.

Although byssally attaching species were never diverse or abundant in the TEP (Fig. 7), they have enjoyed spectacular success in the SWC, where they are the group with the greatest increase in diversity (Fig. 6). Their increase is correlated ($r^2 = 0.418$, $p = 0.059$) with the widespread expansion of high-carbonate environments (Appendix 2; O'Dea et al. 2007) and increase in the development of coral reefs since 4 Ma (Collins et al. 1996a; Johnson et al. 1995; Budd and Johnson 1999; Jain and Collins 2006; Johnson et al. 2007). Indeed, many byssally attaching species live attached to corals (Waller 1993). Although they also increased markedly in abundance, byssally attaching species never achieved the abundance characteristic of free-living species (Fig. 6).

The coexistence for 2 Myr of faunules with widely divergent Lyellian percentages (Fig. 11) strongly supports Petuch's (1982) hypothesis of "geographic heterochrony." However, we found no evidence that local communities with low Lyellian percentages were restricted to marginal environments, according to measurements of MART, percent carbonate in sediments, and water depth. One possible explanation for a lack of environmental effect is that faunules were sampled on the wrong spatial and temporal scales relative to environmental variability, but this seems highly unlikely for two reasons. First, pervasive time-averaging of sediments and fossils by bioturbation and other forms of disturbance should eliminate any fine-scale differences in distributions in level-bottom environments (Kidwell and Flessa 1996; Best and Kidwell 2000a,b; Kidwell 2002). Second, the scale and density of sampling were sufficient to identify strong relationships between benthic community composition and these same environmental parameters (O'Dea et al. 2007).

An entirely different possible explanation stems from metapopulation theory and the concept of extinction debt under conditions of pervasive environmental change (Jackson et al. 1996a; Hanski and Gilpin 1997). By this argument, species naturally exist in patches of high abundance in a landscape of low abundance or absence, and the persistence of the species depends on the number of patches occupied, the rate of colonization of new patches, and the rate of extinction in patches already occupied. Changes in these three parameters depend in turn upon the specific life-history characteristics of the species in relation to their environment (Nee and May 1992; Tilman et al. 1994). Thus, species soon fated to go extinct may nevertheless persist in a declining frequency of patches until the last patch becomes extinct.

Our data are in agreement with such a scenario (Fig. 11A,B). First, faunules within any 1-Myr interval typically include only a small fraction of the scallop species that existed during that interval. This was particularly true during the 4–3 Ma interval when no single faunule contained more than 13 of the 41 species that inhabited the SWC at that time. Overall differences in molluscan community composition were also extremely high among different faunules of the same age during this time (Jackson et al. 1999: Fig. 16). Thus, differences in species composition among faunules were extremely high during this period of maximum faunal and environmental change, and these differences persisted, albeit at decreasing frequency, for 2 Myr. Moreover, some of the ill fated species were abundant within some faunules until very near the end as seen by the greater number of faunules with Lyellian percentages less than 30–40% when relative abundance of species is included in the calculation (cf. Fig. 11B and 11A). Most importantly, species that survived had larger eggs and shorter larval durations than those that became extinct (Smith et al. 2003; Smith and Jackson 2004). Such differences in life history are the very essence of the model of extinction debt (Nee and May 1992; Tilman et al. 1994).

In summary, the extreme faunal turnover of scallops in the SWC has a strong ecological signature that is apparent only when the life habits of the different species and their abundance are fully taken into account. Moreover, and despite these considerable differences, the patterns of diversity, origination, and extinction for scallops as a whole are qualitatively very different from patterns for gastropods, reef corals, and erect bryozoans from the same region (Cheetham and Jackson 1996; Budd and Johnson 1999; Todd et al. 2002). Greater understanding of such major episodes of faunal turnover and extinction fundamentally depends upon exploiting such ecological differences to factor out the processes responsible.

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Appendix 1

List of species with fauna, first (FO) and last (LO) occurrence, and ecological group.

Species	Fauna	FO (Ma)	LO (Ma)	Ecological group
"*Amusium*" *bocasense* (Olsson, 1922)	SWC	4.5	2.05	Free-swimming
"*A.*" *laurenti* (Gmelin, 1791)	SWC	3.55	Recent	Free-swimming
"*A.*" sp. 2	SWC	8.6	6.9	Free-swimming
"*A.*" *toulae* (Brown and Pilsbry, 1913)	SWC	6.95	3.55	Free-swimming
"*Chlamys*" *onzola* (Olsson, 1964)	TEP	9.65	3.35	Byssal
Aequipecten canalis (Brown and Pilsbry, 1913)	SWC	18	3.55	Mixed
A. plurinomis (Pilsbry and Johnson, 1917)	SWC	12.6	3.55	Mixed
A. sp. 3	SWC	9.6	3.55	Mixed
A. sp. 4	SWC	8.6	8.6	Mixed
A. sua (Olsson, 1964)	TEP	9.65	9.65	Mixed
Argopecten costaricaensis (Olsson, 1922)	SWC	4.5	1.6	Argopecten
A. gibbus (Linnaeus, 1758)	SWC	3.55	Recent	Argopecten
A. levicostatus (Toula, 1909)	SWC	9.6	2.75	Argopecten
A. nerterus (Woodring, 1982)	SWC	9.6	3.55	Argopecten
A. sp. A	TEP	7.3	7.3	Argopecten
A. sp. 1	Both	9.65	3.55	Argopecten
A. sp. 4	SWC	2.05	2.05	Argopecten
A. sp. 5	SWC	3.55	1.4	Argopecten
A. sp. 8	SWC	4	4	Argopecten
A. uselmae (Pilsbry and Johnson, 1917)	SWC	12.6	1.6	Argopecten
A. ventricosus (Sowerby II, 1842)	TEP	9	Recent	Argopecten
Bractechlamys antillarum (Recluz, 1853)	SWC	3.55	Recent	Byssal
Caribachlamys imbricata (Gmelin, 1791)	SWC	2.05	Recent	Byssal
C. sentis (Reeve, 1853)	SWC	3.55	Recent	Byssal
Cryptopecten cactaceus (Dall, 1898)	SWC	6.95	3.45	Mixed
C. phrygium (Dall, 1886)	SWC	1.6	Recent	Mixed
C. woodringi (Olsson, 1964)	TEP	3.6	3.35	Mixed
Demarzipecten sp. 1	SWC	6.9	3.45	Byssal
D. sp. 2	SWC	6.95	6.95	Byssal
Euvola gordus (Olsson, 1964)	TEP	9.65	9.65	Free-swimming
E. perulus (Olsson, 1961)	TEP	3.35	Recent	Free-swimming
E. sp. (cf. *E. perulus*)	SWC	—	Recent	Free-swimming
E. reliquus (Brown and Pilsbry, 1913)	SWC	9.6	3.55	Free-swimming
E. ziczac (Linnaeus, 1758)	SWC	3.55	Recent	Free-swimming
Laevichlamys multisquamata (Dunker, 1864)	SWC	3.55	Recent	Byssal
Leopecten antiguensis (Brown, 1913)	SWC	9.6	9.6	Free-swimming
L. catianus (Weisbord, 1964)	SWC	9.6	3.55	Free-swimming
L. chazaliei (Dautzenberg, 1900)	SWC	3.55	Recent	Free-swimming
L. coralliphila (Olsson, 1922)	SWC	3.55	1.4	Free-swimming
L. gatunensis (Toula, 1909)	Both	12.6	2.75	Free-swimming
L. macdonaldi (Olsson, 1922)	Both	9.6	6.9	Free-swimming

Appendix 1. Continued.

Species	Fauna	FO (Ma)	LO (Ma)	Ecological group
L. marquerensis (Durham, 1950)	TEP	9	9	Free-swimming
L. sericeus (Hinds, 1845)	TEP	9	Recent	Free-swimming
L. sp. (cf. *L. sericeus*)	SWC	2.05	Recent	Free-swimming
L. sp. 4	SWC	3.55	3.55	Free-swimming
L. sp. 5	SWC	3.55	3.55	Free-swimming
Lepidopecten scissuratus (Dall, 1898)	SWC	12.6	6.9	Mixed
Leptopecten bavayi (Dautzenberg, 1900)	SWC	4.25	Recent	Leptopecten
L. biolleyi (Hertlein and Strong, 1946)	TEP	1.85	Recent	Leptopecten
L. sp. (cf. *L. biolleyi*)	SWC	3.55	Recent	Leptopecten
L. cracens (Olsson, 1964)	TEP	9.65	7.35	Leptopecten
L. ecnomius (Woodring, 1982)	SWC	11.6	3.45	Leptopecten
L. euterpes (Berry, 1957)	TEP	1.6	Recent	Leptopecten
L. sp. 2	SWC	9.6	3.05	Leptopecten
L. sp. 4	SWC	11.6	3.55	Leptopecten
L. velero (Hertlein, 1935)	TEP	1.85	Recent	Leptopecten
Lindapecten acanthodes (Dall, 1925)	SWC	4	Recent	Byssal
L. sp. 1	SWC	4.5	3.05	Byssal
Nodipecten arthriticus (Reeve, 1853)	TEP	1.6	Recent	Mixed
N. sp. (cf. *N. arthriticus)*	SWC	—	Recent	Mixed
N. nodosus (Linnaeus, 1758)	SWC	2.6	Recent	Mixed
Pacipecten linki (Dall, 1926)	SWC	3.55	Recent	Leptopecten
P. maturensis (Maury, 1925)	SWC	4.5	2.6	Leptopecten
P. sp. A	TEP	9.65	9.65	Leptopecten
P. sp. 1	SWC	4.5	3.5	Leptopecten
P. sp. 3	SWC	2.05	2.05	Leptopecten
P. tumbezensis (d'Orbigny, 1846)	TEP	9	Recent	Leptopecten
Pectinid A lineolaris (Lamarck, 1819)	SWC	—	Recent	Mixed
P. A. mimyum (Woodring, 1982)	SWC	8.6	3.45	Mixed
P. A. sol (Brown and Pilsbry, 1913)	SWC	4.25	4.25	Mixed
Pseudamusium (*Peplum*) *fasciculatum* (Hinds, 1845)	TEP	1.6	Recent	Mixed
P. (*P.*) sp. (cf. *P.* (*P.*) *fasciculatum*)	SWC	—	Recent	Mixed
Spathochlamys benedicti (Verrill and Bush, 1897)	SWC	3.55	Recent	Byssal
S. lowei (Hertlein, 1935)	TEP	3.35	Recent	Byssal
S. sp. 1	SWC	6.3	6.3	Byssal
S. sp. 2	SWC	2.6	2.6	Byssal
S. sp. 3	SWC	4	2.05	Byssal
S. sp. 4	SWC	7.3	7.3	Byssal
S. sp. 5	SWC	3.55	3.55	Byssal
S. sp. 6	SWC	2.05	2.05	Byssal
S. sp. 7	SWC	2.05	2.05	Byssal
S. vestalis (Reeve, 1853)	SWC	4.5	Recent	Byssal

Appendix 2

List of faunules used in this study with age estimate, mean percent carbonate, estimates of MART, species richness, and Shannon's *H*.

	Basin	Median age (Ma) (±)	S_{obs}	H	% CO3	MART
SWC, Nicaragua and Honduras						
Bahía Almirante	Panama	Recent	15	1.95	28.06	3.80
Bocas del Toro	Panama	Recent	20	1.63	33.58	3.39
Cayos Moskitos	Nicaragua	Recent	14	1.44	84.15	1.80
Golfo de los Moskitos	Panama	Recent	16	1.4	44.29	2.20
Laguna Chiriquí	Panama	Recent	17	1.33	35.24	3.80
Los Cochinos	Honduras	Recent	16	2.06	62.83	2.60
San Blas	Panama	Recent	14	2.11	67.37	3.13
Swan Cay	Bocas del Toro	1.4 (0.6)	6	1.19	63.49	3.22
Cangrejos Creek	Limón	1.55 (0.05)	2	—	36.1	—
Empalme	Limón	1.6 (0.1)	6	1.08	41.07	—
Cerro Mocho	Limón	1.6 (0.1)	1	—	—	—
Upper Lomas del Mar	Limón	1.6 (0.1)	9	1.45	43.28	2.82
Lower Lomas del Mar	Limón	1.7 (0.2)	4	0.91	38.83	3.08
Pueblo Nuevo	Limón	1.95 (0.15)	4	—	—	—

Appendix 2. Continued.

	Basin	Median age (Ma) (±)	S_{obs}	*H*	% CO3	MART
NW Escudo de Veraguas	Bocas del Toro	2.0 (0.1)	9	1.12	37.66	3.88
Wild Cane Key	Bocas del Toro	2.05 (0.15)	7	1.42	45.76	4.19
Ground Creek	Bocas del Toro	2.05 (0.15)	10	1.07	39.40	—
Fish Hole	Bocas del Toro	2.6 (0.4)	13	1.96	19.55	2.36
NC Escudo de Veraguas	Bocas del Toro	2.75 (0.85)	6	0.77	35.44	2.68
Bomba	Limón	3.05 (0.15)	7	1.26	68.96	3.13
Old Bank	Bocas del Toro	3.3 (0.3)	7	1.49	50.68	—
Bruno Bluff	Bocas del Toro	3.45 (0.15)	9	1.51	13.52	6.95
Quitaría	Limón	3.5 (0.1)	3	—	24.53	—
Isla Solarte	Bocas del Toro	3.55 (0.05)	7	0.88	54.10	6.68
Santa Rita	Limón	3.55 (0.05)	9	1.84	44.40	5.73
Cayo Agua: Punta Nispero South	Bocas del Toro	3.55 (0.05)	9	0.91	31.18	7.23
Cayo Agua: Punta Nispero West	Bocas del Toro	3.55 (0.05)	7	1.43	14.04	—
Cayo Agua: Punta Tiburón	Bocas del Toro	3.55 (0.05)	10	1.13	30.73	4.23
SE Escudo de Veraguas	Bocas del Toro	3.55 (0.05)	5	0.64	28.10	—
NE Escudo de Veraguas	Bocas del Toro	3.55 (0.05)	11	0.86	41.40	2.68
Río Bananito	Limón	3.55 (0.05)	1	—	—	—
Río Vizcaya	Limón	3.55 (0.05)	1	—	17.34	—
Cayo Agua: Punta Norte East	Bocas del Toro	4.25 (0.75)	11	1.51	18.87	4.11
Cayo Agua: Piedra Roja	Bocas del Toro	4.25 (0.75)	11	1.31	27.73	3.52
Cayo Agua: Punta Norte West	Bocas del Toro	4.25 (0.75)	10	0.91	15.93	6.25
Isla Popa	Bocas del Toro	4.25 (0.75)	10	1.53	19.77	6.65
Cayo Zapatilla	Bocas del Toro	4.25 (0.75)	6	0.90	14.61	5.62
Shark Hole Point	Bocas del Toro	5.65 (0.05)	3	0.8	14.25	5.22
South Valiente West	Bocas del Toro	6.29 (0.97)	5	1.21	18.22	6.16
Finger Island	Bocas del Toro	6.9 (1.3)	2	0.41	16.55	6.17
Plantain Cay	Bocas del Toro	6.9 (1.3)	2	—	—	—
Patterson Cay	Bocas del Toro	6.9 (1.3)	2	—	—	—
Playa Lorenzo	Bocas del Toro	6.9 (1.3)	4	—	—	—
Toro Cay	Bocas del Toro	7.3 (1.3)	4	0.64	54.17	—
Río Tuba	Limón	7.7 (0.5)			—	—
Isthmian						
Gatún	Canal	6.0 (2.5)	9	1.2	28.27	—
Río Tupisa	Chucunaque	6.35 (0.75)	5	1.19	15.28	6.65
Río Chico N17	Chucunaque	6.35 (0.75)	7	0.94	20.11	8.67
Río Icuanati	Chucunaque	6.95 (1.35)	4	1.18	24.88	—
Río Tuquesa	Chucunaque	6.95 (1.35)	6	1.29	17.48	—
Yaviza	Chucunaque	6.95 (1.35)	2	—	—	—
Río Indio	North Coast	6.95 (1.35)	3	0.1	18.47	—
Río Chucunaque	Chucunaque	7.05 (1.25)	1	—	9.46	—
Río Calzones	North Coast	8.25 (2.95)	4	0.8	15.02	4.57
Miguel de la Borda	North Coast	8.6 (1.8)	3	0.52	23.57	—
Mattress Factory	Canal	9.0 (0.4)	10	1.37	24.55	6.18
Isla Payardi	Canal	9.6 (1.3)	7	0.35	25.15	—
Río Tuira	Chucunaque	10.15 (0.75)	4	0.64	14.22	—
Martin Luther King	Canal	11.6 (0.2)	2	—	—	—
Río Chico N11	Chucunaque	12.6 (0.1)	4	0.68	18.36	—
Eastern Pacific						
Gulf of Chiriqui	Panama	Recent	11	1.72	25.92	5.92
Gulf of Panama	Panama	Recent	8	1.3	30.26	5.92
Tablazo	Manabí	1.4 (0.4)	5	1.08	15.36	—
Armuelles	Burica	1.6 (0.1)	9	—	—	—
Nicoya	Nicoya	1.6 (0.1)	8	—	—	—
Punta Canoa	Manabí	1.6 (0.6)	4	0.54	23.00	—
Golfo Dulce	Burica	1.85 (0.35)	6	—	—	—
Calle Esmeralda	Borbon	3.35 (0.25)	7	1.24	15.39	—
Río Camarones: Onzole	Borbon	3.6 (0.4)	1	—	20.62	—
Jama	Manabí	7.3 (1.3)	2	—	13.36	—
Favio Alfaro	Manabí	7.35 (1.35)	4	0.5	11.13	—
Palma Royal	Borbon	9 (0.4)	3	0.53	34.01	—
Punta Verde: Onzole	Borbon	9 (0.4)	3	—	—	—
Cueva de Angostura	Borbon	9.65 (1.25)	4	0.66	15.54	—
Punta Verde: Angostura	Borbon	9.65 (1.25)	4	0.67	17.11	—
Río Cayapas	Borbon	9.65 (1.25)	2	0.12	16.10	—