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Evolution of large body size in abalones (*Haliotis*): patterns and implications

James A. Estes, David R. Lindberg, and Charlie Wray

Abstract.—Kelps and other fleshy macroalgae—dominant reef-inhabiting organisms in cool seas—may have radiated extensively following late Cenozoic polar cooling, thus triggering a chain of evolutionary change in the trophic ecology of nearshore temperate ecosystems. We explore this hypothesis through an analysis of body size in the abalones (Gastropoda; Haliotidae), a widely distributed group in modern oceans that displays a broad range of body sizes and contains fossil representatives from the late Cretaceous (60–75 Ma). Geographic analysis of maximum shell length in living abalones showed that small-bodied species, while most common in the Tropics, have a cosmopolitan distribution, whereas large-bodied species occur exclusively in cold-water ecosystems dominated by kelps and other macroalgae. The phylogeography of body size evolution in extant abalones was assessed by constructing a molecular phylogeny in a mix of large and small species obtained from different regions of the world. This analysis demonstrates that small body size is the plesiomorphic state and largeness has likely arisen at least twice. Finally, we compiled data on shell length from the fossil record to determine how (slowly or suddenly) and when large body size arose in the abalones. These data indicate that large body size appears suddenly at the Miocene/Pliocene boundary. Our findings support the view that fleshy-algal dominated ecosystems radiated rapidly in the coastal oceans with the onset of the most recent glacial age. We conclude with a discussion of the broader implications of this change.

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Introduction

Major patterns of organic evolution over the course of earth history are known almost entirely from the fossil record. However, the resulting view of the history of life has a well recognized but poorly understood bias: species or taxa that were not preserved can never be identified from direct fossil evidence. The probability of a species' preservation, and thus its representation in the fossil record, is influenced by many factors, including abundance, habitat, and the existence of preservable structures, such as bones or other calcified tissues. Important species, and indeed even entire higher-level taxa, undoubtedly have come and gone without leaving a single direct record of their existence, much less their functional role in paleoecosystems. Nevertheless, in some cases these taphonomic ghosts may have left indirect evidence of their existence, and even their ecological function, through the fossil record of associated species with which they interacted strongly.

The kelps (Order Laminariales) are an important group of marine autotrophs that has left little or nothing in the way of a direct fossil record. In terms of biomass, organic carbon fixation, space occupation, and biogenic habitat, kelps are the dominant reef-inhabiting organisms in cool seas, especially in the Northern Hemisphere (Steneck et al. 2003). They also occur in the nearshore environment, a habitat where other organisms have been well fossilized (Valentine 1989). Nonetheless, only one fossil kelp (*Julescrania*; late Miocene [Parker and Dawson 1965]) has been described, and the taxonomic affinity of this species to the Laminariales might even be questioned (Estes and Steinberg 1989). The dearth of fossil kelps is almost certainly due to the absence of preservable structures.

Despite the absence of a fossil record, geo-

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graphic patterns to the diversity and distribution of extant kelp species, habitat requirements of extant species, and historical reconstructions of where and when these habitats existed, combined with the fossil record of species that associated with kelps in an obligate or strongly facultative manner, have been used to infer that the kelps originated in the late Oligocene/early Miocene (Domning 1989; Vermeij 1992, 2001) and diversified relatively recently from the North Pacific basin (Estes and Steinberg 1988). Although these analyses and their interpretations focused exclusively on kelps, they should apply to other groups of large fleshy marine algae, most of which are larger and more abundant in cool seas than in tropical/subtropical marine ecosystems because of elevated productivity and reduced intensities of herbivory (Gaines and Lubchenco 1982; Duffy and Hay 2001). Tropical to warm temperate conditions predominated in coastal environments worldwide at the end of the Mesozoic followed by stepwise global cooling during the Cenozoic (Cervato and Burckle 2003). The southern oceans cooled first with expansive glaciation of Antarctica by at least 43–42 Ma (Browning et al. 1996), and Barron et al. (1991) argued for the presence of Antarctic ice sheets by the late middle Eocene. Increased high-latitude cooling in the North Pacific Ocean has been dated between 10.0 and 4.5 Ma (Barron 2003). Intensification of costal upwelling also occurred in the late Neogene (Jacobs et al. 2004), which further contributed to the cooling of coastal waters in the North Pacific (Barron 1998).

With the onset of polar cooling, fleshy macroalgae probably assumed an increasingly important ecological role in high-latitude coastal oceans. If this hypothesis is correct, then signals of the transition from macroalgal-impoverished to macroalgal-enriched ecosystems should be found in other groups of organisms that experienced the transition. Here we explore this hypothesis through an analysis of body size in the abalones (Gastropoda; Haliotidae). The abalones are a potentially informative group because they are widely distributed in modern oceans; extant species display a broad range of maximum body sizes; and they are an old group (earliest fossils assigned to the genus *Haliotis* are from the late Cretaceous, 60–75 Ma) with an adequate fossil record, especially in the Neogene.

Our analysis has three parts. The first is a geographical assessment of maximum body size in extant abalones. Specifically, we evaluate the hypothesis that large abalones occur most commonly in cold-water ecosystems dominated by fleshy macroalgae by examining the distributional patterns of maximum body size in the extant fauna. This analysis confirms that all of the extant large-bodied abalones live in kelp-forests or other fleshy-algal dominated ecosystems at high latitudes. Next, we explore the patterns of body size evolution in extant abalones by constructing a molecular phylogeny in a mix of large and small species obtained from different regions of the world. This analysis demonstrates that small body size is a plesiomorphic trait, and that largeness arose at least twice in the abalones. Finally, we reanalyze data on shell length from the fossil record to determine how (slowly or suddenly) and when (recently or long ago) large body size evolved in the abalones. This analysis indicates that large body size appears suddenly at the Miocene/Pliocene boundary.

Our findings provide further support for the view that fleshy-algal dominated ecosystems radiated rapidly in coastal oceans with the onset of late Cenozoic regional cooling. We conclude by discussing the implications of this change.

Methods and Materials

Maximum Body Size Variation in Extant and Fossil Abalones.—There are approximately 56 extant species of abalones (Geiger 1998, 2000) and 42 species known from the fossil record (Geiger and Groves 1999) (Table 1). Abalones are exclusively marine-living and occur from the Tropics to cool temperate regions in both the Southern and Northern Hemispheres. The highest latitudinal record is 58°N for *H. kamtschatkana* Jonas in southeastern Alaska (Geiger 2000). Within their latitudinal range, extant abalones have a nearly cosmopolitan distribution, being absent only from the western North Atlantic Ocean and the Pacific coast of South America (Fig. 1).

Records of geographical distribution and

TABLE 1. Occurrences of fossil *Haliotis* taxa (including first occurrences of extant species) with maximum size data. Size data from Lindberg (1992), Geiger (1998, 2000), and Hutsell et al. (1999). Fossil occurrence data from Geiger and Groves (1999).

Taxon	Period	Extant	Locality	Size (mm)
H. antillesensis	Cretaceous		Caribbean	25
H. lomaensis	Cretaceous		California	12
H. waitemataensis	Oligocene		New Zealand	90
H. benoisti	Oligocene		France	21
H. kochibei	L. Miocene		Japan	77
H. koikei	L. Miocene		Japan	108
H. glabrosa	L. Miocene		Japan	85
H. japonica	L. Miocene		Japan	50
H. powelli	L. Miocene		New Zealand	47
H. koticki	L. Miocene		California	99
H. notoensis	M. Miocene		Japan	54
H. fuijokai	M. Miocene		Japan	43
H. amabilis	M. Miocene		Japan	57
H. lasia	U. Miocene		California	75
H. kurosakiensis	U. Miocene		Japan	81
H. clathrata	U. Miocene	*	Guam	43
H. moniwaensis	Miocene		Japan	50
H. palaea	Miocene		California	52
H. iris	Miocene	*	New Zealand	183
H. discus	U. Pliocene	*	Japan	225
H. diversicolor	U. Pliocene	*	Japan	109
H. gigantea	U. Pliocene	*	Japan	226
H. pourtalesi	L. Pliocene	*	California	20
H. elsmerensis	L. Pliocene		California	62
H. fulgens	L. Pliocene	*	California	225
H. cracherodii	Pliocene	*	California	216
H. rufescens	Pliocene	*	California	313
H. corrugata	Pliocene	*	California	245
H. assimilis	Pliocene	*	California	184
H. walallensis	Pliocene	*	California	176
H. ovina	Pliocene	*	Guam	90
H. varia	Pliocene	*	Sri Lanka	82
H. tuberculata	Pliocene	*	Italy	117
H. australis	U. Pleistocene	*	New Zealand	107
H. virginea	U. Pleistocene	*	New Zealand	67
H. cyclobates	Pleistocene	*	Australia	88
H. emmae	Pleistocene	*	Australia	105
H. laevigata	Pleistocene	*	Australia	228
H. rubra	Pleistocene	*	Australia	194
H. kamtschatkana	Pleistocene	*	California	159
H. sorenseni	Pleistocene	*	California	230
H. midae	Pleistocene	*	South Africa	220

maximum size for living and fossil abalone species were obtained from various sources, including Lindberg (1992), Geiger (1998, 2000), and Geiger and Groves (1999). The geographical distribution of modern kelp forests was obtained from Steneck et al. (2003) and references therein. Modern abalone species were divided into two groups, hereafter termed ''temperate'' or ''tropical,'' depending on whether their geographical ranges occur primarily within or outside the geographical range of modern kelp forests. Because kelps and other fleshy algae extend into seasonally ice-covered regions of the Northern and Southern Hemispheres and no extant abalone species range to such high latitudes, the poleward distribution of all temperate abalones was taken to occur within the geographical range of kelp forest ecosystems. Determination of the degree of overlap with kelp forest ecosystems for warm-water species at higher latitudes and for cold-water species at lower latitudes was potentially more problematic. However, most species distributions do not transcend the tropical range limits of kelp forest ecosystems, instead occurring exclusively

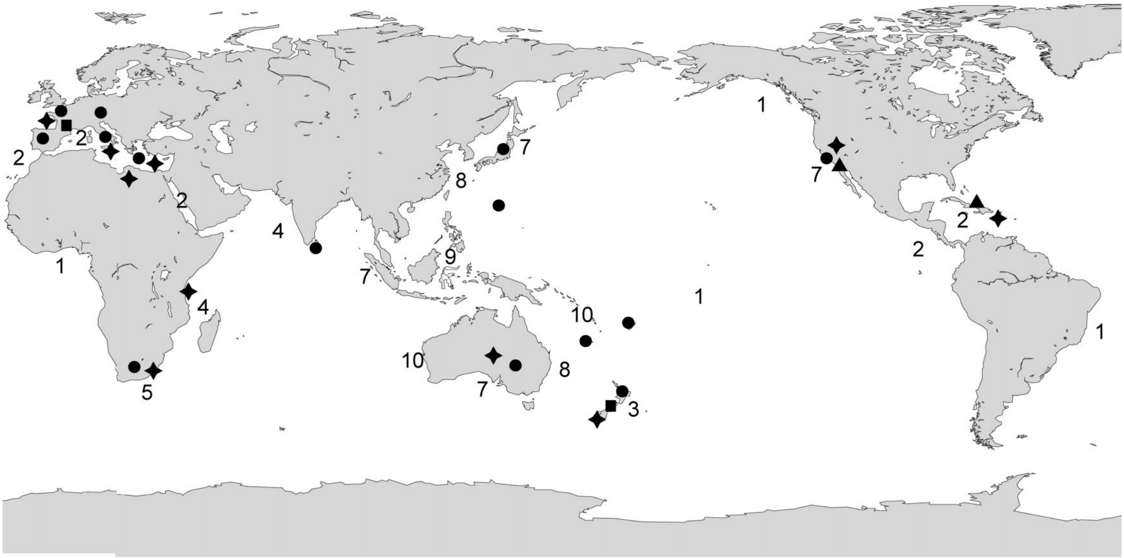

FIGURE 1. Worldwide distribution of living and fossil abalone. Numerals indicate approximate number of living species in each region. Fossil distribution represent by symbols ▲ = Cretaceous, ■ = Paleogene, ● = Neogene, ♦ = Pleistocene. Distributional data from Geiger (1998, 2000); fossil data from Geiger and Groves (1999).

in one habitat type or the other. Maximum size was taken as the greatest reported shell length. These values are minimum proxies for maximum size.

Abalone Phylogeny and Biogeography.—Tissue samples were obtained for 29 (about 50%) of the 56 extant abalone species and the large ribosomal subunit (mt 16S rRNA) was partially sequenced (517 BP). All available *Haliotis* sequences for three additional genes (COI [499 BP], ITS [795 BP], and Lysin [712 BP]) were retrieved from Genbank and combined with the 16S data (Table 2). Sequences were initially aligned using the Clustal W (Thompson et al. 1994) accessory application of BioEdit (Hall 1999), and then by hand. Ambiguities resulting from poorly aligned positions were identified and minimized with GBlocks (Castresana 2000).

The combined four-gene data set (30 taxa, 2523 characters) was subjected to maximum parsimony analysis using PAUP* Version 4.0b10 (Swofford 1998). All characters were equally weighted and unordered. The tree-bisection-reconnection (TBR) branch-swapping algorithm was used with a random addition sequence (1000 replicates), and one tree was held at each step during stepwise addition. Bootstrap support values were calculated using the Bootstrap option in PAUP* and Bremer support values using the clade decay option in MacClade 4.0 (Madison and Madison 1992).

An area cladogram was produced using Component Ver. 2.00a (Page 1993). Biogeographic areas generally followed Geiger's (2000) distributional mapping of the Haliotidae except we incorporated East African species within the Indo-Pacific region. Heuristic search options included nearest-neighbor interchange branch swapping, and the number of leaves added was used as the minimization criterion in calculating the area cladogram. Trees from both PAUP* and Component analyses were visualized and printed using TreeView Version 1.6.6 (Page 1996).

Results

Body Size Variation in Extant and Fossil Abalones.—Maximum shell length distributions differed significantly (two-sample *t*-test) between tropical and temperate abalone species (Fig. 2A). Further analyses of these data by region show that the northwestern and northeastern Pacific (temperate) faunas contain markedly larger abalones than other faunas (Fig. 3), and an analysis of variance of abalone size by regions revealed significant differences between both the East African and Indo-Pa-

TABLE 2. Taxa used in molecular phylogenetic analysis. Reference numbers refer to Genbank accession numbers. 16S = 16S ribosomal RNA gene; COI = cytochrome c oxidase subunit I gene; ITS = internal transcribed spacer 1, 5.8S ribosomal RNA gene, and internal transcribed spacer 2; Lysin = sperm lysin mRNA, complete coding sequence.

Taxon	16S	COI	ITS	Lysin
H. asinine	AY650173			
H. australis	AY650157			L26270
H. conicopora				L26281
H. corrugata	AY650172	AF060849	AF296856	M34389
H. cracherodii	AY650159	AF060848	AF296857	L59971
H. cyclobates	AY650153	AF60851	AF296865	L26271
H. discus	AY650174	AY146398	AY146403	M98875
H. diversicolor	AY650171	AY146402	AY146406	L26272
H. dohrniana	AY650152			
H. fulgens	AY650158	AF060850	AF296859	L59972
H. gigantea	AY650160	AY146400	AY146405	L26283
H. glabra	AY650151			
H. iris	AY650166	AF060854	AF296869*	L26273
H. kamtschatkana	AY650163	AF060845	AF296853	L59970
H. laevigata	AY650169			L26274
H. madaka	AY650177	AY146399	AY146404	
H. midae	AY650167	AF060853	AF296863	L26275
H. ovina	AY650154			M26276
H. pourtalesii	AY650165		AF296871	
H. pustulata	AY650175			L35180
H. roberti	AY650150		AF306942	
H. roei	AY650170		AF296866	M98874
H. rubra	AY650155	AF060852	AF296868	L26277
H. rufescens	AY650164	AF060842	AF296855	M34388
H. rugosa	AY650176			
H. scalaris	AY650156		AF296864	M26278
H. sorenseni	AY650161	AF060844	AF296850	M59968
H. tuberculata	AY650168		AF296860	L26280
H. varia	AY650149			L35181
H. walallensis	AY650162	AF060846	AF296854	M59969

* 5.8S only; ITS1 and ITS2 were unalignable with the remaining abalone species (see Coleman and Vacquier 2002).

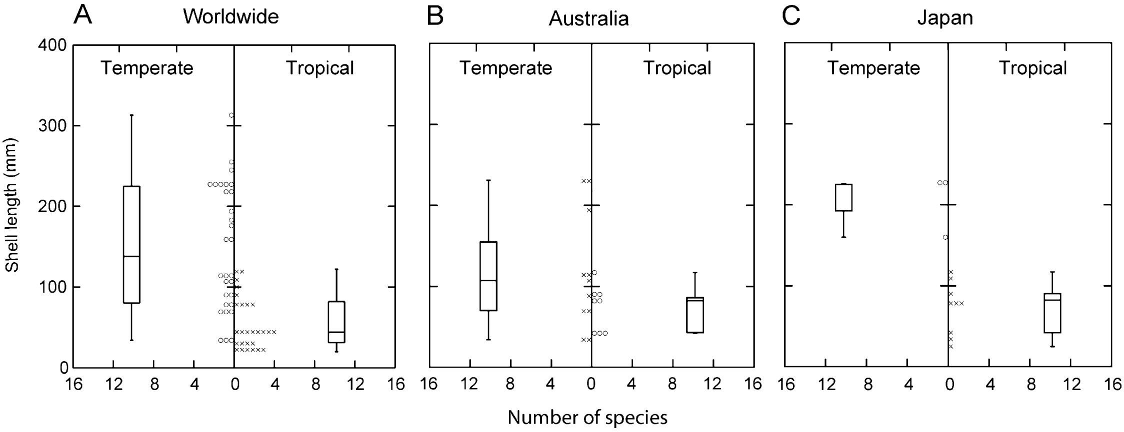

FIGURE 2. Size distributions of temperate and tropical abalones. A, Worldwide fauna. B, Latitudinal gradient from north (tropical) to south (temperate) along the western and eastern coasts of Australia. C, Latitudinal gradient from north (temperate) to south (tropical) along the western and eastern coasts of Japan. Box plots display sample means and quartiles. Two-sample *t*-test probabilities (Bonferroni adjusted—all corrected on the basis of same number of tests) on size grouped by regions: tropical vs. temperate ($t_{55} = 5.881$, $p < 0.0001$); Japan tropical vs. Japan temperate ($t_{10} = 5.821$; $p < 0.0001$); Australian tropical vs. Australian temperate ($t_{17} = 1.674$; $p = 0.112$). Size data from Lindberg (1992), Geiger (1998, 2000), and Hutsell et al. (1999); distributional data from Geiger (2000).

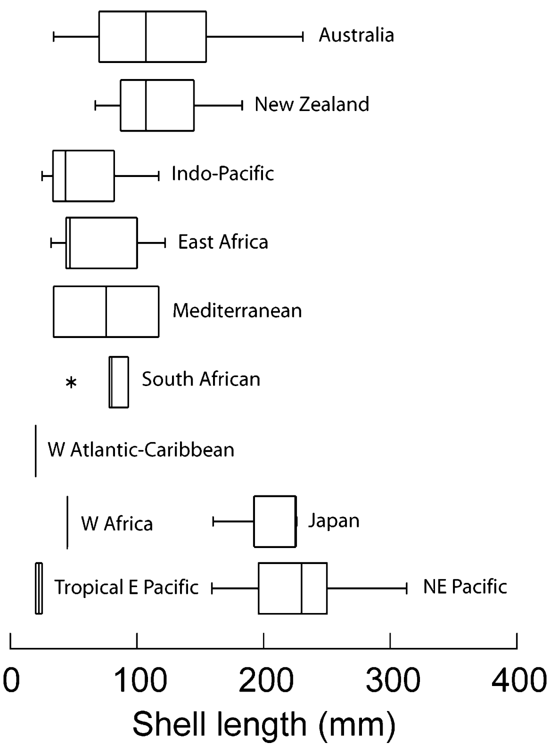

FIGURE 3. Size distributions of living abalone taxa by regions. Box plots display sample medians and quartiles; * = outliers. Size data from Lindberg (1992), Geiger (1998, 2000), and Hutsell et al. (1999); distributional data from Geiger (2000).

cific faunas (tropical) and the northwestern and northeastern Pacific (temperate) faunas (Table 3). The temperate Australian fauna showed a similar pattern of increased size compared with the Indo-Pacific, but the difference was not statistically significant. The northwestern and northeastern Pacific (temperate) faunas were also significantly larger than both the tropical eastern Pacific fauna and the tropical western Atlantic fauna (Table 3).

The smallest reported maximum shell lengths for tropical and temperate abalone species are roughly similar—20 mm for the tropical eastern Pacific *H. roberti* and 34 mm for the temperate Australia *H. hargravesi*. However, all of the larger-bodied species occur in temperate habitats. The greatest reported shell length in a tropical abalone is 122 mm for *H. mariae* of the Arabian Peninsula, although *Ecklonia radiata* (a kelp) and *Sargassum* spp. (rockweeds) occur in that region (Shepherd and Steinberg 1992), which thus might be classified as kelp-dominated despite its tropical location. Fifteen species (50% of the temperate species) have maximum reported shell lengths that exceed this value. The largest reported shell length of any extant abalone is 313 mm for *H. rufescens*, which ranges from southern Oregon (United States) to the Pacific coast of

TABLE 3. Least significant difference pairwise comparison probabilities from ANOVA of abalone size by geographical regions. Significant comparisons remaining after Bonferroni adjustment (Miller 1985) in bold. Data from Lindberg (1992), Geiger (1998, 2000), and Hutsell et al. (1999).

Region	Australia	East Africa	Indo-Pacific	N.W. Pacific	Mediterranean	New Zealand	South Africa	N.E. Pacific	Tropical E. Pacific	Tropical W. Atlantic
Australia										
East Africa	0.086									
Indo-Pacific	0.006	0.723								
N.W. Pacific	0.012	**0.001**	**<0.0001**							
Mediterranean	0.292	0.879	0.680	0.008						
New Zealand	0.952	0.1830	0.069	0.046	0.352					
South Africa	0.642	0.278	0.094	0.010	0.502	0.691				
N.E. Pacific	**<0.0001**	**<0.0001**	**<0.0001**	0.495	**<0.0001**	0.003	**<0.0001**			
Tropical E. Pacific	0.019	0.278	0.332	**<0.0001**	0.301	0.043	0.060	**<0.0001**		
Tropical W. Atlantic	0.0164	0.254	0.301	**<0.0001**	0.279	0.038	0.053	**<0.0001**	0.9610	
West Africa	0.180	0.667	0.7790	0.009	0.625	0.212	0.292	0.002	0.719	0.689

northern Baja California, Mexico (Hutsell et al. 1999).

Similar patterns of variation in maximum body size occur along continental margins that correspond to tropical/temperate latitudinal gradients, and significant size differences exist along these gradients in the Australian (Fig. 2B) and Japanese (Fig. 2C) faunas (Table 2). A longitudinal gradient in maximum shell length also occurs in the Mediterranean and eastern Atlantic *H. tuberculata*. In the eastern part of its range (Israel, Greece) this species seldom attains shell lengths greater than 40 mm (Owen et al. 2001). In the central Mediterranean (Italy), maximum shell lengths approach 70 mm, whereas shell lengths exceeding 90 mm are attained on the Atlantic coasts of France and England (Geiger 2000: Figs. 4–9). This latter shell length gradient corresponds to both water temperature and the abundance of laminarian algae.

Altogether, 42 abalone species are known from the fossil record (Geiger and Groves 1999). The earliest species (*H. antillesensis*) is from the Cretaceous (Table 1). This species, which has a maximum reported shell length of 25 mm, is similar in gross morphological features to the extant haliotids. Relatively few fossil abalones (4 species) have been described through the Oligocene. Larger numbers of species (39) are known from the Miocene through the Pleistocene. Whether this proliferation of fossil species represents a post-Oligocene radiation or a time-related taphonomic bias is unknown. Nonetheless, abalones have been continuously present in the world's oceans for at least 60–75 million years.

We divided the fossil abalones into small or large species depending on whether maximum reported shell length was <150 mm or >150 mm, a size break that appears significant for extant abalone faunas (Fig. 3). Based on this criterion, 28 of the fossil species were designated as small and 14 as large. Small-bodied species occur in the fossil record from the Cretaceous through the Pleistocene. One large-bodied species appears in the Miocene, the first occurrence of the extant *H. iris* in New Zealand. The remaining 13 large-bodied species do not appear until the Pliocene (Fig. 4B). Maximum size distributions for fossil taxa differ significantly (two sample t-test) between pre-Pliocene and post-Miocene occurrences (Table 4), and are markedly similar to those of extant tropical and temperate faunas (cf. Fig. 4A, B). There is no significant difference between the sizes of fossil abalone species that have first occurrences in either the Pliocene and Pleistocene (Table 4, Fig. 4C).

TABLE 4. Two-sample t-test probabilities (Bonferroni adjusted) on maximum reported abalone shell length grouped by period as indicated in Table 1 (extinct and extant taxa pooled). Shell length data from Lindberg (1992), Geiger (1998, 2000), and Hutsell et al. (1999). Fossil occurrence data from Geiger and Groves (1999).

Group	n	Mean shell length (mm)	SD	p
Pre-Pliocene	19	65.9	38.6	<0.0001
Post-Miocene	23	160.3	75.7	
Pliocene	14	163.6	84.1	0.794
Pleistocene	9	155.3	65.0	

Abalone Phylogeny and Biogeography.—During hand alignment the ITS1 and ITS2 regions of *H. iris* were found to be unalignable with the remaining abalone species and only the 5.8S gene was included in the analysis (see Coleman and Vacquier 2002). The maximum parsimony analysis of the complete data matrix found eight trees of 2321 steps on a single tree island (consistency index [CI] = 0.6049, CI excluding uninformative characters = 0.5244, and retention index [RI] = 0.7092). The strict consensus tree with bootstrap and Bremer support values is presented in Figure 5A. Polytomies exist in the relationships of the northwestern and northeastern Pacific faunas with the tropical eastern Pacific and tropical western Atlantic faunas, and the relationship of *H. cyclobates* with the other temperate Australian taxa (Fig. 5A).

The GBlocks analysis (Castresana 2000) removed 602 poorly aligned positions leaving 1928 (76%) of the original 2523 characters. The reduced matrix was then subjected to a maximum parsimony analysis under the same parameters and options used for the original matrix. The topology of the strict consensus tree from the reanalysis (Fig. 5B) did not substantially differ from the strict consensus tree of the original analysis (Fig. 5A). In the re-

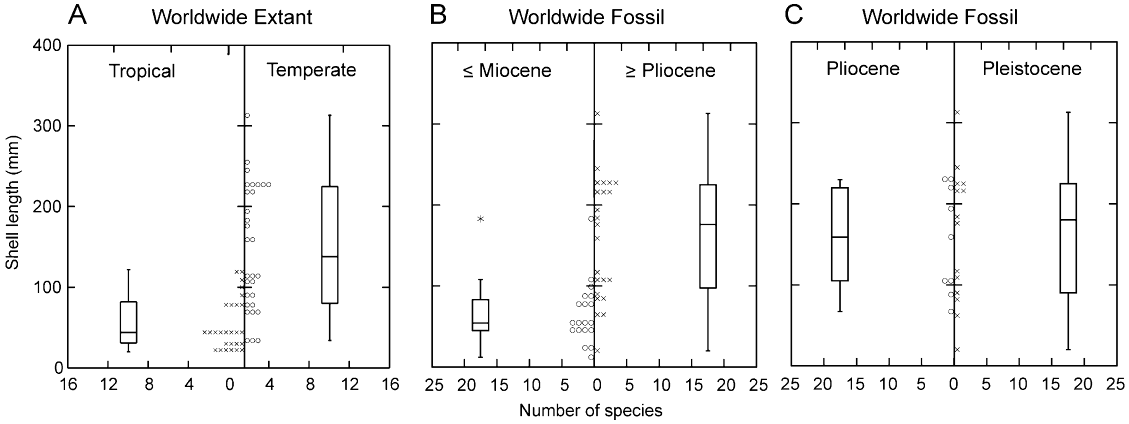

FIGURE 4. Size distributions of living and extinct abalone taxa. A, Living taxa. B, Pre-Pliocene taxa vs. post Miocene taxa. C, Pliocene taxa vs. Pleistocene taxa. Box plots display sample mean and quartiles; * = outliers. See Figure 2 for data sources for living taxa. Fossil occurrences for *Haliotis* species from Geiger and Groves (1999).

analysis three nodes (* in Fig, 5A) collapsed, producing polytomies, and the polytomy among the Australian taxa resolved with the alternative clade (cf. Fig. 5B, C). Neither of these changes affects either the biogeographical or size patterns discussed below.

To select a fully resolved tree for biogeographical analysis we parsed the Pacific-based polytomy (Fig. 5A) by considering the northwestern and northeastern Pacific clades to share a more recent common ancestor rather than either having a sister-taxon relationship with the tropical eastern Pacific and tropical western Atlantic faunas. This resolution was based, in part, on the first occurrences of extant taxa in both temperate faunas (Table 1), and the closing of the Panamic Portal and isolation of the tropical eastern Pacific fauna from the tropical western Atlantic fauna. Two trees (3 and 7) had the Pacific topology resolved as above, but differed in the resolution of the Australian polytomy. We had no opinion regarding the Australian polytomy and therefore randomly chose Tree 3 (Fig. 5C).

Two large clades are evident in all trees: one includes the temperate Australian and South African taxa; the other, the Mediterranean + several Indo-Pacific taxa, New Zealand, North Pacific, and tropical New World faunas. A grade of Indo-Pacific species are sister taxa to the two aforementioned clades (Fig. 5C.) The latter large clade can be further resolved into two subclades: Mediterranean + several Indian Ocean taxa, and New Zealand + North Pacific + tropical New World taxa. Temperate and tropical species are mixed in this clade but not in the Australian and South African clade or in the grade of Indo-Pacific taxa. Support (bootstrap/Bremer) for the placement of these larger clades is good: Mediterranean + Indian Ocean taxa (92/8), New Zealand + North Pacific + tropical New World (99/23), and the temperate Australian and South African (84/10) (Fig. 5A). Weaker support exists for the placement of an additional New Zealand taxon (*H. australis*) as the sister taxon of these two clades (62/2), and for the sister relationship between the Mediterranean + Indian Ocean clade and the New Zealand + North Pacific + tropical New World clade (62/4) (Fig. 5A).

Graphing body size of extant species on the strict consensus tree (Fig. 5D) suggests that small body size is the plesiomorphic character state; tropical lineages rarely, if ever, produced large-bodied species; small body size was retained in some temperate abalones but most cold-water lineages became large; and large body size in the abalones independently evolved at least twice, once in the temperate North Pacific and once in temperate Australia + South Africa, or possibly independently in South Africa.

The fact that all extant large-bodied abalones live in association with kelp forests strongly suggests that the kelp forest environment was a necessary condition for the evolution and maintenance of this trait. Further-more, the fact that large body size is a polyphyletic trait in the abalones suggests that it is evolutionarily labile—i.e., it might be expected to arise whenever small haliotid taxa radiated into regions supporting kelp forest ecosystems.

The unrooted area cladogram for Tree 3 also reflects separate originations of large body size in abalone, and two originations of tropical faunas (Fig. 6). The Mediterranean, Indian Ocean and tropical western Pacific taxa form a nexus that likely reflects the Tethyan origin of this clade (see also Lindberg 1992; Geiger and Groves 1999. Subsequent division of this clade into eastern and western Tethyan components is also suggested (Fig. 6). Australian and South African taxa group next, followed by the New Zealand fauna; all three of these faunas are Southern Hemisphere. The remaining three faunas represent a northward excursion and the subsequent divergence of a second tropical group into the tropical eastern Pacific and Caribbean, and lastly the divergence of the northeastern and northwestern Pacific faunas (Fig. 6). This pattern suggests that the occurrence of *Haliotis* species in the Cretaceous of California and the Caribbean likely represent components of the western Tethyan lineage that subsequently went extinct in the New World, but the region was then recolonized from the southwestern Pacific in the Tertiary prior to the closing of the Panamic Portal (see also Lee and Vacquier 1995).

Discussion

Extant abalones live in intertidal and shallow subtidal habitats from tropical to cold temperate latitudes (Geiger 2000). We have shown that the smaller species occur throughout this range whereas the larger species (i.e., shell lengths >150mm) occur exclusively in cold-water habitats. However, this pattern and its purported explanation is not a universal or perhaps even a widely recurrent theme in herbivorous marine gastropods. Other groups tend to be larger at higher latitudes, but apparently for different reasons. For example, lottiid and especially fissurelid limpets, neither of which feed predominately on macroalgae, also have given rise to large-bodied taxa in certain temperate oceans. In other families of marine gastropods with broad latitudinal ranges (e.g., Trochidae, Conidae, Mitridae, Olividae), it is often the smaller species that occur in temperate waters (Lindberg unpublished data). The larger and more robust shell morphologies of these latter families in tropical environments are thought to result from two main factors: the greater potential for calcification and an evolutionary escape response from benthic-feeding, shell-crushing predators (Vermeij 1978, Palmer 1979). Thus, the geographical patterns of body size in marine gastropods no doubt have varied explanations. Although an overview of this broad-scale variation is a potentially fertile area of future inquiry, our focus here is specifically on the abalones, a group for which the evolution of body size variation seems to be related to primary production and mode of foraging.

Geographical Patterns of Production and Herbivory.—The distinct latitudinal pattern of maximum size in the abalones probably results from differences between temperate and tropical reef systems in both the rate of primary production and the mode of organic carbon fixation and transfer from autotrophs to primary consumers. Fleshy macroalgae are generally rare on tropical reefs (Gaines and Lubchenco 1982), or were until recently (Hughes 1994; Jackson et al. 2001; Pandolfi et al. 2003), owing in part to high intensities of disturbance by herbivorous fishes and invertebrates and in part to the nutrient-impoverished nature of warm seawater. Overall production rates are relatively low in the Tropics, where microalgae (phytoplankton, diatoms, and zooxanthellae) are the main autotrophs, many of which (the zooxanthellae) are unavailable to herbivores because of their endosymbiotic relationship with corals. These conditions do not favor growth or production in herbivorous invertebrates, perhaps thus explaining why tropical abalones are so small. In contrast, most temperate reef habitats support dense stands of fleshy macroalgae, in part because herbivorous vertebrates are comparatively rare (Gaines and Lubchenco 1982; Steneck et al. 2003) and in part because the typically cold, nutrient-rich water of higher-latitude seas promotes high production. Kelps, rock-

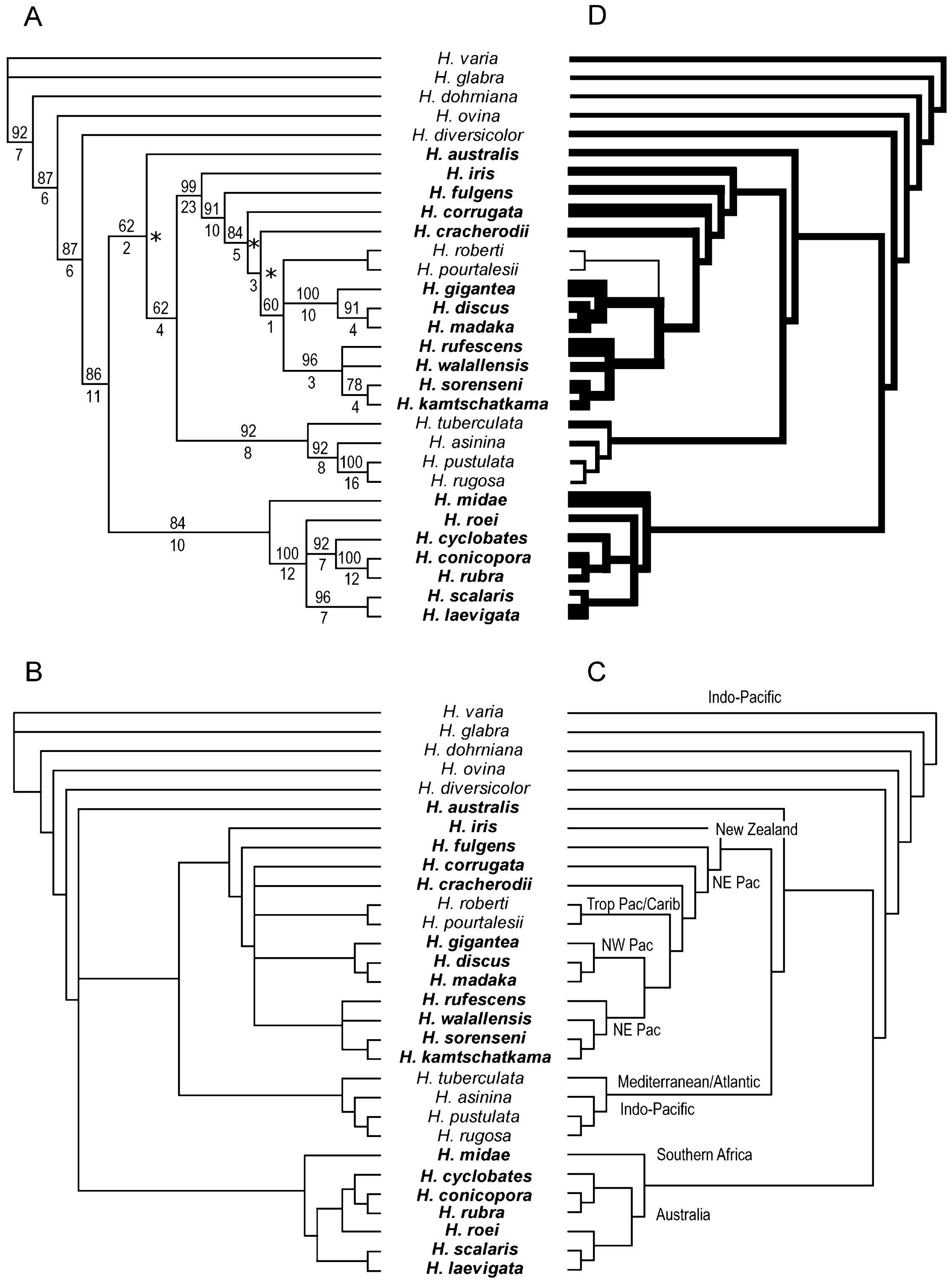

FIGURE 5. *Haliotis* molecular phylogenies (maximum parsimony analysis of 16S, COI, ITS, and lysin sequence data). A, Unrooted strict consensus tree from analysis of complete character matrix. Values above branch = bootstrap value; values below = Bremer support (clade decay). * = unsupported nodes in reduced character matrix. B, Unrooted strict consensus tree from analysis of GBlocks (Castresana 2000) reduced character matrix. C, Tree number

weeds (Order Fucales), and various red (Rhodophyta) and green (Chlorophyta) algae dominate temperate algal assemblages; all of these grow rapidly (especially the kelps [Mann and Lazier 1996]) and produce large quantities of particulate organic carbon (often termed ''drift algae'' [Harrold and Reed 1985; Konar 2000]). Seagrasses potentially serve an analogous ecological role in the Tropics; although most herbivorous gastropods only rasp their cortical cells or consume their algal epiphytes, seagrass abundance and detrital production may have been much less when herbivorous vertebrates (such as sea turtles, sirenians, and various fishes) were more common in tropical oceans (Jackson et al. 2001; McClenachan et al. 2005), and we are unaware of any evidence that tropical abalones feed on seagrasses in any form.

Drift algae, which are largely absent from tropical reefs, fuel secondary production on temperate reefs by convecting organic carbon from the water column to the seafloor (Duggins et al. 1989). This mode of organic carbon fixation and transport can subsidize local secondary production to levels far exceeding those achievable solely through in situ photosynthesis (Bustamante and Branch 1996; Polis et al. 1997). Algal drift also enables herbivorous invertebrates to employ a sit-and-wait foraging strategy, something tropical species seemingly cannot afford to do. This drift-algae-driven sit-and-wait foraging strategy occurs in several groups of macroinvertebrate herbivores, with substantial ecological and life-history consequences in each case. For example, temperate-latitude sea urchins in the family Strongylocentrotidae employ fundamentally different foraging strategies depending upon whether algal drift is abundant or rare (Ebeling et al. 1985; Harrold and Reed 1985; Konar and Estes 2003). When algal drift is abundant, urchins are sessile, sit-and-wait consumers, whereas when drift is rare or absent, they become highly mobile in their search for food. Foraging mode has fitness consequences to the herbivores as drift-feeding urchins have larger gonads and higher growth rates and achieve larger body sizes (Larson et al. 1980); it also has important ecological consequences because mobile sea urchins destructively consume living macroalgae, thus creating areas in which fleshy macroalgae are grazed to local extinction (reviewed by Steneck et al. 2003).

The importance of drift feeding is also apparent in temperate limpet faunas. Most limpet species that occur in rocky intertidal and shallow subtidal communities obtain their nutrition by consuming diatoms, algal spores, and other microscopic materials while actively moving over rock surfaces (Castenholtz 1961). The influence of nutritional limitation on these species is evident in a variety of interesting variations on this theme, such as the development of territoriality (Branch 1975) and the enhancement of local production by fertilization from the limpets' nutrient-rich excrement and other metabolic products (Connor and Quinn 1984; Plaganyi and Branch 2000). Nonetheless, microalgal feeding through active movement and searching typifies the foraging behavior of limpets in most temperate, fleshy-algal dominated systems, including the eastern North Pacific (Cubit 1984), the western North Atlantic (Steneck 1982), Australia (Creese and Underwood 1982), and New Zealand (Menge et al. 1999). In South Africa, two species of limpets have departed from this foraging mode by becoming macroalgal feeders (Bustamante et al. 1995). Here, dense stands of the kelps *Ecklonia maxima* and *Laminaria pallida* produce large quantities of drift that is convected by waves and currents into the rocky intertidal zone where it is consumed by *Patella granatina*. In a variation on this theme, *Scutellastra argenvillei* traps living kelp fronds under its shell and

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←

3 of eight most parsimonious trees from complete character matrix analysis. D, Unrooted strict consensus tree from complete character matrix analysis with relative maximum shell length represented as branch width. Substantial increases are present in *H. iris–H. kamtschatkama* (New Zealand, Japan, and N.E. Pacific) and *H. midae–H. laevigata* (South Africa and Australia). A single reversal (large → small body size) occurs in the *H. roberti–H. pourtalesii* group (tropical Eastern Pacific and Caribbean). Cold-water species are in bold.

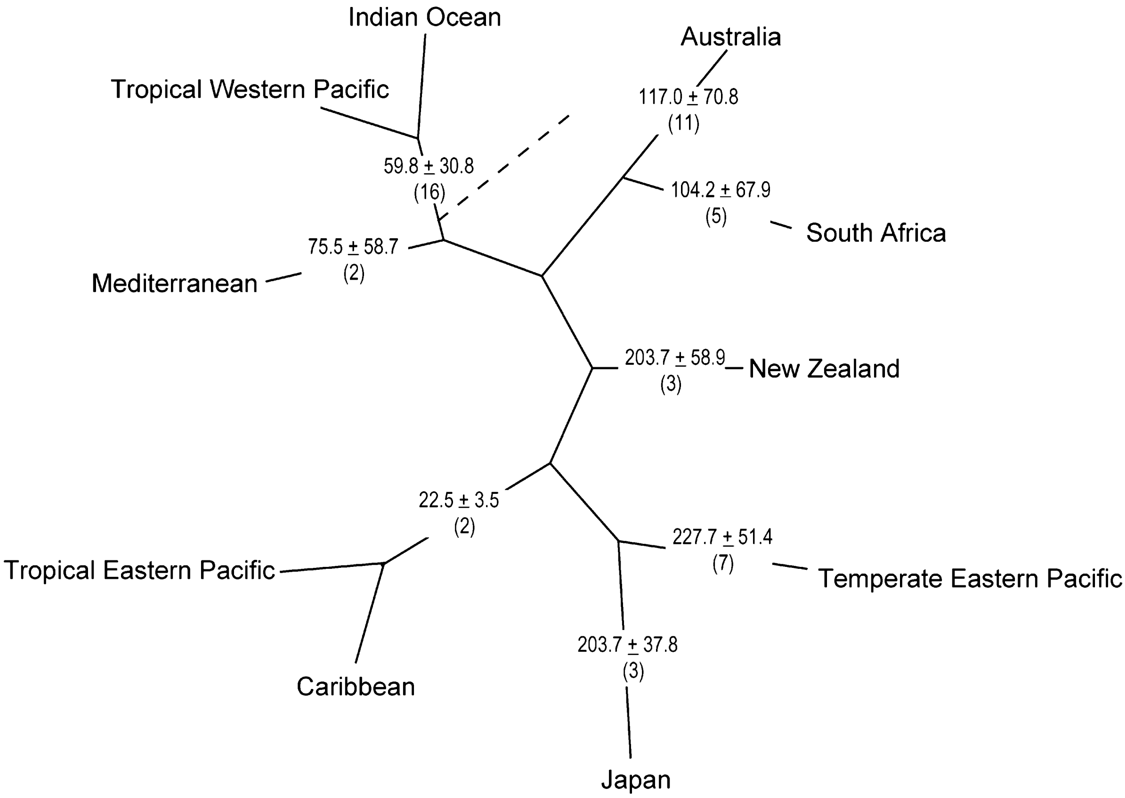

FIGURE 6. Area network of *Haliotis* taxa from tree number 3, regions modified from Geiger (2000). Values represent mean shell length ± standard deviation and (number of taxa). Dashed line indicates probable rooting. Overall pattern suggests dispersal with vicariance events in tropical New World and North Pacific regions.

several individuals collectively feed on the trapped algae. The consequence of this change from micro- to macroalgal feeding is a spectacular increase in population density (200 limpets/m^2) and biomass (10–13 kg/ m^2)—the highest values for any of the diverse South African limpets (Branch 1976), and indeed among the highest values for comparably sized limpet species anywhere in the world.

So far as presently known, tropical haliotids are predominately nocturnal algal feeders, a similar foraging strategy to that used by other tropical vetigastropods (Tahil and Juinio-Menez 1999). A transition from micro- to macroalgal feeding in tropical haliotids is seen in the ontogeny of their radula as they switch from grazing diatoms and blue-green algae when they are small to red (Rhodophyta) macroalgae as they grow larger (Kawamura et al. 2001; Tahil and Juinio-Menez 1999). Temperate abalones also feed on microalgae early in life (Garland et al. 1985; Roberts et al. 1999). As they grow larger, most or perhaps all of these temperate abalone species become obligate or strongly facultative macroalgal drift feeders (Tutschulte and Connell 1988; Shepherd and Steinberg 1992), and in so doing they switch to a more sessile, sit-and-wait foraging strategy.

Haliotid Phylogeography.—When considered together, the above data and patterns suggest the following ecological and biogeographical scenario for the evolution of large body size in the abalones. The earliest abalones appeared during the Late Cretaceous (Maastrichtian), when tropical and subtropical conditions dominated the world oceans. These species probably lived under ecological conditions that were broadly similar to those experienced by modern tropical reef abalones, although much of the reef framework was made up of rudistid bivalves rather than scleractinian corals (Durham 1979). We envision that these early abalones, like extant tropical species, were mobile microalgal grazers.

The earliest haliotids were of Tethyan origin, and although they ultimately became extinct in the New World, our area cladogram suggests that lineages remained in what is now the Mediterranean, and in tropical seas to the east following the closure of the eastern Mediterranean and the Red Sea (Fig. 6). These early tropical abalones gave rise to a Southern Hemisphere fauna that ultimately led to the extant abalones in South Africa, Australia, and New Zealand, and the abalone fauna of the tropical western Pacific. Another lineage subsequently spread northeastward, occupying the New World in the eastern Pacific (Fig. 6). Northeastern Pacific lineages developed from these early ancestors, and New World tropical taxa reappeared before being subsequently divided by the Pliocene closure (3.5 Ma) of the Panamic Portal (Fig. 6). The temperate North Pacific was then occupied and subsequently divided into western and eastern subclades (Fig. 6).

Body Size Evolution.—The onset of the current glacial age caused the coastal oceans at high latitudes to cool, in turn resulting in elevated production, reduced grazing by herbivorous fishes, and the rapid proliferation of fleshy macroalgae on high-latitude reefs. Although these events purportedly led to the evolution of large body size in temperate abalones, both the timing and strength of this effect apparently differed between the Southern and Northern Hemispheres. The onset of polar cooling in the Southern Hemisphere occurred in the late Eocene/Oligocene (Nelson and Cooke 2001; DeConto and Pollard 2003) and thus the temperate Australian, South African, and New Zealand taxa could have originated as early as 40 Ma (Browning et al. 1996). In contrast, polar cooling in the Northern Hemisphere did not begin until the Miocene, around 10 Ma (Barron 2003).

These differences in the timing of polar cooling between the Southern and Northern Hemispheres raise an apparent paradox. If southern temperate systems are so much older than their Northern Hemisphere counterparts, why did the North Pacific abalones become larger (Fig. 3)? The explanation, we propose, lies in regional differences in algal nutritional quality and secondary chemistry. That is, while conditions in the Southern Hemisphere were seemingly well suited for abalone growth, the increases in body size of Southern Hemisphere haliotids were comparatively modest because of the broad occurrence of chemical deterrents to herbivory in Southern Hemisphere macroalgae (Steinberg 1989). Northern Hemisphere algae, in contrast, contain substantially lower concentrations of deterrent secondary metabolites.

Estes and Steinberg (1988) and Steinberg et al. (1995) have argued that this interhemispheric difference in secondary metabolites between Australasian and North Pacific marine algae was driven largely by fundamental differences in food chain length and their resulting influences through top-down forcing (Hunter and Price 1992) and trophic cascades (Paine 1980; Carpenter and Kitchell 1993) on the strength of plant-herbivore interactions. More specifically, Steinberg et al. (1995) argued that Australasian temperate reef systems evolved in the absence of effective predators on benthic macroherbivores, thus resulting in abundant macroherbivore populations and an evolutionary arms race between plant deterrents to herbivory and herbivore resistance to plant defenses. The temperate North Pacific, in contrast, purportedly evolved as a three-trophic-level system with more substantial predator limitation on benthic macroherbivore populations, decoupling in turn the evolutionary arms race between macroalgae and their herbivores. In particular, sea otters (*Enhydra lutris*) and their ecologically analogous ancestors likely provided a setting for the evolution of fleshy macroalgae with low levels of chemical deterrents (Estes and Steinberg 1988). We propose that the emergence of this high quality food source was an important factor in the markedly different evolutionary size increases in these regional haliotid faunas (Figs. 3, 6). Although some of the kelps subsequently spread to the North Atlantic and Southern Hemisphere (Estes and Steinberg 1988; Lindberg 1991; Yoon et al. 2001), this probably did not occur until very recently, and the kelps are not preferentially consumed by Southern Hemisphere haliotids despite their low levels of chemical deterrents (Shepherd and Steinberg 1992).

A seemingly paradoxical consequence in our proposed scenario is that the largest haliotid species known (*H. rufescens*) and one of the most diverse large abalone faunas in the world (eight species) all co-occur in the eastern North Pacific Ocean with what is arguably the large abalones' most devastating natural predator—the sea otter. The sea otter's range was restricted to the North Pacific basin, at least from the Pleistocene onward (Berta and Morgan 1986). As sea otters recovered from the Pacific maritime fur trade, and their numbers and range in central California spread during the mid-1900s, abalone numbers plummeted (Estes and VanBlaricom 1985; Fanshawe et al. 2003). Sea otters are also known to be strongly size-selective consumers (VanBlaricom 1988; Estes and Duggins 1995), preferring the largest available individuals as their prey. How can these patterns be reconciled with our proposed explanation for the evolution of large body size under such relentless predation pressure?

Shallow reefs often are interspersed with cryptic habitats—cracks and crevices in the rocky substrate that provide refuges from predation, and where macroalgal drift accumulates. When sea otters are abundant, abalones and other species of macroinvertebrates occur almost exclusively within these cryptic habitats (Lowry and Pearse 1973; Fanshawe et al. 2003). Living macroalgae, in contrast, occur primarily in exposed, non-cryptic habitats where the intensity of herbivory is low. Thus, we propose that benthic-feeding predators in the North Pacific Ocean have created a small-scale spatial separation in the distribution of plants and their principal herbivores. The production and transport of algal drift provides a trophic connection between the plants and consumers but the disparate spatial distributions of these groups prevent the herbivores from negatively affecting the living plants. The spatial dissociation of plants and their potentially most dangerous enemies, the herbivorous macroinvertebrates, would have prevented the coevolutionary escalation of defense and resistance in this consumer-prey system. The resulting high quality of drift algae in the North Pacific may be responsible for the particularly large body sizes that have been attained by the regional abalone fauna. There is some evidence for this hypothesis in that chemically defended brown algae inhibit growth in various herbivorous macroinvertebrates in the Northern Hemisphere (Vadas 1977; Larson et al. 1980), including the abalones (Winter and Estes 1992). The restricted distribution of abalones to isolated cryptic habitats together with their limited capacity for both gametic and larval dispersal (Prince et al. 1987; Shanks et al. 2003) may also have facilitated speciation by reducing gene flow among isolated populations. Thus, in an indirect way, intense predation may have promoted the evolution of the remarkably large-bodied and diverse abalone fauna in the eastern North Pacific Ocean.

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