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The evolution of gigantism on temperate seashores

GEERAT J. VERMEIJ*

University of California Davis, Department of Geology, One Shields Avenue, Davis, CA 95616

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The extent to which animal lineages achieve large body size, a trait with broad advantages in competition and defence, varies in space and time according to the supply of (and demand for) resources, as well as the magnitude and effects of extinction. Using the maximum sizes of shallow-water marine shell-bearing molluscs belonging to nineteen guilds (groups of species with similar habits and food sources) in seven temperate regions from the Early Miocene to the Recent, the present study examined the controls on productivity and predation that enable and compel large size to evolve. The North Pacific (especially its eastern sector) has been most favourable to large-bodied species from the Pliocene onward. Large productive kelps (Laminariales) evolved there in conjunction with herbivorous mammals, setting the stage through positive feedbacks between production and consumption for the evolution of large molluscan herbivores and suspension-feeders. The evolution of bottom-feeding predatory mammals together with other large predators created intense selection for large molluscan sizes. Very large molluscs in the Early Miocene were concentrated in the southern hemisphere, especially among metabolically passive species. Extinctions, which preferentially targeted the largest members of guilds in most regions, were more numerous in the southern hemisphere and the North Atlantic than in the North Pacific. Minimal disruption, together with the early evolution of metabolically-active consumers and the positive feedbacks they engendered, accounts for the evolution of molluscan gigantism in the North Pacific. *Biological Journal of the Linnean Society*, 2012, **106**, 776–793.

ADDITIONAL KEYWORDS: extinction – Miocene – Mollusca – New Zealand – North Atlantic – North Pacific – Pliocene – South Africa – South America.

INTRODUCTION

When humans began to exploit marine shellfish for food at least 164 000 years ago in South Africa (Marean, 2011) and later elsewhere, they encountered many exceptionally large and abundant edible animal species. Had humans instead begun to search for food on temperate seashores during the Oligocene (32 to 23 million years ago), they would have encountered much smaller shellfish. How this potential food source affected (and was affected by) consumers on the demand side and producers on the supply side over geological time is the subject of the present study. The aim is to probe the circumstances that permitted, compelled, and sometimes disallowed large body size to evolve and be maintained in some of the world's most productive and accessible ecosystems. To that end, geographical and historical comparisons are made of shallow-water marine ecosystems from climatically similar times and places aiming to ascertain when, where, in which ecological guilds, and in which clades very large body size evolved and disappeared.

Adult body size evolutionarily integrates predictable aspects of the demand for (and supply of) resources. Demand is created by the costs of doing the work of life (i.e. metabolism) and by natural selection stemming from competition in its broadest sense including predation (Van Valen, 1976) for locally limiting resources. Natural selection results in large size when being larger confers advantages in acquiring and defending sufficient resources to survive and leave offspring. Within a guild (a group of co-occurring species with similar habits, habitats, metabolic rates, and food sources), large-bodied species tend to be competitive dominants that control a disproportionately large fraction of available resources (Brown & Maurer, 1986). In addition, they enjoy a partial refuge in large size from their most potent predators because the costs in time, energy,

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*E-mail: gjvermeij@ucdavis.edu

and risk of injury required for predators to kill and consume victims rise faster than the benefits with increasing prey size (Palmer, 1990). The vulnerable part of the life cycle, when individuals are small and young, is characterized by rapid growth in places that are relatively safe from enemies, as in the pelagic realm, under stones, in a resistant egg capsule or inside the parent's body. In this way, large-bodied species with high metabolic demands reduce the functional trade-offs between traits necessary for survival early in life and the benefits associated with a large body in the reproductive adult stage.

The extent to which selection drives species toward larger body size depends on enabling factors, which control the supply of (and access to) food. The enabling factors that permit large size to evolve in metabolically active species with high demand include: (1) reliably high productivity (the rate at which food is made available); (2) the existence of technology to tap, defend, and capitalize on available resources; (3) high oxygen availability, especially in cold water; and (4) minimal constraints on access to food from either enemies or from excessive heat, cold, turbulence, and toxicity. Maximum adult size in marine animal species is known to increase along geographical gradients of increasing primary productivity in suspension-feeding bivalves, herbivorous gastropods, and many predatory gastropods and crustaceans (Vermeij, 1978, 1980; Bosman, Hockey & Siegfried, 1987; Reaka-Kudla, 2000; Linse, Barnes & Enderlein, 2006; Sejr, Blicher & Rysgaard, 2009). Species with low metabolism and minimal maintenance costs can attain large size under less productive conditions, although they can do so only if mortality during the slow-growing, small-bodied young stages is low. These latter circumstances produce the 'gentle giant' syndrome of many soft-bodied Antarctic marine animals (Arnaud, 1974; Rosa & Seibel, 2010) and island tortoises.

The conditions that enable and compel the evolution of large body size in consumers vary in space and time. Suspension-feeders are supported by primary production of phytoplankton, which peaks at mid latitudes, especially in regions where nutrients enter from the land via rivers or are brought up to the sea surface from deep reservoirs by upwelling (Mann, 2000). Herbivores depend on primary production on the seafloor, which, on temperate coasts, is highest where nutrient-rich waters wash over extensive beds of large seaweeds and meadows of seagrass (Mann, 2000). The release of copious dissolved organic matter from living and decaying seaweeds also benefits phytoplankton production (Duggins, Simenstad & Estes, 1989; Mann, 2000). In temperate regions, high primary productivity should therefore allow large-bodied species to evolve among both suspension-feeders and herbivores. On the demand side, basal metabolic rates and the intensity of directional selection for traits that enhance competitive ability and antipredatory defence generally increase with higher temperatures and greater food abundance (Vermeij, 2011a, b). Competition and selection may be intense when food is globally scarce, although the ability of a population to respond to selection is minimal (Vermeij, 2004a). There is mounting evidence that demand, especially predation, stimulates primary production (Vermeij, 2010; Vermeij & Leigh, 2011). Enabling factors, metabolism, and selection are thus connected through strong positive feedbacks between consumers and producers. These feedbacks arise because consumers with large appetites exert strong selection on their victim species in favour of rapid growth and therefore higher biomass turnover and productivity. This selection, in turn, permits consumers to become larger, more abundant, and metabolically more active. These feedbacks may become evolutionarily best developed in regions when production and consumption remain relatively undisturbed for long periods of time.

Large body size becomes disadvantageous when the food supply declines or becomes unstable, or when access to food is restricted by conditions unfavourable to biological activity. These adverse circumstances arise during times of widespread extinction, when primary productivity is reduced and positive feedbacks between producers and consumers are disrupted. Such crises place the largest species in a guild at greatest risk of extinction because it is these species that rely most heavily on a predictably prolific supply of food (Vermeij, 2004b; Vermeij, Dietl & Reid, 2008). Regions in which extinction has been minor should therefore have been most favourable to the evolution of very large size.

In the light of these expected patterns, the present study examined how production and consumption together have affected the evolution of gigantism in bottom-dwelling shallow-water molluscs. As an extension of previous work in the North Atlantic (Vermeij *et al*., 2008) and the tropics (Vermeij, 2011a), this present study reports and interprets spatial and temporal patterns in maximum body size in molluscan guilds from four northern and three southern temperate regions. No attempt has been made to quantify the roles of supply and demand because doing so implies that these factors act independently, when in fact they are inextricably linked through feedbacks. Instead, the conditions that have influenced production and consumption in each region are analyzed, showing how far selection has driven species in different trophic categories toward gigantism given the enabling factors prevailing on temperate coasts over approximately the last 20 million years.

MATERIAL AND METHODS

The study concentrated on nineteen guilds containing large-bodied species of shallow-water shell-bearing molluscs representing five ecological categories. These are (1) three guilds of grazers (chitons; limpet-like gastropods including haliotids and patellogastropods; and coiled trochoidean and littorinid gastropods); (2) ten guilds of suspension-feeders (byssally attached epifaunal mytilid mussels; oysters and oyster-like cemented bivalves; pectinid scallops; nonsiphonate shallow-burrowing bivalves in Arcoida and Crassatelloidea; siphonate shallow-burrowing veneroidean bivalves; active shallow-burrowing cardiid bivalves; shallow-burrowing active mactrid bivalves; deep-burrowing mactrid and myoidean bivalves; epifaunal calyptraeid slipper limpets; and high-spired epifaunal to shallowly burrowing turritellid gastropods); (3) deposit-feeders (tellinoidean bivalves); (4) chemosymbiotic bivalves (lucinids and thyasirids); and (5) four guilds of predators (drilling soft-bottom naticids; drilling muricids, mainly on hard bottoms; shell-wedging and generalized predatory buccinoidean whelks; and shell-enveloping volutids). These trophic guilds incorporate considerable variation: most large grazers have broad diets that often include sessile animals, as well as primary producers (Otaíza & Santelices, 1985; Briscoe & Sebens, 1988; Camus, Daroch & Opazo, 2008; Sanhueza *et al*., 2008; Aguilera, 2011); and suspension-feeders take up dissolved organic matter and food particles from the sediment in addition to particulate food suspended in water (Compton *et al*., 2008).

Although several additional guilds contain notably large species, these are excluded because they have not achieved a cosmopolitan distribution in the temperate zones either in the living biota or in the recent geological past. For example, ranellid gastropods are unknown from the Miocene to the Recent in the north-western Atlantic; byssally attached isognomonid and pinnid bivalves on unconsolidated bottoms have never penetrated the temperate zone in the North Pacific and are absent in the Recent faunas of the north-western Atlantic, South America, and southern Africa. Fast-burrowing razor clams have never lived in New Zealand. Other guilds are analyzed only for certain time intervals because of their restricted distribution at other times. For example, volutid gastropods were temperate-cosmopolitan until the Pliocene but are not represented in the living biotas of the North Atlantic; and shallow-water cardiids are unknown in South America and New Zealand today, even though large-bodied fossil species are prominent in both regions.

Seven temperate regions were considered: four in the northern hemisphere (north-east Atlantic, north-west Atlantic, north-east Pacific, and north-west Pacific) and three in the southern hemisphere (southern Africa, South America, and New Zealand). Most South American data come from the west coast (Peru and Chile) but Argentina, whose biota differs somewhat from that of the Pacific side and where most species do not reach the large sizes of those in western South America, was also considered. The only temperate region not considered is Australia, for which shallow-water faunas comparable to those in other temperate regions are poorly represented in the fossil record. Three time periods were chosen for comparison: the Early to Early Middle Miocene (23 to 16 million years ago), Pliocene (5.3 to 2.5 million years ago), and Recent. A latest Oligocene limpet has been included in the Early Miocene time bin for New Zealand.

Data on the maximum adult shell size (largest linear dimension) of the largest species in each guild, region, and time period were taken from the taxonomic literature, supplemented by specimens in the author's collection and in the following museums: California Academy of Sciences (San Francisco), University of California Museum of Paleontology (Berkeley), Los Angeles County Museum of Natural History, US National Museum of Natural History (Washington), National Museum of Natural History (Leiden), and University Museum of the University of Tokyo. Kazutaka Amano provided some data for Japanese fossil species, and Thomas DeVries and Sven Nielsen supplied additional information about western South American fossils. The largest species of guilds were identified from complete faunal lists and by scanning all available museum collections.

Emphasis on maximum size of the largest species, especially of metabolically active ones, is justified because these species are least constrained (and most benefited) by enabling factors and have been most susceptible to selection by powerful predators (Vermeij *et al*., 2008; Vermeij, 2011a). The choice was to read the fossil record literally and to ignore potential artefacts and biases associated with preservation and collection effort. Attempts to eliminate or compensate for such sampling problems result in unacceptable loss of data and introduce many new problems.

For each guild and each time interval, temperate regions were assigned a rank according to the maximum size of the largest species, with a rank of 1 representing the largest-bodied species in that guild among the regions considered. Species with 10% of each other's maximum length were assigned the same rank. For example, the largest known living temperate muricids are the north-west Pacific *Rapana venosa* (Valenciennes, 1846; 190 mm), the north-east Pacific *Forreria belcheri* (Hinds, 1843; 177 mm), and the western South American *Concholepas concholepas* (Bruguiére, 1789; 179 mm). All three species were assigned the rank of 2. The next largest species, *Dicathais orbita* (Gmelin, 1791) from New Zealand, is ranked fourth. For a given time interval, a mean rank was calculated for each region by adding the ranks of each guild and dividing by the number of guilds. All seven temperate regions were considered for the Recent and the Pliocene but, for the Early Miocene, southern Africa was excluded owing to the absence of fossils. To facilitate temporal comparisons, Pliocene rankings of regions were calculated with and without southern Africa.

RESULTS AND DISCUSSION

Maximum size in living faunas

Of the seven living temperate faunas considered, the north-east and north-west Pacific together stand out as housing exceptionally large-bodied species (Tables 1, 2). Guilds whose largest temperate species worldwide occur in the North Pacific (14 of 19, 74%) are found on hard as well as soft bottoms and represent all trophic categories; their number significantly exceeds the $19*(2/7) = 5.4$ expected if the largest species were distributed evenly among regions (chi-squared, $P < 0.01$). At the other end of the spectrum are the two North Atlantic faunas, which lack large coiled herbivorous gastropods, chemosymbiotic bivalves, suspension-feeding turritellids, and predatory muricids. Compared to the north-east Atlantic, the north-west Atlantic supports markedly larger species in eight of 11 guilds on soft bottoms, confirming earlier results (Vermeij *et al.*, 2008). The three southern-hemisphere faunas have mean ranks between those of the two North Pacific and the two North Atlantic faunas (Table 1). Suspension-feeding guilds, however, hold the lowest average rank in western South America, followed closely by southern Africa (Table 1).

Table 1. Mean ranks of temperate regions according to the maximum sizes of the largest species in molluscan guilds

Period and region	Mean ranks and number of guilds: All guilds		Suspension-feeders	
Recent				
North-east Pacific	2.4	16	2.7	9
North-west Pacific	2.4	16	2.3	9
South America	4.5	16	4.9	9
New Zealand	4.5	16	4.6	9
Southern Africa	4.3	16	4.8	9
North-east Atlantic	5.1	16	4.5	9
North-west Atlantic	4.8	16	4.3	9
Pliocene with southern Africa				
North-east Pacific	3.2	12	4.1	6
North-west Pacific	3.3	12	3.6	6
South America	4.3	12	4.5	6
New Zealand	3.8	12	3.1	6
Southern Africa	4.8	12	5.1	6
North-east Atlantic	5.0	12	4.4	6
North-west Atlantic	3.5	12	3.1	6
Pliocene without southern Africa				
North-east Pacific	2.8	17	3.0	10
North-west Pacific	3.0	17	3.1	10
South America	3.9	17	4.2	10
New Zealand	3.4	17	3.0	10
North-east Atlantic	4.5	17	4.4	10
North-west Atlantic	3.4	17	3.6	10
Early Miocene				
North-east Pacific	3.7	13	4.3	7
North-west Pacific	3.3	13	2.9	7
South America	2.9	13	2.8	7
New Zealand	2.2	13	2.2	7
North-east Atlantic	4.0	13	4.7	7
North-west Atlantic	3.9	13	3.4	7

Maximum size is greater in at least one tropical region, which is usually the Indo-West Pacific or eastern Pacific (Vermeij, 2011a), than in any temperate area in eight guilds (low-coiled hard-bottom grazing gastropods, chemosymbiotic lucinids, inactive turritellid and nonsiphonate burrowing bivalves, cockles, and predatory muricids, whelks, and volutids). Guilds with very large-bodied species in the tropics that are only sporadically represented or entirely absent from temperate regions include high-spired and stromboidean herbivores, cowrie-like gastropods, worm-eating gastropods, and echinoderm-feeders. Guilds that reach larger sizes in one or more temperate regions include chitons, limpets feeding on fleshy seaweeds, suspension-feeders in seven guilds (mussels, scallops, oysters, mactrids, veneroids, deep-burrowing bivalves, and slipper limpets), deposit-feeding tellinoideans, and predatory naticids. These geographical patterns reflect the greater abundance and productivity of phytoplankton and the larger size of fleshy seaweeds in the temperate zones.

Size patterns in the past

The distribution of maximum size among temperate regions has changed substantially over the course of the last twenty million years. During the Early Miocene, the largest temperate species in most (13 of 18) guilds lived in the southern hemisphere (New Zealand and South America), representing more than

Table 2. Maximum sizes in molluscan guilds by period and region

	Maximum size (mm) by region						
Guild and period	NEP	NWP	SAM	NZ	SAF	NEA	NWA
Herbivores							
Chitons							
Recent	350	350	200	87	100	70	50
Limpets							
Recent	313	210	135	162	190	100	31
Pliocene	225	200	209	160	148	43	55
Early Miocene	99	120	50	200	–	29	44
Coiled gastropods							
Recent	154	130	57	120	132	53	42
Pliocene	75	85	40	90	70	20	24
Early Miocene	34	65	–	80	–	–	19
Suspension-feeders							
Turritellids							
Recent	54	80	58	86	106	58	25
Pliocene	60	110	70	170	47	70	110
Early Miocene	80	110	110	170	–	35	95
Slipper limpets							
Recent	57	60	100	62	45	23	59
Pliocene	108	50	85	76	36	35	65
Early Miocene	72	75	50	50	–	38	48
Mussels							
Recent	255	217	208	163	160	220	140
Pliocene	285	180	100	132	–	150	125
Early Miocene	135	131	155	182	–	–	155
Nonsiphonate burrowers							
Recent	45	127	40	118	70	70	43
Pliocene	95	100	47	90	100	90	105
Early Miocene	44	98	128	153	–	65	81
Scallops							
Recent	228	200	140	157	106	148	174
Pliocene	228	220	138	175	–	168	200
Early Miocene	220	150	200	200	–	75	120
Veneroids							
Recent	160	127	86	81	88	125	120
Pliocene	74	95	142	109	97	103	150
Early Miocene	64	88	98	85	–	74	97
Matricids							
Recent	155	145	123	111	113	114	175
Pliocene	85	125	113	84	68	130	130
Early Miocene	85	101	–	–	–	10	51
Deep burrowers							
Recent	280	260	110	121	137	144	183
Pliocene	200	165	46	160	244	129	135
Early Miocene	82	111	80	105	–	90	115
Cardiids							
Recent	140	128	–	–	–	103	131
Early Pliocene	105	91	155	155	–	68	68
Early Miocene	58	102	146	130	–	60	65
Oysters							
Recent	228	450	50	109	183	180	150
Pliocene	384	300	217	300	93	100	122
Early Miocene	113	–	172	136	–	40	184

Table 2. *Continued*

	Maximum size (mm) by region						
Guild and period	NEP	NWP	SAM	NZ	SAF	NEA	NWA
Deposit-feeders							
Tellinoids							
Recent	150	135	94	65	85	55	55
Pliocene	100	126	77	35	72	64	61
Early Miocene	61	114	54	–	–	62	59
Chemosymbiotic bivalves							
Recent	250	70	–	43	34	40	48
Pliocene	–	76	–	97	–	23	60
Early Miocene	61	76	78	97	–	31	51
Predators							
Naticids							
Recent	166	73	85	33	41	38	100
Pliocene	102	48	44	51	21	50	56
Early Miocene	59	52	57	70	–	40	48
Muricids							
Recent	177	190	179	118	83	63	68
Pliocene	92	50	130	80	110	63	120
Early Miocene	110	–	45	80	–	93	84
Volutids							
Recent	125	220	500	205	235	–	–
Pliocene	160	100	200	180	–	200	350
Early Miocene	170	163	195	135	–	125	73
Whelks							
Recent	170	210	128	235	237	189	253
Pliocene	170	169	100	–	101	130	250
Early Miocene	74	80	110	160	–	99	173

NEA, north-east Atlantic; NEP, north-east Pacific; NWA, north-west Atlantic; NWP, north-west Pacific; NZ, New Zealand; SAF, southern Africa; SAM, South America.

Literature sources: North-east Pacific: Addicott (1970); Addicott (1976); Allison & Marincovich (1982); Clark & Arnold (1923); Coan *et al*. (2000); Grant & Gale (1931); Hertlein (1937); Marincovich (1977, 1981, 1983, 1988); Smith (1991).

North-west Pacific: Amano & Ogihara (2012); Chinzei (1959, 1961); Egorov (1992); Gladenkov & Sinelnikova (1990); Gladenkov *et al*. (1984, 1988); Golikov & Gulbin (1978); Hatai *et al*. (1970); Kurihara (2010); Majima (1989); H. Noda *et al*. (1995); Y. Noda (1992); Ogasawara *et al*. (1988); Ozawa and Tomida (1996); Scarlato (1981); Shibata (1957); Titova (1994); Yokoyama (1922).

South America: Castilla *et al*. (1994); DeVries (1997, 2007); DeVries & Hess (2004); Frassinetti (1993); Genta-Iturrería *et al*. (2011); Griffin & Nielsen (2008); Herm (1969); von Ihering (1907); Marincovich (1977); Morsán & Ciocco (2004); Nielsen & Frassinetti (2007); Osorio & Ramajo (2007); Pastorino (2005); McLean (1984); del Río (2004); del Río & Camacho (1998); del Río & Martinez (2006); Sanhueza *et al*. (2008); Signorelli & Pastorino (2011); Taylor & Smythe (1985); Waller (1969).

New Zealand: Beu (1995, 2004, 2006, 2010); Beu & Maxwell (1990); Eagle (1996); Fleming (1973); King (1934); Marwick (1948, 1965); Powell (1938, 1979); Powell & Bartrum (1929).

South Africa: Carrington & Kensley (1969); Kensley (1972, 1974); Kensley & Pether (1986); Kilburn & Rippey (1982); Kilburn & Tankard (1975).

North-east Atlantic: Warén & Klitgaard (1991); Vermeij *et al*. (2008).

North-west Atlantic: Petuch & Drolshagen (2010); Vermeij *et al*. (2008).

twice the number that would be expected from a random distribution of maximum sizes across regions (chi-squared, $P < 0.01$). The two North Atlantic regions occupy the lowest rank: the number of guilds with the smallest maximum size in either the north-east or north-west Atlantic (ten of 18) is significantly higher than the six expected (chi-squared, $P < 0.05$). In the Early Pliocene, the two North Pacific regions hold the top ranks of all guilds taken together but, with predatory guilds treated separately, the north-west Atlantic ranks highest (Table 1). Overall, the largest temperate Pliocene species are distributed evenly across regions. From the Early Miocene to the Recent, there is a general northward shift in gigantism from the southern hemisphere to the North Pacific.

Temporal trends in maximum body size within guilds can be characterized either as increases (including cases of no significant change) or decreases. From the Early Miocene to the Pliocene, maximum size increased in a majority of guilds in all regions (Table 3). The number of increases significantly exceeds the number of decreases in the four northern regions (chi-squared, $P < 0.01$) but not in the two southern ones. From the Pliocene to the Recent, increases outnumbered decreases in most regions but significantly so only in the north-west Pacific (Table 3). The north-west Atlantic is the only region where maximum size decreased in a majority of guilds (nine versus eight). From the Early Miocene to the Recent, increases in maximum size exceeded decreases significantly (chi-squared, $P < 0.05$) in the north-east and north-west Pacific and in the north-east Atlantic but did not do so in South America or the north-west Atlantic; in New Zealand, decreases slightly outnumbered increases (Table 3).

Table 3. Proportion of decreases in maximum body size in guilds

Interval and region	Number of decreases/ total number of guilds
Pliocene to Recent	
North-east Pacific	6/17 = 0.35
North-west Pacific	1/17 = 0.059
South America	5/16 = 0.31
New Zealand	8/17 = 0.47
Southern Africa	4/13 = 0.31
North-east Atlantic	7/16 = 0.44
North-west Atlantic	9/16 = 0.56
Early Miocene to Pliocene	
North-east Pacific	2/17 = 0.12
North-west Pacific	4/16 = 0.25
South America	7/15 = 0.47
New Zealand	6/16 = 0.37
North-east Atlantic	3/16 = 0.19
North-west Atlantic	2/18 = 0.11
Early Miocene to Recent	
North-east Pacific	3/18 = 0.17
North-west Pacific	1/16 = 0.06
South America	5/14 = 0.36
New Zealand	9/15 = 0.60
North-east Atlantic	4/15 = 0.27
North-west Atlantic	8/18 = 0.44

The six guilds of sedentary suspension-feeders as adults (turritellids, slipper limpets, mussels, scallops, oysters, and nonsiphonate burrowers) show a larger number of decreases in maximum size than the four guilds of suspension-feeders in which individuals are either mobile or produce powerful feeding currents (veneroids, mactrids, cockles, and deep burrowers). From the Pliocene to the Recent, decreases account for 24 of 41 cases (59%) in the sedentary group and only five of 25 cases (20%) in the active group (chi-squared, $P < 0.01$). From the Early Miocene to the Pliocene, the trend is the same but is not quite statistically significant at the 0.05 level: sedentary guilds witnessed decreases in maximum size in 13 of 35 cases (37%), whereas active guilds saw decreases in only two of 22 cases (9.1%). A similar difference between passive and active suspension-feeding guilds was noted for size patterns in the Late Neogene tropics (Vermeij, 2011a).

Overall, these data indicate that maximum size increased most consistently and to the greatest extent in the North Pacific. They therefore suggest that conditions in the North Pacific (i.e. high productivity, intense selection by enemies, and minimal disruption) were particularly favourable for the evolution and maintenance of very large size in shallow-water molluscs.

THE ROLE OF PRODUCTIVITY

Planktonic production and suspension-feeding

The temperate regions with the highest estimated planktonic primary productivity (up to 800 g C m^{-2} $year^{-1}$) are the upwelling zones in the Benguela Current system off southwestern Africa and the Humboldt Current system off Peru and northern Chile (Walsh, 1988; Mann, 2000). These are not, however, the regions with the largest suspension-feeding molluscs. In fact, the mean rank of nine suspension-feeding guilds in southern Africa (4.7) and western South America (5.1) are the lowest among the seven regions considered (Table 1). These same regions rank lowest among suspension-feeders in the Early Pliocene as well, when intense upwelling was already a prominent feature of ocean conditions there (Dunbar, Marty & Baker, 1990; Diesterh-Haass, Meyers & Vidal, 2002; Heinrich *et al.*, 2011; Rommerskirchen *et al.*, 2011). The upwelling systems of the California Current in the north-east Pacific are less productive (150 g C m^{-2} $year^{-1}$) but support the next-to-largest suspension-feeders (mean rank 2.7). The upwelling regime in California has existed with varying intensities since Late Miocene times (Barron, 1998; Jacobs, Haney & Louie, 2004) but upwelling may have been reduced (or been less effective at bringing up nutrients from deep water) during the Early Pliocene; yet the mean rank of suspension-feeding guilds in the Early Pliocene north-east Pacific is tied for highest place when South African data are excluded (Table 1).

A possible explanation for the lack of correspondence between maximum size of suspension-feeders and estimated planktonic productivity is that peak production and nutrient concentrations in upwelling regions occur well offshore (Barber, 1988; Walsh, 1988; Mann, 2000), whereas the suspension-feeders are found nearshore in shallow subtidal and lowest intertidal habitats. Unpredictability in the intensity of upwelling, nutrient levels, and planktonic productivity from year to year may be another contributing factor, especially on the west coast of South America, where normally high rates of production plummet during EI Niño-Southern Oscillation events (Barber, 1988). The largest suspension-feeding mussels, barnacles, and burrowing bivalves in western South America are found not in the zone of upwelling but in the quiet waters of southern Chile, where strong tidal currents sweep nutrients over the bottom but upwelling does not occur. In the Late Miocene and Early Pliocene of California, exceptionally large mussels, scallops, oysters, and slipper limpets are found in embayments and in the inland sea of the San Joaquin Basin, where nutrient enrichment occurs by the incursion of waters from the adjacent open Pacific Ocean (Kirby, 2001; Bowersox, 2005). Embayments and lagoons were also much more extensive on the western coast of South America during the Early Pliocene, when sea levels were higher and uplift of the coast had not proceeded as far (Dunbar *et al*., 1990).

Benthic productivity and herbivory

Benthic primary productivity in the temperate zones is 1.5 to 10 times higher than planktonic productivity (Smith, 1981; Mann, 2000; Worm, 2000) and is concentrated nearshore. By releasing large quantities of dissolved organic matter, which is subsequently absorbed by bacteria or coagulated into particles and therefore accessible to suspension-feeders (Duggins *et al*., 1989; Mann, 2000), algal primary producers on the seafloor contribute to the food supply of all shallow-water consumers. On temperate coasts, therefore, benthic producers should have a greater overall influence on primary consumers (suspension-feeders as well as herbivores) than pelagic producers.

The highest estimated rates of benthic production are for kelps of the genus *Postelsia* in Washington State in the north-east Pacific (Leigh *et al*., 1987; 8.6 kg C m^{-2} $year^{-1}$), although even higher rates are likely in the absence of herbivores (Paine, 2002). Typical rates of primary production by large seaweeds along temperate coasts range from 1.0 to almost 1.8 kg C m^{-2} $year^{-1}$ (Mann, 2000), with north-east Atlantic maxima being somewhat lower than those in the north-west Atlantic, north-east Pacific, southern Africa, and temperate Australia. Productivity of temperate seagrass beds is less well known, although the highest estimates are 0.8 kg C m^{-2} $year^{-1}$ for *Zostera* meadows in Denmark (Mann, 2000). From these estimates, the north-east Pacific might be expected to support the largest herbivores and suspension-feeders, as is indeed the case (Tables 1, 2). Questions remain, however, about how regional differences in productivity and herbivory have arisen.

Very large brown seaweeds, which account for the highest rates of primary production on temperate coasts, arose in only two regions. Kelps (order Laminariales) originated in the North Pacific, with the largest species evolving on its eastern side. By the Early Pliocene at the latest, kelps had spread to the North Atlantic, southern Africa, South America, and temperate Australasia (Estes & Steinberg, 1988; Coyer, Smith & Andersen, 2001; Lane *et al*., 2006). The fucoid *Durvillaea* likely arose in the southwestern Pacific and has subsequently spread to western South America (Fraser *et al*., 2010).

The North Pacific is also the only region where seaweed-eating marine mammals evolved. Land-derived desmostylians, which lived on North Pacific shores from the Early Oligocene to the Late Miocene (Domning, Ray & McKenna, 1986; Ray, Domning & McKenna, 1994; Beatty, 2009), are inferred to have fed on seagrasses, although some species may also have included algae in their diet (Domning, 1989; Clementz, Hoppe & Koch, 2003). Seagrass feeding sirenians of the genus *Dusisiren* extended to the north-east Pacific from warmer American waters during the Early Middle Miocene and had spread to Japan by the Late Miocene. By the Early Pliocene, one lineage of *Dusisiren* had given rise to the much larger *Hydrodamalis*, represented in the Recent fauna by *Hydrodamalis gigas*, a species hunted to extinction by humans (Domning, 1976, 1978; Takahashi, Domning & Saito, 1986).

Kelps differ from other seaweeds by their rapid growth, high productivity, large standing crop, nutrient storage, and vascular system (Mann, 1973; Mann, Chapman & Gagné, 1980). These traits may have evolved in response to natural selection by endothermic herbivores with large appetites (Vermeij, 2004a, 2010). Seaweed-eating marine mammals are unknown outside the North Pacific. Many anseriform birds (geese, swans, and ducks) feed on seagrasses, and some gulls (*Larus*) and geese (*Branta* in the northern hemisphere, *Chloephaga* in southern South America) occasionally consume ephemeral algae

(Summers & Grieve, 1982; Hori, Noda & Nakao, 2006), although specialized kelp-eating birds have not evolved. Mammals therefore appear to be largely responsible for the evolution of highly productive seaweeds in the North Pacific.

In southern New Zealand, *Durvillaea* is consumed by the large (45 cm) wrasse *Odax* (Taylor & Schiel, 2010), which belongs to a lineage originating approximately 38 Mya during the Late Eocene (Clements *et al*., 2004). Species of the southern-hemisphere lobster genus *Jasus* consume large brown seaweeds on islands in the southern Indian and Atlantic Oceans (Beurois, 1975) and may well do so in southern Africa, South America, and New Zealand as well. One or more of these large ectothermic herbivores may thus have influenced the evolution and adaptive characteristics of *Durvillaea*.

The ability of some abalones (*Haliotis* spp.), South African limpets (*Cymbula* spp.), and sea urchins to capture and consume large drifting seaweeds not only increased the effective productivity and stock of algal foods (Bustamante, Branch & Eekhout, 1995), but also could have contributed to the evolution of large size in these herbivores, as suggested for kelp-eating abalone by Estes, Lindberg & Wray (2005). Consumption of large drifting seaweeds is known in the North Pacific, South Africa, South America, and New Zealand (Branch, 1971; Tegner, 1980; Duggins, 1981; Moreno & Sutherland, 1982; Dayton, 1985; Vásquez & Buschmann, 1997).

It is noteworthy and puzzling that the presence of productive kelps and high-shore fucoids elicited feeding specialization by small littorinid and patellid gastropods in the north-eastern Atlantic (Vermeij, 1992) but did not lead to the evolution of large herbivores anywhere in the North Atlantic. Although the north-eastern Atlantic limpet *Patella vulgata* Linnaeus, 1758, can trap and feed on drifting upper-shore fucoids (Lorenzen, 2007), no North Atlantic herbivorous mollusc is sufficiently large to catch and eat drifting kelp.

In short, very large herbivorous molluscs arose in regions where other high-energy herbivores (mammals in the North Pacific, fish in the southwestern Pacific) selected for fast-growing, large seaweeds, and where the ability to capture drifting kelps evolved. The region with the largest seaweeds, highest-energy herbivores, and most diverse herbivores capable of trapping drifting kelps is the North Pacific.

Despite their high productivity and the presence of endothermic herbivorous mammals and birds since the Early Oligocene in the North Pacific and the Miocene in the North Atlantic and South America, temperate seagrass meadows lack herbivorous molluscs greater than 15 mm in length. This situation contrasts markedly with tropical seagrass communities, which have supported herbivorous gastropods of 100 mm length or more from the Early Eocene onward (Vermeij, 2011a). The reasons for this contrast remain unclear.

PREDATION

If competition among, and selection by, predators is a primary agency in the evolution of large body size in prey species, the spatial and temporal patterns in maximum body size described in the present study would imply that: (1) predation is most intense, or has been least constrained, in the north-east Pacific and most encumbered in the North Atlantic and (2) predators have become increasingly powerful agents of selection on many temperate shores since Early Miocene times, especially in the North Pacific. As shown below, there is substantial but not complete support for these predictions.

The north-east Pacific stands out as a region with exceptionally large and diverse predators of shell-bearing molluscs. The largest species worldwide in four guilds of ectothermic predators in addition to drilling naticid gastropods are found in the north-east Pacific: octopods (*Enteroctopus dofleini*, with a lateral spread of 9.6 m and weighing up to 330 kg; Newman, 1994); sea stars ingesting whole prey (*Pycnopodia helianthoides*, subtidal individuals up to 1.5 m in diameter; Mauzey, Birkeland & Dayton, 1968); sea stars using force to open bivalves (*Pisaster ochraceus*, subtidal individuals at least 45 cm in diameter and weighing more than 3 kg; Paine, 1976); and cancrid crabs (*Cancer productus*, up to 267 mm wide; Harrison & Crespi, 1999).

Endothermic predators capable of eating large molluscan prey have evolved only in the North Pacific, the western coast of South America, and as minor players in the north-west Atlantic. The earliest to do so were Early Miocene amphicynodontid bear-like carnivores of the genus *Kolponomos* in the north-east Pacific. According to Tedford, Barnes & Ray (1994), they had shell-crushing dentition and strong neck musculature consistent with a diet of large intertidal molluscs. The otariid seal *Gomphotaria* from the Late Miocene of southern California was likely also a shellcrusher (Barnes & Raschke, 1991). Walruses (Odobenidae), which feed on burrowing bivalves by using suction to remove the soft parts from the shell (Lowry, Frost & Burns, 1980; Oliver *et al*., 1983; Fukuyama & Oliver, 1985), have Early Middle Miocene origins in the North Pacific (Deméré & Berta, 2001; Kohno, 2006), although when fish-eating was replaced by benthic predation on molluscs in this group remains unknown. The sea-otter genus *Enhydra* in the Mustelidae is a member of an Old

World clade of otters that likely became marine in the north-west Pacific (Koepfli *et al*., 2008). It preys on sea urchins, large rocky-shore and soft-bottom molluscs, and many other animals (Calkins, 1978; VanBlaricom, 1988; Kvitek *et al*., 1992) on both sides of the North Pacific. The fossil record of *Enhydra* (Willemsen, 1992) begins in the earliest Pleistocene.

On the western temperate coast of South America, the sea otter *Lontra felina* (Molina, 1782) is an important shell-crushing predator of large molluscs on exposed rocky shores (Castilla & Bahamondes, 1979). Phylogenetic analyses show this species is derived from a Patagonian lineage of otters that became marine in the Late Pleistocene (Koepfli *et al*., 2008; Vianna *et al*., 2010, 2011).

Three lineages of benthically feeding marine mammals are known from the North Atlantic, although only one originated there and none survives on temperate Atlantic shores. The walrus lineage (*Odobenus*) entered the Atlantic during the Early Pliocene and persists in the Arctic sector (Repenning, 1976). *Enhydra* was present in the Pleistocene of the North Sea Basin (Willemsen, 1992). An Early Pleistocene occurrence of *Enhydra* in Arctic Alaska (Hopkins & Marincovich, 1984; Carter *et al*., 1986) supports the hypothesis that *Enhydra* entered the temperate Atlantic by way of the Arctic from the North Pacific. Finally, the eastern North American sea mink (*Mustela macrodon*) became an intertidal shell-crusher during the latest Pleistocene or Holocene and has become extinct in historic time (Waters & Ray, 1961; Sealfon, 2007). The bearded seal (*Erignathus barbatus*) has a broad diet including small molluscs (Lowry *et al*., 1980; Marshall, Kovacs & Lydersen, 2008). This mainly Arctic species, which extends into the northern Bering Sea as well, has not invaded the temperate waters of the Atlantic and is not considered further here.

Although birds are important endothermic predators of molluscs and other shore animals in all temperate and polar regions, their small size and limited capacity to handle large prey make birds poor candidates as major agents of selection favouring large size in molluscs. The birds capable of taking the largest prey (i.e. gulls, oystercatchers, crows, and eider ducks of the genus *Somateria*) are limited to prey smaller than 55 to 73 mm in maximum dimension (Webster, 1941; Harris, 1965; Norton-Griffiths, 1967; Brun, 1971; Dunthorn, 1971; Baker, 1974; Hartwick, 1976; Zach, 1978; Hockey & Branch, 1984; Lindberg, Warheit & Estes, 1987; Cadée, 2008a, b). This upper size limit is smaller than that of co-occurring predators such as sea otters, muricids, anticids, large whelks, octopods, lobsters, crabs, and sea stars that use force to open bivalves. Other molluscivorous birds are restricted to much smaller prey (Navarro, Velasquez & Schlatter, 1989; González, Piersma & Verkuil, 1996; Piersma *et al*., 2003; Cadée, 2011).

Ectotherms, especially sea stars and crustaceans, are likely to be important agents of selection for large size in molluscan prey in all temperate regions. In South America, they include species of the crab genus *Cancer*, the octopod *Enteroctopus*, and sea stars of the genera *Heliaster* and *Meyenaster*, as well as muricid gastropods and, on the Patagonian coast, large volutids (Dayton *et al*., 1977; Ortiz *et al*., 2003; Escobar & Navarrete, 2011). In New Zealand, where no molluscivorous marine mammals occur, the top predators of molluscs are clawless palinurid lobsters of the genus *Jasus* and the sea star *Stichaster*. Southern Africa also lacks marine mammals; top predators there include *Jasus* and the sea star *Marthasterias* (Griffiths & Seiderer, 1980; Butler, Steneck & Herrnkind, 2006). Finally, in the North Atlantic, the largest living molluscivores are cod and clawed nephropid lobsters of the genus *Homarus* (Butler *et al*., 2006).

In summary, the available evidence indicates that large endothermic predators capable of eating large molluscs appeared early in the North Pacific, and much later if at all in other temperate regions. These predators may account for the very large size of species in many molluscan and non-molluscan guilds in the North Pacific. It remains a mystery, however, which selective agents were responsible for the large size of many Miocene species in the southern hemisphere.

EXTINCTION AND SIZE

The magnitude of species-level extinction among molluscs since the Early Pleistocene in the temperate marine realm varies from a low of 30% to 39% in the north-east and north-west Pacific (Stanley, 1986b; Bowersox, 2005), to highs of 79% in the north-west Atlantic (Vermeij *et al*., 2008) and 83% to 88% in South America (Guzmán *et al*., 2000; Rivadeneira & Marquet, 2007). The Spearman rank correlation between the post-Pliocene magnitude of extinction and the mean rank of the largest species in Recent guilds in the seven regions is –0.72, indicating that extinction interferes with the evolution of large body size. Indeed, extinction was more severe among the largest members of guilds than among molluscs as a whole in all temperate regions except South America, confirming previous work in the North Atlantic (Vermeij *et al*., 2008). Pliocene to Early Pleistocene giants had magnitudes of extinction varying from 56% in the north-west Pacific and 76% in the north-east Atlantic to 88% in the north-west Atlantic and 94% in New Zealand. Stanley (1986a) previously suggested that Pliocene extinctions in the warm-temperate western Atlantic were not size-biased; and Smith & Roy (2006) showed that large north-east

Pacific scallops had, on average, a lower magnitude of extinction than smaller species. The latter study, however, included several species in their largest size class. Reexamination of their data shows that the single largest species in each Pliocene guild was more prone to extinction than other large species, consistent with the present findings.

Several large-shelled taxa became extinct during or after the Pliocene without being replaced by modern equivalents. They include the pteriodean bivalves *Hippochaeta* in the north-west Atlantic, *Neopanis* in New Zealand, and '*Isognomon*' in Chile and South Africa; the large New Zealand cardiid *Maoricardium*; and the volutids *Volutifusus* in the north-west Atlantic and 'S*caphella*' in the north-east Atlantic. The inclusion of these taxa would have made the difference between the magnitude of extinction of the largest members of guilds and that of molluscs as a whole even more stark. It is noteworthy that all these unreplaced taxa, as well as other large-bodied species that became extinct and were ecologically replaced by large species in different clades, lived in nutrient-rich lagoons and bays, environments that were largely obliterated in the north-east Pacific and in western South America (Jacobs *et al*., 2004; Bowersox, 2005; Kiel & Nielsen, 2010).

Clade identity and contingency

The identity of clades to which the largest members of a guild belong varies both in space and over time. In the guild of living limpet-like herbivores, for example, the largest species belong to Fissurellidae in South America, to a clade within Haliotidae in the North Pacific, and to a separate haliotid clade in New Zealand and southern Africa (Estes *et al*., 2005). Among scallops, comprising the single clade Pectinidae, the largest living species belong to the clades Pectinini (*Pecten* in New Zealand, South Africa, and the north-east Atlantic), Palliolini (*Placopecten* in the north-west Atlantic), Aequipectinini (*Argopecten* in western South America), and Chlamydini (*Mizuhopecten* in the north-west Pacific, *Patinopecten* in the north-east Pacific). In the Pliocene, still other pectinid subclades contained the largest species: Mesopeplini (*Phialopecten* in New Zealand), Decatopectinini (*Lyropecten* in the north-east Pacific), and a separate clade within Palliolini (*Pseudamussium* in the north-east Atlantic; for phylogeny, see Waller, 2006).

Of the 19 guilds examined in the present study, eight comprise large-bodied species for which a robust phylogenetic hypothesis has been proposed. Of the 144 species in these eight guilds (42% of the 347 largest-bodied species considered in the present study), 84 (58%) represent distinct clades, in which large size evolved independently. The present study identified 85 cases of temporal succession of phylogenetically well characterized species within guilds. Of this number, 51 (60%) represent clear instances of temporal clade substitution among largest-bodied species within a guild. These data strongly indicate that lineages hold the status of largest-bodied member of a guild within a region only briefly, and that phylogenetic usurpation of this top status is the rule.

The largest Pliocene and Recent members of guilds in a region usually belong to clades with a long history in that region. Of 125 Recent species, only ten (8.0%) are immigrants from elsewhere, nine from the North Pacific to the North Atlantic, and one (*Pecten*) from South Africa to New Zealand via Australia (Vermeij, 1991; Beu, 2004). Without the North Pacific immigrants, decreases in maximum size from the Pliocene to the Recent would have outnumbered increases by 12 : 5 instead of 9 : 8 in the north-west Atlantic and by 11 : 5 instead of 7 : 9 in the north-east Atlantic. Clades of large-bodied non-molluscan predators and herbivores show the same pattern of long history in most regions and recent immigration to the North Atlantic. Fossil and phylogenetic evidence indicates that large North Pacific and southern-hemisphere forcipulate sea stars, North Atlantic gadid fishes including cod, North Atlantic and southern-hemisphere lobsters, north-east Pacific cancrid crabs, and the herbivorous mammals and wrasses discussed earlier all belong to clades with long pre-Pliocene histories in their respective regions (Harrison & Crespi, 1999; Patek *et al*., 2006; Teletchea, Laudet & Hanni, 2006; Mah & Foltz, 2011). Newcomers include sea otters (see above) and North Atlantic forcipulate sea stars (Mah & Foltz, 2011), large cancrid crabs (Harrison & Crespi, 1999), sea mink, and walrus (see above). The cod *Gadus morhua*, although it belongs to the clade Gadinae with a long Atlantic history, may represent a re-invasion to the North Atlantic by a lineage that had previously entered the North Pacific via the Arctic Ocean (Coulson *et al*., 2006). Geologically recent immigration from the North Pacific by large-bodied molluscs and many of their enemies thus partially reversed the effects of widespread Pliocene and Early Pleistocene extinctions in the North Atlantic.

These data support the general conclusion that a given trait with a large, broadly adaptive advantage (i.e. large size in the present case) is very much less contingent on the unique events and circumstances of history than are the identities of the clades with that trait or the sources of selection favouring the trait. Of the many clades in which the potential for evolving large body size exists, only a few achieve the highest size rank in their respective guilds. Which clades are involved and which are responsible for pushing them there depends on quirks of geography and on the fates of potential competitors. In short, the outcomes and directions of evolution are more predictable than the players in the evolutionary drama (Vermeij, 2006, 2010, 2011c).

CONCLUSIONS

Even under climatically similar circumstances, biotas in different parts of the world have separate histories and often diverge from one another in the prevailing biological conditions that the resident species respond to and create. Comparative studies of the kind undertaken in the present study not only help to identify similarities and contrasts between biotas that have developed independently, but also expose long-term evolutionary agencies (i.e. ecological feedbacks, natural selection and its consequences, and extinction) that shape the composition of, and relationships in, those biotas. They show that current conditions are insufficient to explain the heterogeneity we observe on biogeographical scales.

Many questions remain. Why did metabolically active herbivorous and predatory marine mammals that feed on bottom-dwelling organisms emerge so early in the north Pacific and so late or not at all elsewhere? What accounts for the large differences among regions in the magnitude of extinction during the Pliocene? Why are there gigantic worm-eating, echinoderm-feeding, and soft-bottom herbivorous gastropods in the tropics and not in the temperate zones? Given the widely held view that dispersibility in the sea is high, why have so few competitively dominant species and the larger clades to which they belong so often remained in one or two regions without spreading more widely as successful invaders?

These and other biogeographical and evolutionary questions require more insights into the biology of individual species and communities. Satisfactory answers will also require a better understanding and measurement of productivity. Finally, it is essential to recognize that a given regime of production or selection does not affect all species in the same way. Some species will have the technology to harvest resources even when other species do not; and prior adaptation greatly affects how a given species responds evolutionarily to a predator. In simplified theoretical models, such heterogeneity is often ignored or relegated as noise. In the real world of economic relationships among organisms, heterogeneity is a key property that must be analyzed and celebrated if we are to understand the processes of history.

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REFERENCES

Addicott WO. 1970. Miocene gastropods and biostratigraphy of the Kern River Area, California. *United States Geological Survey, Professional Paper* **642:** 1–174.

Addicott WO. 1976. Molluscan paleontology of the Lower Miocene Clallam Formation, northwestern Washington. *US Geological Survey Professional Paper* **976:** 1–67.

Aguilera MA. 2011. The functional roles of herbivores in the rocky intertidal systems in Chile: review of food preferences and consumptive effects. *Revista Chilena de Historia Natural* **84:** 241–261.

Allison RC, Marincovich L. 1982. A Late Oligocene or earliest Miocene molluscan fauna from Sitkinak Island, Alaska. *US Geological Survey Professional Paper* **1233:** 1–11.

Amano K, Ogihara R. 2012. Taxonomy of large *Nuttallia* (Bivalvia: Psammobiidae) in the northwestern Pacific, with remarks on the evolution of the genus. *Paleontological Research* in press.

Arnaud PM. 1974. Contribution á la bionomie marine benthique des régions antarctiques et subantarctiques. *Tethys* **6:** 567–653.

Baker AJ. 1974. Prey-specific feeding methods of New Zealand oystercatchers. *Notornis* **21:** 219–233.

Barber RT. 1988. Ocean basin ecosystems. In: Pomeroy LR, Alberts JJ, eds. *Concepts of ecosystem ecology: a comparative view*. New York, NY: Springer, 171–193.

Barnes LG, Raschke RE. 1991. *Gomphotaria pugnax*, a new genus and species of Late Miocene dusignathine otariid pinniped (Mammalia: Carnivora) from California. *Contributions in Science of the Natural History Museum of Los Angeles County* **426:** 1–16.

Barron JA. 1998. Late Neogene changes in diatom sedimentation in the North Pacific. *Journal of Asian Earth Sciences* **16:** 85–95.

Beatty BL. 2009. New material of *Cornwallius sookensis* (Mammalia: Desmostylia) from the Yaquina Formation of Oregon. *Journal of Vertebrate Paleontology* **29:** 894–909.

Beu AG. 1995. Pliocene limestones and their scallops: lithostratigraphy, pectinid biostratigraphy and paleogeography of eastern North Island Late Neogene limestone. *New Zealand Geological Survey Paleontological Bulletin* **68:** 1–243.

Beu AG. 2004. Marine Mollusca of oxygen isotope stages of the last 2 million years in New Zealand. Part 1. Revised generic positions and recognition of warm-water and cool-water migrants [with an Appendix: age and correlation of Ototoka tephra B. V. Alloway, B. J. Pillans, J. R. Naish and J. A. Westgate]. *Journal of the Royal Society of New Zealand* **34:** 111–265.

Beu AG. 2006. Marine Mollusca of oxygen isotope stages of the last 2 million years in New Zealand. Part 2. Biostratigraphically useful and new Pliocene to Recent bivalves. *Journal of the Royal Society of New Zealand* **36:** 151–338.

Beu AG. 2010. Marine Mollusca of isotope stages of the last 2 million years in New Zealand. Part 3. Gastropoda (Vetigastropoda – Littorinimorpha). *Journal of the Royal Society of New Zealand* **40:** 59–180.

Beu AG, Maxwell PA. 1990. Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey Paleontological Bulletin* **58:** 1–518.

Beurois J. 1975. Étude écologique et halieutique des fondes de pêche et des especes d'intérêt commerciel (langoustes et poissons) des îles Saint-Paul et Amsterdam (Océan Indien). *Comité National Française de Recherches Antarctiques Publication* **No. 37:** 1–91.

Bosman AL, Hockey PAR, Siegfried WR. 1987. The influence of coastal upwelling on the functional structure of rocky intertidal communities. *Oecologia (Berlin)* **72:** 226–232.

Bowersox JR. 2005. Reassessment of extinction patterns of Pliocene molluscs from California and environmental forcing of extinction in the San Joaquin Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* **221:** 55–82.

Branch GM. 1971. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. I Zonation, movements and feeding. *Zoologica Africana* **6:** 1–38.

Briscoe CS, Sebens KP. 1988. Omnivory in *Strongylocentrotus droebachiensis* (Müller) (Echinodermata: Echinoidea): predation on subtidal mussels. *Journal of Experimental Marine Biology and Ecology* **115:** 1–24.

Brown JL, Maurer BA. 1986. Body size, ecological dominance and Cope's Rule. *Nature* **324:** 248–250.

Brun E. 1971. Predation of *Chlamys islandica* (O. F. Müller) by eiders *Somateria* spp. *Astarte* **4:** 23–29.

Bustamante RH, Branch GM, Eekhout S. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* **76:** 2314–2319.

Butler MJ, Steneck RS, Herrnkind WG. 2006. Juvenile and adult ecology. In: Phillips B, ed. *Lobsters: ecology, management, aquaculture and fisheries*. Oxford: Blackwell, 263–309.

Cadée GC. 2008a. Oystercatchers *Haematopus ostralegus* catching Pacific oysters *Crassostrea gigas*. *Basteria* **72:** 25–31.

Cadée GC. 2008b. Herring gulls feeding again on Pacific oysters *Crassostrea gigas* in the Dutch Wadden Sea near Texel. *Basteria* **72:** 33–36.

Cadée GC. 2011. *Hydrobia* as 'Jonah in the whale': shell repair after passing through the digestive tract of shelducks alive. *Palaios* **26:** 245–249.

Calkins DG. 1978. Feeding behavior and major prey species of the sea otter, *Enhydra lutris*, in Montague Strait, Prince William Sound, Alaska. *Fisheries Bulletin* **76:** 125–131.

Camus PA, Daroch K, Opazo LF. 2008. Potential for omnivory and apparent intraguild predation in rocky intertidal herbivore assemblages from northern Chile. *Marine Ecology Progress Series* **361:** 35–45.

Carrington AJ, Kensley BE. 1969. Pleistocene molluscs from the Namaqualand coast. *Annals of the South African Museum* **52:** 189–223.

Carter LD, Brigham-Grette J, Marincovich L Jr, Pease VL, Hillhouse JW. 1986. Late Cenozoic Arctic Ocean sea ice and terrestrial paleoclimate. *Geology* **14:** 675–678.

Castilla JC, Bahamondes I. 1979. Observaciones conductuales y ecológicas sobre *Lutra felina* (Molina) 1782 (Carnivora: Mustelidae) en las zonas central y centro-norte de Chile. *Archivos de Biologiá y Medicina Experimentales (Chile)* **12:** 119–132.

Castilla JC, Branch GM, Barkai A. 1994. Exploitation of two critical predators: the gastropod *Concholepas concholepas* and the rock lobster *Jasus lalandii*. In: Siegfried WR, ed. *Rocky shores: exploitation in Chile and South Africa*. Berlin: Springer, 101–130.

Chinzei K. 1959. Molluscan fauna of the Pliocene Sannohe Group of northeast Honshu, Japan. 1. The faunule of the Kubo Formation. *Journal of the Faculty of Science, University of Tokyo, Section II* **12:** 103–132.

Chinzei K. 1961. Molluscan fauna of the Pliocene Sannohe group of northeast Honshu, Japan. 2. The faunule of the Togawa Formation. *Journal of the Faculty of Science, University of Tokyo, Section II* **13:** 81–131.

Clark BL, Arnold R. 1923. Fauna of the Sooke Formation, Vancouver Island. University of California Publications. *Bulletin of the Department of Geological Sciences* **14:** 123–234.

Clements KD, Alfaro ME, Fessler JL, Westneat MW. 2004. Relationships of the temperate Australasian labrid fish tribe Odacini (Perciformes; Teleostei). *Molecular Phylogenetics and Evolution* **32:** 575–587.

Clementz MT, Hoppe KA, Koch PL. 2003. A paleoecological paradox: the habit and dietary preferences of the extinct tethythere *Desmostylus*, inferred from stable isotope analysis. *Paleobiology* **29:** 506–519.

Coan EV, Scott PV, Bernard FR. 2000. *Bivalve seashells of western North America: marine bivalve mollusks from Arctic Alaska to Baja California*. Santa Barbara, CA: Santa Barbara Museum of Natural History.

Compton TJ, Kentie R, Storey AW, Veltheim I, Pearson GB, Piersma T. 2008. Carbon isotope signatures reveal that diet is related to the relative sizes of the gills and palps in bivalves. *Journal of Experimental Marine Biology and Ecology* **361:** 104–110.

Coulson MW, Marshall HD, Pepin P, Carr SM. 2006. Mitochondrial genomics of gadine fishes: implications for taxonomy and biogeographic origins from whole-genome data sets. *Genome* **49:** 1115–1130.

Coyer JA, Smith GJ, Andersen RA. 2001. Evolution of *Macrocystis* spp. (Phaeophyceae) as determined by ISS1 and ISS2 sequences. *Journal of Phycology* **37:** 574–585.

Dayton PK. 1985. The structure and regulation of some South American kelp communities. *Ecological Monographs* **55:** 447–468.

Dayton PK, Rosenthal RJ, Mahen LC, Antezana T. 1977. Population structure arid foraging biology of the predaceous Chilean asteroid *Meyenaster gelatinosus* and the escape biology of its prey. *Marine Biology* **39:** 361–370.

Deméré TA, Berta A. 2001. A reevaluation of *Proneotherium repenningi* from the Miocene Astoria Formation of Oregon and its position as a basal odobenid (Pinnipedia: Mammalia). *Journal of Vertebrate Paleontology* **21:** 279–310.

DeVries TJ. 1997. A review of the genus *Chorus* Gray, 1847 (Gastropoda: Muricidae) from western South America. *Tulane Studies in Geology and Paleontology* **30:** 125–145.

DeVries TJ. 2007. Cenozoic Turritellidae (Gastropoda) from southern Peru. *Journal of Paleontology* **81:** 331–351.

DeVries TJ, Hess B. 2004. *Piscoacritia*, gen. nov.: first account of tribe Trochini (Gastropoda: Trochidae: Trochinae) from the Cenozoic of western South America. *Veliger* **47:** 6–12.

Diesterh-Haass L, Meyers PA, Vidal L. 2002. The Late Miocene onset of high productivity in the Benguela Current upwelling system as part of a global pattern. *Marine Geology* **180:** 87–103.

Domning DP. 1976. An ecological model for Late Tertiary sirenian evolution in the North Pacific Ocean. *Systematic Zoology* **25:** 352–362.

Domning DP. 1978. Sirenian evolution in the North Pacific Ocean. *University of California Publications in Geological Science* **118:** 1–176.

Domning DP. 1989. Kelp evolution: a comment. *Paleobiology* **15:** 53–56.

Domning DP, Ray CE, McKenna ME. 1986. Two new Oligocene desmostylians and a discussion of tethytherian systematics. *Smithsonian Contributions to Paleobiology* **59:** 1–56.

Duggins DO. 1981. Urchins and kelp: the effects of short term changes in urchin diet. *Limnology and Oceanography* **26:** 391–394.

Duggins DO, Simenstad CA, Estes JA. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* **245:** 170–173.

Dunbar RB, Marty RC, Baker PA. 1990. Cenozoic marine sedimentation in the Sechura and Pidsco Basins, Peru. *Palaeogeography, Palaeoclimatology, Palaeoecology* **77:** 235–261.

Dunthorn AA. 1971. The predation of cultivated mussels by eiders. *Bird Study* **18:** 107–112.

Eagle MK. 1996. A new species of *Haliotis* (Mollusca) from the Early Miocene basal Waitemata beds, Rodney District, North Auckland. *Records of the Auckland Institute and Museum* **33:** 159–171.

Egorov RV. 1992. Gastropods of the families Muricidae and Thaididae from the seas of Russia. *Ruthenica* **2:** 63–75.

Escobar JB, Navarrete SA. 2011. Risk recognition and variability in escape responses among intertidal molluscan grazers to the sun star *Heliaster helianthus*. *Marine Ecology Progress Series* **421:** 151–161.

Estes JA, Lindberg DR, Wray C. 2005. Evolution of large body size in abalones (*Haliotis*): patterns and implications. *Paleobiology* **31:** 591–606.

Estes JA, Steinberg PD. 1988. Predation, herbivory, and kelp evolution. *Paleobiology* **14:** 19–36.

Fleming CA. 1973. Kermadec Island giant limpet occurring fossil in New Zealand, and relict distributions in the tropics. *New Zealand Journal of Marine and Freshwater Research* **7:** 159–164.

Fraser CI, Winter DJ, Spencer HG, Waters JM. 2010. Multigene phylogeny of the southern bull-kelp genus *Durvillaea* (Phaeophyceae: Fucales). *Molecular Phylogenetics and Evolution* **57:** 1301–1311.

Frassinetti DC. 1993. Bivalvos de Mioceno marino de Matanzas (formación Navidad, Chile central). *Boletin del Museo Nacional de Historia Natural, Santiago de Chile* **44:** 73–97.

Fukuyama AK, Oliver JS. 1985. Sea star and walrus predation on bivalves in Norton Sound, Bering Sea, Alaska. *Ophelia* **24:** 17–36.

Genta-Iturrería SF, Griffin M, Raising M. 2011. Redescription of the genus *Modiomytilus* Griffin, 1990 (Bivalvia: Mytilidae) from southern Patagonia with remarks on the paleobiogeography of the genus. *Nautilus* **125:** 213–220.

Gladenkov YB, Gladikova VM, Kafanov AN, Konova LL, Krishtofovich LV, Sinelnikova VN, Popov SV. 1984. Sea mollusks. Atlas of fauna and flora of the Neogene sediments of the Far East: Tochilinski section of western Kamchatka. *Academy of Sciences of the USSR, Geological Institute Transactions* **385:** 152–250.

Gladenkov YB, Sinelnikova VN. 1990. Miocene mollusks and climatic optima in Kamchatka. *Academy of Science of the USSR Order of the Red Banner of Labour Geological Institute Transactions* **453:** 1–172.

Gladenkov YB, Sinelnikova VN, Titova LV. 1988. Etapnost razvitiya fauny shelfovykh bassenov neogena kamchatki (na primere buktsinid). In: Timofeyev P, ed. *Litologiya i stratigrafiya mezonoya i kainozoya vostocknykh raionov SSSR*. Moscow: 'Nauka', 58–135.

Golikov AN, Gulbin VV. 1978. Prosobranchial gastropods of the Kurile Islands. I. Orders Docoglossa -Entomostoma. In: Kussakin OG, ed. *Fauna and vegetation of the shelf of the Kurile Islands*. Vladivostok: Academy of Sciences of the USSR, Far East Science Center, Institute of Marine Biology, 159–223.

González PM, Piersma T, Verkuil Y. 1996. Food, feeding, and refueling of red knots during northward migration at San Antonio Oeste, Rio Negro, Argentina. *Journal of Field Ornithology* **67:** 575–591.

Grant USIV, Gale HR. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. *Memoir of the San Diego Society of Natural History* **1:** 1–1035.

Griffin M, Nielsen SN. 2008. A revision of the type specimens of Tertiary molluscs from Chile and Argentina described by d'Orbigny (1842), Sowerby (1846) and Hupé (1854). *Journal of Systematic Palaeontology* **6:** 251–316.

Griffiths CL, Seiderer JL. 1980. Rock-lobsters and mussels – limitations on preferences in a predator-prey interaction. *Journal of Experimental Marine Biology and Ecology* **44:** 95–109.

Guzmán N, Marquardt C, Ortlieb L, Frassinetti D. 2000. La malacofauna neógena y quaternaria del area de Caldera (27°–28° S): especies y rangos bioestratigráficos. *IX Congreso Geológico Chileno, Actas Volumen 1. Santiago: Universidad de Chile*, 476–481.

Harris MP. 1965. The food of some *Larus* gulls. *Ibis* **107:** 43–51.

Harrison MK, Crespi BJ. 1999. Phylogenetics of Cancer crabs (Crustacea: Decapoda: Brachyura). *Molecular Phylogenetics and Evolution* **12:** 186–199.

Hartwick EB. 1976. Foraging strategy of the black oyster catcher (*Haematopus bachmani* Audubon). *Canadian Journal of Zoology* **54:** 142–155.

Hatai K, Kotaka T, Noda H. 1970. Some marine fossils from southwest of Shiroishi City, Miyagi Prefecture, northeast Honshu, Japan. *Saito Ho-On Kai Museum Research Bulletin* **39:** 13–23.

Heinrich S, Zonneveld KAF, Bickert T, Willems H. 2011. The Benguela upwelling related to the Miocene cooling event and the development of the Antarctic Circumpolar Current: evidence from calcareous dinoflagellate cysts. *Paleoceanography* **26:** PA3209.

Herm D. 1969. Marines Pliozän und Pleistozän in Nord-und Mittel-Chile unter besonderer Berücksichtigung der Entwicklung der Mollusken-Faunen. *Zitteliana* **2:** 1–159.

Hertlein LG. 1937. *Haliotis koticki*, a new species from the Lower Miocene of California. *Bulletin of the Southern California Academy of Sciences* **36:** 93–97.

Hockey PAR, Branch GM. 1984. Oystercatchers and limpets: impact and implications – a preliminary assessment. *Ardea* **72:** 199–206.

Hopkins DM, Marincovich L Jr. 1984. Whale biogeography and the history of the Arctic Basin. *University of Groningen, Works of the Arctic Center* **8:** 7–24.

Hori M, Noda T, Nakao S. 2006. Effects of avian grazing on the algal community and small invertebrates in the rocky intertidal zone. *Ecological Research* **21:** 768–775.

von Ihering H. 1907. Les mollusques fossiles du Tertiaire et du Crétacé supérieur de l'Argentine. *Annales del Museo Nacional de Buenos Aires (Ser. III)* **7:** 1–611.

Jacobs DK, Haney TA, Louie KD. 2004. Genes, diversity, and geologic process on the Pacific coast. *Annual Reviews of Earth and Planetary Sciences* **32:** 601–652.

Kensley B. 1972. Pliocene marine invertebrates from Langebaanweg, Cape Province. *Annals of the South African Museum* **60:** 173–191.

Kensley B. 1974. The status of the Plio-Pleistocene *Panopea* in southern Africa (Mollusca, Bivalvia, Hiatellidae). *Annals of the South African Museum* **65:** 199–215.

Kensley B, Pether J. 1986. Late Tertiary and Early Quaternary fossil Mollusca of the Hondeklip area, Cape Province, South Africa. *Annals of the South African Museum* **97:** 141–225.

Kiel S, Nielsen SN. 2010. Quaternary origin of the inverse latitudinal diversity gradient among southern Chilean mollusks. *Geology* **38:** 955–958.

Kilburn RN, Rippey E. 1982. *Sea shells of southern Africa*. Johannesburg: Macmillan South Africa Limited.

Kilburn RN, Tankard AJ. 1975. Pleistocene molluscs from the west and south coasts of the Cape Province, South Africa. *Annals of the South African Museum* **67:** 183–226.

King LC. 1934. The geology of the Lower Awatere District, Marlborough, New Zealand. *New Zealand Geological Survey Memoir* **2:** 1–49.

Kirby MX. 2001. Differences in growth rate and environment between Tertiary and Quaternary *Crassostrea* oysters. *Paleobiology* **27:** 84–103.

Koepfli KP, Deere KA, Slater GJ, Begg C, Begg K, Grassman L, Lucherini M, Veron G, Wayne RK. 2008. Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biology* **6:** 10.

Kohno N. 2006. A new Miocene odobenid (Mammalia: Carnivora) and its implications for odobenid phylogeny. *Journal of Vertebrate Paleontology* **26:** 411–421.

Kurihara Y. 2010. Middle and Late Miocene Bivalvia from the northern Kanto region, central Japan. *National Museum of Nature and Science Monographs* **41:** 1–87.

Kvitek RG, Oliver JS, DeGange AR, Anderson BS. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. *Ecology* **73:** 41l–428.

Lane CE, Mayes C, Druehl LD, Saunders GW. 2006. A multi-gene molecular investigation of the kelp (Laminariales, Phaeophyceae) supports substantial taxonomic re-organization. *Journal of Phycology* **42:** 493–512.

Leigh EG Jr, Paine RT, Quinn JF, Suchanek TH. 1987. Wave energy and intertidal productivity. *Proceedings of the National Academy of Sciences of the United States of America* **84:** 1314–1318.

Lindberg DR, Warheit KI, Estes JA. 1987. Prey preference and seasonal predation by oystercatchers on limpets at San Nicolas Island, California, USA. *Marine Ecology Progress Series* **39:** 105–113.

Linse K, Barnes DKA, Enderlein P. 2006. Body size and growth of benthic invertebrates along an Antarctic latitudinal gradient. *Deep-Sea Research II* **53:** 921–931.

Lorenzen S. 2007. The limpet *Patella vulgata* L. at night in air: effective feeding on *Ascophyllum nodosum* monocultures and stranded seaweeds. *Journal of Molluscan Studies* **73:** 267–274.

Lowry LF, Frost KJ, Burns JJ. 1980. Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walruses. *Arctic* **33:** 330–342.

Mah C, Foltz D. 2011. Molecular phylogeny of the Forcipulatacea (Asteroidea: Echinodermata): systematics and biogeography. *Zoological Journal of the Linnean Society* **162:** 646–660.

Majima S. 1989. Cenozoic fossil Naticidae (Mollusca: Gastropoda) in Japan. *Bulletins of American Paleontology* **96:** 1–159.

Mann KH. 1973. Seaweeds: their productivity and strategy of growth. *Science* **182:** 975–981.

Mann KH. 2000. *Ecology of coastal waters, with implications for management*, 2nd edn. Malden, MA: Blackwell.

Mann KH, Chapman ARO, Gagné JA. 1980. Productivity of seaweeds: the potential and the reality. In: Falkowski PG, ed. *Primary productivity in the sea*. New York, NY: Plenum, 363–380.

Marean CW. 2011. Coastal South Africa and the coevolution of the modern human lineage and the coastal adaptation.

In: Bicho N, Haws JA, Davis LG, eds. *Trekking the shore: changing coastlines and the antiquity of coastal settlement*. New York, NY: Springer, 421–440.

Marincovich L Jr. 1977. Cenozoic Naticidae (Mollusca: Gastropoda) of the northeastern Pacific. *Bulletins of American Paleontology* **70:** 169–494.

Marincovich L Jr. 1981. *Tyrannoberingius rex*, new genus and species of Miocene gastropod from Alaska. *Journal of Paleontology* **55:** 176–179.

Marincovich L Jr. 1983. Molluscan paleontology, paleoecology, and North Pacific correlations of the Miocene Tachilni Formation, Alaska Peninsula, Alaska. *Bulletins of American Paleontology* **84:** 59–155.

Marincovich L Jr. 1988. Miocene mollusks from the lower part of the Bear Lake Formation on Ukolnoi Island, Alaska Peninsula, Alaska. *Contributions in Science, Natural History Museum of Los Angeles County* **397:** 1–20.

Marshall CB, Kovacs KM, Lydersen C. 2008. Feeding kinematics, suction and hydraulic jetting capabilities in bearded seals (*Erignathus barbatus*). *Journal of Experimental Biology* **211:** 699–708.

Marwick J. 1948. Lower Pliocene Mollusca from Otahuhu, Auckland. *New Zealand Geological Survey Geological Survey Paleontological Bulletin* **16:** 1–38.

Marwick J. 1965. Upper Cenozoic Mollusca of Wairoa District, Hawke's Bay. *New Zealand Geological Survey Paleontological Bulletin* **39:** 1–83.

Mauzey KP, Birkeland C, Dayton PK. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. *Ecology* **49:** 603–619.

McLean JH. 1984. Systematics of *Fissurella* in the Peruvian and Magellanic faunal provinces (Gastropoda: Prosobranchia). *Contributions in Science of the Natural History Museum of Los Angeles County* **354:** 1–69.

Moreno CA, Sutherland JP. 1982. Physical and biological processes in a *Macrocystis pyrifera* community near Valdivia, Chile. *Oecologia (Berlin)* **55:** 1–6.

Morsán E, Ciocco NF. 2004. Age and growth model for the southern geoduck, *Panopea abbreviata*, off Puerto Lobos (Patagonia, Argentina). *Fisheries Research* **69:** 343–348.

Navarro RA, Velasquez CR, Schlatter RP. 1989. Diet of the surfbird in southern Chile. *Wilson Bulletin* **101:** 137–141.

Newman M. 1994. *Life in a fishbowl: confessions of an aquarium director*. Vancouver: Douglas and McIntyre.

Nielsen SN, Frassinetti DC. 2007. The Neogene Volutidae (Gastropoda: Neogastropoda) from the Pacific coast of Chile. *Journal of Paleontology* **81:** 82–102.

Noda H, Watanabe R, Kikuchi Y. 1995. Pliocene marine molluscan fauna from the Hitachi Formation in the northeastern part of Ibaraki Prefecture, Japan. *Science Reports, Institute of Geoscience, University of Tsukuba, Section B, Geological Sciences* **16:** 39–63.

Noda Y. 1992. Neogene molluscan faunas from the Haboro Coalfield, Hokkaido, Japan. *Science Reports of Tohoku University (2, Geology)* **62:** 1–140.

Norton-Griffiths M. 1967. Some ecological aspects of the feeding behaviour of the oystercatcher *Haematopus ostralegus* on the edible mussel *Mytilus edulis*. *Ibis* **109:** 412–424.

Ogasawara K, Sasaki O, Chiba N. 1988. The Dainenjian molluscan association from the environs of Sendai, northeast Honshu and its zoogeographic significance. *Saito Ho-On Kai Natural History Research Bulletin* **56:** 1–15.

Oliver JS, Slattery PN, O'Connor EF, Lowry LF. 1983. Walrus, *Odobenus rosmarus*, feeding in the Bering Sea: a benthic perspective. *Fisheries Bulletin* **81:** 501–512.

Ortiz M, Jesse S, Stotz W, Wolff M. 2003. Feeding behaviour of the asteroid *Meyenaster gelatinosus* in response to changes in abundance of the scallop *Argopecten purpuratus* in northern Chile. *Archiv für Hydrobiologie* **157:** 211–225.

Osorio RC, Ramajo GL. 2007. Morphologic and reproductive biology of two species of the buccinid gastropod genus *Aeneator* Finlay, 1927, from southern Chilean fjords. *Veliger* **49:** 70–78.

Otaíza RD, Santelices B. 1985. Vertical distribution of chitons (Mollusca: Polyplacophora) in the rocky intertidal zone of central Chile. *Journal of Experimental Marine Biology and Ecology* **86:** 229–240.

Ozawa T, Tomida T. 1996. Systematic study of fossil *Turbo* (*Batillus*) from Japan. *Venus* **55:** 281–297.

Paine RT. 1976. Biological observations on a subtidal *Mytilus californianus* bed. *Veliger* **19:** 125–130.

Paine RT. 2002. Trophic control of production in a rocky intertidal community. *Science* **296:** 636–639.

Palmer AR. 1990. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. *Ecology* **71:** 759–775.

Pastorino G. 2005. Recent Naticidae (Mollusca: Gastropoda) from the Patagonian coast. *Veliger* **47:** 225–258.

Patek SN, Feldmann RM, Porter M, Tshudy D. 2006. Phylogeny and evolution. In: Phillips BF, ed. *Lobsters: biology, management, aquaculture and fisheries*. Oxford: Blackwell, 113–145.

Petuch EJ, Drolshagen M. 2010. *Molluscan paleontology of the Chesapeake Miocene*. Boca Raton, FL: CRC Press.

Piersma T, Dekinga A, van Gils JA, Achterkamp B, Visser GH. 2003. Cost-benefit analysis of mollusk-eating in a shorebird. I. Foraging and processing costs estimated by the doubly labeled water method. *Journal of Experimental Biology* **206:** 3361–3368.

Powell AWB. 1938. Tertiary molluscan faunules from the Waitemata beds. *Transactions of the Royal Society of New Zealand* **68:** 362–379.

Powell AWB. 1979. *New Zealand Mollusca: marine, land and freshwater shells*. Auckland: Collins.

Powell AWB, Bartrum JA. 1929. The Tertiary (Waitematan) molluscan fauna of Oneroa, Waiheke Island. *Transactions of the Royal Society of New Zealand* **60:** 395–447.

Ray CE, Domning DP, McKenna MC. 1994. A new specimen of *Behemetops proteus* (order Desmostylia) from the marine Oligocene of Washington. *Proceedings of the San Diego Society of Natural History* **20:** 205–222.

Reaka-Kudla ML. 2000. The evolution of endemism in Pacific faunas: coral-dwelling stomatopods. *Journal of Crustacean Biology* **20** special number 2: 56–70.

Repenning CA. 1976. Adaptive evolution of sea lions and walruses. *Systematic Zoology* **25:** 385–390.

del Río CJ. 2004. Revision of the large Neogene pectinids (Mollusca: Bivalvia) of eastern Santa Cruz and Chubut Provinces (Patagonia: Argentina). *Journal of Paleontology* **78:** 690–699.

del Río CJ, Camacho HH. 1998. Tertiary nuculoids and arcoids of eastern Patagonia (Argentina). *Palaeontographica Abstract A* **250:** 47–88.

del Río CJ, Martinez S. 2006. The family Volutidae (Mollusca-Gastropoda) in the Tertiary of Patagonia (Argentina). *Journal of Paleontology* **80:** 919–945.

Rivadeneira MM, Marquet PA. 2007. Selective extinction of Late Neogene bivalves on the temperate Pacific coast of South America. *Paleobiology* **33:** 455–468.

Rommerskirchen F, Condon T, Mollenhauer G, Dupont L, Schefuss E. 2011. Miocene to Pliocene development of surface and subsurface temperatures in the Benguela Current system. *Paleoceanography* **26:** PA3216.

Rosa R, Seibel BA. 2010. Slow pace of life of the Antarctic colossal squid. *Journal of the Marine Biological Association of the United Kingdom* **90:** 1375–1378.

Sanhueza AG, Navarrete AH, Opazo LF, Camus PA. 2008. Trophic characterization of the intertidal placophoran *Enoplochiton niger* in northern Chile: environmental variation and dietary patterns at local and regional levels. *Revista Chilena de Historia Natural* **81:** 533–546.

Scarlato OA. 1981. *Dvustvorchatye molliuski umerennych shirot zapadnoi chasti tichogo okeana*. Leningrad: 'Nauka'.

Sealfon RA. 2007. Dental divergence supports species status of the extinct sea mink (Carnivora: Mustelidae: *Neovison macrodon*). *Journal of Mammalogy* **88:** 371–383.

Sejr MK, Blicher ME, Rysgaard S. 2009. Sea ice cover affects inter-annual and geographic variation in growth of the Arctic cockle *Clinocardium ciliatum* (Bivalvia) in Greenland. *Marine Ecology Progress Series* **389:** 149–158.

Shibata M. 1957. Some molluscan fossils from the eastern part of the Kanzawa mountainland. *Transactions and Proceedings of the Palaeontological Society of Japan n.s.* **25:** 21–25.

Signorelli JH, Pastorino G. 2011. Revision of the Magellanic Mactridae Lamarck, 1809 (Bivalvia: Heterodonta). *Zootaxa* **2757:** 47–67.

Smith JT. 1991. Cenozoic giant pectinids from California and the Tertiary Caribbean Province: *Lyropecten*, '*Macrochlamis*,' *Vertipecten*, and *Nodipecten* species. *US Geological Survey Professional Paper* **1391:** 1–155.

Smith JT, Roy K. 2006. Selectivity during background extinction: Plio-Pleistocene scallops in California. *Paleobiology* **32:** 408–416.

Smith SV. 1981. Marine macrophytes as a global carbon sink. *Science* **211:** 838–840.

Stanley SM. 1986a. Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the western Atlantic bivalve fauna. *Palaios* **1:** 17–36.

Stanley SM. 1986b. Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. *Paleobiology* **12:** 89–110.

Summers RW, Grieve A. 1982. Diet, feeding behaviour and food intake of the upland goose (*Chloephaga picta*) and the ruddy-headed goose (*C. rubidiceps*). *Journal of Applied Ecology* **19:** 783–804.

Takahashi S, Domning DP, Saito T. 1986. *Dusisiren dewana*, n. sp. (Mammalia: Sirenia), a new ancestor of Steller's sea cow from the Upper Miocene of Yamagata Prefecture, northeastern Japan. *Transactions and Proceedings of the Palaeontological Society of Japan* **141:** 296–321.

Taylor DI, Schiel DR. 2010. Algal populations controlled by fish herbivory across a wave-exposure gradient on southern temperate shores. *Ecology* **91:** 201–211.

Taylor JD, Smythe KR. 1985. A new species of Trochita (Gastropoda: Calyptraeidae) from Oman: relict distribution and association with upwelling areas. *Journal of Conchology* **32:** 39–48.

Tedford RH, Barnes LG, Ray CE. 1994. The Early Miocene littoral ursoid *Kolponomos*: systematics and mode of life. *Proceedings of the San Diego Society of Natural History* **29:** 11–32.

Tegner MJ. 1980. Multispecies considerations of resource management in southern California kelp beds. *Canadian Technical Report, Fisheries and Aquatic Sciences* **954:** 125–143.

Teletchea F, Laudet V, Hanni C. 2006. Phylogeny of the Gadidae (sensu Svetovidov, 1948) based on their morphology and two mitochondrial genes. *Molecular Phylogenetics and Evolution* **38:** 189–199.

Titova LV. 1994. Revision of the Neogene Turritellidae (Mollusca: Gastropoda) from Kamchatka. *Ruthenica* **4:** 1–20.

Van Valen L. 1976. Energy and evolution. *Evolutionary Theory* **1:** 179–229.

VanBlaricom GR. 1988. Effects of foraging by sea otters on mussel-dominated intertidal communities. In: VanBlaricom GR, Estes JA, eds. *The community ecology of sea otters*. Berlin: Springer, 48–91.

Vásquez JA, Buschmann AH. 1997. Herbivore-kelp interactions in Chilean subtidal communities: a review. *Revista Chilena de Historia Natural* **79:** 41–52.

Vermeij GJ. 1978. *Biogeography and adaptation: patterns of marine life*. Cambridge, MA: Harvard University Press.

Vermeij GJ. 1980. Gastropod growth rate, allometry, and adult size: environmental implications. In: Rhoads DC, Lutz RA, eds. *Skeletal growth of aquatic organisms: biological records of environmental change*. New York, NY: Plenum, 379–394.

Vermeij GJ. 1991. Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology* **17:** 281–307.

Vermeij GJ. 1992. Time of origin and biogeographical history of specialized relationships between northern marine plants and herbivorous molluscs. *Evolution* **46:** 657–664.

Vermeij GJ. 2004a. *Nature: an economic history*. Princeton, NJ: Princeton University Press.

Vermeij GJ. 2004b. Ecological avalanches and the two kinds of extinction. *Evolutionary Ecology Research* **6:** 315–337.

Vermeij GJ. 2006. Historical contingency and the purported uniqueness of evolutionary innovations. *Proceedings of the National Academy of Sciences of the United States of America* **103:** 1804–1809.

Vermeij GJ. 2010. *The evolutionary world: how adaptation explains everything from seashells to civilization*. New York, NY: Thomas Dunne Books, St. Martin's Press.

Vermeij GJ. 2011a. Shifting sources of productivity in the coastal marine tropics during the Cenozoic era. *Proceedings of the Royal Society of London Series B, Biological Sciences* **278:** 2362–2368.

Vermeij GJ. 2011b. The energetics of modernization: the last one hundred million years of biotic history. *Paleontological Research* **15:** 54–61.

Vermeij GJ. 2011c. A historical conspiracy: competition, opportunity, and the emergence of direction in history. *Cliodynamics* **2:** 187–207.

Vermeij GJ, Dietl GP, Reid DG. 2008. The trans-Atlantic history of diversity and body size in ecological guilds. *Ecology* **89:** S39–S52.

Vermeij GJ, Leigh EG Jr. 2011. Natural and human economies compared. *Ecosphere* **2 Article 39:** 1–16.

Vianna JA, Ayerdi P, Medina-Vogel G, Mangeo JC, Zeballos H, Apaza M, Gaugeron S. 2010. Phylogeography of the marine otter (*Lontra felina*): historical and contemporary factors determining its distribution. *Journal of Heredity* **101:** 676–689.

Vianna JA, Medina-Vogel G, Chehébar C, Sielfeld W, Olivarría C, Faugeron S. 2011. Phylogeography of the Patagonian otter *Lontra provocax*: adaptive divergence to marine habitat or signature of southern glacial refugia? *BMC Evolutionary Biology* **11:** 53.

Waller TR. 1969. The evolution of the Argopecten gibbus stock (Mollusca: Bivalvia) with emphasis on the Tertiary and Quaternary species of eastern North America. *Paleontological Society Memoir* **3:** 1–125.

Waller TR. 2006. New phylogenies of the Pectinidae (Mollusca: Bivalvia): reconciling morphological and molecular approaches. In: Shumway SE, Parsons GJ, eds. *Scallops: biology, ecology and aquaculture*. Amsterdam: Elsevier, 1–44.

Walsh JJ. 1988. *On the nature of continental shelves*. San Diego, CA: Academic Press.

Warén A, Klitgaard A. 1991. Hanleya nagelfar, a sponge-feeding ecotype of H. hanleyi or a distinct species of chiton? *Ophelia* **34:** 51–70.

Waters JH, Ray CE. 1961. Former range of the sea mink. *Journal of Mammalogy* **42:** 380–383.

Webster JD. 1941. Feeding habits of the black oystercatcher. *Condor* **43:** 175–179.

Willemsen GF. 1992. A revision of the Pliocene and Quaternary Lutrinae from Europe. *Scripta Geologica* **101:** 1–115.

Worm B. 2000. Consumer versus resource control in rocky shore food webs: Baltic Sea and northwest Atlantic Ocean. *Berichte aus dem Institut für Meereskunde an der Christian-Albrechts-Universität Kiel no* **316:** 1–147.

Yokoyama M. 1922. Fossils from the Upper Musashino of Kazusa and Shimosa. *Journal of the College of Science, Imperial University of Tokyo* **44:** 1–200.

Zach M. 1978. Selection and dropping of whelks by Northwestern crows. *Behaviour* **67:** 134–148.