Drilling predation increased in response to changing environments in the Caribbean Neogene

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Abstract.—Changes in the physical environment are major drivers of evolutionary change, either through direct effects on the distribution and abundance of species or more subtle shifts in the outcome of biological interactions. To investigate this phenomenon, we built a fossil data set of drilling gastropod predation on bivalve prey for the last 11 Myr to determine how the regional collapse in Caribbean upwelling and planktonic productivity affected predator–prey interactions. Contrary to theoretical expectations, predation increased nearly twofold after productivity declined, while the ratio of drilling predators to prey remained unchanged. This increase reflects a gradual, several-fold increase in the extent of shallow-water coral reefs and seagrass meadows in response to the drop in productivity that extended over several million years. Drilling predation is uniformly higher in biogenic habitats than in soft sediments. Thus, changes in predation intensity were driven by a shift in dominant habitats rather than a direct effect of decreased productivity. Most previous analyses of predation through time have not accounted for variations in environmental conditions, raising questions about the patterns observed. More fundamentally, however, the consequences of large-scale environmental perturbations may not be instantaneous, especially when changes in habitat and other aspects of local environmental conditions cause cascading series of effects.

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Introduction

Changing physical environments play a critical role in ecology and evolution (Schindler 1990; Wootton et al. 1996; Jablonski 2003; Vrba 2005; Jackson and Erwin 2006). However, predicting how specific environmental changes will influence biotic systems is difficult, because the changes may influence biological interactions over multiple temporal and spatial scales (Levin 1992; Lynch and Lande 1993; Lavergne et al. 2010; Pereira et al. 2010; Dawson et al. 2011). Fortunately, the fossil record provides an unique opportunity to assess the effect of changing environmental conditions on biotic interactions over extended timescales (Marx and Uhen 2010) and to disentangle complicated biotic responses to environmental change (Terry et al. 2011; Blois et al. 2013, 2014).

Predation is a biotic interaction that plays an especially important role in shaping ecosystems through cascading effects (Harriston et al. 1960; Paine 1966; Pace et al. 1999; Roemer et al. 2009; Estes et al. 2011). A number of variables influence predator–prey interactions, including productivity (Leibold 1989; Holt et al. 1994; Bohannan and Lenski 2000), temperature (Elliott and Leggett 1996), environmental disturbance (Bertness 1981; Menge and Sutherland 1987), and habitat complexity (Almany 2004). The fossil record provides the opportunity to directly examine how environmental perturbations influence predation over long timescales, because certain predators leave distinctive traces of their predation on the hard parts of their prey (Kitchell et al. 1981; Kowalewski 2002).

The fossil record of drilling gastropod predators represents one of the few direct records of predation (Kowalewski 2002). Although several families of gastropods produce drill holes, most reported in the fossil record, including this study, closely resemble

those made by muricid and naticid gastropods (Kelley and Hansen 2003). Both naticids and muricids create bore holes using a combination of mechanical and chemical processes in which the proboscis/radula and the accessory boring organ are used alternately to rasp and soften the shell chemically (Carriker 1981). Naticids are infaunal (live within the sediment) and usually prefer infaunal prey, whereas muricids are primarily epifaunal (live on the surface of the seafloor) and therefore search for and drill primarily epifaunal prey (Kelley and Hansen 2003). Naticid and muricid gastropods both produce regular holes that can be distinguished from the more irregular drill holes produced by other predators (principally octopods and worms). Naticid drill holes are normally beveled, while muricids more commonly produce smooth-sided, cylindrical drill holes, but shell structure and thickness of prey may influence the shape of the drill hole (Kowalewski 1993; Kelley and Hansen 2003).

Here, we use the fossil record of gastropod predation on bivalves to test the effect of changes in the physical environment on trophic interactions in the Caribbean during the Neogene. The final closure of the Central America Seaway (CAS) by the emergence of the Isthmus of Panama approximately 3.5 Ma (Coates et al. 1992, 2004; Coates and Stallard 2013; Jackson and O'Dea 2013) caused a decrease in upwelling and planktonic productivity that provides a natural experiment for testing how changes in the physical environment may have influenced the structure and function of Caribbean near-shore marine communities (Woodring 1966; Vermeij and Petuch 1986; Johnson et al. 1995, 2007, 2008; Jackson et al. 1999; Todd et al. 2002; O'Dea et al. 2007; O'Dea and Jackson 2009; Smith and Jackson 2009; Leonard-Pingel et al. 2012). The fossil record is rich and well dated, and changes in physical environments are well documented based on independent proxy data (O'Dea et al. 2007). We use this excellent framework to quantify changes in drilling predation through time and assess potential causes of change in predation, specifically addressing two alternative hypotheses:

H1: Decline in regional planktonic productivity directly resulted in decreased

intensity of predation as expected from ecological theory and from laboratory experiments. Theoretically, as a prey population grows, predators respond behaviorally (functional response) by increasing their rate of prey consumption (Holling 1959). This has been observed in both field and laboratory experiments (Ricker 1941; Holling 1959; Kauzinger and Morin 1998) and is well established in theoretical ecology (e.g., Case 2000). Conversely, then, if the prey population decreases in size due a decrease in productivity, one might expect to see a decrease in the intensity of predation.

H2: Changes in predation intensity were the result of changes in habitats and the species that inhabited them rather than a direct effect of changes in productivity on predation intensity.

Materials and Methods

Sample Collection and Predation Measures

We collected 189 fossil samples from 28 faunules across Panama and Costa Rica that span 11 Myr (Table 1, Fig. 1). Here, we define a "faunule" as a pooled collection of bulk samples from a locality that we believe reasonably represents a fossil community (e.g., bulk samples that are pooled into a faunule are from the same environment, time, and geographic location) (see also Jackson et al. 1999; Johnson et al. 2007; O'Dea et al. 2007; Smith and Jackson 2009; Leonard-Pingel et al. 2012). We collected between 1 and 21 approximately 10 kg bulk sediment samples (collection bag of loosely consolidated sediment, rock, and fossils) from each locality, carefully controlling for stratigraphy and geographic extent (e.g., closely spaced sampling from the same geologic horizon and paleoenvironment). The use of several bulk samples for each locality allowed us to attain an adequate sample size. In addition, individual bulk samples are combined into faunules to avoid pseudoreplication—each individual bulk sample is not an independent replicate (Hurlburt 1984); however, each faunule does represent an

TABLE 1. Age, geologic formation, and locality information for each faunule. Numbers correspond to locations mapped in Figure 1.

Faunule	Age (Ma)	Geologic formation	Latitude	Longitude
Lennond (1)	0.007	Unnamed Holocene	9.354883	−82.26635
Swan Cay (2)	1.4	Swan Cay	9.453347	−82.299414
Empalme (3)	1.6	Moin	9.985583	−83.06125
Upper Lomas (4)	1.6	Moin	9.99195	−83.03672
Wild Cane Reef (5)	2.05	Ground Creek	9.349978	−82.167983
Wild Cane Key (6)	2.05	Ground Creek	9.351047	−82.1687
Ground Creek: porites (7)	2.05	Ground Creek	9.416992	−82.304567
Ground Creek: mud (8)	2.05	Ground Creek	9.407367	−82.301983
Fish Hole (9)	2.6	Ground Creek	9.318311	−82.110838
Bomba (10)	3.05	Quebrada Chocolate	9.913861	−83.066306
Quebrada Chocolate (11)	3.1	Quebrada Chocolate	9.973608	−83.084728
Quitaria (12)	3.5	Quebrada Chocolate	9.910228	−83.08575
Cayo Agua: Punta Níspero West (13)	3.55	Lower Cayo Agua	9.168555	−82.031914
Cayo Agua: Punta Tiburón - Punta Piedra (14)	3.55	Upper Cayo Agua	9.151892	−82.023775
Río Vizcaya (15)	3.55	Quebrada Chocolate Formation	9.880608	−83.069381
Santa Rita (16)	3.55	Quebrada Chocolate	9.97038	−83.12991
Isla Solarte (17)	3.55	Ground Creek	9.333214	−82.218714
Cayo Agua: Punta Níspero South (18)	3.55	Lower Cayo Agua	9.167275	−82.030579
Isla Popa (19)	4.25	Cayo Agua	9.21452	−82.107
Cayo Agua: Punta Norte West (20)	4.25	Lower Cayo Agua	9.178117	−82.053814
Cayo Agua: Punta Piedra Roja West (21)	4.25	Upper Cayo Agua	9.139444	−82.016778
Cayo Agua: Punta Norte East (22)	4.25	Lower Cayo Agua	9.174883	−82.042417
Río Chico N17 (23)	6.35	Chucunaque	8.257639	−77.531889
Río Tupisa (24)	6.35	Chucunaque	8.308611	−77.610417
Río Indio (25)	6.95	Gatun Formation	9.179083	−80.241389
Mattress Factory (26)	9	Gatun Formation	9.36006	−79.83093
Isla Payardi (27)	9.6	Gatun Formation	9.382722	−79.821389
Sand Dollar Hill (28)	11	Gatun Formation	9.3515	−79.810472

independent sample. Faunules were assigned to one of four habitat types: reef, seagrass, mixed reef and seagrass, or soft sediment based on lithologic descriptions, total faunal assemblages, and the percent mud and carbonate in sediments (Coates 1999; Jackson et al. 1999; O'Dea et al. 2007; see Table 2). Although identified by a suite of descriptive characters, reef habitats were identified either by the presence of large–reef building corals, which remained uncollected but were noted in stratigraphic descriptions, or by a high proportion of coral debris found in the fossil assemblages. Seagrass environments are also identified primarily by faunal composition, either by bivalves commonly associated with seagrass beds, or the presence of small, solitary corals typical of seagrass beds (see Leonard-Pingel et al. 2012). Soft-sediment habitats were recognized by faunal assemblages typical of sandy or muddy bottoms, particularly a very low proportion of coral debris in the fossil assemblages (mean = 1.26% by weight, SD = 1.71).

We washed bulk samples on a 2 mm sieve and sorted them to gross taxonomic groups. We then sorted bivalves to genus and gastropods to family following the nomenclature of Todd (2001). Identification of bivalves to the generic level is based on dentition (number and arrangement of teeth on the hinge plate), shell shape, and ornament; all characters that are readily preserved in the fossil record. Morphological characters that distinguish gastropod families are also well preserved. Individuals that we could not identify to at least family with a high degree of certainty, particularly due to poor preservation, represent <1% of the total number of bivalve valves (~109,000) identified and counted. Unidentified individuals were not included in this analysis. For bivalves, numbers of individuals were estimated from the number of valves with a hinge and umbo and divided in half to account for disarticulation; gastropods with an apex were counted as individuals (Gilinsky and Bennington 1994). We examined bivalves for the presence of
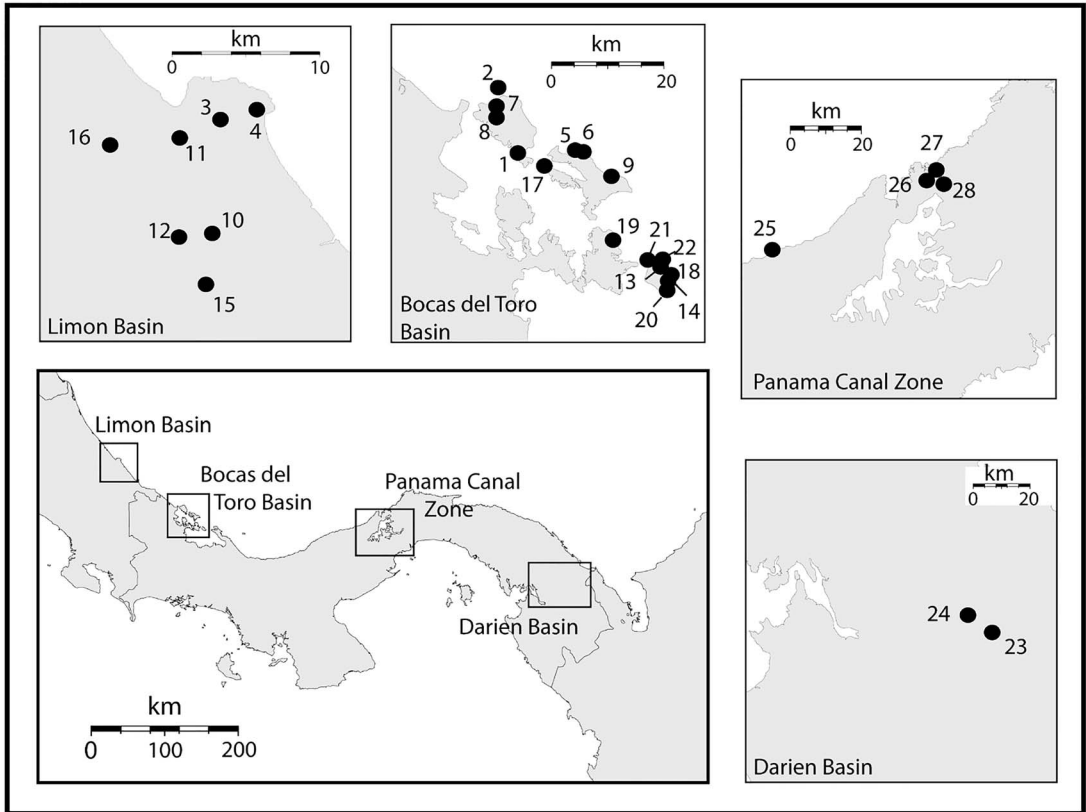
FIGURE 1. Map of Panama and eastern Costa Rica, with insets showing the four basins from which collections were taken; Limon Basin, Costa Rica; Bocas del Toro Basin, Panama; Panama Canal Zone, Panama; and Darien Basin, Panama. Numbers correspond to faunules listed in Table 1.

distinctive traces left by naticids or muricids (Kitchell et al. 1981; Vermeij 1987; Kelley et al. 2001; Leighton 2002; Walker 2007). However, we did not distinguish between muricid and naticid drill traces in the final analyses because of ambiguity introduced by differential shell preservation, variability in drill shape among individuals (Kowalewski 2004), and variability in drill shape among prey with different microstructures (Hoffman et al. 1974). We then tallied the number of valves displaying at least one successful drilling trace (Kowalewski 2002). We did not observe unambiguous edge drilling of bivalves (Dietl and Herbert 2005; Chattopadhyay et al. 2014). We calculated the drilling frequency (number of bivalve valves drilled/half of the total number of bivalve valves in the sample) at the assemblage level for each faunule as a proxy for predation intensity sensu Kowalewski (2002) (Table 2).

We also calculated the drilling frequency for each bivalve genus with at least 25 valves pooled over all samples (see Table 3).

Statistical Analyses

Bivalves.—We performed a Spearman rank correlation on the assemblage-level drilling frequency in relation to faunule age to test for changes in predatory drilling through time. To test for the effect of habitat on drilling we used Wilcoxon rank-sum tests to compare the drilling frequency of faunule assemblages categorized as either soft-sediment or biogenic habitats (reefs, seagrasses, or a combination of both). We also compared drilling frequency for genera characteristic of biogenic versus soft-sediment environments using data pooled across all the faunules. Assignment of genera to different habitat

TABLE 2. Age, habitat designation, environmental data, and abundance data for each faunule (O'Dea et al. 2007; Leonard-Pingel et al. 2012). Mixed habitat refers to a combination of seagrass and coral dominated environments.

Faunule	Number of samples	Age (Ma)	Habitat	Depth (m)	Mean annual range in temperature	Percent carbonate	Percent mud	Percent coral	Number of bivalve valves	Drilling frequency (percent bivalves drilled)	Number of gastropods	Number of muricids	Number of naticids
Lennond	10	0.007	Mixed	15	3.8	85.18	39.03	94.98	1313	20.72	2680	55	3
Swan Cay	11	1.4	Reef	100	3.22	63.49	20.9	15.74	1327	21.7	3560	115	51
Empalme	6	1.6	Reef	20	2.82	43.43	32.55	3.45	3646	23.64	1994	74	5
Upper Lomas	21	1.6	Reef	75	2.82	43.28	21.33	35.7	14793	36.87	6204	158	83
Wild Cane Reef	7	2.05	Reef	25	4.19	56.4	28.29	67.05	279	18.64	1403	23	36
Wild Cane Key	4	2.05	Mixed	30	4.19	45.76	33.11	52.62	360	22.22	605	16	7
Ground Creek: porites	9	2.05	Reef	10	4.19	51.41	53.01	93.79	2119	6.51	1202	5	7
Ground Creek: seagrass	6	2.05	Seagrass	10	4.19	29.6	30.78	9.45	24476	18.72	1653	20	94
Fish Hole	4	2.6	Mixed	88	2.36	19.55	59.34	34.64	329	17.02	438	2	26
Bomba	10	3.05	Soft sediment	30	3.13	68.96	29.78	1.65	2339	14.11	1503	7	128
Quebrada Chocolate	1	3.1	Reef	25	3.13	31.98	17.22	0.17	8438	12.66	509	15	27
Quitaria	1	3.5	Soft sediment	30	3.13	20.83	20.19	2.67	478	7.11	630	1	34
Cayo Agua: Punta Nispero West	3	3.55	Soft sediment	60	7.23	26.1	33.85	1.56	989	10.52	402	2	13
Cayo Agua: Punta Tiburon	4	3.55	Seagrass	60	5.68	32.01	30.14	25.02	1055	18.77	200	6	5
Rio Vizcaya	3	3.55	Soft sediment	12	3.13	31.66	15.47	0.19	1651	10.3	1155	13	56
Santa Rita	6	3.55	Soft sediment	30	5.73	44.4	28.88	5.86	1236	14.89	274	9	22
Isla Solarte	3	3.55	Soft sediment	75	6.68	54.1	14.79	3.28	3016	13.13	2142	124	33
Cayo Agua: Punta Nispero South	3	3.55	Seagrass	60	7.23	26.1	15.34	3	1922	30.49	132	7	2
Isla Popa	6	4.25	Soft sediment	50	6.65	19.77	56.69	0.02	11067	17.46	141	6	33
Cayo Agua: Punta Norte West	9	4.25	Seagrass	30	6.25	15.93	42.59	8.08	3161	15.56	637	45	18
Cayo Agua: Punta Piedra Roja West	10	4.25	Seagrass	42	3.52	27.73	18.72	17.32	10616	28.86	1841	43	99
Cayo Agua: Punta Norte East	7	4.25	Soft sediment	60	4.11	18.87	49.57	1.6	1493	17.41	368	6	26
Rio Chico N17	4	6.35	Soft sediment	30	8.67	20.11	36.02	0	5282	13.59	854	0	63
Rio Tupisa	3	6.35	Soft sediment	100	6.65	15.28	41.2	0	1103	14.14	376	0	26
Rio Indio	11	6.95	Soft sediment	25	6.77	9.76	12.13	0.09	619	11.95	202	3	35
Mattress Factory	2	9	Soft sediment	28	6.18	24.55	35.3	0.25	1388	31.84	158	6	9
Isla Payardi	9	9.6	Soft sediment	27.5	6.18	25.73	47.9	0	3184	11.24	3548	0	570
Sand Dollar Hill	3	11	Soft sediment	27.5	6.18	20.24	8.6	0.43	1551	6.58	120	0	52

TABLE 3. Bivalve genera pooled across all samples with drilling frequency and preferred habitat. Preferred habitat is inferred from a reivew of the literature with key references cited.

Genus	Family	Number of valves	Valves/2	Number of drilled valves	Drilling frequency	Preferred habitat	Habitat references
Anomia	Anomiidae	299	149.5	8	5.35	Reef	Díaz et al. 1990
Anadara	Arcidae	3961	1980.5	250	12.62	Soft sediment	Taylor 1968; Stanley 1970; Chinzei 1984; Fortunato and Schafer 2009
Barbatia	Arcidae	827	413.5	29	7.01	Reef	Taylor 1968; Taylor and Reid 1969; Work 1969; Stanley 1970; Díaz et al. 1990; Zuschin et al. 2001
Arca	Arcidae	296	148	16	10.81	Reef	Taylor and Reid 1969; Work 1969; Stanley 1970; Díaz et al. 1990
Acar	Arcidae	162	81	8	9.88	Reef	Taylor 1968; Tayler and Reid 1969
Lunarca	Arcidae	36	18	2	11.11	Soft sediment	Pires 1992
Trigoniocardia	Cardiidae	1548	774	53	6.85	Soft sediment	Keen 1971
Trachycardium	Cardiidae	321	160.5	2	1.25	Seagrass	Stanley 1970
Laevicardium	Cardiidae	210	105	4	3.81	Soft sediment	Stanley 1970; Chinzei 1984
Americardia	Cardiidae	32	16	2	12.50	Soft sediment	Stanley 1970
Cardites	Carditidae	908	454	87	19.16	Soft sediment	Yonge 1969
Chama	Chamidae	1085	542.5	146	26.91	Reef	Taylor and Reid 1969; Díaz et al. 1990; Zuschin et al. 2001
Arcinella	Chamidae	254	127	18	14.17	Reef	Slack-Smith 1998
Caryocorbula	Corbulidae	18526	9263	3247	35.05	Soft sediment	Stanley 1970; Anderson 1992, 1994; Fortunato and Schafer 2009
Varicorbula	Corbulidae	16997	8498.5	2161	25.43	Soft sediment	Yonge 1946; Anderson 1992, 1994
Crassinella	Crassatellidae	878	439	86	19.59	Seagrass	Hauser et al. 2007
Eucrassatella	Crassatellidae	72	36	5	13.89	Soft sediment	Coan 1984
Cardiomya	Cuspidariidae	119	59.5	2	3.36	Soft sediment	Prezant 1998
Dimya	Dimyidae	359	179.5	104	57.94	Reef	Yonge 1978
Donax	Donacidae	72	36	0	0.00	Soft sediment	Taylor 1968; Stanley 1970
Tucetona	Glycymerididae	4471	2235.5	568	25.41	Soft sediment	Thomas 1975
Axinactis	Glycymerididae	65	32.5	3	9.23	Soft sediment	Thomas 1975
Hyotissa	Gryphaeidae	253	126.5	41	32.41	Reef	Taylor and Reid 1969; Zuschin et al. 2001
Isognommon	Isognomonidae	77	38.5	4	10.39	Reef	Taylor and Reid 1969; Work 1969; Díaz et al. 1990; Zuschin et al. 2001
Temblornia	Leptonidae	28	14	0	0.00	Symbiotic in soft-sediment burrows	Keen 1971
Ctenoides	Limidae	51	25.5	2	7.84	Reef	Zuschin et al. 2001
Limea	Limidae	29	14.5	3	20.69	Soft sediment	Allen 2004
Limopsis	Limopsodae	486	243	74	30.45	Reef/Hard Substrate	Oliver 1981
Lucina	Lucinidae	2134	1067	137	12.84	Seagrass	Stanley 1970; Hauser et al. 2007
Myrtea	Lucinidae	1243	621.5	175	28.16	Soft sediment	Dando et al. 1985
Parvilucina	Lucinidae	787	393.5	197	50.06	Seagrass	Jackson 1973; Hauser et al. 2007
Phacoides	Lucinidae	208	104	23	22.12	Seagrass	Stanley 1970
Radiolucina	Lucinidae	106	53	18	33.96	Seagrass	See references for *Parvilucina*; Britton 1972
Codakia	Lucinidae	45	22.5	6	26.67	Seagrass	Taylor 1968; Stanley 1970; Jackson 1973; Bitter-Soto 1999
Cavilinga	Lucinidae	39	19.5	9	46.15	Seagrass	See references for *Lucina*; Britton 1972
Mulinia	Mactridae	26	13	1	7.69	Soft sediment	Stanley 1970; Rudnick et al. 1985
Crenella	Mytilidae	119	59.5	6	10.08	Reef	Taylor and Reid 1969
Arcopsis	Noetiidae	820	410	76	18.54	Reef	Stanley 1970; Díaz et al. 1990
Noetia	Noetiidae	225	112.5	5	4.44	Soft sediment	Stanley 1970
Sheldonella	Noetiidae	61	30.5	6	19.67	Soft sediment	Thomas 1978
Saccella	Nuculanidae	3064	1532	165	10.77	Soft sediment	Chinzei 1984; Probert and Grove 1998
Costelloleda	Nuculanidae	102	51	2	3.92	Soft sediment	Olsson 1971
Adrana	Nuculanidae	60	30	1	3.33	Soft sediment	Olsson 1971
Propeleda	Nuculanidae	27	13.5	1	7.41	Soft sediment	Arnaud et al. 2001

Table 3. *Continued*

Genus	Family	Number of valves	Valves/ 2	Number of drilled valves	Drilling frequency	Preferred habitat	Habitat references
Nucula	Nuculidae	2688	1344	144	10.71	Soft sediment	Yonge 1946; Stanley 1970; Rudnick et al. 1985; Probert and Grove 1998
Acila	Nuculidae	166	83	2	2.41	Soft sediment	Stasek 1961
Varinucula	Nuculidae	128	64	4	6.25	Soft sediment	Probert and Grove 1998
Dendostrea	Ostreidae	5151	2575.5	332	12.89	Reef	Díaz et al. 1990; Zuschin et al. 2001
Ostreola	Ostreidae	549	274.5	71	25.87	Reef	Taylor 1968; Taylor and Reid 1969; Díaz et al. 1990
Crassostrea	Ostreidae	172	86	4	4.65	Reef, Hard Substrate	Taylor 1968
Argopecten	Pectinidae	3765	1882.5	33	1.75	Soft sediment	Haaker et al. 1988; Fortunato and Schafer 2009
Spathochlamys	Pectinidae	582	291	4	1.37	Reef	Taylor 1968; Smith 2006
Leptopecten	Pectinidae	538	269	1	0.37	Reef/Hard Substrate	Morton 1980
Leopecten	Pectinidae	482	241	2	0.83	Soft sediment	Shumway and Parsons 2006
Pacipecten	Pectinidae	70	35	8	22.86	Reef/Hard Substrate	Morton 1980
Amusium	Pectinidae	56	28	1	3.57	Soft sediment	Morton 1980
Aequipecten	Pectinidae	40	20	0	0.00	Seagrass	Stanley 1970
Flabellipecten	Pectinidae	36	18	0	0.00	Soft sediment	Shumway and Parsons 2006
Plicatula	Plicatulidae	753	376.5	130	34.53	Reef	Taylor 1968; Taylor and Reid 1969; Díaz et al. 1990
Cyclopecten	Propeamussiidae	612	306	23	7.52	Soft sediment	Probert and Grove 1998
Spondylus	Propeamussiidae	60	30	4	13.33	Reef	Taylor and Reid 1969; Díaz et al. 1990; Zuschin et al. 2001
Pteria	Pteriidae	169	84.5	6	7.10	Reef	Taylor 1968; Díaz et al. 1990
Yoldia	Sareptidae	108	54	6	11.11	Soft sediment	Stanley 1970; Rudnick et al. 1985
Ervilia	Semelidae	598	299	50	16.72	Seagrass	Taylor 1968
Cumingia	Semelidae	61	30.5	4	13.11	Soft sediment	Stanley 1970
Semele	Semelidae	49	24.5	0	0.00	Soft sediment	Urban and Campos 1994
Tagelus	Solecurtidae	1240	620	14	2.26	Soft sediment	Stanley 1970
Angulus	Tellinidae	853	426.5	28	6.57	Soft sediment	Chinzei 1984
Merisca	Tellinidae	563	281.5	6	2.13	Soft sediment	Based on the *Tellina* classification - still considered a subgenus in most classification regimes
Eurytellina	Tellinidae	536	268	22	8.21	Soft sediment	Based on the *Tellina* classification - still considered a subgenus in most classification regimes
Tellina	Tellinidae	332	166	12	7.23	Soft sediment	Stanley 1970
Moerella	Tellinidae	285	142.5	44	30.88	Soft sediment	Probery and Grove 1998; Simone and Wilkinson 2008
Elpidollina	Tellinidae	88	44	5	11.36	Soft sediment	Simone and Wilkinson 2008
Strigilla	Tellinidae	85	42.5	3	7.06	Soft sediment	Stanley 1970
Felaniella	Ungulinidae	100	50	9	18.00	Soft sediment	Hayward et al. 1997
Chione	Veneridae	15317	7658.5	1780	23.24	Seagrass	Jackson 1973; Bitter-Soto 1999; Hauser et al. 2007
Macrocallista	Veneridae	4405	2202.5	267	12.12	Soft sediment	Stanley 1970
Gouldia	Veneridae	1982	991	230	23.21	Seagrass	Hauser et al. 2007
Pitar	Veneridae	990	495	65	13.13	Soft sediment	Taylor 1968; Chinzei 1984
Lirophora	Veneridae	839	419.5	44	10.49	Soft sediment	Stanley 1970; Fortunato and Schafer 2009
Lamelliconcha	Veneridae	302	151	19	12.58	Soft sediment	Taylor 1968; Pilsbry 1931; Chinzei 1984
Panchione	Veneridae	150	75	15	20.00	Soft sediment	See references for *Lirophora;* Roopnarine 1996
Dosinia	Veneridae	117	58.5	5	8.55	Soft sediment	Stanley 1970; Chinzei 1984
Cyclinella	Veneridae	92	46	2	4.35	Soft sediment	Stanley 1970
Ventricolaria	Veneridae	73	36.5	6	16.44	Soft sediment	Jones 1984
Anomalocardia	Veneridae	55	27.5	0	0.00	Soft sediment	Stanley 1970
Chionista	Veneridae	36	18	1	5.56	Seagrass	See references for *Chione;* Roopnarine 1996
Trigonulina	Verticordiidae	70	35	4	11.43	Soft sediment	Allen and Turner 1974

types was based on a literature survey (Table 3). Additionally, we used drilling frequency data on individual genera to determine whether the same genus living in different habitats had similar drilling frequencies. We chose four common genera typical of soft-sediment habitats and four common genera typical of biogenic habitats, calculated the drilling frequency for each genus in each faunule where it occurred in a reasonable abundance (>5 valves), and then compared the drilling frequencies in soft-sediment and biogenic habitats for each genus using Wilcoxon rank-sum tests.

We also looked for significant differences in drilling frequency between functional groups that are strongly related to habitat (i.e., infaunal vs. epifaunal bivalves and chemosymbiotic vs. siphonate bivalves) using G-tests of independence. For comparison of predation frequency upon infaunal versus epifaunal bivalves, we excluded groups whose life habits do not fit well within either of these broad functional types. The most abundant of these are small corbulid bivalves that live byssally attached to sediment grains upon or immediately below the sediment surface in gregarious clusters (Mikkelsen and Bieler 2001). We also excluded Pectinidae (scallops) because of their ability to move freely or swim away from predators, a trait that is rare among other epifaunal bivalves (Joll 1989). For comparison of drilling on chemosymbiotic and siphonate bivalves, the chemosymbiotic group includes all the lucinid bivalves; the siphonate group includes families of suspension-feeding or deposit-feeding bivalves with siphons long enough to facilitate relatively deep burrowing. The latter include members of the families Semelidae, Solecurtidae, Tellinidae, Thraciidae, and Veneridae.

Gastropods.—The abundance of predators (Naticidae and Muricidae gastropods) or changes in their relative abundance (ratio of Muricidae to Natidicae) might also influence drilling frequency. To investigate this, we binned faunules according to age—11–6.35 Ma (before major restriction of shallow-water connections between the Caribbean and eastern Pacific), 4.25–3.05 Ma (transitional period of increasing restriction between the oceans), and 2.6–0.007 Ma (modern Caribbean)—and

performed Kruskal-Wallis tests to determine whether there were significant differences in the ratio of predators to prey or shifts in the dominant drilling predators through time. In cases in which Kruskal-Wallis tests showed significant differences, Wilcoxon rank-sum tests were performed a posteriori. We also performed G-tests of independence to test for significant differences in relative abundance of muricid and naticid gastropods in soft-sediment and biogenic habitats

Results

We examined a total of 109,202 bivalve valves from 145 genera and found 11,405 valves with unambiguous drill holes. We also counted 34,931 gastropods and identified 1563 naticid gastropods and 761 muricid gastropods. Analysis of this data shows that the drilling frequency of bivalves significantly increases through time despite high variability among faunules ($\rho = 0.33$, $p < 0.05$) (Fig. 2). However, when faunules are grouped by habitat, the percentage of drilled bivalves is uncorrelated with faunule age (soft-sediment habitats: $\rho = 0.04$, $p = 0.44$; biogenic habitats: $\rho = -0.19$, $p = 0.26$). Assemblage-level drilling frequencies of biogenic (seagrass meadow, coral reef, or mixed reef–seagrass) habitats are nearly double those of assemblage-level drilling frequencies in soft-sediment faunules ($W = 159$, $p < 0.01$; Fig. 3A). Drilling frequencies for bivalve genera characteristic of biogenic habitats experience significantly higher drilling frequencies than genera characteristic of soft-sediment habitats ($W = 1299.5$, $p < 0.01$; Fig. 3B). Furthermore, bivalve functional groups typically associated with biogenic habitats experience more drilling than bivalve functional groups associated with soft-sediment habitats. The drilling frequency of epifaunal bivalves characteristic of reef-associated habitats and chemosymbiotic bivalves characteristic of seagrasses is 2 to 4 times higher than the drilling frequency of infaunal bivalves characteristic of soft sediments ($G = 322.89$, $p < 0.0001$ and $G = 680.59$, $p < 0.0001$, respectively; Fig. 3C,D). However, drilling frequencies for individual genera that occur in both soft-sediment and biogenic habitats show only one case of a
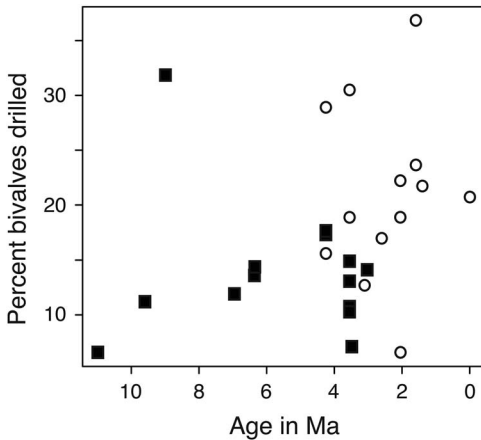
FIGURE 2. Percentage of bivalves drilled for each faunule. The percentage of drilled bivalves significantly increased through time ($\rho = 0.33$, $p < 0.05$), but there is no correlation between percentage of drilled bivalves and time when faunules are analyzed by habitat (soft-sediment habitats (squares): $\rho = 0.04$, $p = 0.44$; biogenic habitats (circles): $\rho = -0.19$, $p = 0.26$). This contradicts the hypothesis that predation is positively correlated with primary productivity.

significant difference between the two habitat groups (Fig. 4).

The ratio of predatory gastropods to bivalve prey was unchanged over the entire interval (Fig. 5A). However, this apparent stability belies a profound shift in the composition of drilling gastropod assemblages. The ratio of epifaunal muricid gastropods to infaunal naticid gastropods shifts among time bins ($\chi^2 = 9.73$, $p < 0.01$), with significantly lower proportions of naticids in younger time bins ($W = 11$, $p < 0.01$; $W = 4$, $p < 0.01$, respectively; Fig. 5B). Muricids comprise more than half the drilling gastropod fauna in biogenic habitats, whereas naticids are nearly 5 times more abundant than muricids in soft-sediment faunules ($G = 473.61$, $p < 0.0001$, df $= 1$, $n = 2324$; see Fig. 6).

Discussion

The results strongly support the hypothesis that frequency of predation is determined by habitat (H2) and not by the regional decrease in planktonic productivity (H1). Bivalves living in and characteristic of biogenic habitats are subject to higher predation intensities than bivalves living in soft-sediment habitats (Fig. 3). There is no evidence, however, that

drilling frequencies increase uniformly in biogenic habitats. Within a genus, drilling frequency is not significantly higher in biogenic environments in seven out of eight genera tested (Fig. 4). We therefore conclude that the regional change in drilling frequency through time (Fig. 1) is due to the increase in the extent of biogenic habitats and the bivalve genera common to these habitats. Consequently, changes in the frequency of drilling predation can ultimately be linked to the final closure of the CAS ca. 3.5 Ma (Keigwin 1982; Haug et al. 2001; Coates and Stallard 2013; Jackson and O'Dea 2013) and the restructuring of benthic communities associated with closure of the CAS.

Closure of the CAS and Oceanographic Changes

Closure of the CAS led to a variety of environmental changes in the Caribbean, including increased salinity (Keigwin 1982; Cronin and Dowsett 1996), a decrease in seasonality (Teranes et al. 1996; O'Dea et al. 2007), and a decrease in regional planktonic productivity as Caribbean upwelling shut down (Allmon 2001; Kirby and Jackson 2004; O'Dea et al. 2007). Isotopic evidence indicates areas of upwelling in the Caribbean in the Miocene and Pliocene and a decrease in upwelling and productivity from the late Pliocene to Pleistocene (Cronin 1991; Cronin and Dowsett 1993, 1996; Jones and Allmon 1995; Allmon et al. 1996). Further evidence for upwelling comes from large Miocene phosphorite deposits in the southeastern United States, Cuba, and Venezuela (Riggs 1984). Vertebrate and invertebrate fossil assemblages also indicate areas of upwelling and high biological productivity throughout the western Atlantic in the Pliocene (Allmon 1993; Allmon et al. 1996). Extinction of organisms that required high planktonic productivity in the late Pliocene provides additional evidence for regional productivity declines (e.g., Kirby and Jackson 2004; O'Dea and Jackson 2009). While we have good proxy evidence for a regional decrease in planktonic productivity after closure of the CAS, we lack proxies for productivity among individual
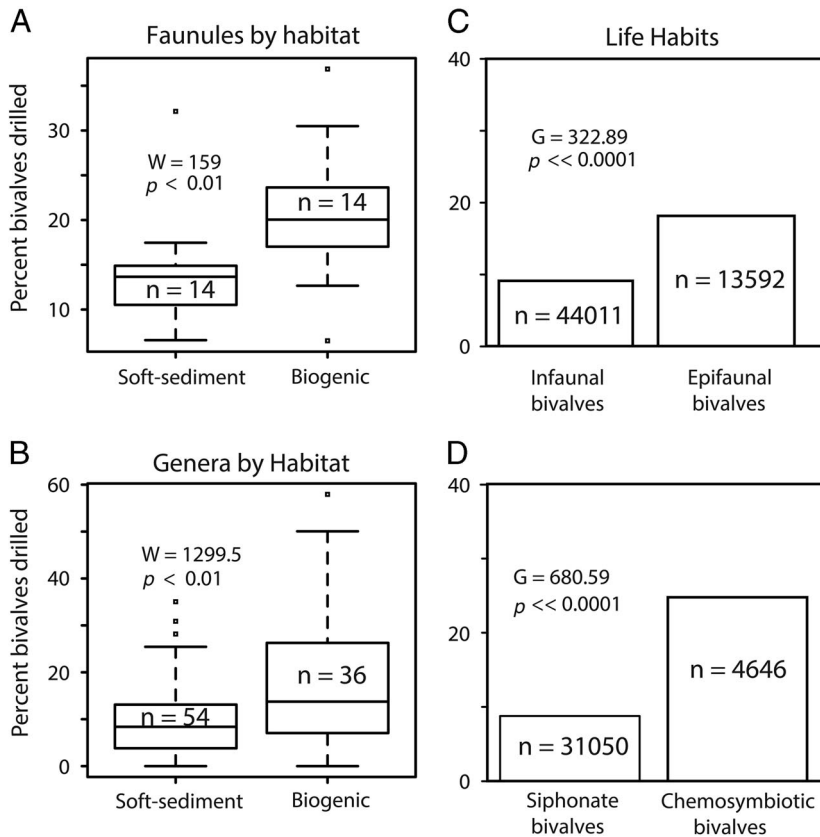
FIGURE 3. Differences in predation rates between habitats and bivalve functional groups. W-values are for Wilcoxon rank-sum tests; G-values are for G-tests. A, Biogenic faunules ($n = 14$) have significantly higher drilling frequencies than do soft-sediment faunules ($n = 14$). B, Genera characteristic of biogenic habitats ($n = 36$) display higher drilling frequencies than do genera characteristic of soft-sediment habitats ($n = 54$). C, The percentage of epifaunal bivalves ($n = 13592$ valves) drilled is more than twice that of infaunal bivalves ($n = 44011$ valves) in all 28 faunules combined. D, The percentage of chemosymbiotic bivalves ($n = 4646$ valves) drilled is more than triple that of siphonate bivalves ($n = 31050$ valves) in all 28 faunules combined.

faunules. Our analysis of the productivity hypothesis (H1) is therefore restricted to a regional scale.

Decreased Productivity, Habitat Change, and Molluscan Assemblages

Reconstructions of paleoenvironments from the fossil record of the southwestern Caribbean demonstrate that reefs and shallow-water seagrass beds were uncommon in geologic formations older than 3.5 Ma (Jackson et al. 1999; Hendy 2013) and that extensive reef development and shallow seagrass beds occurred only after seaway closure and a shift to oligotrophic conditions (Jackson et al. 1999;

Domning 2001; Todd et al. 2002; Johnson et al. 2007, 2008; O'Dea et al. 2007; Jagadeeshan and O'Dea 2012). Bivalve assemblages from biogenic habitats are strikingly different from those in soft-sediment environments (Jackson 1972, 1973; Todd et al. 2002; Johnson et al. 2007; Smith and Jackson 2009; Leonard-Pingel et al. 2012). In particular, hard substrata associated with reefs are dominated by epifaunal bivalves and their predominantly muricid gastropod predators, whereas seagrasses are commonly dominated by infaunal chemosymbiotic bivalves and their naticid gastropod predators. Previous analysis of the bivalve assemblages used in this study showed a significant increase in the abundance of epifaunal suspension
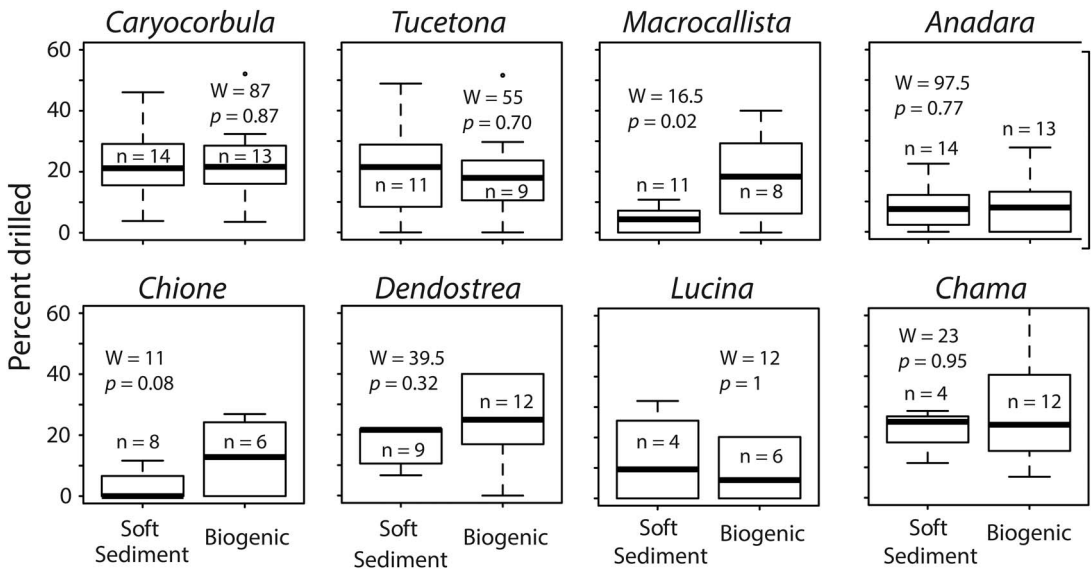
FIGURE 4. Box plots of eight common bivalve genera that occur in both soft-sediment and biogenic faunules. *W*-values are for Wilcoxon rank-sum tests; *n* denotes the number of faunules. The percentage of valves drilled (drilling frequency) generally remains constant within a genus, with the single exception of *Macrocallista*.

feeders and chemosymbiotic feeders after closure of the Isthmian Seaway—this diversification in diets was attributed to a shift toward a detritus-based trophic ecology after closure of the CAS (Leonard-Pingel et al. 2012). Our results further demonstrate that the dominant drilling gastropods also shifted through time. Muricid gastropods increase in abundance and are more abundant in both reef and seagrass environments. On the other hand, naticid gastropods dominate soft-sediment communities but are less dominant (although still abundant) in seagrass and reef environments (Figs. 5B and 6). Epifaunal and chemosymbiotic bivalves from the Caribbean experience much higher predation intensities than do many other bivalve guilds (Leonard-Pingel and Jackson 2013). Independent work in Adriatic ecosystems shows a similar pattern (Sawyer and Zuschin 2010). Increases in the abundance of guilds and taxa that are more susceptible to predation may impact the drilling frequency of the entire faunule, driving regional trends in drilling frequency.

Productivity and Predation

Our results clearly demonstrate that drilling frequency increased while regional planktonic productivity plummeted, contrary to earlier predictions (Todd et al. 2002; Johnson et al. 2007). However, biogenic ecosystems on the seafloor, including coral reefs, algae, and seagrasses, exhibit very high benthic primary production that may rival or even exceed primary production of phytoplankton (Odum and Odum 1955; Zieman and Wetzel 1980; Hatcher 1988, 1990; Gallegos et al. 1993). Thus the relationship between the incidence of predation and total community primary production is still unresolved.

Implication for Drilling Frequency in the Fossil Record

The fossil record of gastropod drilling predation on prey with hard parts, primarily bivalves, provides the tantalizing potential to examine changes in predation through time and therefore draw conclusions about escalation and coevolution (Vermeij 1987). However, recent studies have shown that drilling frequencies can be influenced by many environmental factors, including latitude (Kelley and Hansen 2007; Martinelli et al. 2013), substrate type (Sawyer and Zuschin 2010), and sedimentary regime (Huntley and Scarponi 2015), indicating that paleontologists
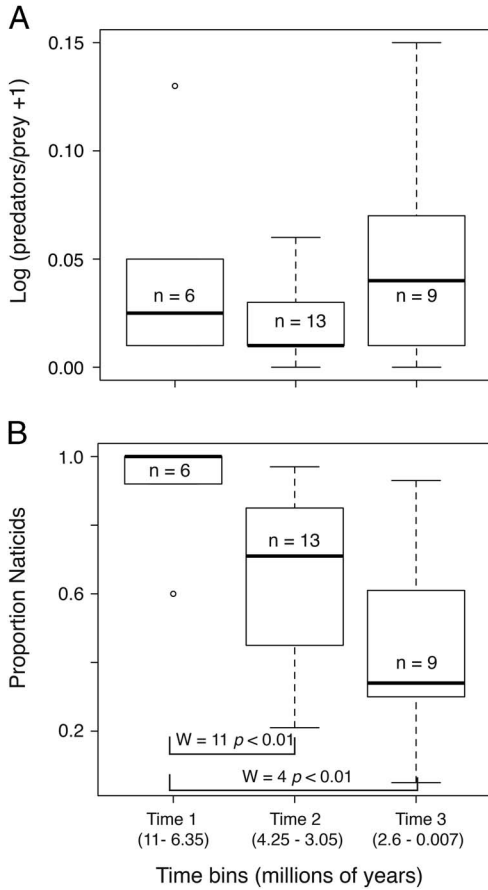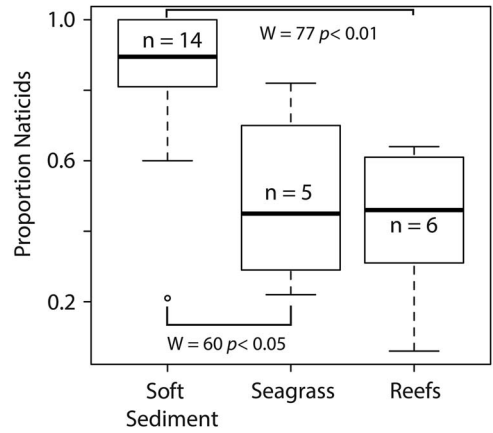
FIGURE 6. Naticid gastropods as a proportion of total drilling gastropods varies significantly among different habitat types ($\chi^2 = 10.99$, $p < 0.01$) and is significantly lower in seagrass and reef habitats than soft-sediment habitats. Faunules binned according to habitat type; n is the number of faunules for each bin.

FIGURE 5. Faunules binned according to age; n is the number of faunules for each bin. A, The relative abundance of gastropod predators and bivalve prey remained constant over the past 11 Myr ($\chi^2 = 1.97$, $p = 0.37$). B, The ratio of muricid gastropods to naticid gastropods increased significantly through time.

frequency (see Kowalewski et al. [2005] for an exception). Larger data sets are more likely to include a diversity of habitats from each time sampled, but efforts should be made to standardize these data sets with respect to the types of habits/environments represented.

Studies of predator–prey dynamics in the fossil record have, since Vermeij's seminal paper on the Mesozoic marine revolution, become focused on the ecological factors (e.g., coevolution, escalation) driving evolutionary changes (Vermeij 1977, 1987; Vermeij et al. 1981; Dietl and Alexander 2000; Dietl and Kelley 2002; Harper 2006). In the absence of environmental data or stratigraphic context, the importance of ecological interactions may be overstated. Surely, both ecology and environment are important in shaping evolutionary trends (Jablonski 2003), and we suggest that future studies on time series of predator–prey dynamics should investigate predation changes in more rigorous stratigraphic and environmental contexts. The court jester of environmental change may merit more attention in studies of predation.

should use caution when making interpretations about temporal changes in drilling frequencies. Our study provides additional evidence that habitat plays an important role in determining predation pressures and drilling frequency.

Regional studies of predation intensity are undoubtedly influenced by the type and diversity of habitats sampled; any trends in predation identified should, therefore, be treated with skepticism until habitat is accounted for. The influence that habitats might have on global studies of predation intensity (e.g., Huntley and Kowalewski 2007) is less apparent. Few of these large-scale global studies have tried to account for environmental influence on drilling

Conclusions

Our results do not negate the importance of the collapse in planktonic productivity for

ecosystem structure and function (O'Dea et al. 2007; Todd and Johnson 2013), nor do they negate the potential impact productivity may have on trophic structure. However, our results do provide an example of the necessity to distinguish between proximate and ultimate factors to unravel cause and effect (Mayr 1961; Didham et al. 2005; Leonard-Pingel et al. 2012). The decline in planktonic productivity extensively changed coastal habitats throughout the region, and these differences in habitat—rather than the changes in planktonic productivity per se—determined the kinds of bivalves present and their susceptibility to predation on smaller scales. The increasing habitat heterogeneity that occurred in the Caribbean, including habitat-level changes in productivity and types of prey, fundamentally drove larger-scale regional trends in predation.

Acknowledgments

Literature Cited

Allen, J. A. 2004. The Recent species of the genera *Limatula* and *Limea* (Bivalvia, Limacea) present in the Atlantic, with particular reference to those in deep water. Journal of Natural History 38:2591–2653.

Allen, J. A., and J. F. Turner. 1974. On the functional morphology of the family Verticordiidae (Bivalvia) with descriptions of new species from the abyssal Atlantic. Philosophical Transactions of the Royal Society of London B 268:401–532.

Allmon, W. D. 2001. Nutrients, temperature, disturbance, and evolution: a model for the late Cenozoic marine record of the western Atlantic. Palaeogeography, Palaeoclimatology, Palaeoecology 166:9–26.

Allmon, W. D., S. D. Emslie, D. S. Jones, and G. S. Morgan. 1996. Late Neogene oceanographic change along Florida's west coast: evidence and mechanisms. Journal of Geology 104:143–162.

Almany, G. R. 2004. Does increased habitat complexity reduce predation and competition in coral reef assemblages? Oikos 106:275–284.

Anderson, L. C. 1992. Naticid gastropod predation on corbulid bivalves: effects of physical factors, morphological features, and statistical artifacts. Palaios 7:602–620.

——. 1994. Paleoenvironmental control of species distributions and intraspecific variability in Neogene Corbulidae (Bivalvia: Myacea) of the Dominican Republic. Journal of Paleontology 68:460–473.

Arnaud, P. M., J. S. Troncoso, and A. Ramos. 2001. Species diversity and assemblages of macrobenthic Mollusca from the South Shetland Islands and Bransfield Strait (Antarctica). Polar Biology 24:105–112.

Bertness, M. D. 1981. Predation, physical stress, and the organization of a tropical rocky intertidal hermit crab community. Ecology 62:411–425.

Bitter-Soto, R. 1999. Benthic communities associated to *Thalassia testudinum* (Hydrocharitaceae) at three localities of Morrocoy National Park, Venezuela. Revista de Biología Tropical 47:443–452.

Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate change and the past, present, and future of biotic interactions. Science 341:499–504.

Blois, J. L., N. J. Gotelli, A. K. Behrensmeyer, J. T. Faith, S. K. Lyons, J. W. Williams, K. L. Amatangelo, et al. 2014. A framework for evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil pollen associations across the late Quaternary. Ecography 37:1095–1108.

Bohannan, B. J. M., and R. E. Lenski. 2000. The relative importance of competition and predation varies with productivity in a model community. American Naturalist 156:329–340.

Britton, J. C. 1972. Two new species and a new subgenus of Lucinidae (Mollusca: Bivalvia), with notes on certain aspects of lucinid phylogeny. Smithsonian Institution Press, Washington, D.C.

Carriker, M. 1981. Shell penetration and feeding by Naticacean and Muricacean predatory gastropods: a synthesis. Malacologia 20:403–422.

Case, T. J. 2000. An illustrated guide to theoretical ecology. Oxford University Press, New York.

Chattopadhyay, D., M. Zuschin, and A. Tomašových. 2014. Effects of a high-risk environment on edge-drilling behavior: inference from Recent bivalves from the Red Sea. Paleobiology 40:34–49.

Chinzei, K. 1984. Ecological parallelism in shallow marine benthic associations of Neogene molluscan faunas of Japan. Geobios 17:135–143.

Coan, E. V. 1984. The Recent Crassatellinae of the eastern Pacific, with some notes on *Crassinella*. Veliger 26:158–160.

Coates, A. G. 1999. Lithostratigraphy of the Neogene strata of the Caribbean coast from Limon, Costa Rica, to Colon, Panama. Bulletins of American Paleontology 113:17–37.

Coates, A. G., and R. F. Stallard. 2013. How old is the Isthmus of Panama? Bulletin of Marine Science 89:801–813.

Coates, A. G., J. B. C. Jackson, L. S. Collins, T. M. Cronin, H. J. Dowsett, L. M. Bybell, P. Jung, and J. A. Obando. 1992. Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and western Panama. Geological Society of America Bulletin 104:814–828.

Coates, A. G., L. S. Collins, M. P. Aubry, and W. A. Berggren. 2004. The geology of the Darien, Panama, and the late Miocene–Pliocene collision of the Panama arc with northwestern South America. Geological Society of America Bulletin 116:1327–1344.

Cronin, T. M. 1991. Pliocene shallow water paleoceanography of the North Atlantic ocean based on marine ostracodes. Quaternary Science Reviews 10:175–188.

Cronin, T. M., and H. J. Dowsett. 1993. Prism: warm waters of the Pliocene. Geotimes 38:17–19.

——. 1996. Biotic and oceanographic response to the Pliocene closing of the Central American Isthmus. Pp. 76–104 in J. B. C. Jackson, A. F. Budd, and A. G. Coates, eds. Evolution and environment in tropical America. University of Chicago Press, Chicago.

Dando, P. R., A. J. Southward, E. C. Southward, N. B. Terwilliger, and R. C. Terwilliger. 1985. Sulfur-oxidizing bacteria and hemoglobin in gills of the bivalve mollusk *Myrtea spinifera*. Marine Ecology Progress Series 23:85–98.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science 332:53–58.

Díaz, J. M., L. A. Escobar, and L. E. Velásquez. 1990. Reef associated molluscan fauna of the Santa Marta area, Caribbean Coast of Colombia. Anales del Instituto de Investigaciones Marinas de Punta Betin 19–20:173–196.

Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmell. 2005. Are invasive species the drivers of ecological change? Trends in Ecology and Evolution 20:470–474.

Dietl, G. P., and R. R. Alexander. 2000. Post-Miocene shift in stereotypic naticid predation on confamilial prey from the Mid-Atlantic shelf: coevolution with dangerous prey. Palaios 15:414–429.

Dietl, G. P., and G. S. Herbert. 2005. Influence of alternative shell-drilling behaviours on attack duration of the predatory snail, *Chicoreus dilectus*. Journal of Zoology 265:201–206.

Dietl, G. P., and P. H. Kelley. 2002. The fossil record of predator–prey arms races: coevolution and escalation hypotheses. Paleontological Society Papers 8:353–374.

Domning, D. 2001. Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean. Palaeogeography, Palaeoclimatology, Palaeoecology 166:27–50.

Elliott, J. K., and W. C. Leggett. 1996. The effect of temperature on predation rates of a fish (*Gasterosteus aculeatus*) and a jellyfish (*Aurelia aurita*) on larval capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences 53:1393–1402.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, et al. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Fortunato, H., and P. Schafer. 2009. Coralline algae as carbonate producers and habitat providers on the eastern Pacific coast of Panama: preliminary assessment. Neues Jahrbuch Geologie und Palontologie-Abhandlungen 253:145–161.

Gallegos, M., M. Merino, N. Marba, and C. Duarte. 1993. Biomass and dynamics of *Thalassia testudinum* in the Mexican Caribbean: elucidating rhizome growth. Marine Ecology Progress Series 95:185–192.

Gilinsky, N., and J. Bennington. 1994. Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record. Paleobiology 20:245–258.

Haaker, P. L., J. M. Duffy, K. C. Henderson, and D. O. Parker. 1988. The speckled scallop, *Argopecten circularis*, in Aqua Hedionda Lagoon, San Diego County, California. California Department of Fish and Game, Long Beach, Calif.

Harper, E. M. 2006. Dissecting post-Paleozoic arms races. Palaeogeography, Palaeoclimatology, Palaeoecology 232:322–343.

Harriston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421–425.

Hatcher, B. G. 1988. Coral reef primary productivity: a beggar's banquet. Trends in Ecology and Evolution 3:106–111.

——. 1990. Coral reef primary productivity: a hierarchy of pattern and process. Trends in Ecology and Evolution 5:149–155.

Haug, G. H., R. Tiedemann, R. Zahn, and A. C. Ravelo. 2001. Role of Panama uplift on Oceanic freshwater balance. Geology 29:207–210.

Hauser, I., W. Oschmann, and E. Gischler. 2007. Modern bivalve shell assemblages on three atolls offshore Belize (Central America, Caribbean Sea). Facies 53:451–478.

Hayward, B. W., A. B. Stephenson, M. Morley, J. L. Riley, and H. R. Grenfell. 1997. Faunal changes in Waitemata Harbour sediments, 1930s–1990s. Journal of the Royal Society of New Zealand 27:1–20.

Hendy, A. J. W. 2013. Spatial and stratigraphic variation of marine paleoenvironments in the Middle–Upper Miocene Gatun Formation, Isthmus of Panama. Palaios 28:210–227.

Hoffman, A., A. Pisera, and M. Ryszkiewicz. 1974. Predation by muricid and naticid gastropods on the Lower Tortonian mollusks from the Korytnica clays. Acta Geologica Polonica 24:249–264.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist 91:293–320.

Holt, R. D., J. Grove, and D. Tilman. 1994. Simple rules for inter-specific dominance in systems with exploitative and apparent competition. American Naturalist 144:741–771.

Huntley, J. W., and M. Kowalewski. 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. Proceedings of the National Academy of Sciences USA 104:15006–15010.

Huntley, J. W., and D. Scarponi. 2015. Geographic variation of parasitic and predatory traces on mollusks in the northern Adriatic Sea, Italy: implications for the stratigraphic paleobiology of biotic interactions. Paleobiology 41:134–153.

Hurlburt, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Jablonski, D. 2003. The interplay of physical and biotic factors in macroevolution. Pp. 235–252 in L. Rothschild and A. Lister, eds. Evolution on planet Earth. Elsevier, Amsterdam.

Jackson, J. B. C. 1972. The ecology of the molluscs of *Thalassia* communities, Jamaica, West Indies. II. Molluscan population variability along an environmental stress gradient. Marine Biology 14:304–337.

——. 1973. The ecology of molluscs of *Thalassia* Communities, Jamaica, West Indies. I. Distribution, environmental physiology, and ecology of common shallow-water species. Bulletin of Marine Science 23:313–350.

Jackson, J. B. C., and D. H. Erwin. 2006. What can we learn about ecology and evolution from the fossil record? Trends in Ecology and Evolution 21:322–328.

Jackson, J. B. C., and A. O'Dea. 2013. Timing of the oceanographic and biological isolation of the Caribbean Sea from the tropical Eastern Pacific. Bulletin of Marine Science 89:779–800.

Jackson, J. B. C., J. A. Todd, H. Fortunato, and P. Jung. 1999. Diversity and assemblages of Neogene Caribbean Mollusca of lower Central America. Bulletin of American Paleontology 357:193–230.

Jagadeeshan, S., and A. O'Dea. 2012. Integrating fossils and molecules to study Cupuladriid evolution in an emerging isthmus. Evolution and Ecology 26:337–355.

Johnson, K. G., A. F. Budd, and T. A. Stemann. 1995. Extinction selectivity and ecology of Neogene Caribbean reef corals. Paleobiology 21:52–73.

Johnson, K. G., J. A. Todd, and J. B. C. Jackson. 2007. Coral reef development drives molluscan diversity increase at local and regional scales in the late Neogene and Quaternary of the southwestern Caribbean. Paleobiology 33:24–52.

Johnson, K. G., J. B. C. Jackson, and A. F. Budd. 2008. Caribbean reef development was independent of coral diversity over 28 million years. Science 319:1521–1523.

Joll, L. M. 1989. Swimming behaviour of the saucer scallop *Amusium balloti* (Mollusca: Pectinidae). Marine Biology 102:299–305.

Jones, C. C. 1984. *Ventricolaria judithae* n. sp. (Bivalvia, Veneridae) from the Oligocene of North Carolina, with comments on ecology. Proceedings of the Academy of Natural Sciences of Philadelphia 136:152–164.

Jones, D. S., and W. D. Allmon. 1995. Records of upwelling, seasonality, and growth in stable-isotope profiles of Pliocene mollusk shells from Florida. Lethaia 28:61–74.

Kaunzinger, C. M. K., and P. J. Morin. 1998. Productivity controls food-chain properties in microbial communities. Nature 1078:495–497.

Keen, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, Calif.

Keigwin, L. 1982. Isotopic paleoceanography of the Caribbean and East Pacific: role of Panama uplift in Late Neogene time. Science 217:350–353.

Kelley, P. H., and T. A. Hansen. 2003. The fossil record of drilling predation on bivalves and gastropods. Pp. 113–139 in P. Kelley, M. Kowalewski, and T. Hansen, eds. Predator–Prey Interactions in the Fossil Record. Kluwer Academic/Plenum, New York.

——. 2007. Latitudinal patterns in Naticid gastropod predation along the east coast of the United States: a modern baseline for interpreting temporal patterns in the fossil record. Pp. 287–299 in R. G. Bromley, L. A. Buatois, G. Mangano, J. F. Genise, and R. N. Melchor, eds. Sediment–organism interactions: a multi-faceted ichnology (SEPM Special Publication Vol. 88). Society for Sedimentary Geology, Tulsa, Okla.

Kelley, P. H, T. A. Hansen, S. E. Graham, and A. G. Huntoon. 2001. Temporal patterns in the efficiency of naticid gastropod predators during the Cretaceous and Cenozoic of the United States Coastal Plain. Palaeogeography Palaeoclimatology Palaeoecology 166:165–176.

Kitchell, J. A., C. H. Boggs, J. F. Kitchell, and J. A. Rice. 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. Paleobiology 7:533–552.

Kirby, M. X., and J. B. C. Jackson. 2004. Extinction of a fast-growing oyster and changing ocean circulation in Pliocene tropical America. Geology 32:1025–1028.

Kowalewski, M. 1993. Morphometric analysis of predatory drillholes. Palaeogeography Palaeoclimatology Palaeoecology 102:69–88.

——. 2002. The fossil record of predation: an overview of analytical methods. Paleontological Society Papers 8:3–42.

——. 2004. Drill holes produced by the predatory gastropod *Nucella lamellosa* (Muricidae): paleobiological and ecological implications. Journal of Molluscan Studies 70:359–370.

Kowalewski, M., A. P. Hoffmeister, T. K. Baumiller, and R. K. Bambach. 2005. Secondary evolutionary escalation between brachiopods and enemies of other prey. Science 308:1774–1777.

Lavergne, S., N. Mouquet, W. Thuiller, and O. Ronce. 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. Annual Reviews in Ecology and Systematics 41:321–350.

Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. American Naturalist 134:922–949.

Leighton, L. R. 2002. Inferring predation intensity in the marine fossil record. Paleobiology 28:328–342.

Leonard-Pingel, J. S., and J. B. C. Jackson. 2013. Drilling intensity varies among Neogene tropical American Bivalvia in relation to shell form and life habit. Bulletin of Marine Science 89:905–909.

Leonard-Pingel, J. S., J. B. C. Jackson, and A. O'Dea. 2012. Changes in bivalve functional and assemblage ecology in response to environmental change in the Caribbean Neogene. Paleobiology 38:509–524.

Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. Ecology 71:1943–1967.

Lynch, M., and R. Lande. 1993. Evolution and extinction in response to environmental change. Pp. 234–250 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, eds. Biotic interactions and global change. Sinauer, Sunderland, Mass.

Martinelli, J. C., S. Gordillo, and F. Archuby. 2013. Muricid drilling predation at high latitudes: insights from the southernmost Atlantic. Palaios 28:33–41.

Marx, F. G., and M. D. Uhen. 2010. Climate, critters, and cetaceans: Cenozoic drivers of the evolution of modern whales. Science 327:993–996.

Mayr, E. 1961. Cause and effect in biology. Science 134:1501–1506.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730–757.

Mikkelsen, P. M., and R. Bieler. 2001. *Varicorbula* (Bivalvia: Corbulidae) of the Western Atlantic: taxonomy, Anatomy, Life Habits, and Distribution. Veliger 44:271–293.

Morton, B. 1980. Swimming in *Amusium pleuronectes* (Bivalvia, Pectinidae). Journal of Zoology 190:375–404.

O'Dea, A., and J. B. C. Jackson. 2009. Environmental change drove macroevolution in cupuladriid bryozoans. Procedings of the Royal Society of London Series B 276:3629–3634.

O'Dea, A., J. B. C. Jackson, H. Fortunato, J. T. Smith, L. D'Croz, K. G. Johnson, and J. A. Todd. 2007. Environmental change preceded Caribbean extinction by 2 million years. Proceedings of the National Academy of Sciences USA 104:5501–5506.

Odum, H. T., and E. P. Odum. 1955. Trophic struture and productivity of a windward coral reef community on Eniwetok Atoll. Ecological Monographs 25:291–320.

Oliver, P. 1981. The functional morphology and evolution of Recent Limopsidae (Bivalvia, Arcoidea). Malacologia 21:61–93.

Olsson, A. A. 1971. Biological results of the University of Miami deep-sea expeditions: mollusks from the Gulf of Panama collected by R/V John Elliott Pillsbury, 1967. Bulletin of Marine Science 21:35–92.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14:483–488.

Paine, R. T. 1966. Food Web Complexity and Species Diversity. American Naturalist 100:65–75.

Pereira, H. M., P. W. Leadley, V. Proença, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarrés, M. B. Araújo, et al. 2010. Scenarios for global biodiversity in the 21st century. Science 330:1496–1501.

Pilsbry, H. A. 1931. The Miocene and Recent Mollusca of Panama Bay. Proceedings of the Academy of Natural Sciences of Philadelphia 83:427–474.

Pires, A. M. S. 1992. Structure and dynamics of benthic megafauna on the continental shelf offshore of Ubatuba, Southeastern Brazil. Marine Ecology Progress Series 86:63–76.

Prezant, R. S. 1998. Superfamily Verticordioidea. Pp. 420–422 in P. L. Beesley, G. J. B. Ross, and A. Wells, eds. Mollusca: the southern synthesis. CSIRO, Melbourne, Australia.

Probert, P. K., and S. L. Grove. 1998. Macrobenthic assemblages of the continental shelf and upper slope off the west coast of South Island, New Zealand. Journal of the Royal Society of New Zealand 28:259–280.

Ricker, W. E. 1941. The consumption of young sockeye salmon by predaceous fish. Journal of the Fisheries Research Board of Canada 5:293–313.

Riggs, S. R. 1984. Paleoceanographic model of Neogene phos-phorite deposition, U.S. Atlantic continental margin. Science 223:123–131.

Roemer, G. W., M. E. Gompper, and B. Van Valkenburgh. 2009. The ecological role of the mammalian mesocarnivore. BioScience 59:165–173.

Roopnarine, P. D. 1996. Systematics, biogeography, and extinction of Chionine bivalves (Bivalvia: Veneridae) in tropical America: Early Oligocene–Recent. Malacologia 38:103–142.

Rudnick, D. T., R. Elmgren, and J. B. Frithsen. 1985. Meiofaunal prominence and benthic seasonality in a coastal marine ecosystem. Oecologia 67:157–168.

Sawyer, J. A., and M. Zuschin. 2010. Intensities of drilling predation of molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea). Palaeogeography, Palaeoclimato-logy, Palaeoecology 285:152–173.

Schindler, D.W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. Oikos 57:25–41.

Shumway, S. E., and G. J. Parsons. 2006. Scallops: biology, ecology and aquaculture. Elsevier Science, Amsterdam.

Simone, L. R. L., and S. Wilkinson. 2008. Comparative morphological study of some Tellinidae from Thailand (Bivalvia: Tellinoidea). Raffles Bulletin of Zoology 18:151–190.

Slack-Smith, S. M. 1998. Superfamily Chamoidea. Pp. 307–309 in P. L. Beesley, G. J. B. Ross, and A. Wells, eds. Mollusca: the Southern Synthesis. CSIRO, Melbourne, Australia.

Smith, J. T. 2006. Ecology and environments of an extreme faunal turnover in tropical American scallops. Ph.D. dissertation. University of California, San Diego, San Diego, Calif.

Smith, J. T., and J. B. C. Jackson. 2009. Ecology of extreme faunal turnover of tropical American scallops. Paleobiology 35:77–93.

Stanley, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Geological Society of America Memoir 125.

Stasek, C. R. 1961. The ciliation and function of the labial palps of *Acila castrensis* (Protobranchia, Nuculidae), with an evaluation of the role of the protobranch organs of feeding in the evolution of the Bivalvia. Proceedings of the Zoological Society of London 137:511–538.

Taylor, J. D. 1968. Coral reef and associated invertebrate communities (mainly Molluscan) around Mahe Seychelles. Philosophical Transactions of the Royal Society of London B 254:129–206.

Taylor, J. D., and D. G. Reid. 1969. The abundance and trophic classification of molluscs upon coral reefs in the Sudanese Red Sea. Journal of Natural History 18:175–209.

Teranes, J. L., D. H. Geary, and B. E. Bemis. 1996. The oxygen isotopic record of seasonality in Neogene bivalves from the Central American Isthmus. Pp. 105–129 in J. B. C. Jackson, A. F. Budd, and A. G. Coates, eds. Evolution and environment in tropical America. University of Chicago Press, Chicago.

Terry, R. C., L. Cheng, and E. A. Hadly. 2011. Predicting small-mammal response to climatic warming: autecology, geographic range, and the Holocene fossil record. Global Change Biology 17:3019–3034.

Thomas, R. 1975. Functional morphology, ecology, and evolutionary conservatism in the Glycymerididae (Bivalvia). Palaeontology 18:217–258.

Thomas, R. D. K. 1978. Shell form and ecological range of living and extinct Arcoida. Paleobiology 4:181–194.

Todd, J. 2001. Identification and taxonomic consistency. Neogene marine biota of tropical America. http://nmita.iowa.uiowa.edu/database/mollusc/molluscintro.htm.

Todd, J. A., and K. G. Johnson. 2013. Dissecting a marine snail species radiation (Conoidea: Turridae: Polystira) over 12 million years in the southwestern Caribbean. Bulletin of Marine Science 89:877–904.

Todd, J. A., J. B. C. Jackson, K. G. Johnson, H. M. Fortunato, A. Heitz, M. Alvarez, and P. Jung. 2002. The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. Proceedings of the Royal Society of London B 269:571–577.

Urban, H. J., and B. Campos. 1994. Population dynamics of the bivalves *Gari solida*, *Semele solida*, and *Protothaca thaca* from a small bay in Chile at 36 degrees S. Marine Ecology Progress Series 115:93–102.

Vermeij, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators, and grazers. Paleobiology 3:245–258.

——. 1987. Evolution and escalation. Princeton University Press, Princeton, N.J.

Vermeij, G. J., and E. Petuch. 1986. Differential extinction in tropical American molluscs: endemism, architecture, and the Panama land bridge. Malacologia 27:29–41.

Vermeij, G. J., D. E. Schindel, and E. Zipser. 1981. Predation through geological time: evidence from gastropod shell repair. Science 214:1024–1026.

Vrba, E. S. 2005. Mass turnover and heterochrony events in response to physical change. Paleobiology 31:157–174.

Walker, S. 2007. Traces of gastropod predation on molluscan prey in tropical reef environments. Pp. 324–344 in W. Miller, ed. Trace fossils: concepts, problems, and prospects. Elsevier, Amsterdam.

Woodring, W. P. 1966. The Panama land bridge as a sea barrier. Proceedings of the American Philosophical Society 110:425–433.

Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. Science 273:1558–1561.

Work, R. C. 1969. Systematics, ecology, and distribution of mollusks of Los Roques, Venezuela. Bulletin of Marine Science 19:614–711.

Yonge, C. M. 1946. On the habits and adaptations of *Aloidis* (*Corbula*) *gibba*. Journal of the Marine Biological Association of the United Kingdom 26:358–376.

——. 1969. Functional morphology and evolution within the Carditacea (Bivalvia). Journal of Molluscan Studies 38:493–527.

——. 1978. Dimyidae (Mollusca, Bivalvia) with special reference to *Dimya corrugata* Hedley and *Basiliomya goreaui* Bayer. Journal of Molluscan Studies 44:357–375.

Zieman, J. C., and R. G. Wetzel. 1980. Methods and rates of productivity in seagrasses. Pp. 87–116. in R. C. Phillips, and G. P. McRoy, eds. Handbook of seagrass biology Garland. New York.

Zuschin, M., J. Hohenegger, and F. F. Steininger. 2001. Molluscan assemblages on coral reefs and associated hard substrata in the northern Red Sea. Coral Reefs 20:107–116.