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PII: S0012-8252(18)30504-X
DOI: https://doi.org/10.1016/j.earscirev.2019.02.020
Reference: EARTH 2803

To appear in: *Earth-Science Reviews*

Received date: 30 August 2018
Revised date: 17 February 2019
Accepted date: 18 February 2019

Please cite this article as: A.A. Klompmaker, P.H. Kelley, D. Chattopadhyay, et al., Predation in the marine fossil record: Studies, data, recognition, environmental factors, and behavior, Earth-Science Reviews, https://doi.org/10.1016/j.earscirev.2019.02.020

Predation in the marine fossil record: studies, data, recognition, environmental factors, and behavior

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ABSTRACT

The fossil record is the primary source of data used to study predator-prey interactions in deep time and to evaluate key questions regarding the evolutionary and ecological importance of predation. Here, we review the types of paleontological data used to infer predation in the marine fossil record, discuss strengths and limitations of paleontological lines of evidence used to recognize and evaluate predatory activity, assess the influence of environmental gradients on predation patterns, and review fossil evidence for predator behavior and prey defense. We assembled a predation database from the literature that documents a steady increase in the number of papers on predation since the 1960s. These studies have become increasingly quantitative and have expanded in focus from reporting cases of predation documented by fossils to using the fossil record of predation to test ecological and evolutionary hypotheses. The data on the fossil record of predation amassed so far in the literature primarily come from trace fossils, mostly drill holes and, to a lesser extent, repair scars, derived predominantly from the Cenozoic of Europe and North America. Mollusks are the clade most often studied as prey and inferred predators. We discuss how to distinguish biotic from abiotic damage and predatory from parasitic traces, and how to recognize failed predation. Our data show that identifying the predator is easiest when predator and prey are preserved in the act of predation or when predators were fossilized with their gut contents preserved. However, determining the culprits responsible for bite traces, drill holes, and other types of predation traces can be more problematic. Taphonomic and other factors can distort patterns of predation, but their potential effects can be minimized by careful study design. With the correct identification and quantification of fossilized traces of predation, ecological trends in predator-prey interactions may be discerned along environmental gradients in water depth, habitat, and oxygen and nutrient availability. However, so far, these trends have not been explored adequately for the fossil record. We also review the effects of climate change and ocean acidification on predator-prey interactions, but, again, few studies consider those factors from a deep-time perspective. Finally, fossils have been used successfully to infer the behavior of ancient predators and identify and interpret active and passive defense strategies employed by their prey. The marine fossil record of predation has become a major field of research over the last 50 years, but many critical gaps remain in our understanding of the evolutionary history of predator-prey interactions.

Keywords: behavior, fossil record, mollusks, parasitism, predation, prey

Contents

1. Introduction

Predation is viewed by many ecologists as one of the most important factors shaping marine ecosystems today (e.g., Langerhans, 2007; Paine, 1966). Similarly, many paleontologists consider predation to have been a major force throughout the evolutionary history of marine ecosystems (e.g., Signor and Brett, 1984; Stanley, 2008; Vermeij, 1977), and ample evidence suggests that predator-prey interactions were common from the Neoproterozoic onward (e.g., Cohen and Riedman, 2018; Harper, 2006; Huntley and Kowalewski, 2007; Kelley et al., 2003; Klompmaker et al., 2017; Kowalewski et al., 1998; Kowalewski and Kelley, 2002; Signor and Brett, 1984; Vermeij, 1987). However, because predators are rarely preserved in the act of catching their prey, fossil evidence of predator-prey interactions is typically indirect (e.g., trace fossils). The correct recognition of predatory traces is paramount to infer the importance and evolution of predation in fossil ecosystems, but no comprehensive review exists regarding how to differentiate evidence of predation from damage caused by other processes (but see Kowalewski, 2002, for some aspects).

Once the evidence for predation has been recognized, patterns in predation can be investigated. Although predation is known to vary among environments today (e.g., Harper and Peck, 2016; Sanford, 1999; Sperling et al., 2013), relatively little attention has been paid to environmental gradients in predation in deep time, despite their potential influence on short- and long-term changes in predation intensity.

Recognizing evidence of predation is also crucial for interpreting the behavior of predators and their prey. Although interactions between predators and their prey can be observed directly today, deducing behavior is more difficult for fossil ecosystems. Nevertheless, trace fossils can be employed to infer predatory behavior in deep time, including the predator's selectivity of prey taxon, size, and site of attack (e.g., Bianucci et al., 2010; Kelley, 1988; Smith et al., 2018). Likewise, information about active and passive prey defenses may also be gleaned from the fossil record, with aid from observations in today's marine environment.

The goals of this paper are to (1) review the type of marine predation studies and data that are available from the fossil record, based on a predation database we assembled; (2) elucidate how to recognize evidence for predation and potentially confounding factors; (3)

evaluate the influences of environmental gradients on predator-prey interactions today and in deep time; and (4) interpret the behavior of predators and their prey in ancient marine ecosystems. These aspects have either not been reviewed previously or were reviewed in the past but new research in the last decade warrants a reappraisal.

2. Predation database, history and types of studies, and types of data

2.1. Predation database

We assembled an occurrence-based database on the marine fossil record of predation, upon which the analyses in the next two sections of this paper are based. We recorded the following data for each predation occurrence in the database: citation information for the predation study, type of evidence (e.g., drill holes), prey taxon, inferred predator, precise locality, stratigraphic level, and inferred age. The database also includes details not analyzed further herein, such as predation intensity, prey size, attack site on the victim, prey ecology, and lithology. The database initially was concentrated on evidence from predatory drill holes (predominantly ascribed to *Oichnus ovalis* Bromley, 1993, *O. paraboloides* Bromley, 1981, and *O. simplex* Bromley, 1981) and repair scars (partly attributable to *Caedichnus spiralis* Stafford et al., 2015), but recently was expanded to include data on other lines of paleontological evidence pertaining to predation that have become available. Some data from modern assemblages were included (though not as comprehensively) for comparison with the fossil data. Coprolites were rarely included in the database because of difficulty in determining their content and the taxonomic identity of the tracemaker. Parts of this database have been used previously (e.g., Huntley and Kowalewski, 2007; Klompmaker et al., 2017; Kowalewski et al., 1998).

2.2. History and types of studies

Studies on predation in the marine fossil record date back to at least 1858 (Buckland, 1858, cited in Massare, 1987). The number of published papers remained low until the 1960s. Since then, the pace of publications has increased steadily and continuously (Fig. 1). Early publications focused on documenting biotic interactions. Later papers used such records to test hypotheses or validate specific predictions of evolutionary paleoecology. The development of the concepts of coevolution and escalation in the 1970s and 1980s (e.g., Dawkins and Krebs, 1979; Smith, 1976; Vermeij, 1977, 1987) fostered tests based on the fossil record, which are probably reflected in the post-1960 rise in the published literature (Fig. 1). More recently, studies of predation in deep time have evaluated macroevolutionary effects of predation (e.g., Dietl and Kelley, 2002; Huntley and Kowalewski, 2007; Jablonski, 2008; Nagel-Myers et al., 2013; Roy, 1996), documented predation on taxa that had not been identified as viable prey or were previously largely overlooked in the fossil record (e.g., Baumiller, 1996, 1990; Baumiller and Bitner, 2004; Bicknell et al., 2018; Gordillo, 2013a; Klompmaker, 2012, 2011; Klompmaker et al., 2015, 2014, 2013; Kowalewski et al., 2005; Rojas et al., 2017, 2014), and explored geologic times and geographic localities that are relatively less known for their predation record (e.g., Chattopadhyay and Dutta, 2013; Kowalewski et al., 2000, 1998; Mallick et al., 2017; Morris and Bengtson, 1994; Villegas-Martín et al., 2016). Many of these studies established temporal trends in predation by compiling data from the existing literature or by processing bulk samples to develop large-scale datasets on predation traces (e.g., Huntley and Kowalewski, 2007; Kelley and Hansen, 2003; Klompmaker et al., 2017). More research should focus on geologic times (pre-Cretaceous) and geographic regions that remain poorly studied, such as Africa, parts of Asia, South America, and Antarctica. Additionally, there is a strong focus on reporting positive evidence of predation, while research on negative evidence or low predation intensities (e.g., Forel et al., 2018; Klompmaker et al., 2016a; Tackett and Tintori, 2018) is equally important to assess temporal trends of predation intensity.

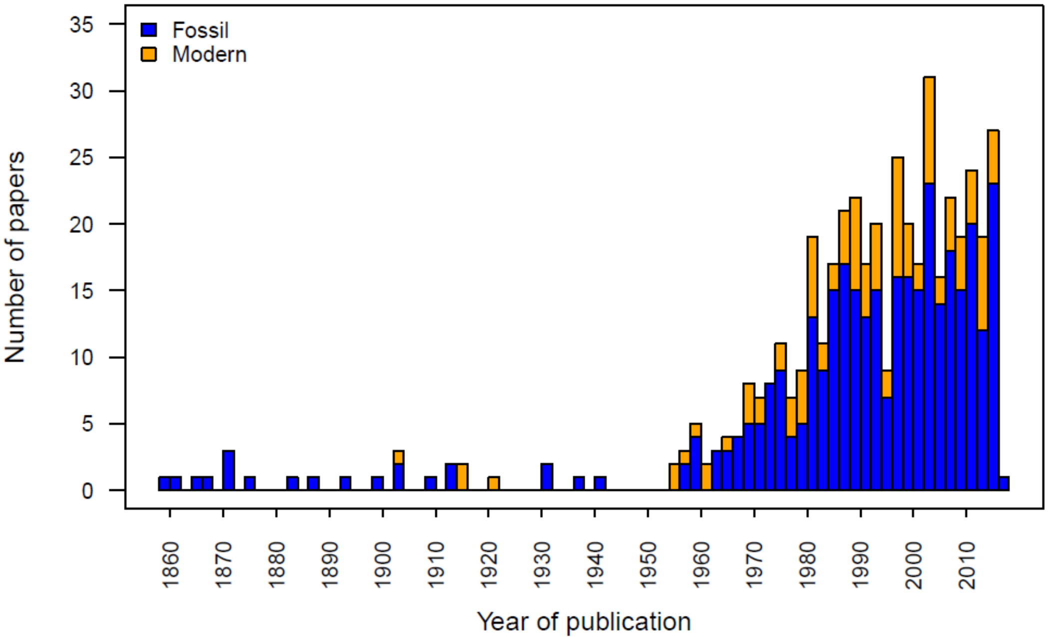

Fig. 1. The number of papers on evidence of predation in the marine fossil record in 2-year intervals based on our predation database (n = 455, of which 350 fossil and 105 modern). “Modern” refers to studies based on live or recently dead specimens.

The neontological studies often involved experiments in which predator-prey interactions were monitored to develop and/or evaluate hypotheses of evolutionary or paleontological significance. A major share of such studies has been performed on molluscan predator-prey systems (e.g., Ansell, 1982a, 1982b, 1982c; Das et al., 2015; Edwards and Huebner, 1977; Hart and Palmer, 1987; Hughes and Dunkin, 1984; Peharda and Morton, 2006); experimental work was also common on durophagous predation by crustacean predators on molluscan or arthropod prey (Barbeau and Scheibling, 1994; Ebling et al., 1964). Fewer studies have examined echinoderms and cnidarians as predators or as prey (e.g., Paine, 1976; Riedel et al., 2008a). Similar lines of ecological investigation have also been pursued in nature rather than in a lab setting (e.g., Aronson, 1989; Dietl and Alexander, 1995, 1997; Kingsley-Smith et al., 2003; Palmer, 1979; Riedel et al., 2008a; Sawyer et al., 2009; Schindler et al., 1994; Vignali and Galleni, 1986).

These studies on modern organisms are crucial in understanding ancient predator-prey interactions. Such studies often discover specific behavioral patterns of extant predators, including selectivity of prey taxon, size, and attack site on the prey – many of which have also been established subsequently in the fossil record of predation. Prey response, including morphological and behavioral defenses, has also been documented in experimental settings (Rovero et al., 1999; Smith and Jennings, 2000). Because the time required for the prey to develop morphological responses is often years longer than the typical duration of experiments, the number of studies exploring morphological changes of prey is small compared to behavioral studies. Only a few studies have combined neontological and paleoecological observations to evaluate specific aspects of biotic interactions, such as research on naticid gastropod predators (Chattopadhyay et al., 2014a; Kitchell et al., 1981). Other neontological studies have used organismal remains to understand the taphonomic aspects of the fossil record of predation and establish guidelines for identifying taphonomically altered assemblages (see section 3.5.).

2.3. Types of data

The main strategies that marine predators use to catch prey are whole organism ingestion, insertion (e.g., of an appendage into the prey) and extraction, pre-ingestive breakage, and drilling (e.g., Harper and Skelton, 1993a; Vermeij, 1987). The first two methods, however important and common in modern marine ecosystems, are rarely recognizable in the fossil record. Hence, the study of fossil predation understandably focuses on the last two types of predation events, which leave recognizable traces. Consequently, the occurrence-based record is dominated by trace fossils such as drill holes (75.8%) and repair scars (12.3%), whereas direct evidence represented by predator digestive tract contents (e.g., bromalites and contents preserved in place) is much rarer (2.6%; Fig. 2A).

Most marine prey items recorded in the literature represent invertebrates, although vertebrate prey are known primarily from preserved stomach contents or scavenging- and/or predation-related bite marks (or bite traces sensu Vallon et al., 2015) on bones of fish (e.g., Amalfitano et al., 2017; Claeson et al., 2015; Collareta et al., 2017a; Hunt and Lucas, 2014; McHenry et al., 2005), reptiles (e.g., Milàn et al., 2011; Noriega et al., 2007; Noto et al., 2012; Rothschild et al., 2018), and mammals (e.g., Boessenecker and Perry, 2011; Deméré and Cerutti, 1982; Ehret et al., 2009). Some of the first documented examples of predation in the fossil record involve vertebrate prey (e.g., Buckland, 1858; Capellini, 1865; Cope, 1872, 1871, 1868; Dollo, 1887; Portis, 1883). Overwhelmingly, however, prey occurrences (Fig. 2B) are dominated by mollusks (77%), followed by brachiopods (9.9%) and arthropods, mostly ostracods (6.2%). Inferred predator occurrences (Fig. 2C) consist primarily of mollusks (69.2%, predominantly drilling gastropods), but arthropods (6.1%, primarily decapod crustaceans) and chordates (3.9%, mostly marine reptiles) are also commonly reported. In 20% of the cases, the predator was either unidentified or, on rare occasions, was ascribed to another taxonomic group (e.g., Cambrian priapulids). In short, the fossil record of marine predation, as reported, is dominated by gastropods that drill their mollusk prey, followed by decapod crustaceans that break mollusk shells. More work is needed on types of predation other than drilling and shell crushing.

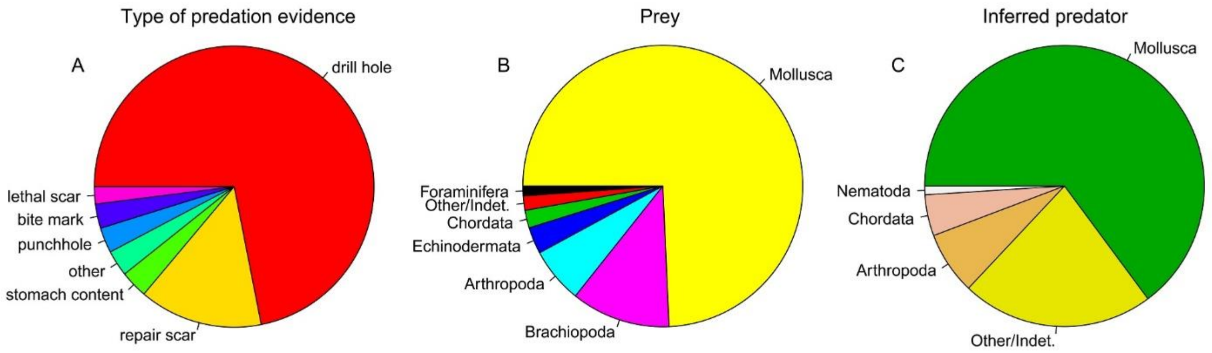

Fig. 2. Prey occurrences in the marine fossil record in our predation database split by (A) types of predation evidence, (B) prey, and (C) inferred predators. n = 3380.

Most reports of predation in the fossil record come from western Europe, the United States, and Japan (Fig. 3). This pattern is roughly comparable to occurrences of marine metazoans in the Paleobiology Database (e.g., Alroy et al., 2001). Stratigraphically, very few prey occurrences are known from the Neoproterozoic (Fig. 4, all prey), except for holes in Ediacaran *Cloudina* (Bengtson and Zhao, 1992; Brain, 2001; Hua et al., 2003) and in Tonian microorganisms (Porter, 2016). More occurrences are known from the Paleozoic and early Mesozoic; a further increase starting in the mid-Cretaceous continues into the Cenozoic, consistent with a previous analysis using drill-hole data only (Kowalewski et al., 1998). The late Cenozoic (Neogene and Quaternary) contains as much as 49.0% of all fossil prey occurrences in our database, most of which are shallow marine. Although research concentrated on predator-prey interactions in the Cretaceous–Cenozoic, this temporally unbalanced focus at least partly refects the dramatic post-Paleozoic increase in the presence of drilling predators and durophagous decapod crustaceans (e.g., Schweitzer and Feldmann, 2010; Walker and Brett, 2002).

The peak in prey occurrences in the late Cenozoic is caused nearly entirely by Mollusca and to some extent by Arthropoda (Fig. 4). Conversely, brachiopod prey occurrences are most abundant in the Paleozoic (Fig. 4), mirroring their relatively high diversity and abundance in that era (e.g., Blois et al., 2013; Payne et al., 2014). Thus, of the shelly benthic prey, it appears that brachiopods were more common prey than mollusks in the Paleozoic, but the opposite applies for the Cenozoic. This pattern is partly reflected in relative drilling intensities within Paleozoic and Cenozoic assemblages that contain both groups (Hoffmeister et al., 2004; Leighton et al., 2013; Simões et al., 2007). Prey occurrences for Echinodermata and Chordata are fewer and increase slightly toward the present (Fig. 4).

Within the diverse phyla, various prey clades have been recognized (see Table 1 for an overview of the literature, particularly for clades that are common prey). In addition to bivalve and gastropod mollusks, which are represented abundantly in the literature, many other clades served as prey. Rare prey occurrences in the marine fossil record are represented by taxa such as Polyplacophora, Xiphosurida, Hoplocarida, Phyllocarida, Eurypterida, Homalozoa, Osteostraci, Agnatha, Aves, Bryozoa, Cnidaria, Graptolithina, and Porifera, and even for taxa that did not inhabit the marine environment (Pterosauria, Dinosauria). Thus far, we have not been able to find references to predation in the fossil record of Rostroconchia, Holothuroidea, Pycnogonida, Edrioasteroidea, and Cystoidea. Many of these clades with rare or no marine predation record do not have an extensive fossil record due to low preservation potential (e.g., Holothuroidea), short stratigraphic range (Cystoidea, Osteostraci), low diversity (Xiphosurida), and/or rarity in marine settings (Pterosauria, Dinosauria). In other cases, more diverse and abundant phyla such as Porifera and Cnidaria may suffer from a lack of research targeting predation. Indeed, studies published in the last 10–15 years have shown that predation may be much more common than previously thought for multiple, previously underappreciated prey groups. These include Cirripedia (e.g., Gordillo, 2013a; Klompmaker et al., 2015), Scaphopoda (Klompmaker, 2011; Li et al., 2011; Mallick et al., 2017), Annelida (Klompmaker, 2012; Martinell et al., 2012; Villegas-Martín et al., 2016), Decapoda (Klompmaker et al., 2013; Pasini and Garassino, 2012), Tentaculita (Vinn, 2012, 2009), and Conodonta (Choo et al., 2009; Zatoń et al., 2017; Zatoń and Rakociński, 2014).

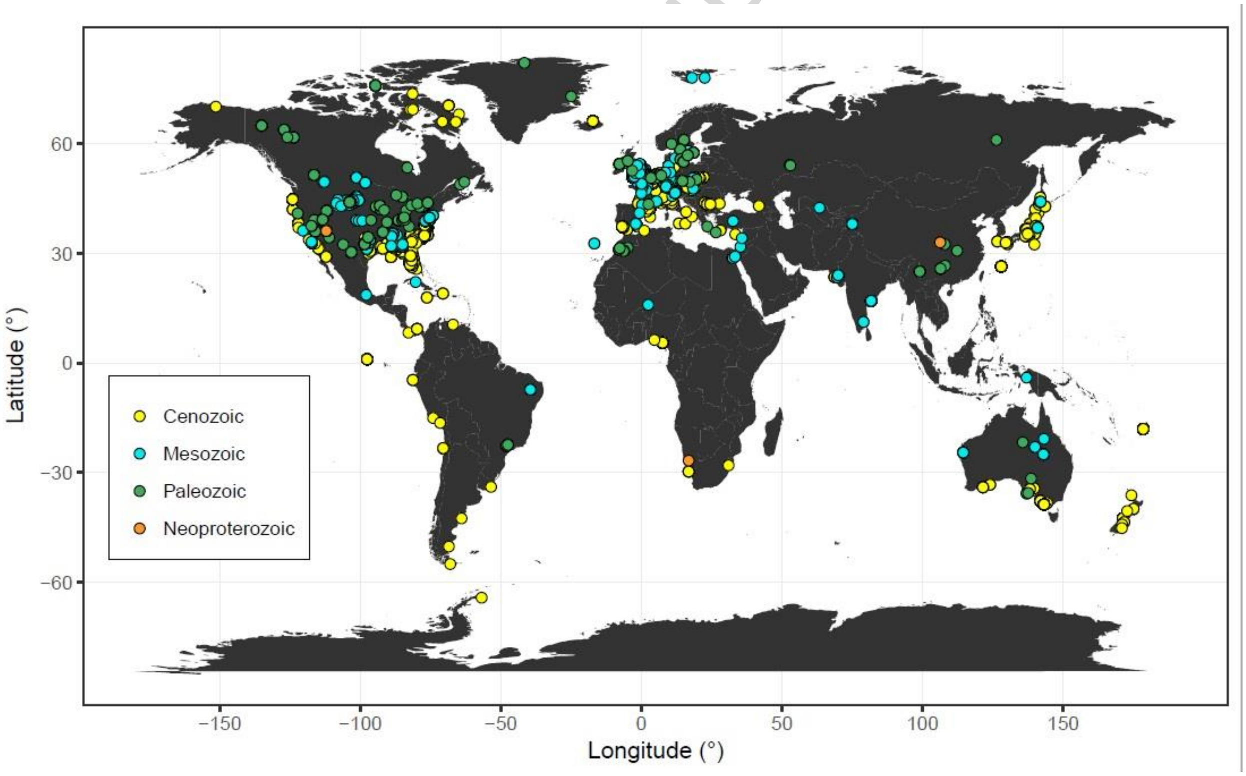

Fig. 3. Geographic location of occurrences of predation on metazoans from the marine fossil record (Neoproterozoic – non-Recent Holocene) per era from our predation database. Older

occurrences are plotted on top of younger ones (covering many Cenozoic occurrences). n total = 3380: Cenozoic = 2237, Mesozoic = 677; Paleozoic = 443; Neoproterozoic: 23.

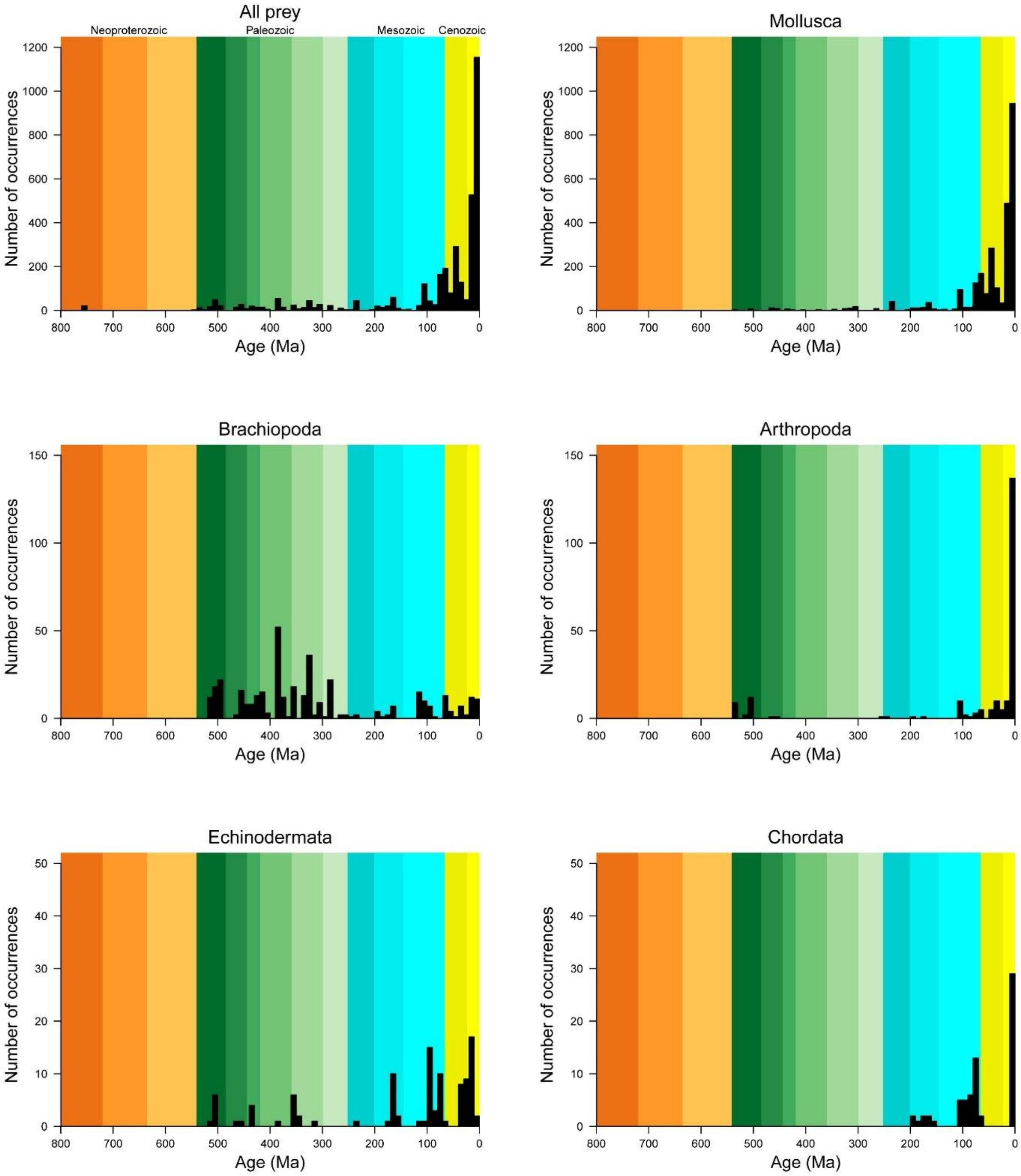

Fig. 4. The number of occurrences of predation in the marine fossil record throughout the Geozoic in 10-my intervals for all prey (n = 3380) and common prey phyla. Each period is highlighted by a different color shade within eras.

Table 1. A non-comprehensive overview of prey in the marine fossil record, arranged alphabetically. For common prey (e.g., bivalves, gastropods), only references with extensive quantitative data are listed.

Prey phylum	**Lower ranked prey clade**	**References**
Annelida		e.g., Conway Morris, 1990; Klompmaker, 2012; Martinell et al., 2012; Müller, 1969; Vannier, 2012; Villegas-Martín et al., 2016; Zatoń and Rakociński, 2014
Arthropoda	Cirripedia	e.g., Donovan and Novak, 2015; Gale and Sørensen, 2015; Gordillo, 2013a; Klompmaker et al., 2015, 2014; Kočí et al., 2015
Arthropoda	Decapoda	e.g., Bishop, 1975, 1972; Ishikawa et al., 2004; Jäger and Fraaye, 1997; Klompmaker et al., 2013; Maisey, 1994; Pasini and Garassino, 2012
Arthropoda	Eurypterida	Caster and Kjellesvig-Waering, 1964
Arthropoda	Hoplocarida	Lund and Lund, 1984, 1985
Arthropoda	Ostracoda	e.g., Aranki, 1987; Bhatia et al., 1989; Maddocks, 1988; Reyment et al., 1987; Reyment and Elewa, 2003; Ruiz et al., 2010b, 2010a; Villegas-Martín et al., 2019
Arthropoda	Phyllocarida	Briggs et al., 2011; Broda et al., 2018
Arthropoda	Thylacocephala	Briggs and Rolfe, 1983; Broda et al., 2015; Pinna et al., 1985; Williams, 1990; Zangerl and Richardson, 1963
Arthropoda	Trilobita	e.g., Alpert and Moore, 1975; Babcock, 2003, 1993; Briggs et al., 1994; Conway Morris and Jenkins, 1985; Kimmig and Pratt, 2018; Ludvigsen, 1977; Nedin, 1999; Pates et al., 2017; Pates and Bicknell, 2019; Pratt, 1998; Zhu et al., 2004
Arthropoda	Xiphosurida	Bicknell et al., 2018
Brachiopoda		e.g., Alexander, 1986a; Daley, 2008; Forcino et al., 2017; Harper and Wharton, 2000; Kowalewski et al., 2000; Leighton, 2003; Rojas et al., 2017; Smith et al., 1985; Tuura et al., 2008
Bryozoa		Berning, 2008; McKinney et al., 2003; Taylor, 1982; Wilson and Taylor, 2006
Chordata	Acanthodii	Arsenault, 1982; Davidson and Trewin, 2005; Janvier, 1996, pp. 297–300; Miles and Westoll, 1968, p. 462
Chordata	Agnatha	Lebedev et al., 2009
Chordata	Aves	Martin and Bjork, 1987
Chordata	Chondrichthyes	e.g., Bjork, 1981; Hlavin, 1990; Wahl, 2005; Williams, 1990
Chordata	Conodonta	Choo et al., 2009; Conway Morris, 1990; Nicoll, 1977; Williams, 1990; Zatoń et al., 2017; Zatoń and Rakociński, 2014

Chordata	Dinosauria	Taylor et al., 1993: predation or scavenging
Chordata	Mammalia	e.g., Bianucci et al., 2010; Boessenecker and Perry, 2011; Ehret et al., 2009; Kallal et al., 2012; Portis, 1883; Voss et al., 2019
Chordata	Osteichthyes	e.g., Bardack, 1965; Buckland, 1858; Cicimurri and Everhart, 2001; Collareta et al., 2017b, 2015; Cope, 1868; Ebert et al., 2015; Kear et al., 2003; Maisey, 1994; McAllister, 2003; McHenry et al., 2005; Viohl, 1990; Wretman and Kear, 2014
Chordata	Osteostraci	Denison, 1956, pp. 425–426
Chordata	Placodermi	e.g., Dennis and Miles, 1981; Lebedev et al., 2009; Long, 1995, pp. 189–190; Zakharenko, 2008
Chordata	Pterosauria	Brown, 1904
Chordata	Reptilia	e.g., Amalfitano et al., 2017; Cope, 1872; Eastman, 1964; Everhart, 2008; Kear et al., 2003; Konishi et al., 2011; Massare, 1987; Myrvold et al., 2018; O'Keefe et al., 2009; Rothschild et al., 2018; Tschanz, 1989
Cnidaria		e.g., Babcock et al., 1987; Galle and Ficner, 2004; Galle and Mikuláš, 2003; Mapes et al., 1989; Webb and Yancey, 2010; Wood, 2003
Echinodermata	Asteroidea	e.g., Breton, 1992; Lehmann, 1951; Neumann, 2000; Wright and Wright, 1940; Zatoń et al., 2007
Echinodermata	Blastoidea	Parasitic drill holes most likely: Baumiller, 1996, 1993; Macurda, 1965; Meyer and Macurda, 1977
Echinodermata	Crinoidea	e.g., Baumiller et al., 2010a; Baumiller and Gahn, 2004, 2003; Brachaniec et al., 2017; Gahn and Baumiller, 2005; Lehmann, 1975; Syverson et al., 2018; Thomka and Eddy, 2018; Zatoń et al., 2007
Echinodermata	Echinoidea	e.g., Beu et al., 1972; Ceranka and Złotnik, 2003; Gibson and Watson, 1989; Gripp, 1929; Grun et al., 2017; Kowalewski and Nebelsick, 2003; McNamara, 1994; Wilson et al., 2015; Zinsmeister, 1980; Złotnik and Ceranka, 2005
Echinodermata	Homalozoa	Deline, 2008: parasitic or predatory
Echinodermata	Ophiuroidea	e.g., Aronson, 1992, 1991, 1987; Aronson et al., 1997; Hess, 1960; Lehmann, 1951; Zatoń et al., 2008
Foraminifera		e.g., Collen, 1973; Culver and Lipps, 2003; Hageman and Kaesler, 2002; Herrero and Canales, 2002; Lehman, 1971; Malumián et al., 2007; Nielsen and Nielsen, 2001; Sliter, 1971; Syed et al., 2014
Hemichordata	Graptolithina	Loydell et al., 1998; Muir and Botting, 2007; Underwood, 1993
Mollusca	Bivalvia	e.g., Adegoke and Tevesz, 1974; Alexander and Dietl, 2003; Chattopadhyay et al., 2016; Chattopadhyay and Baumiller, 2010; Dietl, 2004; Fischer, 1966; Harper, 1994; Hoffman et al., 1974; Kelley et al., 2001; Kelley and Hansen, 2003, 1993; Klompmaker, 2009; Klompmaker et al., 2016a; Kojumdjieva, 1974; Kowalewski, 1990; Leonard-Pingel and Jackson, 2016; Ozanne and Harries, 2002; Taylor, 1970; Taylor et al., 1983
Mollusca	Cephalopoda	e.g., Andrew et al., 2015; Bond and Saunders, 1989; Hansen and Mapes, 1990; Kauffman and Kesling, 1960; Klompmaker et al., 2009; Klug and Vallon, 2018; Kröger, 2004, 2002; Landman and Waage, 1986; Mapes et al., 1995; Mapes and Chaffin, 2003; Martill, 1990; Pollard, 1968; Sato and Tanabe, 1998; Takeda et

		al., 2016
Mollusca	Gastropoda	e.g., Adegoke and Tevesz, 1974; Alexander and Dietl, 2003; Allmon et al., 1990; Bałuk and Radwański, 1996; Chattopadhyay et al., 2016; Chattopadhyay and Baumiller, 2010; Fischer, 1966; Hagadorn and Boyajian, 1997; Hoffman et al., 1974; Hoffman and Martinell, 1984; Kelley et al., 2001; Kelley and Hansen, 2003; Kohn and Arua, 1999; Kojumdjieva, 1974; Kowalewski, 1990; Mallick et al., 2014; Maxwell, 1988; Taylor, 1970; Taylor et al., 1983; Vermeij and Dudley, 1982; Walker, 2001
Mollusca	Helcionelloida	Skovsted, 2004; Skovsted et al., 2007
Mollusca	Hyolitha	e.g., Baumiller et al., 2010b; Briggs et al., 1994; Conway Morris, 1979; Kimmig and Pratt, 2018; Malinky and Skovsted, 2004
Mollusca	Polyplacophora	Rojas et al., 2014
Mollusca	Scaphopoda	e.g., Klompmaker, 2011; Li et al., 2011; Mallick et al., 2017; Robba and Ostinelli, 1975; Yochelson et al., 1983
Mollusca	Tergomya	Ebbestad et al., 2009
Porifera		Blake and Elliott, 2003; Elliott, 2008
	Cloudinidae	Becker-Kerber et al., 2017; Bengtson and Zhao, 1992; Brain, 2001; Hua et al., 2003
	Mobergellidae	Bengtson, 1968
	Neoproterozoic Eukaryota	Porter, 2016
	Tentaculita	Berkyová et al., 2007; Larsson, 1979; Vinn, 2009, 2012

3. Recognizing and identifying predation

3.1. Biotic and abiotic shell damage

Bromalites of carnivores (fossilized products of digestion, including cololites, coprolites, enterospirae, gastrolites, and regurgitalites; see Hunt, 1992) provide relatively unequivocal evidence of biotic activities when properly recognized. Drawing a distinction between biotic and abiotic traces can be more challenging for shell and bone damage, such as circular to irregular holes, shell fragments, non-lethal scars, and bite marks. Nevertheless, a number of general criteria can be used to establish a biotic origin of such traces (expanded from Kowalewski, 2002). These include: (1) distinct geometric shape; (2) narrow size range; (3) geometry consistent with penetrative activities aimed at gaining access to tissue inside protective housing; (4) non-random distribution across prey taxa; (5) non-random spatial distribution on prey skeletons (behavioral stereotypy); (6) non-random distribution across prey size classes; (7) presence of complementary scars on both sides of the prey; (8) presence of attachment scars; (9) correlation between trace size and prey size; (10) presence of the hypothesized trace maker in the same stratigraphic unit as the trace; (11) morphological similarity to traces made by extant predators or parasites; and (12) absence of unequivocal evidence for abiotic damage. More detailed criteria for each trace type are discussed below.

3.1.1. Circular and irregular holes

Millimeter to centimeter-sized (sub)circular holes in shells are created by predators such as drilling organisms (Klompmaker et al., 2017; Kowalewski, 2002), stomatopods (Geary et al., 1991; Pether, 1995), crabs (Fraaye, 1996; Krantz and Chamberlin, 1978; Turra et al., 2005), humans (Kubicka et al., 2017), birds (Cadée, 1994; Harper and Kelley, 2012), fishes (Norton, 1988; Rasser and Covich, 2014), durophagous cephalopods (Klompmaker et al., 2009; Takeda et al., 2016), sharks (Mapes et al., 1995, 1989), and mosasaurs (Kauffman and Kesling, 1960; Tsujita and Westermann, 2001). Boring, including by domicile seekers, may cause non-predatory holes (Ebbestad and Tapanila, 2005; Richards and Shabica, 1969; Wilson and Palmer, 2001). Holes or perforations are also created by abiotic processes, including pressure solution due to compaction of sediments (Lescinsky and Benninger, 1994) and abrasion, as observed in natural and experimental settings (Brom, 2014; Cadée, 2016; Chojnacki and Leighton, 2014; Gorzelak et al., 2013; Salamon et al., 2014).

Distinguishing biotic from abiotic holes is simplest for circular drill holes. Holes produced by abrasion tend to be more irregular and less smooth than predatory or parasitic holes (Brom, 2014; Chojnacki and Leighton, 2014; Salamon et al., 2014) and lack both rasp marks produced by radular teeth (Schiffbauer et al., 2008) and beveled edges characteristic of drill holes produced by naticid gastropods (Kelley and Hansen, 2003). Drill holes produced by cassid gastropods in echinoid prey are exceptions; because prey tests consist of small calcitic plates, drill-hole boundaries tend to be irregular (Kowalewski and Nebelsick, 2003; Nebelsick and Kowalewski, 1999). Predatory and parasitic drill holes in otherwise complete gastropod shells can be widened by abrasion, and their distinct geometric signatures (e.g., smooth regular margins, beveled edges) may be obscured or obliterated, but only after prolonged tumbling (~144 hrs, Chojnacki and Leighton, 2014). Circular holes between the septa of ammonite phragmocones, chambers containing gas and water rather than soft tissue, were interpreted as evidence of implosion (Keupp, 1991).

Irregular holes of biotic origin can be more difficult to distinguish from holes induced abiotically, but there are ways to minimize confusion. Pressure solution is likely to have occurred when damage resembles the cross-sectional outline of plicate shells and specimens contain an embedded shell (Lescinsky and Benninger, 1994). Specimens with abrasion-induced holes can show evidence of thinning of the shell around the hole (Brom, 2014; Chojnacki and Leighton, 2014), which is rarely observed for irregular holes produced by predators (Geary et al., 1991; Pether, 1995; Turra et al., 2005). Additionally, absence of abrasion or other signs of transport or reworking in otherwise pristine shells favors a biotic origin of holes. For *Nautilus* shells, tumbling experiments resulted in irregular holes on the ventral side of the phragmocone and in the body chamber that appear relatively straight in lateral view (Wani, 2004). Inferred ventral bite marks in ammonites (Andrew et al., 2010; Klompmaker et al., 2009; Takeda et al., 2016) are found exclusively on the body chamber, and such damage reaches much deeper into the body whorl (i.e., is much more angular in lateral view). Similarly, vertebrate bite marks in shells and bones of their prey most often show distinct depressions that can be related explicitly to the dental and jaw morphology of the predator (e.g., Bianucci et al., 2010; Boessenecker and Perry, 2011; Kear and Godthelp, 2008).

3.1.2. Shell fragments

Shell fragments can be produced by both abiotic processes and shell-crushing predators, including arthropods, cephalopods, and a variety of vertebrates (Brett and Walker, 2002; Cadée, 1994; Walker and Brett, 2002; see also Zuschin et al., 2003, for a review of abiotic and biotic shell breakage). Abiotic factors that produce shell fragments include compaction, tectonic shear, impacts from shells and other objects, and implosion (Checa, 1993; Klompmaker, 2009; Leighton et al., 2016; Shanks and Wright, 1986; Wani, 2004; Zuschin et al., 2003); such fragments can be modified by impacts and abrasion, primarily in the surf zone or during storms. In lithified sediments, compaction and tectonic shear are generally easy to recognize because broken parts remain next to one another. Unlike for lithified sediments, breakage due to compaction in unlithified sediments (Fig. 5) can be more challenging to distinguish from other types of breakage, as pieces from a single shell disassociate during collecting and processing of samples. Compaction can result in angular fragments, as shown experimentally for scaphopods and bivalves (Klompmaker, 2011; Kosloski, 2011; Zuschin and Stanton, 2001), or breakage along growth lines of *Nautilus* shells (Wani, 2004). Kosloski (2011) showed that, for the bivalve

Mercenaria mercenaria, fragments caused by compaction can be differentiated from those caused by a predator. Specifically, fragments formed under uniaxial compression display plumose structures in homogeneous inner shell layers and step-like breakage patterns in the outer prismatic layer, whereas fragments produced by the stone crab *Menippe mercenaria* show shear fracture surfaces (Kosloski, 2011).

Implosion of nautiloid shells is suggested to occur due to increasing hydrostatic pressure during post-mortem sinking of the shell (Kanie et al., 1980; Saunders and Wehman, 1977; Ward and Martin, 1980) if the chambers retain some gas and are negatively buoyant (Maeda and Seilacher, 1996). Similarly, implosion may have occurred in ammonites, and the resultant fragments may resemble those produced by large durophagous predators (i.e., sharks, Mesozoic marine reptiles). Fossil cephalopod fragments attributed to implosion are few, most likely because most sedimentary rocks containing fossil cephalopods were deposited at shallower depths than those at which *Nautilus* shells implode (depths below ~300–800 m; see references above).

Multiple studies have shown differences between fragments produced by predators and those caused by other types of breakage. Fragments with angular margins commonly are attributed to fishes and crabs (Cintra-Buenrostro, 2007; Salamon et al., 2014), whereas tumbling experiments involving mollusk shells typically do not produce such angular fragments but instead yield more abraded, rounded shell pieces (Cintra-Buenrostro, 2007; Oji et al., 2003; Salamon et al., 2014) (Fig. 6). Field studies support these experimental data. For example, Leighton et al. (2016) found that sharp mollusk fragments are much more abundant at localities in which more durophagous predators were observed than at low-predation sites in British Columbia, Canada. Crab-induced damage to bivalve shells represented by peeling and nibbling traces along shell margins differed from damage induced by tumbling experiments, in which mechanical breakage also occurred away from the margin and the resulting damage pattern was more ragged (Cintra-Buenrostro et al., 2005). Trampling of shells by humans, possibly an analog for other animals walking on the sea bottom or along the shoreline, can also result in angular fragments, but only 20% of such shells could be confused with crab damage (Cintra-Buenrostro, 2007). Nevertheless, sharp-edged fragments produced by predators may be rounded over time by abrasion (Cintra-Buenrostro, 2007), which occurs most rapidly in the surf zone (Driscoll, 1970). Similarly, transport-induced breakage and abrasion to shells would lead to the preservation of only the most durable parts, whereas damage by predation would lead to a higher fidelity of the death assemblage (Cadée, 1994).

In the case of non-benthic mollusks such as some cephalopods, additional abiotic causes of fragmentation are possible. For example, collision of experimental floating *Nautilus* shells with other objects caused apertural damage only during storms and probably resulted from impacts of *Nautilus* shells against the cage edge rather than collisions between shells (Wani, 2004). Although floating of *Nautilus* shells is rare (Mapes et al., 2010), extensive damage to shells transported to shallow waters by storms (Hembree et al., 2014) is possible. However, this damage is unlikely to be confused with predatory damage to the aperture or the ventral side of the shell.

In contrast to mollusks, distinguishing between biotic and abiotic damage in echinoid tests may be challenging because cross-plate fractures can result from both predation and physical agitation, as shown by tumbling experiments (Kidwell and Baumiller, 1990). Tumbling experiments represent extreme conditions of storms or intertidal environments (Driscoll, 1967) that do not apply to all sedimentary regimes in which echinoids live. Many predators of echinoids leave ambiguous damage that may be confused with abiotic damage (Grun, 2016; Kowalewski and Nebelsick, 2003; Sievers and Nebelsick, 2018), but no detailed study has compared biotic traces with abiotic damage thus far. For trilobites, it is difficult to distinguish the shape of damages attributed to predation/scavenging versus abiotically broken sclerites (Pates et al., 2017).

In sum, shell damage with a biotic origin can be distinguished from abiotic damage in many cases. Thus, changes in the frequency of damage through time may be meaningful. In particular, shifts through time in the type of fragments dominating fossil assemblages can be useful in tracking changes in the intensity of durophagous predation (e.g., Oji et al., 2003).

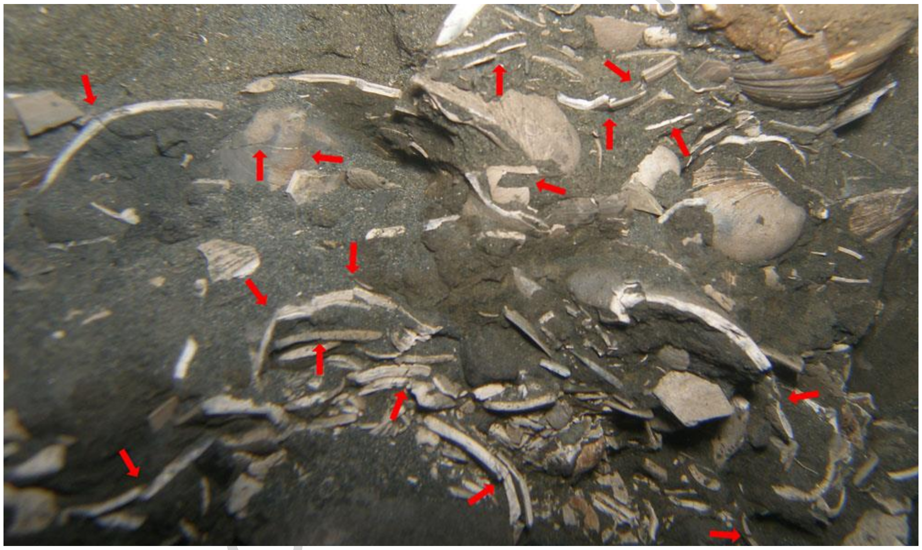

Fig. 5. Possible evidence of breakage due to compaction (see arrows) of Pliocene bivalves from the Mill-Langenboom locality in the Netherlands. Underwater photo is from a subvertical wall in an artificial lake. Photo by Ron Derks.

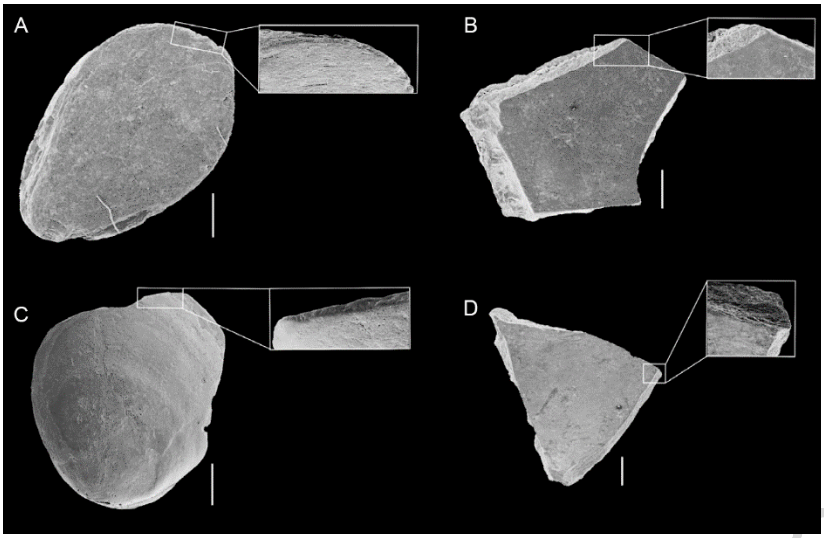

Fig. 6. Abiotic- (A and C) and biotic-induced (B and D) damage in shells. Rounded fragments after a tumbling experiment (A) and from the Baltic Sea surf zone (C). Angular fragments from a locality where fish and bivalves were observed to interact (B), and from the Carboniferous (Mississippian) of the Holy Cross Mountains, Central Poland (D). Insets show details of shell margins. Scale bars are 1 mm. Figure modified from Salamon et al. (2014: fig. 1C–F).

3.1.3. Non-lethal damage

Non-lethal damage on the exterior of a shell is often attributed to failed durophagous attacks (Alexander and Dietl, 2003; Gahn and Baumiller, 2005; Kröger, 2002; Vermeij et al., 1981), but predation by whole-animal ingestion can also produce non-lethal damage if the prey survives passage through the digestive tract of the predator (Cadée, 2011). Various shell breakage morphologies have been attributed to predation on mollusks (Alexander and Dietl, 2003), but non-lethal damage may also be self-inflicted, as shown by whelks preying on bivalves (Dietl, 2003a, 2003b; Nielsen, 1975) and by bivalves burrowing into shell hash (Alexander and Dietl, 2001a). Both extant and Neogene deep-burrowing bivalves contain repairs of breakage that cannot be attributed to predation (Alexander and Dietl, 2005; Checa, 1993); instead, such breaks formed during burrowing. In addition, diverse abiotic factors can produce non-lethal shell damage, including rolling rocks (Bulkley, 1968; Cadée, 1999; Raffaelli, 1978; Savazzi, 1984a, 1984b; Shanks and Wright, 1986) and moving ice (Cadée, 1999; Harper et al., 2012). In this section we discuss methods to determine reliably whether non-lethal damage resulted from predation, non-predatory biotic causes, or abiotic causes.

Whelk gastropods use their thick outer lips to chip or wedge open the shells of bivalve prey (Fig. 7), thereby often damaging their lips (Dietl, 2003a, 2003b; Nielsen, 1975). This type of damage appears less jagged, is located more often at the mid-part of the lip or last growth episode, and shows less relief at the repaired fracture compared to evidence of crab-induced predation on the whelk *Sinistrofulgur* (Dietl, 2003a). Triangular divots (triangular depressions in the valve where the shell was removed) on the posterior margin of shallow-burrowing bivalves are interpreted as evidence of predation by siphon-nipping fishes and shore birds, whereas such damage found anteriorly on deep infaunal bivalves is harder to attribute to a specific predator (Alexander and Dietl, 2003). However, for the same shallow-burrowing bivalve species, Alexander and Dietl (2001a) reported an apparently self-inflicted triangular divot on a ventral-posterior position, likely caused by burrowing into shell hash. Experiments with bivalves further showed that triangular divots can form due to burrowing (Checa, 1993). Thus, divots cannot be attributed unequivocally to predation, although they seem to occur more frequently in shallow-burrowing or epifaunal bivalves (Alexander and Dietl, 2005) for which predation intensity may be higher.

Checa (1993) showed a variety of repair scar types in deep-burrowing extant bivalves from Spain. This non-lethal damage is unlikely to be caused by predators because of (1) damage morphologies said to differ from predatory damage, (2) anomalously high repair scar frequencies compared to scars attributed to predation in general, (3) shell fragments that are retained in the shell, and (4) the fact that deep-burrowing bivalves are less accessible to predators. Subsequent work on Neogene bivalves from the USA (Alexander and Dietl, 2005) confirmed that those repair scars were different from repairs of damage by predators. Alexander and Dietl (2005) added that the repair scars occurred only late in life, when specimens burrowed deeper, and that the scars were found mostly on the anterior portion of the shell, which is poorly accessible to predators. Rather, more likely causes of non-lethal breakage in deep burrowers include burrowing to avoid predators and sediment overburden or erosion during storms (Alexander and Dietl, 2005; Checa, 1993). Non-predatory breakage can also result from trapping of particles between valves, colliding with hard objects within the sediment, and sediment loading (Alexander and Dietl, 2005). Experiments indeed show that damage along the commissure, especially posteriorly, can form through burrowing (Checa, 1993). Scar shape, scar position on the shell, burrowing behavior, life habit, and estimated storm and predatory activities in the studied unit are useful in assessing whether scars in burrowing bivalves are non-predatory in origin (Alexander and Dietl, 2005).

Semi-infaunal and epifaunal bivalves face the threat of other non-predatory damage such as impacts with ice and rocks, but the resultant traces often differ from biotic traces. Unlike damage to shells by predators, breakage of bivalve shells attributed to moving ice was positioned away from the shell margin, was present in one valve only, and did not result in shell loss (i.e., pieces were retained; Harper et al., 2012). Iceberg scour also may cause sediment particles to become trapped between calcium carbonate shell layers (Harper et al., 2012), a phenomenon not known to be caused by predatory attacks. Moreover, shell-crushing predators are rare to absent in modern polar marine ecosystems in which bivalves are subject to ice damage (Cadée, 1999; Harper et al., 2012). Experiments mimicking impacts of wave-borne rocks on limpets showed that breakage patterns differed among species and included chipping of the shell edge, spalling of the anterior shell, or collapse of the apex (Shanks and Wright, 1986). However, these damage patterns are similar to those reported in laboratory experiments involving crabs attacking three limpet species (Tyler et al., 2014), but detailed comparisons have not been performed so far. Damage induced by ice and rocks is restricted to certain types of environments and should not affect most assemblages preserved in the fossil record.

Much less has been published on taxa other than bivalves and gastropods. Regenerated crinoid arms are typically interpreted as records of non-lethal predatory attacks (Syverson et al., 2018, and references therein). Crinoids are resistant to wave stress or transport (Baumiller, 2003a; Gorzelak and Salamon, 2013; Meyer, 1985) and purposeful shedding of body parts (autotomy) may happen under high abiotic stresses (oxygen deficiency, tumbling, temperature change, hypersalinity) or in the presence of predators (Oji and Okamoto, 1994). Autotomy may have also occurred in Devonian ophiuroids with damage possibly resulting from an attempt to dig out from a storm event bed (Reid et al., in press), although cases when autotomy likely records a reponse to predators have also been reported (Fell, 1966). Non-lethal shell breakage in ammonoids and nautiloids is typically linked to the activities of predators (Kerr and Kelley, 2015; Klug, 2007; Kröger, 2004, 2002; Mironenko, 2017).

Holes that do not fully penetrate the shell are usually attributed to failed drilling predation by gastropods (e.g., Kelley et al., 2001). However, some incomplete circular holes may also be caused by other processes, such as dissolution and pressure solution due to point contacts with other shells. Such holes are likely to be accompanied by additional holes, their placement on prey skeleton may be more random, and their shape tends to be less circular than is typically observed for gastropod drill holes.

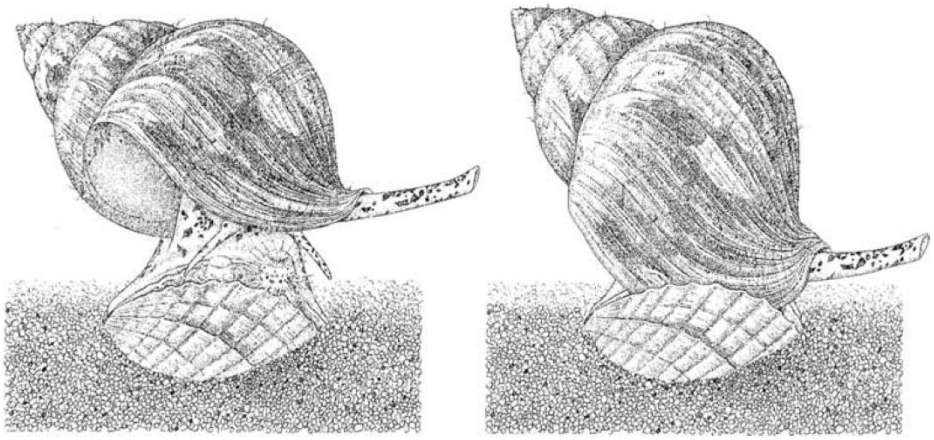

Fig. 7. The whelk *Buccinum undatum* mounts (A) and then attempts to chip the shell of the bivalve *Cerastoderma edule* by first inserting its outer lip between the valves (B). From Nielsen (1975: fig. 1).

3.1.4. Correcting for abiotic damage

Despite challenges in differentiating abiotic and biotic damage, some research has moved forward by excluding inferred taphonomic breakage when estimating predation intensity. For gastropods, Vermeij (1982a) proposed to use the proportion of drilled shells that were broken to quantify post-mortem breakage, because breakage of such shells would have occurred after the death of the animal by a drilling predator. To obtain a frequency of lethal breakage (F_B) by durophagous predators, Vermeij (1982a) proposed the following formula:

$$F_B = \frac{N_B}{N} \times \left(1 - \frac{N_{BD}}{N_D}\right)$$

where N_B is the number of broken shells, N is the total number of shells (drilled + non-drilled), N_{BD} is the number of broken drilled shells, and N_D is the number of drilled shells. Vermeij's analysis was modified and named Vermeij Crushing Analysis by Stafford and Leighton (2011). They identified different types of damage in gastropods and compared the percentages of these types for drilled versus non-drilled shells. The difference per species represents the Estimated Crushing Mortality (ECM) (Stafford and Leighton, 2011):

$$ECM = \left(\frac{N_{BND}}{N_{ND}} - \frac{N_{BD}}{N_D}\right)$$

where N_{BND} is the number of broken non-drilled shells, N_{ND} is the total number of non-drilled shells, and N_{BD} and N_D are abbreviated as above. This method was subsequently used, for example, to calculate lethal breakage for bivalves from the late Cenozoic of Florida (Mondal et al., 2014; Mondal and Harries, 2015). Both methods assume that death from drilling made drilled individuals unavailable to durophages as prey; however, these prey may not have been drilled yet when the durophages were present and therefore were available to crushing predators. We here propose the Predatory Breakage Frequency (P_{BF}) for this scenario (Fig. 8):

$$P_{BF} = \frac{\left(\frac{N_{BND}}{N_{ND}} - \frac{N_{BD}}{N_D}\right) \times N_{ND}}{N}$$

Abbreviations are specified above. The P_{BF} can be used for individual species of interest, for an entire assemblage, and for every species within the assemblage individually (if all taxa are drilled) and then weighted for the abundance of each species to estimate the P_{BF}. The ECM and P_{BF} may be seen as extreme endmembers that provide a range of likely lethal breakages. All methods are based on the following assumptions: drilled shells do not break more easily than non-drilled shells (e.g., Kelley, 2008), broken shells have the same preservation potential as complete shells, hermit crabs have not preferentially reused undamaged gastropod shells (but see Hazlett, 1970), all specimens were collected regardless of the quality of preservation, fragments and drilled shells have not been preferentially transported into or out of the studied assemblage (Lever et al., 1961, for a beach setting), mistaken attacks on shells that were already preyed upon have not occurred (Kelley et al., 2001, for rare multiply drilled shells, which might indicate mistaken predation), specimens with a complete drill hole were dead and not in the process of starting to repair the drill hole (e.g., Robinson, 2014), and holes represent predatory drill holes (see section 3.2. for criteria). The three methods are most straightforward to use for the single-shelled gastropods, but the fact that bivalves consist of two valves needs to be taken into account (i.e., a drill hole in one valve of a specimen is usually lethal, whereas durophagous breakage may be expected to affect both valves).

As for predatory breakage frequencies, drilling intensities can also be affected when post-mortem breakage is not taken into account. Often, only complete fossil specimens are used to quantify the frequency of predatory drill holes, whereas fragments are disregarded (but see Klompmaker, 2009). If fragmentation happened post-mortem and specimens with and without drill holes were equally likely to be fragmented across all taxa, no correction is needed. However, many marine predators are durophagous and can also destroy prey skeletons. In such cases, the surviving subset of complete skeletal remains can be severely biased. For example, the frequency of drilled specimens will be inflated, because the fossil record does not include potential prey destroyed by durophagous predators. To illustrate this issue, suppose that 1000 gastropod prey were present at a given site and 200 were killed by drilling (yielding a true drilling intensity of 20%). In addition, 400 were killed, and their shells were damaged beyond recognition by durophagous decapods and/or fish. In this example, 600 specimens would remain to be preserved in the fossil record, of which 200 bear drill holes (yielding an observed drilling intensity of 33%). This issue was first recognized explicitly by Vermeij (1980). Recently, a more formalized approach was proposed and illustrated with examples (Smith et al., 2019), also taking into account post-mortem breakage.

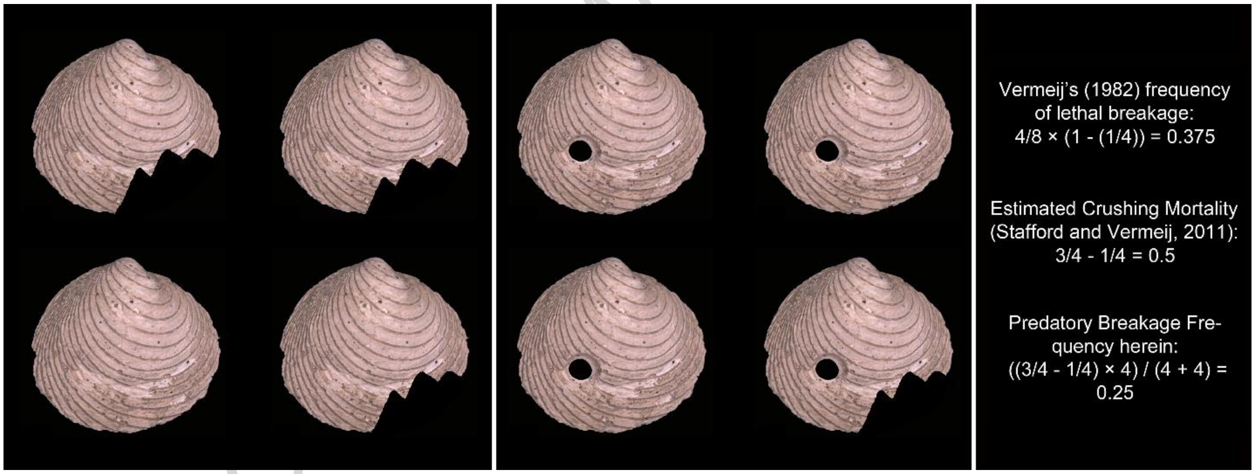

Fig. 8. Methods to account for taphonomic breakage by using broken drilled shells to obtain a predatory breakage frequency. For this example, one valve is presumed to represent one specimen. Specimen image modified after Klompmaker (2009: fig. 2A).

3.2. Predatory versus parasitic traces

Studies of predation need to distinguish traces made by predators from those produced by parasites. Among trace fossils, morphologically similar drill holes are produced by several clades in both groups. Predatory and parasitic drill holes are particularly challenging to differentiate when found in assemblages that include both parasitic and predatory drillers and also in the early Phanerozoic when representatives of modern driller groups were absent (Table 2). Many studies have attempted to differentiate the two types of culprits with varying levels of detail (Ausich and Gurrola, 1979; Baumiller, 2003b, 1990; Baumiller et al., 1999; Brett, 2003; Daley, 2008; Hoffmeister et al., 2003; Kier, 1981; Klompmaker et al., 2016a; Kowalewski, 2002; Kowalewski et al., 2000; Leighton, 2001; Nebelsick and Kowalewski, 1999; Schimmel et al., 2012). We recognize the following 16 distinguishing criteria (see also Table 3):

(1) Both drilling predators and parasites can produce multiple drill holes per shell (e.g., Brown and Alexander, 1994; Hutchings and Herbert, 2013; Kelley et al., 2001; Warén et al., 1994). Because interactions between hosts and parasites should not be lethal, a victim may be attacked by another driller, at the same or later time. In contrast, an attack by a predator usually leads to the death of the animal and thus only one drill hole is produced. Therefore, shells with multiple drill holes should more commonly record parasitic attacks. For example, the predatory cassid gastropods usually drill one hole per echinoid test today (Nebelsick and Kowalewski, 1999; but see Złotnik and Ceranka, 2005, for multiple inferred Miocene cassid drill holes per test), whereas parasitic eulimid gastropods often penetrate the echinoid test multiple times (Kowalewski and Nebelsick, 2003; Warén et al., 1994). Although rare, multiple platyceratid gastropods, often interpreted to be parasitic, have been found on crinoids (Baumiller, 2002). The frequency of multiple drill holes may differ depending on the prey: multiple drill holes per shell

produced by the predatory octopods are common in *Nautilus* (30% of drilled shells; Saunders et al., 1991) but less so in mussels (1% of drilled shells; Nixon, 1979).

(2) Healed or repaired drill holes should be much more common for parasites than for predators. During the long-term interaction between parasite and host, the parasite may get dislodged, after which the hole can be repaired. Healing is known for holes made by modern parasitic eulimid gastropods (Warén et al., 1994; Warén and Crossland, 1991) and most likely by a parasitic capulid gastropod (Orr, 1962). Healed drill holes, which can show a blister on the inside of the shell, are also known from the fossil record (Ausich and Gurrola, 1979; Baumiller and Macurda, 1995; Klompmaker et al., 2015; Robinson, 2014; Smith et al., 1985). However, healed holes can also occur following failed predation attempts, if the predator was interrupted (e.g., by its own predator or prey movement) after penetrating the shell but before killing the prey (Kitchell et al., 1986).

(3) The location of drill holes relative to the prey's internal anatomy can give important clues about the type of driller. A drill hole that is located above the soft tissue (e.g., Chattopadhyay and Dutta, 2013; Hoffmeister et al., 2003; Klompmaker, 2011; Klompmaker et al., 2015; Leighton, 2001) is likely caused by a predator. If the hole is not located near the visceral mass (Baumiller et al., 1999), a parasite driller may be more likely.

(4) Drill-hole size of predators, as a proxy for predator size (Klompmaker et al., 2017), frequently has been reported to be significantly positively correlated to prey size to maximize energy intake (Grun et al., 2017; Kitchell et al., 1981; Klompmaker et al., 2015; Kowalewski, 2004). Conversely, little evidence of significant positive correlation between drill-hole size and host size has been found for parasitic drillers (no significant correlation (Baumiller, 1996, 1993; Orr, 1962), and a weak significant correlation (Baumiller and Macurda, 1995)). This result is not

surprising because parasites only rely on a portion of the food of their host, implying that the size of the host is less critical to meet the food requirements of parasites.

(5) Predatory drillers tend to be larger than their prey, facilitating prey subjugation. On the other hand, parasites are usually smaller than their host. As a consequence, parasite-host body size ratios tend to be < 1, whereas predator-prey size ratios are usually > 1 (Klompmaker et al., 2017: fig. S18).

(6) As drill hole size and body size are positively correlated across drillers (Klompmaker et al., 2017), drill holes are expected to be smaller for parasitic drillers relative to predatory drillers for equal-sized prey/hosts.

(7) As interactions between predators and their prey are brief, only rarely are predators preserved in the act of predation in the fossil record (exceptions: Blake and Guensburg, 1994; Boucot, 1990: p. 179). We do not know of a fossilized instance of a predatory driller atop a prey. Parasites are expected to be found more often attached to their host. Multiple examples have been found of extinct platyceratid gastropods, inferred to have been parasitic drillers of at least echinoderms (Baumiller, 2003b, 1996, 1990) and brachiopods (Deline et al., 2003), preserved on top of their echinoderm host (e.g., Baumiller, 2003b, 1996, 1990; Kluessendorf, 1983).

(8) A long-term association between parasite and host is expected to result in a tight fit between the shell of a parasite and its host, which is not the case for predator-prey interactions. Tight fits have been shown for platyceratids (e.g., Baumiller, 1990; Bowsher, 1955; Clarke, 1908; Keyes, 1888) and capulids (Orr, 1962).

(9) Etching scars indicating long-term association of likely parasites with their host are known for Paleozoic platyceratids (Baumiller, 1990; Gahn and Baumiller, 2006; Keyes, 1888),

?Cretaceous – Recent capulids (Breton et al., 2017; Kabat, 1990; Matsukuma, 1978; Orr, 1962), and modern eulimids (Warén et al., 1994; Warén and Crossland, 1991).

(10) Embedment structures of the echinoderm host around the parasite have been figured for eulimids (Neumann and Wisshak, 2009; Warén, 1981).

(11) In some cases, long-term maintenance of the drill hole can be inferred, indicating parasitism as the most probable biotic interaction. Kier (1981) argued that the size of a Cretaceous echinoid could be inferred at the time drilling by a probable eulimid gastropod commenced. The production of new plates was halted after drilling when only 48 porepairs were present in the drilled petal. Echinoids with 48 porepairs in the same assemblage are 21 mm long, whereas the drilled echinoid has a length of 42 mm, implying that the drill holes were not lethal to the echinoid. This method may work only for echinoids.

(12) The ecology of the driller itself, if preserved, can be deduced from the ecology of modern representatives if there are any (i.e. phylogenetic inference). If no modern representatives are known, which is the case for the Paleozoic and early Mesozoic, a morphology close to that of an extant parasite or predator may help to infer the life mode of the drill-hole producer (i.e. morphological inference; see Brett, 2003; Klompmaker et al., 2016a).

(13) The amount of soft tissue of the prey provides an additional clue as to whether a given drill hole records an attack by a predator or parasite. Mollusks tend to possess more soft tissue than similar-sized brachiopods (Peck, 1993), so that a drill hole in a mollusk is more likely to be predatory than parasitic (but see capulids). Conversely, drill holes in brachiopods have been variously interpreted (Baumiller et al., 2006, 1999; Daley, 2008; Harper and Wharton, 2000; Hiller, 2014; Rojas et al., 2017; Schimmel et al., 2012). Compared to mollusks, most crinoids contain little soft tissue (Baumiller, 2003b), and these echinoderms were infested by parasitic

platyceratid gastropods in the Paleozoic (see above). In turn, the meaty platyceratid gastropods, rather than their crinoid hosts, may have been targeted by predators (Brett, 2003; Syverson et al., 2018).

(14) Assuming that parasitic and predatory drillers preserve equally well despite their size differences (Klompmaker et al., 2017: fig. S18), the relative abundance of the two groups in an assemblage may provide clues as to the nature of the drill-hole producer.

(15) Drill-hole morphology may be useful to some extent. Beveled drill holes with a parabolic cross-section (*Oichnus paraboloides*) are most often attributed to naticid gastropods (Kelley and Hansen, 2003), and we know of no modern parasitic drillers that make similar-shaped drill holes. Similar-shaped drill holes, not to be confused with holes in echinoderms that may have been partially caused by embedment (e.g., Brett, 1985), are also known from the Triassic (Fürsich and Jablonski, 1984; Klompmaker et al., 2016a) and the Devonian (Smith et al., 1985) when naticids had not evolved yet (Kase and Ishikawa, 2003; Klompmaker et al., 2016a). Unlike the Cretaceous and Cenozoic drill holes, early Phanerozoic drill holes need to be interpreted more cautiously because, thus far, only platyceratid gastropods are known to drill in the Paleozoic (Baumiller, 1990), but drill-hole morphology varies (Brett, 2003; Klompmaker et al., 2016a).

(16) Because parasites are a metabolic drain for the host, infested hosts can have a smaller average and maximum size compared to conspecifics that are not parasitized (Baumiller and Gahn, 2002; Gahn and Baumiller, 2003, for fossil crinoids; not the case for infested fossil decapods, pers. obs. AAK), although this interpretation may be confounded if castration occurs (O’Brien and Van Wyk, 1985). If prey have not reached a size refugium for a predator, at least the maximum size should be similar between individuals that were preyed upon and those that

were not attacked. Hence, the maximum size of specimens of the same species drilled by a parasite may be smaller than those drilled by a predator. Studies have yet to test this possible difference.

Table 2. Extant and fossil marine predatory and parasitic drillers and their stratigraphic ranges. PBDB = Paleobiology Database (https://paleobiodb.org).

Phylum	Class	Family (Genus species)	Life habit drillers	Known stratigraphic range taxon with lowest taxonomic rank	Reference (s) stratigraphic range	Reference(s) documenting drilling habit of taxon
Mollusca	Gastropoda	Buccinidae (*Cominella* spp.)	Predatory	Paleocene – Recent	PBDB	Larcombe (1971); Peterson and Black (1995); Stewart and Creese (2004)
Mollusca	Gastropoda	Capulidae (*Capulus danieli* (=*Capulus sycophanta* & *Capulus dilatatus*))	Parasitic	?Pleistocene – Recent	Matsukuma (1978)	Bromley (1981); Kosuge and Hayashi (1967); Matsukuma (1978); Orr (1962)
Mollusca	Gastropoda	Cassidae (various genera)	Predatory	Cretaceous – Recent	Beu (2008); PBDB	Grun (2017); Hughes and Hughes (1971, 1981); Nebelsick and Kowalewski (1999)
Mollusca	Gastropoda	Eulimidae (various genera)	Parasitic	Cretaceous – Recent	Kier (1981); Neumann and Wisshak (2009)	Kosuge (1971); Schiaparelli et al. (2007); Warén (1981); Warén et al. (1994); Warén and Crossland (1991)
Mollusca	Gastropoda	Marginellidae (*Austroginella* spp.)	Predatory	Miocene – Recent	Coovert and Coovert (1995); Harris (1897); Laseron (1957)	Ponder and Taylor (1992)
Mollusca	Gastropoda	Muricidae (various genera)	Predatory, some parasitic	Cretaceous – Recent	Barco et al. (2012); Merle et al. (2011)	Herbert et al. (2009); Kowalewski (2004);

						Matsukuma (1977); Morton et al. (2007); Palmer (1988)
Mollusca	Gastropoda	Nassariidae (various genera)	Predatory	Paleocene – Recent	Galindo et al. (2016); PBDB	Chiu et al. (2010); Morton and Britton (2002); Morton and Chan (1997)
Mollusca	Gastropoda	Naticidae (various genera)	Predatory, some omnivorous	Cretaceous – Recent	Kase and Ishikawa (2003)	Casey et al. (2016); Kingsley-Smith et al. (2003); Kitchell et al. (1981); Wiltse (1980)
Mollusca	Gastropoda	Okadaiidae (*Vayssierea elegans*)	Predatory	Recent	-	Kabat (1990); Young (1969)
Mollusca	Gastropoda	Dotidae (*Doto coronata*)	Predatory	Recent	-	Lambert (1991)
Mollusca	Gastropoda	Platyceratidae (?various genera)	Parasitic	Ordovician – Permian	Bowsher (1955); Sutton et al. (2006)	Baumiller (2003b, 1990); Baumiller et al. (1999); Baumiller and Gahn (2018); Gahn and Baumiller (2003)
Mollusca	Cephalopoda	Octopodidae (various genera)	Predatory	Cretaceous – Recent	Kröger et al. (2011); Strugnell et al. (2006)	Anderson et al. (2008); Arnold and Arnold (1969); Nixon and Maconnachie (1988); Runham et al. (1997)
Foraminifera	Globothalamea	Turrilinidae (*Floresina amphiphaga*)	Parasitic	Recent	Walker et al. (2017)	Hallock et al. (1998); Hallock and Talge (1994); Nielsen et al. (2002)
Foraminifera	Globothalamea	Cibicididae (*Cibicides antarcticus*)	Parasitic	Pliocene – Recent	Walker et al. (2017)	Walker et al. (2017)
Foraminifera	Globothalamea	Rosalinidae (*Hyrrokkin* spp.)	Parasitic	Pleistocene – Recent	Walker et al. (2017)	Walker et al. (2017)
Nematoda			Predatory	?Cretaceous – Recent	Sliter (1971,	Douglas (1973);

					1975)	Kabat (1990); Sliter (1971, 1975)
Platyhelminthes	Rhabditophora	Callioplanidae (*Koinostylochus ostreophagus*)	Predatory	Recent	-	Woelke (1957); Yonge (1964)

Table 3. Criteria to distinguish between parasitic and predatory activity, explained in more detail in the text.

Characteristic	**Parasitism**	**Predation**
(1) Multiple drill holes	more common	less common
(2) Healed or repaired drill holes (incomplete drill holes)	more common	less common
(3) Drill site directly over soft tissue (positioning drill hole)	N	Y
(4) Drill-hole size and prey size correlated	less likely	more likely
(5) Size attacker relative to prey	usually small	usually large
(6) Average drill-hole size	relatively small	relatively large
(7) Attacker found on prey	more likely	less likely
(8) Tight fit of attacker with prey	Y	N
(9) Attachment scars of attacker on prey	possibly present	absent
(10) Embedment structure of prey around attacker	possibly present	absent
(11) Evidence of long-term maintenance of drill hole	possibly present	absent
(12) Ecology of extant members of group	parasitic	predatory
(13) Amount of soft tissue of host/prey	less	more
(14) Relative abundance of body fossils in assemblage	abundant parasites	abundant predators
(15) Drill hole morphology	not beveled	may be beveled
(16) Maximum size of host/prey	may be smaller	may be larger

3.3. Identifying the predator

Once a fossilized predation event has been detected, the identification of the predator may be pursued. Theoretically, the taxonomic identification of a predator is possible for any type of predation indicator (e.g., direct indicators: trace fossils, gut contents, coprolites, preserved predation events; indirect indicators: taphonomic patterns, comparative anatomy; Kowalewski, 2002). Identifying the predator with high taxonomic resolution, however, can be quite difficult, particularly for trace fossils (e.g., Bromley, 1996, 1993), as detailed below. The probability of accurate identification at high taxonomic resolution depends on the type of evidence for and nature of a given predation event. Predators are most easily identified when preserved in the act of predation. Such fossils are rare, however, and constitute only a small percentage of predation-related fossils (Fig. 9; for exceptions see Blake and Guensburg, 1994; Boucot, 1990: p. 179). Similarly, fossils in which predators and their gut contents are preserved together often contain sufficient material to identify the predator to at least the family level, and often to the genus and species levels (Fig. 9).

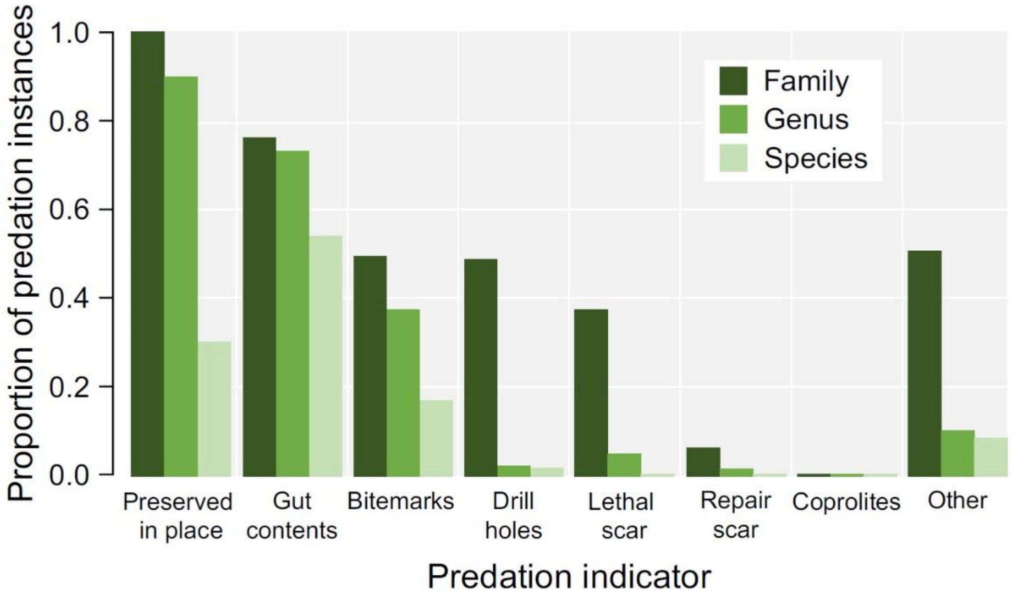

Fig. 9. The proportion of predation instances reported in published literature in which the predator was identified to the level of family, genus, and species for various indicators of predation: predation event preserved in place (n = 10; includes embedded teeth), gut contents (n = 142), bite marks (n = 124), drill holes (n = 3321), lethal scars (n = 81), repair scars (n = 504), coprolites (n = 43), and other (n = 190; includes irregular holes and other depressions, regurgitates, prey shell breakage, comparative anatomy, and organismal associations). A

'predation instance' was defined by the association of a predator consuming a particular prey taxon within a given study. The taxonomic resolution of prey varied across studies; the lowest taxonomic rank was used on a per case basis.

Identifying the predator from trace fossils such as bite marks, drill holes, and lethal and repaired scars can be more difficult (Fig. 9). Such predation indicators often do not contain remains of the predator; rather they consist of evidence of predator activity preserved on fossilized prey skeletons. Numerous methods and criteria have been proposed to assist in identifying predators from such trace fossils. For example, bite marks on fossilized prey can be compared to preserved jaws or teeth of predators from the same assemblage (or nearby assemblages) to derive a comparative interpretation of predator identity (e.g., Gorzelak et al., 2010; Mapes and Hansen, 1984; Neumann and Hampe, 2018), and may be supported by experiments (e.g., Neumann and Hampe, 2018). The drill hole of a given drilling predator may be morphologically distinct (i.e., in shape) from that of other predators, allowing for reasonable identification of the driller through quantitative or qualitative analyses (e.g., Dietl et al., 2004; Dietl and Kelley, 2006; Grey et al., 2005; Kowalewski, 2004; Paul and Herbert, 2014), although drill-hole convergence (i.e. different predators making similar drill holes) does occur (Klompmaker et al., 2016a). Other types of traces that may be diagnostic include irregular holes and other depressions (e.g., stomatopod punctures; Bałuk and Radwański, 1996; Geary et al., 1991; Pether, 1995), and distinct prey shell breakage patterns (e.g., Klompmaker et al., 2009; Landman and Klofak, 2012; Oji et al., 2003; Takeda et al., 2016). Of these additional types of traces, punctures are usually attributed to stomatopod predators, although crabs can also produce irregular holes (e.g., Krantz and Chamberlin, 1978). Various other attributes of a predatory trace (e.g., size selectivity and site stereotypy; Leighton, 2001) may be used to distinguish predators. Experiments comparing predatory traces of modern predators to those found in fossilized prey can also shed light on predator identities (e.g., Dietl et al., 2004; Pierrehumbert and Allmon, 2018).

Recent technological advances can be adopted by paleontologists for identifying predators from trace fossils. For example, the advancement in 3D-imaging technology may allow for more precise descriptions of predatory traces in prey remains (e.g., Micro-CT and X-Ray imaging; Kiel et al., 2010; Sutton, 2008; Wisshak et al., 2017) that can be linked to particular predators. For example, microrasp marks in the vertical walls of drill holes attributed to scraping by radular teeth of muricid gastropods have been recorded in modern and fossil shells (Schiffbauer et al., 2008; Tyler and Schiffbauer, 2012). The patterns of microrasp traces could be explored to further identify the predator.

Although multiple studies have attempted to specify criteria for identifying predators based on trace fossil evidence, identification of predators is not trivial. Such techniques can sometimes reveal predator identity with high taxonomic resolution (e.g., species level: Li et al., 2011; Martinell et al., 2012; Morton and Harper, 2009), especially when multiple methods are employed at the same time (Dietl et al., 2004). However, the current literature review (Fig. 9) suggests that identifying the predator below the family level is rarely possible for such indicators of predation, as a diverse range of potential predators can produce a given trace type. Thus, identifying a specific predator with high taxonomic resolution can be difficult for a given predation event (e.g., Klompmaker et al., 2016a; Leighton et al., 2013; Pierrehumbert and Allmon, 2018). For example, for the late Cenozoic, Kubicka et al. (2017) reported that predatory drill holes and holes produced by humans for body adornments tended to be located in similar positions on mollusk shells. The same predator may also leave different morphological traces across individual prey items (Arnold and Arnold, 1969; Bromley, 1970; Wodinsky, 1969). Taphonomic alteration of a predation trace after the predation event can also hamper predator identification (e.g., Chojnacki and Leighton, 2014). Further, changes in ocean chemistry can influence dissolution rates of empty mollusk shells (e.g., Clements et al., 2018; Waldbusser et al., 2011) and potentially alter the morphology of a predation trace.

Alongside trace fossils of predatory activity preserved in the remains of prey, bromalites (fossilized digestive material, see section 3.1.) from predators can also be used to indicate potential predation. Bromalites include fossilized regurgitates, intestinal contents (cololites), stomach contents (gastrolites), or, more commonly, fossilized feces (coprolites). In bromalites, identifiable remains of particular prey species contained within the regurgitates or feces can be preserved (e.g., Conway Morris and Robison, 1988, 1986; Nedin, 1999; Reboulet and Rard, 2008; Salamon et al., 2012). Identifying the producer of bromalites, however, is difficult unless bromalites are preserved in association with the predator. In the studies we analyzed, identification of the producer(s) of bromalites such as coprolites was unsuccessful below the phylum level for marine fossils (Fig. 9). This uncertainty is primarily due to the fact that fecal preservations are highly variable in space and time, and because the fecal remains of many animal taxa are highly similar in appearance, making predator identification with high taxonomic resolution highly unlikely (Chin, 2002; Northwood, 2005). Various techniques can aid in the identification of bromalite depositors. For example, DNA analysis, combined with radiocarbon dating, has been used to determine the producer of bromalites (Wood et al., 2012); however, to our knowledge, such analyses remain elusive for marine bromalites.

Other evidence of predation in fossil assemblages can also be used to identify the predator, including comparative anatomy (Butterfield, 2002) and organismal associations (Brandt et al., 1995; Jensen, 1990; Schwimmer et al., 1997). Community structure and the abundance of preserved predators in a given fossil assemblage can also be valuable in identifying likely culprits of predation events when coupled with the type of predation indicator (e.g., Brachaniec et al., 2017; Ganić et al., 2016; Klompmaker, 2009). Nevertheless, below the level of family, the identity of most predators remains difficult to determine (Fig. 9).

3.4. Recognizing and interpreting failed predation

For the purposes of this section, we define failed predation as instances in which an attack did not result in the death of the prey, although the attack might be considered successful from the perspective of the predator if soft tissue was obtained. In many predator-prey systems, failed predation might not leave an identifiable trace, especially when the failure occurs during the early phase of the attack. However, once the predator makes a predatory trace on the prey's shell, the failed predation attempt can often be identified for both drilling and durophagous predation. In the case of vertebrate bite marks in large and robust prey, it can be difficult to determine whether a bite was lethal. However, if the anatomy of the prey is known, the location of the bite mark can indicate whether a bite was likely to have been fatal (e.g., Bianucci et al., 2010). The most common types of failed predation in the fossil record are represented by incomplete drill holes and repair scars in marine invertebrate shells. Repaired holes, healed crinoid arms, and regenerated bone (Fig. 10) are also known from the fossil record. Other types of failed attack are items that are mistakenly perceived as prey (Gaemers and Langeveld, 2015) or shells that are already empty (Walker and Behrens Yamada, 1993).

Incomplete drill holes are those that do not penetrate the entire thickness of the shell of the prey, precluding access by the driller to the prey's soft parts. An incomplete hole is often accompanied by a central boss on the bottom of the drill hole for naticid gastropod drillers (e.g., Kabat, 1990). Some workers (see review by Visaggi et al., 2013) have argued that incomplete holes need not represent failed predation; a bivalve prey that is suffocated may gape, allowing the predator to feed without completing the drill hole. However, prey suffocation reported in the literature usually can be attributed to poor prey health or other laboratory effects (Visaggi et al., 2013) and is unlikely to be common in natural environments. Penetration of the shell by a drill hole does not necessarily mean that predation was successful, as Kitchell et al. (1986) have argued that drill holes are not functional when the ratio of inner drill hole diameter to outer drill-hole diameter is < 0.5 for naticid drillers.

Several methods have been used to quantify failed drilling predation. The most commonly used metric, prey effectiveness, was defined by Vermeij (1987) as the ratio of the number of incomplete drill holes to the total number of attempted holes (complete and incomplete). Hansen and Kelley (1995) calculated the percent of individuals with an incomplete drill hole. Similarly, Sawyer and Zuschin (2010) calculated an Incomplete Drilling Frequency as the number of incomplete drill holes divided by the number of prey individuals. Similar metrics could be developed for repaired drill holes, but such holes are likely to be too rare for metrics to be meaningful. The occurrence of multiple drill holes (whether complete or incomplete) has also been used to indicate failed drilling by naticid gastropods (Kelley et al., 2001), as prey with more than one drill hole survived an attack to be drilled again (Kitchell et al., 1986). Kelley and Hansen (1993) defined MULT as the proportion of drill holes in multiply drilled specimens.

Repair scars result when prey of a durophagous predator survive and secrete new shell material to repair the damage caused by the attack. Metrics for calculating repair frequency include the number of scars in a sample divided by the total number of specimens (scars per shell), the percent of individuals with repair scars (e.g., Dietl and Kosloski, 2013; Lindström and Peel, 2010; Nagel-Myers et al., 2013, 2009), and the number of scars per shell surface area (Preston et al., 1993). These methods are useful in different situations; the percent of shells with scars most closely reflects selection pressure (Alexander and Dietl, 2003). Arm regeneration in crinoids has been quantified in a similar manner, i.e., as percent of individuals with at least one regenerated arm (Aronson et al., 1997; Baumiller and Gahn, 2003). Repair frequencies are often standardized by prey age (or size as a proxy of age) because older individuals accumulated repair scars over a longer period of exposure to durophagous hazards (Vermeij et al., 1981). Interpretation of the incidence of failed durophagous predation is challenging (Leighton, 2002); increases in repair frequencies can result either from more attacks or from decreased success of those attacks.

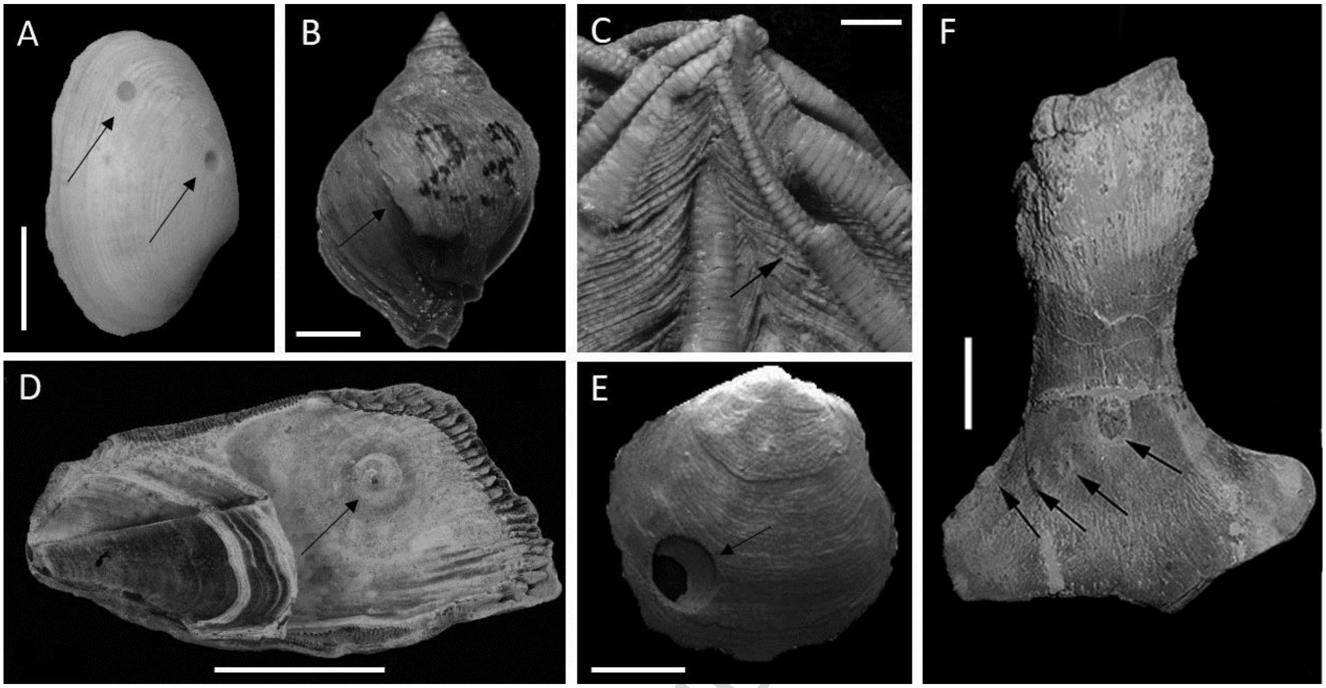

Fig. 10. Traces caused by failed predation, indicated by arrows. (A) Recent bivalve showing two incomplete drill holes, and (B) Recent gastropod with a repair scar developed after a durophagous attack, scale bars = 10 mm. (C) Examples of a regenerated arm in a Paleozoic crinoid (image courtesy: Forest J. Gahn), scale bar = 5 mm. (D) Repaired drill hole on the inside of a Miocene barnacle plate (modified from Klompmaker et al., 2015), scale bar = 10 mm. (E) Partially repaired drill hole on a Recent brachiopod shell (modified from Robinson, 2014), scale bar = 1 mm. (F) Example of a healed Middle Jurassic plesiosaur bone after an attack (modified from Rothschild et al., 2018), scale bar = 50 mm.

Interpretation of the causes of failed predation is far from simple. Failure may be related to the efficiency of the predatory group; for example, Vermeij (1982b) showed that muricid gastropods exhibit a higher incidence of failure in drilling compared to naticid gastropods. He attributed the incidence of failure in a prey population to the abundance and efficiency of predators in relation to the prey and the availability of other prey species. If predator abundance guides the incidence of failure, then the frequencies of successful and failed predation should be positively correlated. However, failure could also result from a behavioral change. For example, many muricids can switch from a drilling to a chipping/wedging strategy (e.g., Sawyer et al., 2009). In such cases, a correlation between successful and failed predation may not be obvious.

Failure of an attack also can be due to the effectiveness of prey-specific defenses. The concept of prey effectiveness as a measure of failure is based on the implicit assumption that the prey contributes to such failure, but prey abandonment by the predator can also be unrelated to prey traits. For example, abandonment can occur when the predator is physically interrupted (e.g., by a storm event) or by an external agent such as its own predator, referred to as a “secondary predator” (Kelley and Hansen, 2003). In fact, predatory or scavenging activities may be abandoned due to the mere presence of a secondary predator. For example, Atema and Burd (1975) demonstrated that the mud gastropod *Nassarius obsoletus*, a scavenger of crushed mollusks, abandoned scavenging in the presence of crushed conspecifics. Similarly, in an experimental study evaluating the non-consumptive effects of a durophagous predator on the drilling performance of muricids, Chattopadhyay and Baumiller (2007) demonstrated that the presence of a secondary predator could deter drilling predators and significantly increase the incidence of voluntary abandonment (see also Hutchings and Herbert, 2013). A strong negative correlation between the frequencies of drill holes that are complete and repair scars observed in the fossil record (Chattopadhyay and Baumiller, 2010) is consistent with those neontological experiments. The relationship between the percentage of successful and unsuccessful attacks may vary with the trophic level of the predator. The number of potential predators is fewer higher up the food chain, suggesting that disruption may occur less frequently. Thus, no strong relationship between successful and unsuccessful attacks is expected for apex predators.

Chattopadhyay and Baumiller (2007) further demonstrated that the decision of abandonment is time dependent: drillers do not abandon their prey if they have invested a significant amount of time before being disturbed. In such cases, prey traits are likely to have contributed to failed drilling, in that prey with thicker shells require a greater time investment by the predator (Kelley et al., 2001).

3.5. Taphonomic and other factors affecting evidence of predation

Deductions about biotic interactions from drill holes and repair scars, two of the most informative predation traces, might not always be flawless. The tacit assumption for interpreting predation is that the quantitative data provided by traces of predation (e.g., frequency of traces, distribution of traces across prey species and prey size classes) are not influenced by taphonomic or other factors. This section focuses on such factors, whereas section 3.1 reviewed abiotic processes that can produce damage similar to predatory traces.

Holes produced by drilling predators may be affected by taphonomic factors (De Cauwer, 1985; Harper et al., 1998; Velbel and Brandt, 1989), including differential preservation and transport of drilled and undrilled valves. The presence of a drill hole in a valve may reduce the resistance to taphonomic forces before or after burial. Roy et al. (1994) found a significant difference in strength between drilled and undrilled bivalves; drilled valves were weaker in point-load compression experiments. This bias, however, appears only to affect shells in high-energy environments and may not have significant impact during natural sediment compaction (Hagstrom, 1996; Kelley, 2008; Nebelsick and Kowalewski, 1999; Zuschin and Stanton, 2001). Experimental fragmentation by sediment compaction using drilled and non-drilled gastropod shells of *Olivella biplicata* did not show elevated breakage of drilled specimens (Dyer et al., 2018), suggesting that compaction did not affect drilling intensity in this case. Nevertheless, criteria for determining the degree of taphonomic bias due to shell breakage and methods for reconstructing the original drilling intensity have been proposed for a few scenarios (Kaplan and Baumiller, 2000; Roy et al., 1994).

Differential transport of valves by currents or other agents may alter drilling frequency in both transported and lag assemblages. The hydrodynamic properties of a shell depend on a number of factors, including its size, shape, and composition. Several studies have examined current velocity required for entrainment and post-transportation alignment of shells of brachiopods (Alexander, 1986b, 1984, 1975; Johnson, 1957; Kornicker and Armstrong, 1959; LaBarbera, 1977; Menard and Boucot, 1951; Nagle, 1967; Quaresma et al., 2007; Savarese, 1994), bivalves (Allen, 1984; Brenchley and Newall, 1970; Chattopadhyay et al., 2013a; Frey and Dörjes, 1988; Futterer, 1982; McKittrick, 1987; Olivera and Wood, 1997; Trewin and Welsh, 1972), and micro-benthos (Ostracoda and Foraminifera; Kontrovitz, 1975; Kontrovitz et al., 1978; Kontrovitz and Snyder, 1981). Transport could alter drilling frequencies by preferential removal of a particular size class, shape class, or taxon from an assemblage. Minor differences in the geometry of opposing valves of a bivalved shell can result in different transportation patterns for the two valves, yielding a sorted assemblage. This phenomenon of preferential valve movement by currents has been reported for brachiopods and bivalves (Behrens and Watson, 1969; Boucot et al., 1958; Chattopadhyay et al., 2013a; Frey and Henderson, 1987; Kornicker et al., 1963; Lever, 1958; Lever and Thijssen, 1968; Martin-Kaye, 1951; Nagle, 1964). If predators preferentially drill one valve, as discussed below, differential transport of valves might alter the true drilling frequency.

Additionally, drilling frequency can be affected by hydrodynamic differences between drilled and undrilled shells. A number of experimental studies have demonstrated that drilled shells entrain at lower velocities than undrilled shells of the same species (Chattopadhyay et al., 2013b; Lever et al., 1961; but see Molinaro et al., 2013). Chattopadhyay et al. (2013b) also demonstrated that the position of the drill hole dictates the entrainment velocity, implying possible sorting based on stereotypic drill-hole site selection by the driller. In explaining differential levels of predation in Cretaceous oysters from Utah, USA, Tapanila et al. (2015) argued for transport-driven mixing; two spatially separated oyster populations that experienced different levels of predation pressure produced a mixed assemblage due to post-mortem transport.

In addition to the effects of differential transportation, unequal preservation of valves can influence measured drilling frequencies. Differences in shape or thickness of two valves of a specimen (a very common phenomenon for brachiopods as well as some groups of bivalves such as Corbulidae) may lead to an unequal preservation probability of the valves (Velbel and Brandt, 1989). Preferential removal of a specific valve might change the original drilling frequency (Kaplan and Baumiller, 2000) if valves are drilled at different frequencies. Valve preference by drillers is not very common for equivalved prey but may occur for unequivalved taxa, such as corbulid bivalves (e.g., De Cauwer, 1985; Kardon, 1998; Kelley, 1988; see section 5). Furthermore, shell preservation can be influenced by chemical factors, possibly leading to different preservation potentials at different times (see sections 4.5. and 4.6.). For example, Clements et al. (2018) showed that higher levels of seawater CO_2 (800 and 4000 μatm) resulted in variably increased shell loss due to dissolution (0 to 7%) for the gastropods *Littorina littorea* and *Euspira heros*. Preferential shell dissolution of taxa due to their shell composition may alter the predation record, if the predation record of those groups significantly deviates from that of more durable species.

Drilling frequencies may also be affected when non-drilling durophages work as taphonomic agents. Drilling frequencies are calculated relative to the total number of shells (drilled and undrilled) in an assemblage. However, if durophages obliterate undrilled shells by crushing, the proportion of drilled shells in an assemblage will be inflated (Vermeij et al., 1989). This problem is most severe when a large fraction of prey specimens was destroyed by durophages (Smith et al., 2019) and they are not accounted for when calculating drilling intensity (see section 3.1.4.).

Factors other than the taphonomic aspects mentioned above may also affect the drilling and durophagous predation records. For instance, the effect of shell morphology on the visibility and the preservation of a repair scar may potentially influence the inferred repair scar frequency. Sime and Kelley (2016) observed an apparent difference in the number of repair scars between two species of the bivalve *Glycymeris* with strikingly different ornamentation. The species with relatively narrow ribs accumulated a higher number of small fractures that could be considered as repair scars; however, fractures of equal severity would not be as recognizable if found on the species with broad ribs. Similarly, Forcino et al. (2017) suggested that repair scars may be more readily visible on finely ornamented brachiopod taxa than in taxa without ornament. Also, some repair scars that are not visible on the shell surface can be seen in a cross-section of the shell (Ramsay et al., 2001).

Sampling and subsequent processing protocols may also affect the inferred drilling intensity. Surface sampling conducted in grids for lithified rocks resulted in a lower observed drilling percentage compared to the actual percentage because shells are not completely exposed

(Chattopadhyay and Bala, 2013). Bulk sampling of unlithified materials, although unaffected by this bias, may still show biases that are introduced during processing. The effects of size filtering (through sieving) on studies of drilling predation may be quite important. A severe bias may creep in through the sieving protocol if the predators exhibit size-specific selection of prey and the study considers samples of only a specific sieve size (Kowalewski, 2002). If the size fraction considered for the study happens to be the preferred size class, observed drilling percentage may be unrealistically inflated; the reverse can occur when the preferred size class is missed by sieving. Nevertheless, only a handful of studies have examined the effects of size filtering on measured drilling intensities in detail (Chattopadhyay et al., 2016; Hattori et al., 2014; Hausmann et al., 2018; Kowalewski and Hoffmeister, 2003; Ottens et al., 2012; Visaggi and Kelley, 2015).

Another common practice that may affect drilling percentage is to consider only valves with complete or near-complete margins (Kosnik, 2005; Leighton, 2002). The effect of such a practice was demonstrated for Pliocene mollusk assemblages (Klompmaker, 2009); a significant increase in drilling intensity was observed when fragmented valves, broken by compaction, were included in the analysis, because specimens that were preferentially broken represented species that were commonly drilled. Likewise, preferential fragmentation of taxa that are rarely drilled would artificially inflate an assemblage drilling percentage. Within-species analyses using a Pliocene turritellid gastropod showed limited differences (Johnson et al., 2017).

Experience in the recognition of drill holes does not seem to influence results on drilling predation. Using bivalves from Pleistocene unlithified sediments, Hattori et al. (2014) observed no significant differences in several predation estimates obtained by trained novice collectors versus veteran collectors.

Finally, the location of prey handling may influence drilling intensity. A recent study on drilling in modern echinoids has shown a 96.8% drilling intensity (Tyler et al., 2018). The authors argued that the predation mode of the cassid predator within the sediment enhanced the survival of drilled tests compared to echinoids that died due to other causes.

4. Environmental gradients

4.1. Depth gradients

Most aspects of the marine physical environment vary with water depth (see, e.g., Dodd and Stanton, 1990) – water energy, probability of disturbance, oxygenation, light penetration, primary productivity, temperature, salinity, nutrients, and the nature of the substrate (e.g., sediment composition, grain size, and texture). Because those factors also control the distribution, diversity, and abundance of species, community composition changes along a depth gradient (see, e.g., Carney, 2005; Sander and Lalli, 1982; Tyler and Kowalewski, 2014). Thus, predator-prey interactions can be expected to vary with depth as different combinations of predators and prey come into contact. Foraging strategies may vary with depth among closely related, morphologically similar species (Zintzen et al., 2013) as food resources change, and trophic structure differs between bathyal and shallower depths (Maxwell, 1988). Physical disruptions related to environmental energy also can affect the activities of predators, and environmental stress can reduce the abundance of predators (McClanahan, 1992); predator-prey interactions should be less important in structuring communities in physically stressful environments (Micheli et al., 2002). In addition, temperature affects metabolic rate and thus influences rates of predation and the lifespan over which prey are exposed to predators (Vermeij, 1987). To some degree, then, patterns of predation along depth gradients might be expected to mirror patterns along latitudinal gradients.

Investigations of the relationship of predation to depth, both in the modern environment and the fossil record, have used a variety of approaches (Table 4). Some studies have inferred the intensity of predation from the diversity, abundance, or density of predators. Stomach contents and, in recent years, isotopes have been used to interpret predator diets. Much of the work comparing the intensity of predation at different depths has used trace fossils and their modern counterparts. In particular, repairs following sublethal damage by durophagous predators and drill holes by shell-drilling gastropod and octopod predators have figured prominently in studies of depth gradients in predation. In other cases, lethal breakage, shell fragmentation, and regeneration of body parts have been used to explore variation in predation with depth.

Despite a growing body of data from both modern environments and the fossil record, the relationship between predation and depth is unclear. Diversity of predators is thought to be less in deep water today (Aronson and Blake, 2001; Harper and Peck, 2016), and the deep sea generally has been regarded as a refuge from predation. Vermeij (1987) argued that many taxa with defensively inferior architecture (e.g., echinoids with flexible tests, loosely coiled or umbilicate gastropods, and bivalves and gastropods with thin, unornamented shells) were once abundant in shallow waters but are now restricted to the deep sea. Perhaps the best-known example is the inferred post-Jurassic retreat of stalked crinoids to deeper waters (Baumiller and Gahn, 2003; Bottjer and Jablonski, 1988; Meyer and Macurda, 1977; Wisshak et al., 2009). Meyer and Macurda (1977) argued that the replacement of stalked crinoids by mobile, better-defended comatulids in waters < 100 m deep was due to increased predation in shallow waters from the late Mesozoic radiation of teleost fish. This conclusion was supported by Oji (1996), who found significantly greater arm regeneration in the extant stalked crinoid *Endoxocrinus parrae* at the upper slope than at deeper sites. Whether stalked crinoids migrated to deeper waters or already were present there is unclear because deep-water deposits are poorly known from the sedimentary record. However, some Triassic and Jurassic deep-water sediments contain stalked crinoids (Salamon and Gorzelak, 2010; Thuy et al., 2012).

Frequencies of shell breakage and repair provide additional evidence for the deep sea as a refuge from predation. Walker et al. (2002) tethered empty gastropod shells at shallow shelf, outer shelf, and slope sites along transects off the Bahamas. Slope samples experienced significantly less "lethal" breakage than did shells deployed on the shelf, with significantly more attacks on tethered shells at 15–30 m depth compared to deeper-water sites. In a study of extant brachiopods by Harper and Peck (2016), repair frequencies (RF) decreased significantly with depth; all samples with RF > 0.105 came from depths < 100 m, with sites deeper than 1000 m exhibiting RF < 0.03. The results of Dietl et al. (2000) also support the view that predation decreases with water depth; Cretaceous and Paleocene gryphaeid oysters exhibited two- to three-times greater repair frequencies in onshore than offshore sites, with a corresponding decline in shell-strengthening ornamentation with depth.

Nevertheless, other studies show no clear-cut pattern in intensity of predation with depth (Table 4). Vale and Rex (1988, see also Vale and Rex, 1989) found no significant relationship between depth and either repair frequencies or percent species with repairs for extant gastropods from depths < 200 – > 4000 m in the western North Atlantic; deep-sea RF were within the range of shallow-water samples. Inner shelf, outer shelf, and upper slope samples off California, USA, yielded different patterns in repair frequency with depth for different groups of mollusks (Kropp, 1992). Nor did Sander and Lalli (1982), sampling from the shelf-slope margin of Barbados, find a consistent trend in drilling predation with depth. In the Red Sea, predation by shell-drilling naticid and muricid gastropods was greatest at depths shallower than 350 m and greater than 1000 m (von Rützen-Kositzkau, 1999), with bivalve and gastropod prey showing slightly different patterns. Tomašových and Zuschin (2009) also did not find a significant relationship between drilling frequency (DF) on Red Sea brachiopods and depth (shallow shelf to basin), although fragmentation (in part due to predation) did decrease significantly with depth. Such work in the modern environment shows that predation can be intense at deep-water sites (see also Carriker, 1998; Walker and Voight, 1994).

Some work in the fossil record is consistent with the conclusion that intense predation can occur in deeper waters. Although Hansen and Kelley (1995) found no trend in DF along a depth gradient from the inner to middle shelf in the Eocene Moodys Branch Formation of Mississippi, USA (see below), drilling frequencies in the outer shelf Yazoo Formation were significantly greater than in the shallower Moodys Branch. Intense predation in deeper water is consistent with results from Pliocene turbidite deposits of Ecuador that contained mid-to-outer shelf and bathyal gastropods; Walker (2001) found repair scars on 68% of species and 25% of individual gastropods, and 66% of species and 32% of individuals were drilled.

Deep-sea hydrothermal vents, hydrocarbon cold seeps, and whale falls (e.g., German et al., 2011), found at variable depths, might be expected to show predation patterns that differ from those of other deep-water environments because they are patchy and transient habitats characterized by chemosynthesis. Few predators are specialized to vent environments, and only those opportunistic predators with sulfide tolerance are able to invade from adjacent areas (Voight, 2000). Nevertheless, predation may still be important in structuring vent communities, as indicated by manipulative field experiments (Micheli et al., 2002). The most extreme but also the most productive environments occur closest to the vent; in those environments, predation exerts the greatest influence on community structure as large epibenthic predators (especially zoarcid fish) selectively remove small mobile grazers and facilitate recruitment of sessile invertebrates (Micheli et al., 2002). Evidence of sublethal predation is common at deep-sea vents (Rhoads et al., 1982; Voight, 2000), although some apparent damage may not be the result of predation (Voight, 2000).

Hydrocarbon seep communities may be structured by predation. Modern cold seeps in the Sea of Okhotsk vary faunally along a depth gradient; a dramatic increase in shelled seep megafauna at 250–450 m depth was attributed to a decline in predators such as crabs, asteroids, and carnivorous gastropods (Sahling et al., 2003). Amano et al. (2010) also observed differences in community structure with depth for Miocene seeps in the Japan Sea back-arc basin and suggested that a lack of predatory gastropods at deeper sites was responsible. Eocene-to-Miocene seep deposits in western Washington state, USA, also showed a decline in predator abundance and increase in proportion of obligate seep taxa with depth (Kiel, 2010). Direct evidence of predation at cold seeps is rare, but drill holes have been reported at low frequencies for some sites of Eocene age and younger (see Amano and Kiel, 2007; Hryniewicz et al., 2019, and references for more examples). Durophagous predation in cold seep environments is also known. For example, Kiel et al. (2016) suggested that repair scar frequencies among Oligocene seep bivalve taxa from Japan attributed to crabs were inversely related to sulfide concentrations. Both durophagous crustaceans and fishes were present in ancient cold seeps, particularly from the Mesozoic onwards for the former (e.g., Klompmaker et al., 2018). The first evidence of drilling on a whale fall community was reported by Amano and Kiel (2007) from the Miocene of Japan.

They stated that drilling frequency for the chemosymbiotic bivalve prey was low (DF = 0.02) in comparison to those reported from shallow-water deposits, likely because the prey may be protected by predation-deterring metabolites produced by their symbionts. However, various authors have reported relatively high predation intensities for shallow-water lucinids, which also bear chemosymbionts (Chattopadhyay et al., 2015; Kelley and Hansen, 2006, 1993; Zuschin and Ebner, 2015).

Thus, the relationship between predation and water depth is not straightforward. Many (but not all) studies support a decline in predation with depth and yet, even in extreme habitats with abundant life such as deep-sea hydrothermal vents and cold seeps, predation plays a substantial role in structuring communities. The factors controlling intensity and nature of predation along depth gradients are complex, as indicated by the contradictory evidence that has been compiled in studies of predation and water depth.

Table 4. Studies that examine relationship of predation to water depth. Abbreviations: pred., predation; RF, repair frequency; DF, drilling frequency; signif., significantly; frag., fragmentation; regen., regeneration; freq., frequency; abund., abundance; ns, non-significant; struc., structure; diff., difference.

Reference	**Pred. metric**	**Age & Taxon**	**Depth**	**Results**
Studies supporting decrease in predation with depth				
Harper and Peck (2016)	RF	Recent brachiopods	0–199, 200–999, > 1000 m	RF decreases w/ depth; all samples w/ RF > 0.105 from < 100 m

Dietl et al. (2000)	RF	Cretaceous-Paleocene oysters	Onshore vs offshore shelf	Onshore > offshore predation (3x for exogyrine, 2x for pycnodont oysters)
Walker et al. (2002)	Lethal breaks	Recent gastropods	Shallow shelf 15–30, outer 70, slope 100–267 m	Signif. more pred. at < 30 m than deeper; pred. on shelf > slope
Tomašových and Zuschin (2009)	DF & frag.	Recent brachiopods	Shallow shelf to basin (~1500 m)	Frag. decrease w/ depth; decrease in DF w/ depth ns
Oji (1996)	Arm regen.	Recent crinoids	178 to ~500 m, ~500 m to 723 m	Regen. freq. for upper slope signif. > deeper (but ns using presence/absence of regen.)
Kiel (2010)	Abund.	Mesozoic & Cenozoic seep faunas	Deep (500–2000 m) vs shallow (16–900 m)	Predator abund. decrease w/ depth in Cenozoic; % obligate seep taxa increase w/ depth (Cenozoic & Mesozoic)
Amano et al. (2010)	Abund.	Miocene mollusks	Deep (1000–2000 m) vs shallower seeps	Deep seeps lack predatory gastropods; diversity lower & % obligate taxa higher
Zintzen et al. (2013)	Stable isotopes	Recent hagfish (predators)	50–900 m	Shallow species = active predators; deeper species = scavengers (e.g., whale falls)
Studies indicating increase in or substantial predation at depth				

Voight (2000)	RF	Recent vent limpets, tubeworms	Deep sea vents	Sublethal pred. common (e.g., on 73 of 74 tube worms) but lethal unknown
Walker and Voight (1994)	RF	Recent archaeo-gastropods	Bathyal (depths 300–1000 m for some samples)	High RF = 0.28–1.0 for *Bathybembex* (small samples), 0.68–0.91 for *Gaza*
Carriker (1998)	DF	Recent mollusks	Deep sea	Drill holes up to 2690 m, naticid gastropods as deep as 6860 m
Sawyer and Zuschin (2010)	DF	Recent mollusks	Intertidal vs sublittoral (4–15 m)	Intertidal DF (1.4%) < sublittoral (27.4%)
Zuschin and Ebner (2015)	DF	Recent mollusks	Intertidal vs shallow subtidal	Intertidal DF (1.2%) < shallow subtidal (25.7%)
Walker (2001)	RF & DF	Pliocene gastropods	mid to outer shelf & bathyal turbidites	RF = 0.25, DF = 0.32; 66% of species had repairs, 68% of species drilled
Maxwell (1988)	Trophic struc.	Miocene mollusks	Upper bathyal (~400–800 m)	Predators & deposit feeders dominant; few suspension feeders
Studies with mixed results or no pattern with depth				
Rhoads et al. (1982)	RF	Recent mussels	Deep sea vents	76% w/ repairs, similar to shallow water

Vale and Rex (1988)	RF	Recent prosobranch gastropods	< 200, 200–1000, 1000–2000, 2000–4000, > 4000 m	Regression of RF or % species w/ repairs vs depth ns, deep sea RF in range of shallow
Vale and Rex (1989)	RF	Recent rissoid gastropods	500, 800, 1100 m	Median RF = 0.11 in range of shallow habitats, diff. among 500, 800, 1100 m ns
Kropp (1992)	RF	Recent mollusks	Inner shelf 90–91 m, outer shelf 145–161 m, upper slope 409–565 m	Prosobranch gastropods: upper slope RF < inner or outer shelf. Scaphopods: upper slope RF > inner shelf). Opisthobranch gastropods: diff. w/ depth ns
Sander and Lalli (1982)	DF	Recent mollusks	125, 175, 225 m (shelf-slope margin)	Avg DF = 0.163, 0.42, 0.30 for 125, 175, 225 m w/ only signif. diff. between 125 and 175 m
von Rützen-Kositzkau (1999)	DF	Recent mollusks	Depths from 4 – 1898 m	DF greatest (up to 0.30) at < 350 m (especially for gastropods) and > 1000 m (especially for bivalves)
Hansen and Kelley (1995)	DF	Eocene bivalves and gastropods	Inner and middle vs outer shelf	No trend w/ depth on inner & middle shelf; outer shelf DF (0.21) > inner to middle (0.08)
Hoffmeister and Kowalewski (2001)	DF	Miocene bivalves and gastropods	Sand vs clay facies in Boreal and Paratethys	Boreal: sand DF (0.28) > clay (0.15); Paratethys clay DF (0.19) > sand (0.13)

Sawyer and Zuschin (2011)	DF	Miocene mollusks	Intertidal vs sublittoral	Results vary with taxonomic level and Miocene stage; in Badenian intertidal DF (6.9%) < subtidal (9.3%)
Chattopadhyay et al. (2015)	DF	Recent bivalves	0–52 m; shallow < 10 deep > 10 m	No signif. relation of depth to DF; shallow DF = 0.17, deep = 0.19, diff. ns
Chattopadhyay et al. (2014b)	EDF	Recent bivalves	0–52 m; shallow < 10, deep > 10 m	Shallow EDF = 0.06, deep = 0.07, diff. ns

4.2. Different habitats and ecology

In addition to broad-scale patterns of predation with water depth, predation also varies with finer-scale differences in depositional environment. Several aspects of the depositional environment are likely to affect patterns in predation. Oxygen and nutrients (discussed in detail below) affect most predator-prey systems, whereas substrate is important mainly for benthic ecosystems. Nektonic predators are less affected by substrate, although depositional environment does affect preservation of evidence of such systems in the fossil record (see examples in Delsett et al., 2016; Godwin, 1998; Joyce, 2000; Zatoń and Rakociński, 2014), as it does for benthic predator-prey systems (Selly et al., 2016).

Work with modern systems indicates that the type of substrate affects the distribution of benthic species (Peterson, 1991). For instance, within the Red Sea (Egypt), regular echinoids most often occur on hard substrates and irregular echinoids in soft substrates, within which species distribution is controlled further by sediment grain size (Nebelsick, 1995). Locomotion operates differently for organisms moving within sand, mud, or on top of hard or soft substrates

(Vermeij, 2017); thus, life mode varies with substrate. Organisms occupy more permanent burrows in cohesive mud, exhibiting morphologies that ensure stability within the substrate, whereas sand dwellers with streamlined morphologies can burrow actively (Vermeij, 2017). Suspension feeders are more common in sandy substrates and deposit feeders in finer-grained sediments that would clog the feeding apparatuses of suspension feeders (Peterson, 1991; Snelgrove, 1999; see also Nesbitt, 1995, for an Eocene example). Life mode may affect prey vulnerability, although those effects may vary depending on predators. For example, epifauna are more exposed than infauna to predators such as crabs and fish, whereas infauna may be more vulnerable to predation by infaunal predators such as naticid gastropods, as exemplified by greater drilling frequency in Red Sea infaunal prey when comparing to epifaunal prey (Chattopadhyay et al., 2015). In addition, Red Sea deposit feeders were less frequently drilled when compared to suspension feeders and chemoautotrophs (Chattopadhyay et al., 2015), perhaps because they tend to be more mobile. Similarly, Sawyer and Zuschin (2010) found that suspension-feeding mollusks in the northern Adriatic experienced more frequent drilling predation than did other life modes, perhaps because they were both highly abundant and less active.

A major factor affecting substrate type (and consequently life modes of the organisms present) is water energy. In general, predation appears to be less intense in high-energy environments. Water turbulence, caused by high flow speed or coarse sediment, may interfere with chemoreception of prey by predators (Weissburg and Zimmer-Faust, 1993) and with predator locomotion and ability to forage (Robles, 1987). Wilson (1991) noted that sediment type affects the ability of predators to excavate prey from the substrate. For example, feeding experiments indicated that the blue crab *Callinectes sapidus* consumed more hard clams

(*Mercenaria mercenaria*) in sand and sand/mud substrates than in shell or gravel substrates that experienced relatively greater water flow velocities (Arnold, 1984).

The effects of differences in water energy are particularly apparent in intertidal areas. Predators such as crabs tend to be smaller and less abundant in higher-energy areas of the intertidal where foraging time is shorter (see Molinaro et al., 2014). Shell repair on the gastropod *Chlorostoma* is less frequent in high-energy compared to sheltered intertidal areas of Barkley Sound, British Columbia, Canada, corresponding to the lower intensity of crab predation (i.e., attack frequency) in the high-energy areas (Molinaro et al., 2014). Cadée et al. (1997) observed a wide range of variation in repair frequency within four gastropod species in different intertidal microhabitats of the northern Gulf of California, but a general decrease of repair frequency with increasing environmental energy occurred (see discussion in Molinaro et al., 2014). However, Schmidt (1989) found greater frequencies of gastropod shell repair in rocky than sandy habitats in the northern Gulf of California.

Other stressors are present in intertidal habitats compared to sublittoral environments (Peterson, 1991). At low tide, organisms are subjected to temperature changes and desiccation, although organisms living within the sediment are buffered somewhat from these stresses compared to those in rocky intertidal habitats. Intertidal areas are also susceptible to salinity changes due to input of fresh water. These stresses all increase with elevation on shore, as does exposure to predation from terrestrial organisms such as shorebirds (e.g., Cadée, 1994, 1995). In contrast, organisms found lower on the shoreline are exposed to predators that follow incoming tides to forage in the intertidal (e.g., crabs and rays). Thus, zonation of both prey and predators can be expected both in rocky and soft-sediment intertidal areas.

Intensity of predation also appears to differ between intertidal and sublittoral areas. For instance, Sawyer and Zuschin (2010) found greater drilling predation on mollusk assemblages and lower taxa in the sublittoral northern Adriatic Sea (4–15 m depth) than in the intertidal (27.4% versus 1.4%), and similar results were obtained for the Red Sea (Zuschin and Ebner, 2015). They linked these differences to deleterious effects of subaerial exposure and variation in salinity and temperature on intertidal predators.

Patterns in predation among sublittoral environments are less clear cut. Studies by Chattopadhyay et al. (2015, 2014b) at depths < 52 m in the Red Sea found no trends in drilling predation on mollusks with depth; fine-grained sediments showed greater DF (0.20) than sandy (0.17) or reef (0.13) substrates, but differences were not statistically significant. Sawyer and Zuschin (2010) found that Adriatic samples from muddy substrates varied more in drilling metrics than did those from sandy bottoms; bivalve families generally had greater DF in muddy than sandy environments but gastropods showed the opposite pattern, although results varied among molluscan families. Among coral reef-associated mollusks of the Gulf of Aqaba (northern Red Sea), bivalves exhibited significantly greater drilling in samples from muddy sand near a patch reef than from gravelly sand near a fringing reef, but gastropod prey showed the opposite pattern of drilling relative to environment (Hausmann et al., 2018). Nebelsick and Kowalewski (1999) found statistically significantly lower DF on echinoids in sand and coral patches in the Red Sea compared to other substrates (muddy sand, sand, sand and seagrass, seagrass, coral carpet); the composition of the echinoid fauna also varied among facies. Drilling frequencies varied widely among sites, even within the same facies, although it was inversely correlated with the abundance of the echinoid species *Fibularia ovulum*. Nebelsick and Kowalewski (1999) hypothesized that the widely varying drilling frequencies were linked to spatial variation in the abundance of predatory cassid gastropods. Predation by cassids in the Caribbean is affected by the presence of reefs (Levitan and Genovese, 1989); mortality of the sea urchin *Diadema* is much greater on sand substrates than in artificial reef or rock environments, suggesting that *Diadema* is commonly associated with reefs because they represent a refuge from their predators.

Seagrass habitats are also thought to provide a refuge from predation for both epifaunal and infaunal prey (Snelgrove, 1999; Wilson, 1991) (see also section 6.1.). Invertebrates occupying areas of dense vegetation are less subject to fish predation (Heck and Thoman, 1981). Seagrass roots bind sediment and are thought to interfere with digging activities of predators; Peterson (1982) found greater densities of the bivalves *Mercenaria* and *Chione* in vegetated habitats and less mortality from whelk predation than in plots from which seagrass was removed experimentally. Increased species richness in seagrass habitats has also been attributed to inhibition of predation by vegetation (Snelgrove, 1999).

How do these observations of environmental variation of predation in the modern environment translate to the fossil record? Relatively few studies in the fossil record address the relationship of predation to depositional environment. Most such work has focused on variation in drilling predation, and results are not straightforward. Hansen and Kelley (1995) compared drilling predation in six facies of the Eocene Moodys Branch Formation from the US Gulf Coastal Plain, ranging from fine sand deposited in an open bay or lagoon to sandy clay deposited on the outer middle shelf. No consistent pattern was found in successful or failed drilling along the environmental gradient for common prey species or the assemblage as a whole, and DF did not correlate with mean grain size. However, DF correlated with relative abundance of both naticid gastropod drillers and the preferred prey species (i.e., lucinid and corbulid bivalves and turritellid and hipponicid gastropods). Thus, the greatest effect of substrate on predation was in determining the taxonomic composition of the prey faunas, a result similar to that reported by Nebelsick and Kowalewski (1999) for modern Red Sea echinoids. Złotnik and Ceranka (2005) also suggested that the abundance of cassid gastropod predators may have been responsible for significantly greater drilling on the echinoid *Echinocyamus pusillus* in lower-energy, fine-grained sand compared to coarse-grained sand in the Miocene of Poland, but they were unable to test that hypothesis. No variation in drilling within sublithofacies was found.

Hoffmeister and Kowalewski (2001) found geographically varying patterns in drilling in the Miocene of Europe; Boreal DF on mollusks were greater in sand facies and Paratethys DF were greater in clay facies, indicating that factors other than substrate affect drilling predation (e.g., salinity, temperature). Paratethys localities experienced fluctuations in salinity that would have been most pronounced in nearshore samples where drilling was less frequent. Hoffmeister and Kowalewski (2001) suggested that the chemical processes employed during drilling by naticid and muricid gastropods may have been affected by salinity. In another study of Miocene Paratethyan mollusks, Sawyer and Zuschin (2011) found variation in the frequency of successful and failed drilling between intertidal and sublittoral samples, but whether the differences were significant depended on the taxonomic level of analysis and which stage of the Miocene was examined. Intertidal habitats may have varied more in drilling predation (4–16%) than did sublittoral (4–13%). The drilling intensity in the more nearshore/estuarine conditions of the regional Karpatian Stage tended to be lower than in the more normal marine conditions of the regional Badenian Stage. These results are consistent with observed differences in drilling between modern Adriatic intertidal and sublittoral environments (Sawyer and Zuschin, 2010). Salinity was also posited by Chattopadhyay et al. (2016) as a factor affecting drilling on mollusks in the Eocene of the Paris Basin. Three localities, representing slightly different depositional environments, differed statistically in DF at the assemblage and genus levels. The locality representing the greatest terrestrial input experienced the lowest drilling frequencies (DF = 0.003), whereas localities from the most stable, deeper water, environment recorded the highest drilling frequencies (DF = 0.25). Conversely, a study on modern mollusks from the Bahamas found no relationship between DF and salinity (Selly et al., 2018).

Unvegetated soft substrates appear to have different patterns of predation in the fossil record than reef or seagrass environments. Daley et al. (2007) compared drilling predation on the infaunal bivalve *Chione elevata* between the Pleistocene Bermont and overlying Fort Thompson formations of Florida, USA. The Bermont exhibited a greater DF and less size selectivity of *Chione* prey. Because the seagrass environment of the Bermont impeded burrowing, infaunal bivalves were less abundant and less diverse than in the Fort Thompson. Daley et al. (2007) concluded that limited prey alternatives in the Bermont led to more intense, less size-selective predation on *Chione* by predatory naticid gastropods. Habitat (seagrass, reef, unvegetated soft sediment) was also considered important in determining differences in predation among families of infaunal bivalves by Leonard-Pingel and Jackson (2013) in the Neogene of Panama and Costa Rica. Genera of venerid bivalves, which mainly occurred in unvegetated sand, were drilled significantly less than lucinid genera, which occupied seagrass habitats. Leonard-Pingel and Jackson (2013) suggested that the small size and shallow depth of burrowing of lucinids made them more vulnerable to drilling predation. They also noted high drilling of cemented epifauna, which are common in reefs. A statistically significant increase in drilling across 11 million years in the Caribbean Neogene was attributed by Leonard-Pingel and Jackson (2016) to an increase in coral reef and seagrass environments; genera typically inhabiting these biogenic habitats were drilled two to four times as much as genera characteristic of soft sediments. This change was accompanied by a shift in dominance of drillers from infaunal naticid gastropods (more common in soft sediments) to epifaunal muricids (dominant in the biogenic environments). Thus, conclusions that seagrass and reefs are refuges from predation, as argued for modern environments, does not seem consistent with observations of drilling predation in the fossil record.

The relationship between predation and depositional environment is not straightforward. Most information from the fossil record comes from drilling gastropod predators and their molluscan and echinoid prey. Drilling appears to vary with environment, but different studies have suggested different, often contradictory, relationships between predation intensity and environmental factors. Most studies have concluded that habitat needs to be taken into account when making comparisons across space and time, but general principles are difficult to derive. Interpretations of long-term patterns in predation must recognize that substrates themselves have evolved; increases in bioturbation, evolution of seagrasses, and the activities of organisms that break up hard substrata (e.g., parrotfishes) have modified depositional environments, especially during the Cenozoic (Vermeij, 2017). These changes have created new habitats and new opportunities for both predators and prey.

4.3. Oxygen

The presence of free oxygen is vital to metazoan predation and, indeed, was a limiting factor in animal physiology and body size through geologic time (Payne et al., 2009). The increasing influence of oxygenic photosynthesis on the hydrosphere and atmosphere, beginning during the Great Oxidation Event (2.5 Ga), led to a protracted and stepwise oxygenation of the

Earth system (Eriksson et al., 2013; Fike et al., 2006; McFadden et al., 2008) with modern pO_2 being reached by the early Paleozoic (Canfield, 2005). Sperling et al. (2013) highlighted the importance of even small increases of dissolved oxygen in enabling the metabolically intense feeding mode of predation through a meta-analysis of polychaete feeding mode in oxygen minimum zones of the modern ocean. They argued that increasing dissolved oxygen in Ediacaran oceans made evolutionary arms races between predators and prey possible, which played a key role in the Cambrian Explosion. Edwards et al. (2017) linked the Great Ordovician Biodiversification Event to increasing oxygenation. Perhaps not coincidentally, predation intensity seems to have increased concurrently during the Late Ordovician (Huntley and Kowalewski, 2007).

Oxygen, though not analyzed as frequently as other environmental factors, is known to influence predator-prey interactions over shorter time scales and in modern ecosystems. The species richness and density of predatory fish (in this case, tuna and billfish) in the open ocean is strongly related to both sea-surface temperature and dissolved oxygen (Worm et al., 2005). This relationship is likely linked to predator physiology, because tuna cardiac function and depth range are limited by oxygen availability (Worm et al., 2005). Conducting a series of in situ hypoxia and anoxia experiments in the northern Adriatic Sea, Riedel et al. (2008b) demonstrated that the anemone *Cereus pedunculatus* and the gastropod *Hexaplex trunculus* continued predatory feeding during moderate hypoxia, whereas decapod crustaceans were more susceptible to hypoxia and anoxia as revealed by altered behavior that exposed them to their own predators and elevated mortality (Haselmair et al., 2010; Riedel et al., 2012). In feeding experiments meant to replicate predation of red sea bream larvae by jellyfish and juvenile Spanish mackerel, Shoji et al. (2005) offered prey items to predators across a range of sub-lethal low dissolved oxygen conditions. The Spanish mackerel individuals swam slower, displayed a higher gill ventilation rate, and consumed fewer bream larvae with less dissolved oxygen. The jellyfish, however, displayed no change in bell contraction rate and consumed more red sea bream larvae under oxygen stress, suggesting that seasonal hypoxia could alter the relative importance of these predators in their natural estuarine habitats in Japan. Breitburg et al. (1994) reported similar results among larval naked goby prey, wherein decreased dissolved oxygen concentrations led to increased predation by the scyphomedusan "sea nettle" and increased physiological stress on and decreased predation by both the adult naked goby and juvenile striped bass from the Chesapeake Bay, eastern USA. In a comprehensive approach integrating live-collected, death assemblage, archaeological, and fossil specimens, Casey et al. (2014) examined community composition and predator-prey interactions along an oxygen stress gradient induced by eutrophication in Long Island Sound, northeastern USA. The authors demonstrated that drilling predation and taxonomic agreement between live-collected and death assemblage samples were greatest in locations most affected by low oxygen levels, contrary to the findings on eutrophication of Kidwell (2013, 2007) and Kidwell and Tomasovych (2013). Rather, disturbance by shell fishing outside of the severely hypoxic zone was the primary source of ecological disruption.

Oxygen stress can, of course, also influence the prey side of predator-prey interactions. The experiments of Long et al. (2008) demonstrated that decreased oxygen significantly reduced the burrowing depth of the estuarine infaunal bivalve *Macoma balthica*, presumably increasing its vulnerability to predatory attacks. Likewise, the duration of time that the freshwater to brackish bivalve *Corbicula fluminea* is able to close its shell in a defensive posture following a simulated attack by a predator is significantly reduced under oxygen stress (Saloom and Scot Duncan, 2005). Even though this taxon is known to reduce its metabolic activity by an order of magnitude when its valves are closed and maintain an aerobic metabolism for 5–10 hours (Ortmann and Grieshaber, 2003), conditions of reduced dissolved oxygen can make it more susceptible to its predators.

In conclusion, free oxygen has likely played an important, though currently understudied, role in shaping predator-prey interactions through geologic time. At the coarsest of time scales, the oxygenation of the atmosphere and hydrosphere enabled, but did not necessarily guarantee, the dramatic increase in body size, diversity, and increasing complexity of metabolically expensive biotic interactions recorded through the Geozoic (Knoll and Bambach, 2000; Payne et al., 2009; Schiffbauer et al., 2016; Sperling et al., 2013). Over shorter time scales, the lack of oxygen has been shown to influence the behaviors of predators and prey and have unexpected consequences to ecosystem function. It is unclear how fluctuations in oxygen throughout the Phanerozoic have modified predator-prey interactions at a variety of temporal and spatial scales and such will likely be a fruitful avenue for future research.

4.4. Nutrients and food scarcity

The relationship between predation and overall nutrient availability or primary productivity is not always clear, even though productivity has been identified as a factor influencing predator–prey interactions (Bohannan and Lenski, 2000; Holt et al., 1994; Leibold, 1989). Both theoretical and experimental studies predict a positive correlation between prey population size and rate of prey consumption by predators (Case, 2000; Holling, 1959; Kaunzinger and Morin, 1998; Ricker, 1941). Because prey population size is often strongly influenced by primary productivity, one might expect a positive correlation between productivity and the intensity of predation. However, this hypothesis may not hold true for all marine invertebrates. In a study of the effects of decreasing planktonic productivity in the Caribbean due to the closure of the Central American Seaway (~3.5 Ma), Leonard-Pingel and Jackson (2016) showed a negative relationship between regional productivity and drilling predation intensity, contrary to the theoretical prediction. They inferred that the changes in predation intensity were driven primarily by a change in habitats rather than a decline in productivity.

Increase in nutrients may also affect predation intensity indirectly. Excess nutrient loading (eutrophication) often causes hypoxia, which in turn may change the prey-predator interaction (see also above). Hypoxia has been linked to a decreased capacity to drill prey by predatory gastropods (Das and Stickle, 1993; Person et al., 1967). Predatory groups may differ in susceptibility to hypoxia (Levin et al., 2009) and their different responses may lead to a complex pattern of predation in an ecosystem affected by hypoxia (Casey et al., 2014; see also section 4.3.). Because of such complex interplay of variables, the relationship between predation intensity and primary production is still unresolved.

In addition to overall nutrient availability, fluctuating levels of local resources also affect organisms. Heterogeneity in environmental attributes leading to ecological patchiness often results in spatial variation in resources (MacArthur and Pianka, 1966). Consequently, a predator may face intermittent events of saturation and starvation (Menge, 1972). The issue of starvation has not been considered directly in the standard cost–benefit analysis of prey profitability. Such models often fail to predict the pattern of prey choice in resource-limited ecosystems. The standard cost–benefit model, developed from optimal foraging theory, addresses optimal diet and optimal allocation of foraging time to patches independently (Heller, 1980). Such models often fail to predict the pattern of prey choice in resource-limited ecosystems. One way to modify the model is to allow the predator's assessment of prey to vary with levels of hunger. In that case, a predator approaching satiation acts as if prey were abundant and demonstrates highly selective behavior (Charnov, 1976; Pulliam, 1974; Schoener, 1971). However, Richards (1983) demonstrated the opposite effect using a two-prey theoretical model. The model showed that predators expand their prey choice near satiation to include lower-value prey. This means that if a small amount of a high-value prey is required, a predator can be satiated faster if it attacks the first item it encounters rather than searching for a high-value prey. With low patch density, where the encounter rate with high-value prey is low, the model predicts that a specialist would expand its prey choice near satiation. A successful predator following this rule becomes an "expanding specialist," starting as a specialist and then expanding its diet after some time in the patch (Heller, 1980).

Experimental studies have demonstrated significantly different behavioral traits among starved predators (including lack of selectivity of prey, higher attack, and feeding rate) compared to satiated ones (Beukema, 1968; Ernsting, 1977; Kislalioglu and Gibson, 1976). Other experiments showed a lack of size selectivity by starved predatory gastropods (Barnett, 1979; Palmer, 1980; Perry, 1987; Wood, 1968), fish (Bence and Murdoch, 1986; Ware, 1972), and a glass worm (Pastorok, 1980). Similar studies showed that the escape response of scavenging snails was diminished by hunger (Morton and Chan, 1999; Stenzler and Atema, 1977). However, the observations for starved predators are not always consistent. For example, Perry (1987) documented a significant drop in attack success for starved predatory gastropods, whereas Das et al. (2015) found a higher rate of attack compared to satiated individuals. Unavailability of preferred prey also has been suggested to initiate change in predatory behavior and often triggered cannibalism in naticid (Chattopadhyay et al., 2014a) and muricid gastropods (Gordillo, 2013b). As starvation is related to prey availability and varies spatially, starvation-induced behavioral change in predation may help explain spatial variation in predation intensity. Prey availability is also thought to change temporally, potentially controlling predatory behavior through time.

4.5. Temperature

Ample evidence suggests that biotic interactions such as predation can be affected by temperature changes in modern marine ecosystems. In turn, whole ecosystems may be influenced. For example, today's Antarctic shelf bottoms are inhabited primarily by ophiuroids, asteroids, echinoids, and gastropods; no shell-breaking predatory crabs are found on the shelf, but they are present on the continental slope (Aronson et al., 2015a, 2015b; Thatje et al., 2005). As seawater temperatures continue to rise, king crabs (Lithodidae) are expected to invade the shelf, along with other shell-breaking invasive crabs (Aronson et al., 2015a, 2015b), most likely resulting in a decreased prey density and diversity (Smith et al., 2017). Predatory decapods were present in Antarctica until the Miocene and Pliocene (Feldmann and Quilty, 1997; Whittle et al., 2014) but may have disappeared since then due to continued cooling (Whittle et al., 2014).

Various examples indicate that entire food chains are altered by increasing temperatures. From a theoretical perspective, an increase in temperature will result in a rise of metabolic rates and thus a higher energetic demand for all species. The latter may not always be met for top predators that have a relatively small population size and are thus more prone to extinction (Kordas et al., 2011). A change in the food chain was shown experimentally for aquatic microbes, as communities in warmer conditions lost proportionally more top predators and herbivores, while autotrophs and bacterivores became more abundant (Petchey et al., 1999). Conversely, experiments on a rocky-intertidal food chain, consisting of a top crab predator, an intermediate drilling gastropod consumer, and a basal mussel prey, showed no negative impact on the crab and mussel with increasing sea temperatures (Miller et al., 2014). However, the intermediate consumer was negatively impacted, showing a reduction in foraging, growth rate, and growth efficiency (Miller et al., 2014).

Most temperature experiments have involved one predator and one prey species from temperate regions. Based on field and lab experiments, rates of predation by a sea star on mussels dropped significantly with a decrease in temperature (Sanford, 2002, 1999). Warming, on the other hand, substantially reduced spaces devoid of predatory sea stars on rocky shores, negatively impacting mussel abundance (Harley, 2011). In another experiment, a gastropod predator and its barnacle prey were subject to changing temperatures (Harvey and Moore, 2017). Tissue production of the prey was reduced in warmer conditions, but feeding rate of the predator decreased rather than increased, despite abundant prey items (Harvey and Moore, 2017). Feeding rates of predatory crabs on bivalves rose as temperature was increased in various experiments (Barbeau and Scheibling, 1994; Matheson and Gagnon, 2012; Sanchez-Salazar et al., 1987; Wu et al., 2017).

For both muricid and naticid (drilling) gastropods, various studies have demonstrated that feeding rates on mollusks increase with higher temperatures in controlled lab settings (Ansell, 1982a, 1982b; Edwards and Huebner, 1977; Garton and Stickle, 1980; Hanks, 1957; Manzi, 1970; Miller, 2013). Likewise, long-term lab experiments with seasonal temperature variations also showed a positive correlation of feeding rates and temperature for muricids and naticids (Kingsley-Smith et al., 2003; Lord and Whitlatch, 2013), as did long-term field-based experiments with a naticid driller (Edwards and Huebner, 1977). In yet another experimental design, muricid consumption, energy intake, and body tissue production based on a mussel diet was positively correlated to sea surface temperature at various sites within the Gulf of Maine, USA, along a temperature gradient (Matassa and Trussell, 2015). Abundant molluscan prey were available in these experiments, which may not always be the case in nature. Thus, whether this change in feeding rates has an effect on overall predation intensity in ecosystems remains to be investigated. Some indication may come from latitudinal trends in drilling frequency across a substantial temperature gradient. Although methods differ, various studies on primarily modern ecosystems have indeed shown decreasing drilling frequencies at higher latitudes (Alexander and Dietl, 2001b; Dudley and Vermeij, 1978; Visaggi and Kelley, 2015), but others have found no obvious correlation (Kelley and Hansen, 2007; Martinelli et al., 2013) or even an opposite trend (Hansen and Kelley, 1995; Vermeij et al., 1989).

Despite the rich molluscan fossil record and dramatic changes in Cenozoic temperature, little is known about the effect of temperature on predator-prey interactions in deep time. An exception is a study on Pleistocene mollusk assemblages from Japan (Chiba and Sato, 2016). Studying drill holes in specimens of the most abundant species in a sequence interpreted to represent a cooling interval from ~0.23–0.15 Ma, they found a significant decrease in drilling frequency as warm-water drillers became less common (Fig. 11A). This decrease coincided with a decline of drill holes located on or near the commissure. Our analysis of the data also indicates that predator-prey size ratios decreased (Fig. 11B), suggesting that predators attacked larger prey relative to their own size. This trend is primarily caused by a decrease in drill-hole size, whereas prey size remained relatively stable throughout this interval. Whether these trends are also observed in other species and within whole assemblages remains to be investigated.

Temperature-related trends in predation may be masked by other factors that can be superimposed on latitudinal or temporal variation in temperature. For example, a study focused on Miocene mollusk assemblages sampled across multiple regions of Europe (Hoffmeister and Kowalewski, 2001) documented less intense drilling predation in the warmer Paratethys basin than in the cooler, higher-latitude region of the northern Atlantic (the Boreal Province). The authors suggested that the observed patterns may be due to fluctuating salinity in the Parathethys that may have limited, at least intermittently, marine drilling predators such as naticids. Conversely, subsequent research found that the complex paleogeographic history of the Paratethys, rather than salinity, might explain the low intensity of drilling (Sawyer and Zuschin, 2011).

A recent study highlighted the effect of cooling on predator-prey interactions during the Eocene in Antarctica (Dietl et al., 2018). Unlike their prediction, cannibalistic drilling among naticids did not decrease during the cooling event, but remained stable. The authors suggested that a coinciding decrease in the abundance of shell-breaking predators stimulated cannibalism in this less risky environment.

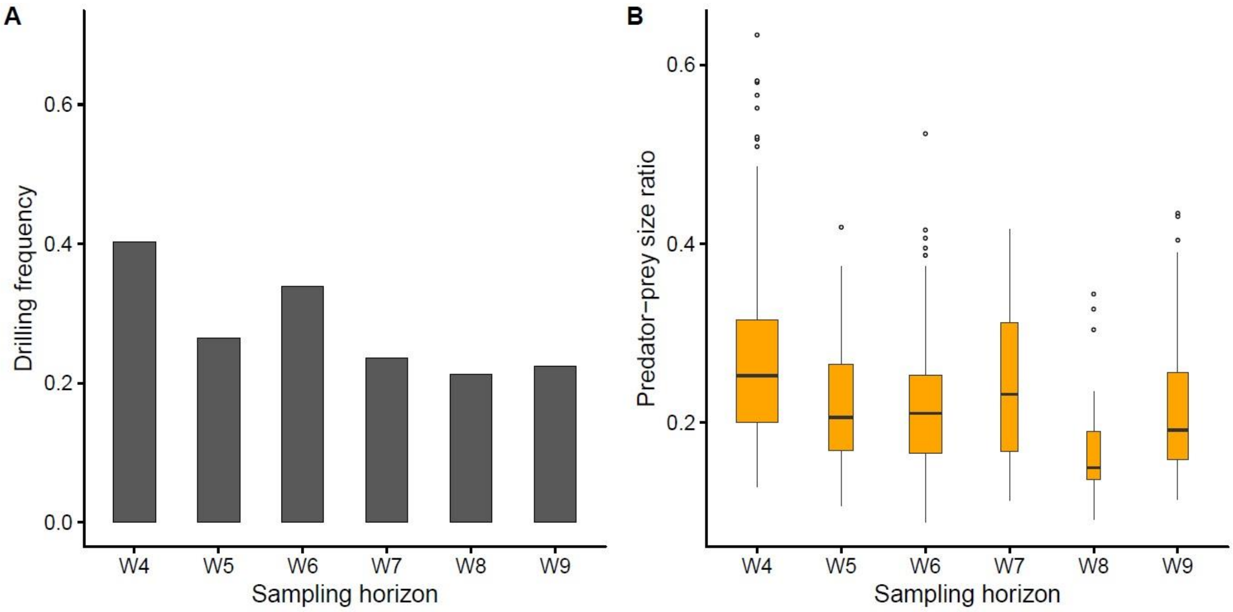

Fig. 11. Decreases in drilling frequencies (A) and predator-prey size ratios (B) during a cooling interval (W4–W9) in the Middle Pleistocene of Japan based on data from Chiba and Sato (2016). The prey used is the bivalve *Glycymeris yessoensis* and the inferred drilling predators are naticid gastropods. Predator-prey size ratios were estimated here by dividing the outer drill-hole diameter by the prey shell length, n = 748.

4.6. Ocean acidification

Ocean acidification (OA) refers to long-term decreases in seawater pH resulting from the uptake of atmospheric CO_2 by the oceans (Doney et al., 2009). This process has received much attention recently, as it has been discovered that current levels of excess CO_2 in the atmosphere have been absorbed by the oceans, resulting in a 0.1 unit drop in surface ocean pH since the Industrial Revolution and a projected further drop of 0.2–0.3 units by 2100 (Hoegh-Guldberg et al., 2014). Although current anthropogenic OA is the focus of most studies, the occurrence of acidification events in the geologic past is well established (D'Hondt et al., 1994; Hönisch et al., 2012; Zachos et al., 2005). Furthermore, these acidification events were likely not benign, and many have been linked to marine mass extinctions (Clarkson et al., 2015; Kiessling and Simpson, 2011; Veron, 2008). The current increase in oceanic CO_2 and the subsequent drop in pH is thus concerning for extant marine organisms and particularly marine calcifiers, due to the susceptibility of calcified shells to dissolution under OA (Hofmann et al., 2010; Kroeker et al., 2013; Orr et al., 2005; Ries et al., 2009). As a result, an outpouring of experimental evidence has tested for the effects of elevated CO_2 on marine organisms, and such evidence may shed light on how acidification events may have affected biotic interactions in the geological past.

Although calcifying marine biota are considered most vulnerable to OA, experimental evidence suggests that species interactions can also be impacted through changes in morphology, physiology, and behavior (see Briffa et al., 2012; Clements and Hunt, 2015; Leduc et al., 2013; Nagelkerken and Munday, 2016, for reviews). For coastal marine mollusks in general, Kroeker et al. (2014) conceptually suggested that energetic and physiological effects of elevated CO_2, along with impacts to chemoreception and behavior, have the capacity to affect predator-prey interactions through altered prey defenses and predator success (Fig. 12). Such impacts have been demonstrated empirically as well. For example, Bibby et al. (2007) reported that OA resulted in thinner shells of the gastropod *Littorina littorea*, which subsequently altered their avoidance behavior of predators (the crab *Carcinus maenas*). Burrowing behavior of infaunal clams is also recognized to be impacted by OA conditions (Clements and Hunt, 2017). Prey defenses in intertidal snails are reportedly affected by OA, rendering snails more susceptible to seastar predation (Jellison et al., 2016). Ocean acidification has also been reported to increase the vulnerability of oysters (*Ostrea lurida*) to drilling predation by invasive oyster drills (*Urosalpinx cinerea*) (Sanford et al., 2014). Wright et al. (2014) also observed increased predation rates of whelks (*Morula marginalba*) feeding on oysters (*Crassostrea gigas*) after 10 days of exposure to OA conditions, although the effect of OA on predation was non-significant after 17 days. Likewise, Amaral et al. (2012) found that oysters (*Saccostrea glomerata*) from more acidic sites were consumed more quickly by whelks (*M. marginalba*) due to their thinner shells. On the other hand, Wu et al. (2017) found that a drop in pH under higher CO_2 conditions resulted in decreased feeding rates of predatory crabs on bivalves. Predator-prey interactions involving a wide variety of mostly fish-eating predatory marine fishes can also be impacted by OA (e.g., Ferrari et al., 2011). Such effects are difficult to establish in the fossil record given the sub-par preservation of predator-prey interactions between fishes. It is thus evident that the nature of biotic interactions across various trophic levels may be affected by acidification, potentially resulting in alterations of entire marine ecosystems (Nagelkerken and Munday, 2016). Furthermore, although multiple-stressor studies remain limited, it is likely that the combined effects of ocean acidification and other environmental stressors (e.g., temperature) can increase the complexity of such ecological effects (Kroeker et al., 2016; Nagelkerken and Munday, 2016); multi-stressor studies in the context of predator-prey interactions are thus deserving of research attention.

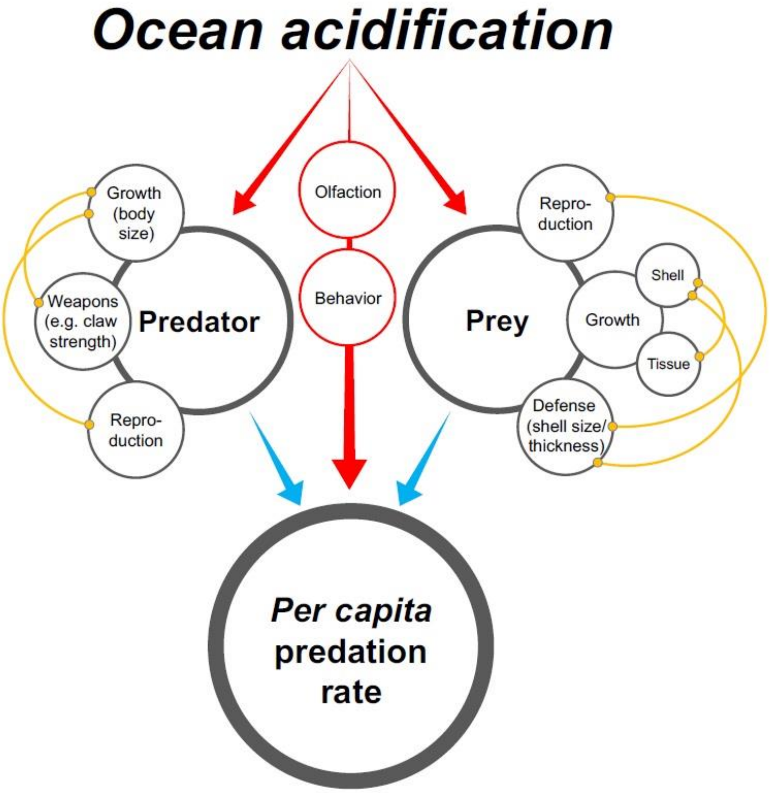

Fig. 12. Conceptual depiction of pathways by which ocean acidification can influence *per capita* predation rates (modified with permission from Kroeker et al., 2014). Yellow lines linking processes indicate potential trade-offs between growth, reproduction, and defenses (prey) and offenses (predator). Olfactory and behavioral effects apply to both predators and prey.

Given the experimental evidence that OA can affect predator-prey relationships, coupled with the notion that biotic interactions can be a function of climate (Blois et al., 2013), the nature of predator-prey interactions throughout geological time may differ between periods of high and low CO_2. Studies have yet to test for effects of acidification events on predator-prey interactions in the fossil record, however. Nonetheless, well-preserved indicators of predator-prey ecology in the fossil record (e.g., drilling predation and repair scars) may shed light on the effect of acidification events on these interactions throughout geological time. Such studies must carefully consider the role of taphonomy, however, given the propensity for increased acidification to weaken shells disproportionately to non-acidification events (e.g., Clements et al., 2018; Waldbusser et al., 2011) and the reported importance of shell dissolution in taphonomy (Cherns et al., 2010; Cherns and Wright, 2009, 2000; Wright et al., 2003). To date, a single study has suggested that OA may have limited effects on shell taphonomy in the context of gastropod drilling predation (Clements et al., 2018); however, much more research is needed regarding the taphonomic role of OA.

5. Behavior of predators

Foraging behaviors by predators have been divided into search, pursuit, and subjugation phases (Griffiths, 1980; Vermeij, 1987; Ziegelmeier, 1954), although these phases are not always easy to separate. Species vary in the proportion of time and energy allocated to each phase of predation. Search and pursuit costs are greater for organisms that forage actively and/or widely, whereas sit-and-wait predators (Pianka, 1974) devote more energy and/or time to subduing their prey (Griffiths, 1980). Hunting mode (sit-and-wait, sit-and-pursue, or active hunting) and habitat domain (the area within the habitat over which foraging occurs) have important consequences for prey behavior, life history, and population demography, which in turn have feedbacks for the predator (Schmitz, 2005). Predator foraging behavior is affected not only by the characteristics and occurrence of the prey but also by the presence of other predators (Chattopadhyay and Baumiller, 2010, 2007; Hutchings and Herbert, 2013; Lima and Bednekoff, 1999; Trussell et al., 2011).

Only certain types of predator foraging behaviors are evidenced in the fossil record. Evidence of search and pursuit behaviors is rarely preserved and is often circumstantial (Bishop, 1975); paleontological studies of such behaviors mostly have been limited to identifying the behaviors characteristic of particular fossil taxa. Trace fossil evidence includes purported "hunting burrows" (e.g., Babcock, 2003; Bergström, 1973; Brandt et al., 1995; Tarhan et al., 2012) of trilobites. Selly et al. (2016) summarized previous work and criteria for demonstrating trace fossil evidence that trilobites pursued and captured soft-bodied prey; Cambrian (of Missouri, USA) *Rusophycus* trilobite burrows and vermiform burrows intersected at a frequency significantly greater than expected by chance and exhibited evidence of size-selective predatory behavior. At the other end of the size/taxon/temporal spectrum is trace fossil evidence of walrus predation on deep-burrowing bivalves (Gingras et al., 2007). Pleistocene marginal-marine sediments of Washington state, USA, contain intersecting bivalve burrows and bowl-shaped excavations interpreted as the result of hydraulic jetting by walruses extracting bivalve prey from the sediment.

More often inferences about search and pursuit behaviors are based on predator morphologies, especially in reference to extant relatives or analogs. For instance, Massare (1988) used functional morphology to infer swimming speeds and foraging strategies of Mesozoic marine tetrapods. She examined hydrodynamic properties of different body shapes and propulsion styles and calculated that, at the same body size, ichthyosaurs were faster swimmers than plesiosaurs and pliosaurs, which in turn outpaced mosasaurs and crocodiles. She suggested that the long-bodied, slower swimmers were more likely ambush predators, whereas faster swimmers such as ichthyosaurs and pliosaurs were more likely pursuit predators. More recently, Motani (2008) described how physical (e.g., hydrodynamic and optical) principles and comparisons to modern swimming vertebrates (sharks and tuna) can be incorporated in functional morphological analysis of extinct marine ichthyopterygians. He concluded that parvipelvian ichthyopterygians had advanced cruising abilities and dark-adapted vision that enabled them to forage over a broader area and at greater depth than more basal ichthyopterygians. Foraging involving deep diving has also been inferred from avascular necrosis of bones (indicating the "bends") in fossil mosasaurs (Martin and Rothschild, 1989; see also Walker and Brett, 2002).

Inferences about the habitat over which a predator searches for prey can also be drawn from prey life mode, at least to a coarse degree. For instance, shell-drilling naticid gastropods usually forage at shallow depths within the substrate (Visaggi et al., 2013), with some exceptions (Grey, 2001; Guerrero and Reyment, 1988; Pahari et al., 2016; Savazzi and Reyment, 1989). However, Dietl (2002) inferred that predators identified as naticids, based on drill-hole shape, hunted and drilled Paleocene pycnodont oysters epifaunally, based on the epifaunal life mode of the prey and the large prey size compared to the predator (as shown by drill-hole size), which would have prevented grappling and transport by the predator.

Evidence of the subjugation (including consumption) phase of predation is preserved more often than evidence of search and pursuit behaviors. Direct evidence of subjugation behaviors occurs in rare cases of exceptional preservation, e.g., an Ordovician asteroid preserved in feeding position on a bivalve, evidencing the early evolution of extraoral feeding by stomach extrusion (Blake and Guensburg, 1994; see also Clarke, 1912, for examples from the Devonian). More often evidence of subjugation activities is provided by trace fossils; such praedichnia are the focus of most of this paper. Gastric residues, regurgitates, and the like can preserve remains of the victim (Bishop, 1975; see summary for fish predation in McAllister, 2003), sometimes with evidence of the mode of subjugation (Neumann, 2000; Zatoń and Salamon, 2008). Bite marks are often attributed to predation, and their morphology has been linked to possible predators (e.g., Gale et al., 2017, and citations therein; Mapes and Hansen, 1984), although scavenging may be difficult to distinguish from predation (e.g., Collareta et al., 2017a; Hill et al., 2015; Neumann, 2000). Activities such as grazing and crushing produce breakage, which may be accompanied by repair scars when damage is sublethal (see, e.g., Nagel-Myers et al., 2013, 2009). Along with breakage and repairs, drill holes yield insight into predator behaviors, including selectivity of prey and prey handling behaviors.

Neontological studies have shown that the degree to which predators are selective of prey differs both among and within taxa as circumstances vary. For instance, predators that are much larger than their prey tend to be less selective (Hawlena and Pérez-Mellado, 2009). Predators tend to be opportunistic if prey are usually scarce (Hughes and Elner, 1989). Predators exposed to increased risk from their own enemies also are less selective (Hawlena and Pérez-Mellado, 2009; Paul and Herbert, 2014). As discussed further in section 4.4, even hunger can affect predator selectivity; for instance, Das et al. (2015) demonstrated that hunger decreases prey size selectivity in the naticid gastropod *Natica tigrina*.

In the fossil record, selectivity with respect to prey taxon is usually determined by comparing statistically some measure of predation frequency with the relative abundance of taxa (Kowalewski, 2002; Smith et al., 2018). When predators are non-selective and choose prey randomly, predation should depend on a taxon's relative abundance or accessibility in an assemblage, which in turn should affect how often that prey taxon is encountered by the predator (Martinelli et al., 2015). Using this line of reasoning, Smith et al. (2018) presented a statistical method that tests for selectivity of prey against a null model in which predator preference (as indicated by drilling frequency) for a given prey type is equivalent to that of all other available prey types in the community. Analyses of prey selectivity must take into account the potential effects of time averaging and other taphonomic factors (see section 3.5.). In addition, the relative abundance of species can be altered if shorter-lived species are disproportionately represented in a fossil assemblage compared to their abundance in life (lifespan bias; Cronin et al., 2018; Kidwell and Rothfus, 2010; Van Valen, 1964; Vermeij and Herbert, 2004) because rapid turnover of generations causes their remains to accumulate faster. Nevertheless, the proportion of specimens of a species exhibiting predation traces should not be affected by lifespan bias. However, apparent selectivity of prey taxa could be affected if different predation tactics were employed on different prey species. For example, if a predator that usually drilled its prey killed a prey item without drilling, as has been reported in some cases (Ansell and Morton, 1987; Kowalewski, 2004; but see Visaggi et al., 2013), no evidence would be left to indicate that the prey item was killed by that predator.

Fossil evidence of breakage and repair has provided some information on taxon selectivity. Although Alexander (1981) concluded that shell-crushing sharks in the upper Mississippian of Utah, USA, were not species-selective of brachiopod prey, other studies have supported selectivity of prey species in the fossil record. For example, the frequency of crinoids with arm regeneration varied significantly among species (0–27%) in the Mississippian of Iowa, USA, with predators targeting the species and individuals with the longest stalks (Gahn and Baumiller, 2005). Paleozoic predators may also have targeted crinoids infested by platyceratid gastropods; Syverson et al. (2018) argued that a correlation between infestation and presence of tegmenal spines in camerate crinoids indicated that spines functioned to deter predation on platyceratids and incidentally on their hosts. Mapes and Chaffin (2003) reported varying percentages (33–83%) of potentially lethal predation breakage among nautiloid genera within the Pennsylvanian Finis Shale of Texas, USA. They concluded that genera with larger-diameter conchs were preferentially selected by predators (probably fish, arthropods, and cephalopods).

Because of problems in interpreting selectivity from repair scars, much of the fossil evidence interpreted as supporting selectivity of prey species comes from shell-drilling predation (but see Leighton, 2002). Examples include prey taxon selectivity of ostracods in the Paleocene of Nigeria (Reyment and Elewa, 2003) and Argentina (Villegas-Martín et al., 2019); mollusks from the Triassic of Italy (Klompmaker et al., 2016a), the Miocene of Bulgaria (Kojumdjieva, 1974) and Poland (Hoffman et al., 1974), and the Pliocene of Spain (Hoffman and Martinell, 1984) and The Netherlands (Klompmaker, 2009); of gastropods in the Miocene of Panama (Fortunato, 2007) and the Pliocene of Ecuador (Walker, 2001); and among brachiopods in the Devonian of New York state, USA (Smith et al., 1985) and the Miocene of Poland (Baumiller and Bitner, 2004). Selectivity of prey taxon is consistent with studies that have found a lack of correlation between drilling frequency and relative abundance (encounter frequency) of taxa (Kelley and Hansen, 2006; Martinelli et al., 2015), although more rigorous tests against null models of predator preference (per Smith et al., 2018) would be welcome. Apparent prey taxon preferences in the fossil record have been linked to various behavioral, ecological, and morphological factors.

Behavioral and ecological factors appear to be important in determining differences in drilling frequencies among fossil taxa (Chattopadhyay and Dutta, 2013; Hoffman et al., 1974). Such factors control the accessibility of prey taxa to predators. For example, Leonard-Pingel and Jackson (2013) found that differential drilling predation on 90 bivalve genera in the Neogene of Panama and Costa Rica was related to position in substrate (deep burrowers experienced less predation than shallow burrowers) and mobility (uncemented epifauna were drilled less frequently than cemented bivalves). Sawyer and Zuschin (2010) also noted a high drilling frequency on cementers from level-bottom sands. These results for drilling predators contrast with Harper's (1991) conclusion that cemented bivalves were less vulnerable than byssally-attached species to predation by asteroids and crustaceans that manipulate their prey.

Morphological features of prey may also contribute to patterns of taxon selectivity. Ornamentation has been proposed to explain differential drilling (and repairs) among taxa (e.g., (e.g., Batllori and Martinell, 1992; Leighton, 2001; Smith et al., 1985), but results are not straightforward (e.g., Allmon et al., 1990; Kerr and Kelley, 2015; Leighton, 2003; Leonard-Pingel and Jackson, 2013). Shell microstructure may also play a role in differential drilling, with taxa such as corbulids that contain organic shell layers being less preferred (Kardon, 1998; Kelley, 1988; Lewy and Samtleben, 1979). Ishikawa and Kase (2007) also reported conchiolin layers in 16 species of *Cardiolucina;* the data of Ishikawa and Kase (2007) produce a correlation coefficient $r = -0.4526$ ($p < 0.01$) between DF and number of conchiolin sheets in the shell, suggesting that predators may avoid (or drill unsuccessfully) taxa with organic sheets. However, Kelley and Hansen (1993, 2006) found corbulids and lucinids (with chemosymbionts, see also section 4.1.) among the preferred prey of naticid drillers across the Cretaceous through Pleistocene of the US Atlantic and Gulf Coastal Plain, attributing their desirability to their sluggish burrowing. In contrast, shell thickness plays an undeniable role in taxon preference of drilling predators (Carriker, 1951; Martinelli et al., 2016). Vermeij (1978) stated that a greatly thickened shell is the only morphological trait known to deter drilling on bivalves.

The importance of shell thickness has been recognized in cost-benefit analysis of prey selectivity by drilling gastropods. Kitchell et al. (1981) argued from experiments and the fossil record (Neogene *Glycymeris* from the US Coastal Plain) that shell-drilling naticid gastropods are optimal foragers that select prey to maximize net energy gain; such predation fits cost-benefit models in which cost is a function of drilling time (i.e., prey shell thickness) and benefit corresponds to biomass (measured as internal volume of the prey shell). Leighton (2001, 2002) argued against the application of optimal foraging theory (Stephens and Krebs, 1986) to predators that encounter prey sequentially (including drillers), but differences in drilling frequencies among taxa appear to fit predictions of cost-benefit analysis in several cases (e.g., Culotta, 1988; Kelley, 1988; Złotnik and Ceranka, 2005; but see Anderson et al., 1991). Confamilial predation, including cannibalism, by naticids was predictable by cost-benefit analysis (Dietl and Alexander, 1995; Kelley, 1991a). Predictability of cannibalism (see also Brezina et al., 2016) suggests that such behavior is not anomalous, contra Hoffman et al. (1974), Pek and Mikuláş (1996), and Stanton and Nelson (1980).

Prey size is an important component in cost-benefit analysis. Several methods have been used to test for size selectivity (Table 5). A common approach compares size-frequency distributions of attacked and unattacked prey (see discussion in Alexander and Dietl, 2003). In the case of drilling predation, a significant correlation between the size of drilled prey and drill-hole size (corresponding to predator size; Carriker and Gruber, 1999; Hughes and Hughes, 1981; Kitchell et al., 1981; Klompmaker et al., 2017; Kowalewski, 2004) has been interpreted to indicate prey size selectivity (Kitchell, 1986). Numerous authors have reported size selectivity by predators in the fossil record (e.g., Ausich and Gurrola, 1979; Chattopadhyay and Dutta, 2013; Geary et al., 1991; Harper et al., 2018; Hoffman and Martinell, 1984; Kabat and Kohn, 1986; Kelley, 1988; Kitchell, 1986; Klompmaker et al., 2015; Mallick et al., 2014, 2013; Martinell et al., 2012; Nagel-Myers et al., 2013; Pek and Mikuláş, 1996; Złotnik and Ceranka, 2005). Such size selectivity may be the result of active predator choice, as predicted by optimal foraging theory, but it may also represent mechanical limits to predation (Brown and Haight, 1992). Rodrigues et al. (1987) argued that foot size of naticid gastropods influences prey size choice; naticids can assess prey size using their foot and reject items that exceed the manipulation size limits of the predator (see also Chiba and Sato, 2012; Kabat, 1990; Kitchell et al., 1981; Pahari et al., 2016). This point is supported by reports of greater size selectivity by naticid than muricid gastropod predators (Casey et al., 2015; Kojumdjieva, 1974); naticids wrap their prey in the foot and muricids do not (Carriker and Yochelson, 1968).

Table 5. Methods used to test size selectivity by predators, with (non-exhaustive) list of studies exemplifying each method.

Method	**Example studies**
Compare size frequency distributions of attacked and non-attacked prey	Kabat and Kohn (1986) - drilling and repair scars on naticid gastropods, Allmon et al. (1990) – drilling on turritelline gastropods, Geary et al. (1991) – stomatopod holes in gastropods, Hoffmeister and Kowalewski (2001) – drilling on mollusks, Martinell et al. (2012) – drilling on serpulids, Grun et al. (2014) – drilling on echinoids, Chattopadhyay and Dutta (2013) – drilling on bivalves, Mallick et al. (2013, 2014) – drilling on gastropods, Selly et al. (2016) – burrow size of attacked and non-attacked trilobite prey, Takeda et al. (2016) – durophagous predation on ammonoids
Compare size frequency distributions of attacked prey and total prey population	Kelley (1982) – drilling on mollusks

Compare size distributions for death assemblage and size at attack based on repair scars	Harper et al. (2009) – durophagous predation on brachiopods, Pruden et al. (2018) – durophagous predation on brachiopods
Compare predation frequencies for different size classes of prey	Złotnik and Ceranka (2005) – drilling on echinoids, Chattopadhyay et al. (2016) – drilling on mollusks
Compare mean and/or median size of attacked and unattacked specimens	Baumiller et al. (2006) – drilling on brachiopods, Daley et al. (2007) – drilling on bivalves, Brezina et al. (2016) – drilling on naticid gastropods
Correlate prey size and predator size proxy (e.g., drill hole size, break length)	Kelley (1982) – drilling on mollusks, Hoffman and Martinell (1984) – drilling on mollusks, Kabat and Kohn (1986) – drilling on naticid gastropods, Kelley (1988) – drilling on bivalves, Allmon et al. (1990) – drilling on turritelline gastropods, Hoffmeister and Kowalewski (2001) – drilling on mollusks, Złotnik and Ceranka (2005) – drilling on echinoids, Daley et al. (2007) – drilling on bivalves, Martinell et al. (2012) – drilling on serpulids, Chattopadhyay and Dutta (2013) – drilling on bivalves, Mallick et al. (2013, 2014) – drilling on gastropods, Klompmaker et al. (2015) – drilling on barnacles, Kong et al. (2015) – drilling on bivalves, Meadows et al. (2015) – drilling on echinoids, Chiba and Sato (2016) – drilling on bivalves, Brezina et al. (2016) – drilling on naticid gastropods, Grun et al. (2014, 2017) – drilling on echinoids, Takeda et al. (2016) – durophagous predation on ammonoids

Some bivalved prey experienced preferential attacks on a particular valve, which may be related to valve accessibility and/or predator handling behaviors. Valve preference has been reported for inequivalved bivalve species. For example, predators prefer drilling the right valve in many species of corbulids (De Cauwer, 1985), which may relate to handling behavior of the predator (Anderson, 1992) or the larger size of the right valve (Taylor et al., 1983; Złotnik, 2001). Species that attach to the substrate by one valve, such as oysters, may also experience valve-selective predation (Chattopadhyay and Dutta, 2013, for the Miocene of India; Taylor, 1970, for the Eocene of the Paris Basin).

Handling behaviors may also affect the site on a prey shell that is attacked. Not all predation is site selective (Adegoke and Tevesz, 1974; Batllori and Martinell, 1992; Kabat and Kohn, 1986). Among drilling gastropods, muricids manipulate their prey less and show more random distributions of drill-hole sites on the prey shell compared to naticids (Carriker and Yochelson, 1968; Casey et al., 2015; Stump, 1975; but see Klompmaker et al., 2015, for muricid drilling on barnacles). However, stereotyped drill-hole positions have been reported on a wide range of prey: bivalves (Kelley, 1988; Kong et al., 2017; Taylor, 1970), gastropods (Berg and Nishenko, 1975; Blustein and Anderson, 2016; Taylor, 1970), scaphopods (Klompmaker, 2011; Yochelson et al., 1983), brachiopods (Ausich and Gurrola, 1979; Harper and Wharton, 2000; Smith et al., 1985), echinoids (Kowalewski and Nebelsick, 2003), barnacles (Donovan and Novak, 2015; Klompmaker et al., 2015), ostracods (Villegas-Martín et al., 2019), serpulid polychaetes (Martinell et al., 2012), and foraminifers (Malumián et al., 2007).

Ease of penetration of hard parts also may influence site of attack on the prey shell. Kitchell (1986) recognized that thickness varies across a prey's shell and proposed that predators situate drill holes on thinner areas of the shell. Allmon et al. (1990) stated that gastropods drilled the thinnest part of the shell of turritelline gastropods. Grun et al. (2017) and Meadows et al. (2015) argued that cassid gastropods preferentially attacked the highly porous, more penetrable central aboral area of fossil echinoid tests. Other authors have linked drill-hole site to the position of soft parts (Arua and Hoque, 1989; Klompmaker, 2011; Smith et al., 1985; Yochelson et al., 1983), including muscles (Chattopadhyay and Dutta, 2013; Leighton, 2001). Todd and Harper (2011) suggested that stereotyped drill-hole position in the bivalve *Venericor* from the

Eocene of England was due to octopods injecting toxins into the posterior adductor muscle. Alexander and Dietl (2001a, 2003) attributed the position of repair scars on bivalve shells to prey anatomy, with attacks focused on areas where soft tissues are exposed, as well as to predator behavior (i.e., posterior repairs resulted from siphon nipping, whereas ventral repairs resulted from shell wedging and chipping or occurred on species with ventral egress of the foot). For gastropod prey, stereotypy of drill-hole site may also reflect handling behaviors that block egress of the prey's foot, thus preventing escape (Berg and Nishenko, 1975; Dietl and Alexander, 2000).

Sometimes the position of attack can be linked to the direction from which predators approached their prey. For example, the position of bite marks on a Pliocene dolphin suggests an attack by a shark from the posterior and subsequently on the dorsal fin (Bianucci et al., 2010; Fig. 13). Although the sample size is small, bite marks on the skulls of Eocene juvenile basilosaurid whales are interpreted to have been made by larger confamilials that attacked primarily from a left lateral position (Fahlke, 2012). Klompmaker et al. (2009) recognized a preference for ventral bite marks near the end of the body chamber, close to the phragmocone, on Mesozoic ammonoids. They concluded that the predators, likely coleoid cephalopods and fish, attacked the ammonoids from behind. Takeda et al. (2016) reached similar conclusions for ventral attacks near the rear of the body chamber of Cretaceous scaphitid ammonoids. Posterior attacks may also have been the norm for predation on trilobites. Babcock (2003) reported that 75% of sublethal predation scars on trilobites occurred on the posterior end and 69% were restricted to the right side of the body. He attributed this lateral preference to the predation tactics suggested by Nedin (1999) for anomalocarids: the predator held one edge of the trilobite in its mouth and flexed the prey back and forth until its exoskeleton broke. Among brachiopods, some studies have found a preference for attacks on the valve closest to the substrate (e.g., Ausich and Gurrola, 1979; Leighton, 2001; Rohr, 1976), which may be consistent with an infaunal predator attacking from beneath the shell.

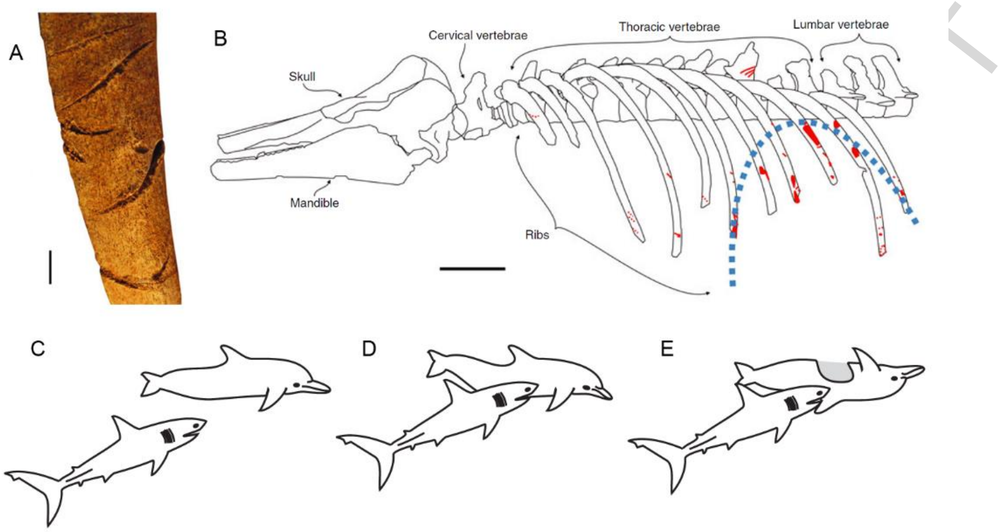

Fig. 13. Inferred shark attack on a dolphin during the Pliocene in Italy. (A) Bite marks on one of the ribs on the right side; scale bar is 50 mm tall. (B) Line drawing of the left side of the dolphin indicating bite marks in red and the location of the possible first main bite with a blue dashed line; scale bar is 100 mm wide. (C–E) Possible sequence of attack by the shark. Modified from Bianucci et al. (2010: figs 3–5).

Handling behavior by a given predator may vary with the type of prey attacked. For instance, octopods drill holes in large prey to inject toxins, but they may not drill smaller prey (Harper, 2006). Similarly, edge-drilling was more frequently used for large bivalve prey of the gastropod *Muricanthus fulvescens*, whereas shell grinding was used often for small prey (Herbert et al., 2016). The muricid gastropod *Hexaplex trunculus* employs both chipping and drilling modes of predation, with large *Hexaplex* preferring to attack mussels by chipping (Sawyer et al., 2009). Gordillo and Archuby (2012) found that the gastropod *Acanthina monodon* used different attack techniques (drilling vs. wedging valves apart) on different species of mussels in Tierra del Fuego, Argentina. Muricid gastropods may employ drilling of prey or kleptoparasitism, in which they "steal" the food from other muricids by feeding through the gape of a bivalve or displacing another muricid from the hole it drilled; Ishida (2005) found muricid species differed in the degree to which they used each technique depending on factors such as proboscis morphology, penetration cost, and ingestion speed. In the fossil record, drilling is likely to be more preservable than alternative techniques, which may lead to underestimation of mortality. Shell-drilling gastropods may employ wall drilling or edge drilling to attack bivalves (Chattopadhyay et al., 2014b; Dietl et al., 2004). In the case of muricids, edge drilling has been linked to the competitiveness of the environment because drilling at the shell margin (where the valve is thinner) is quicker than wall drilling, but the muricid risks amputation of its drilling apparatus by closure of the valves of the prey (Burrell, 1975; Herbert, 2018). Behavioral changes in wall drilling vs edge drilling are readily traceable in the fossil record (Dietl et al., 2004).

Prey handling behaviors also determine whether feeding is solitary or aggregative. Because they use the foot to envelop individual prey items, naticid gastropods typically forage singly (although group scavenging has been observed; JCC, pers. obs.). In contrast, group foraging is possible for gastropods that do not wrap the foot around victims. The muricid gastropod *Stramonita haemastoma* (oyster drill) frequently exhibits group foraging in the field (Brown and Alexander, 1994). In the laboratory, snails were more likely to join an ongoing attack, especially on a large oyster, than initiate an attack on a different prey. Most snails attempted to drill their prey, suggesting that multiple drill holes in single prey items in the fossil record could represent aggregative feeding by muricids. Złotnik and Ceranka (2005) concluded that, in the Miocene of Poland, small cassid gastropods often attacked echinoids through group attacks, as occurs in the Recent (Hughes and Hughes, 1971). However, larger cassids, which cover their prey more entirely with the foot (Hughes and Hughes, 1981), were only able to attack singly, based on evidence from drill holes (Złotnik and Ceranka, 2005). Multiple drill holes on an echinoid specimen varied slightly in size but were all small and widely spaced, indicating that more than one small cassid, spaced across the echinoid test, was responsible for the drilling. However, large holes drilled by large cassids were almost always found singly. Thus, ontogenetic changes in behavior occurred, which concurs with studies reporting ontogenetic behavioral changes in various Recent drilling gastropods (Berg, 1976; Clements and Rawlings, 2014; Gosselin and Chia, 1996; Urrutia and Navarro, 2001). In the fossil record, Złotnik (2001) also documented ontogenetic changes in naticid behavior in the Miocene of Poland; small naticid drill holes on *Corbula gibba* were less stereotyped in position and more occurred on the left valve, compared to larger drill holes. Likewise, Klompmaker (2012) reported that Pliocene serpulids from the Netherlands were primarily drilled by small naticids, suggesting an ontogenetic change in diet.

Kelley (1988) found that, among Miocene bivalves of Maryland, USA, prey species that displayed the most stereotyped drill-hole positions and greatest prey size selectivity also exhibited higher percentages of successful drill holes. If stereotyped behavior leads to greater success by the predator, it might be expected that stereotypy would increase through deep time. Some evidence exists to support this hypothesis. Shell-drilling naticid and muricid gastropods diversified during the Cretaceous. Taylor et al. (1983) reported a lack of size selectivity of mollusk prey of drilling gastropods in the Albian Blackdown Greensand of England, early in this diversification. Reyment et al. (1987) found that drill-hole size was not correlated with ostracod prey size in the Late Cretaceous (Santonian) of Israel but was strongly correlated in the Paleocene of Nigeria. Also, drill-hole site stereotypy may have been less pronounced during the Cretaceous (Berg, 1978; Kitchell, 1986; but see Kelley and Hansen, 1993, 1996). In addition, cost-benefit analyses of prey selectivity based on the model of Kitchell et al. (1981) were more consistent with drilling frequencies for Neogene than Paleogene assemblages (Kelley and Hansen, 1996, 2003). Hagadorn and Boyajian (1997) found that size selectivity by drilling gastropods on US Coastal Plain specimens of *Turritella*, as indicated by correlations of drill-hole diameter and prey size, increased between the Miocene and Pliocene. However, Paul and Herbert (2014) found decreasing size stereotypy of naticid and muricid predation on Neogene *Chione* bivalves of Florida, USA, as did Dietl and Alexander (2000) for Miocene to Recent confamilial predation on naticids of the mid-Atlantic Coastal Plain, USA.

Some authors have reported an increase in efficiency of predators through time. Babcock (2003) interpreted a decrease in frequency of sublethal scars on trilobites after the Cambrian as indicative of attacks by more efficient predators. Dietl (2003a) found that stereotypy of attack site by shell-chipping *Sinistrofulgur* gastropods on the bivalve *Mercenaria* increased from the Pliocene to Pleistocene of Florida. The increased proportion of attacks at the ventral shell margin of *Mercenaria* was accompanied by a decrease in failed attacks and interpreted as an improvement in the gastropod's predatory efficiency. *Sinistrofulgur* may break its own shell while attempting to chip open prey; truncate-embayed scars occur when the predator prematurely resumes feeding without adequately repairing such breaks (Dietl, 2003a). A Plio-Pleistocene decline in the frequency of truncate-embayed scars on the predator's shell was interpreted as evolutionary change in predator behavior to limit such premature feeding (Dietl, 2003a). For drilling predation, prey effectiveness (proportion of drill holes that are incomplete, i.e., unsuccessful) was assessed for Cretaceous - Quaternary gastropod and bivalve samples from the US Coastal Plain. Although fluctuations occurred among samples, Kelley et al. (2001) found a significant decrease in failed drilling, consistent with an increase in predator efficiency after the Paleogene.

Other reported temporal trends in predatory behavior involve a shift in the position of attack on the prey. For instance, Dietl and Alexander (2000) found drill-hole site shifted to a position closer to the umbilicus in confamilial predation of naticid gastropods from the Miocene to Recent; this position would have prevented egress of the prey's foot. Hagadorn and Boyajian (1997) found that the preferred site for drilling on *Turritella* shifted away from the aperture in the Miocene to Pliocene of the US Coastal Plain, and Mondal et al. (2017) reported that confamilial drill holes in naticids became more randomly positioned after the Oligocene. In many cases a shift in attack site may involve a change of predator, rather than an evolutionary change in behavior within a lineage of predator. Thomas (1976) found that drill-hole positions on bivalves of the *Glycymeris americana* lineage shifted from the umbo in the Miocene to a central position in the Plio-Pleistocene of the US Coastal Plain, which he hypothesized represented either a shift in predatory behavior or predator species. Amano (2006) likewise observed a shift in drill-hole position on *Glycymeris* from Japan between the Miocene and Pleistocene, but different predators were involved. Similar conclusions were reached by Chiba and Sato (2016) for *Glycymeris* in the Pleistocene of Japan; changes in drill-hole site and predator-prey size relationships were linked to the abundance of warm- and cool-climate naticid species. Babcock (2003) noted a shift in position of repair scars on trilobites after the Cambrian, with an increase in the percent of scars on the left side or occurring on both sides of trilobites. He linked these changes to a change in predators, from anomalocarids to the adaptive radiation of cephalopods and fish.

6. Antipredatory features and other defense strategies in deep time

Extant and ancient marine organisms use a variety of active defensive behavioral strategies, such as hiding and active movements once caught (e.g., Harper and Skelton, 1993a; Kohn, 1999), and passive defense strategies, including camouflage, toxicity, shell structure, thickness, and ornamentation. Several authors have summarized the literature about defensive traits and behavior of shelled prey (Brett and Walker, 2002; Harper and Kelley, 2012; Harper and Skelton, 1993a; Kohn, 1999; Vermeij, 1995, 1987; Walker and Brett, 2002; Zuschin et al., 2003), drawing heavily from modern observations. Therefore, we review the types of defenses with a strong focus on studies that include fossils or have implications for the fossil record. Notably, the development of defensive traits, such as the type of coiling and the degree of ornamentation, in response to increased predation intensity is one of the cornerstones of the Mesozoic Marine Revolution and its mid-Paleozoic precursor during which predation intensity is thought to have increased (Signor and Brett, 1984; Vermeij, 1977).

6.1. Active defenses

Active defense strategies (see also Vermeij, 1987) by modern marine prey include mobility (e.g., Baumiller and Messing, 2007), immobilization of predators with byssal threads (e.g., Day et al., 1991; Petraitis, 1987), deep burrowing (e.g., Fregeau, 1991; Visaggi et al., 2013; Walker and

Brett, 2002), hiding on the sea bottom (e.g., Klompmaker and Fraaije, 2012), enrollment (e.g., Babcock, 2003), wounding the feeding apparatus of predators (e.g., Burrell, 1975), active movements to dislodge the predator or avoid being caught (e.g., Edwards, 1969; Laws and Laws, 1972; Pratt, 1974), and autotomy (Baumiller et al., 2008; Oji and Okamoto, 1994). Of those, only mobility, burrowing/hiding, and enrollment may be evaluated in detail for the fossil record.

Prey that are more mobile have a greater chance of escaping predators. Although the absolute speed of prey is difficult to determine from marine body fossils or trackways, whether animals were able to move at all is easier to infer for some fossil taxa. Over the Mesozoic, Gorzelak et al. (2012) found that genus richness of sessile crinoids is negatively correlated with that of predatory sea urchins, whereas a positive correlation was suggested between motile crinoids and predatory sea urchins. They argued that crinoid motility is an effective escape strategy, which is consistent with evidence of crawling by extant and fossil stalked crinoids and the crawling and swimming abilities of comatulid crinoids (Baumiller and Messing, 2007; Brom et al., 2018; Meyer and Macurda, 1977; Neto de Carvalho et al., 2016). A similar conclusion was reached for post-Paleozoic crinoids: the appearance and evolutionary success of motile crinoids starting in the Triassic was suggested to be related to the radiation of echinoid predators with more advanced feeding apparatuses (Baumiller et al., 2010a) or the rise of bony fishes (Meyer and Macurda, 1977). Conversely, motility was not found to be an important factor, explaining drilling frequency for modern bivalves in the Red Sea (Chattopadhyay et al., 2015). On very long time scales, Bambach et al. (2002) documented a proportional increase of motile marine metazoan genera throughout the Phanerozoic, from ~20% in the Cambrian to ~80% in the late Cenozoic.

Some marine organisms may have evolved burrowing behavior to gain access to food within the sediment. However, for some taxa, including filter-feeding siphonate bivalves, the ability to burrow may represent an escape strategy from predators. Burrowing is effective against various predators because crustaceans, fishes, and epifaunal drilling predators have more difficulty in detecting and accessing buried prey. An example from the fossil record (Miocene of the Netherlands) illustrates the effect of depth: Van Schooten (1998) inferred that specimens of the bivalve *Pelecyora polytropa nysti* up to 7 cm in size were drilled by (infaunal) naticid gastropods only in the upper half of the shell in its buried life position. Further evidence is provided by Neogene bivalves from Panama: infaunal bivalves, especially deep burrowers, exhibit relatively low drilling frequencies (Leonard-Pingel and Jackson, 2013, but see Chattopadhyay et al., 2015, for extant bivalves from the Red Sea). Over the course of the Phanerozoic, the proportion of genera interpreted to live infaunally increased from ~5% in the early Cambrian to ~20% in the Cenozoic, with a major rise starting in the Mesozoic (Bush and Bambach, 2011). Burrowing depth has also increased throughout the Phanerozoic (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986; Thayer, 1983).

Enrollment, often interpreted as a defense mechanism against predators or adverse environmental conditions, is found primarily in fossil arthropods such as trilobites (Clarkson and Henry, 1973; Esteve et al., 2011; Ortega-Hernandez et al., 2013), horseshoe crabs (Anderson and Selden, 1997), and isopods (Fraaije et al., in revision). Other enrolled specimens include annelid-like animals from the Cambrian (e.g., Chen and Zhou, 1997; Yang et al., 2014). The best-studied temporal patterns in enrollment (or conglobation) are for trilobites; the percentage of enrolled specimens increased throughout the Paleozoic as trilobite enrollment became more efficient due to skeletal modifications (Esteve et al., 2011, 2017). Differentiating environmentally and predatory-induced enrollment appears difficult, but most enrollments may be environmentally induced by sedimentation events that buried the enrolled specimens, because an attack typically does not bury the prey specimens (see also Brett et al., 2012).

Preventative defense may occur when organisms seek shelter within shells, bore into hard substrates, or live in cryptic habitats. Hermit crabs, which have taken up residency in gastropod and ammonite shells, represent a prime example of such behavior (e.g., Fraaije, 2003; Jagt et al., 2006). Many examples of specimens found in shells are known from the fossil record, including trilobites in Paleozoic brachiopods, hyoliths, nautiloids, and trilobites (Brett, 1977; Davis et al., 2001; Fatka et al., 2009; Fatka and Budil, 2014; Zong et al., 2016); echinoids, bivalves, heteromorph ammonites, and ophiuroids in Mesozoic ammonites (Ernst, 1967; Hagdorn, 1998; Matsumoto and Nihongi, 1979), decapods in Triassic–Miocene cephalopods, echinoids, and bivalves (Fraaije and Pennings, 2006; Fraaye and Jäger, 1995a; Gašparič et al., 2015; Klompmaker and Fraaije, 2012; Landman et al., 2014; Schulz, 2002) (Fig. 14); and fishes in Jurassic–Cretaceous ammonites and inoceramid bivalves (Fraaye and Jäger, 1995b; Nyborg et al., 2014; Stewart, 1990; Vullo et al., 2009), among others. Refuge from predators, including long-term residency (=inquilinism), is a potential reason for the co-occurrences, but it is difficult to exclude other possibilities, such as scavenging upon the decaying soft tissue inside the host's shell; a place to reproduce, die, or molt for arthropods; post-mortem transport into the shell; or even accidental trapping due to shelter closure (e.g., Campbell et al., 1997). The preservation style, motility of the animal inside the shell, relative abundance of the animal outside the shell, sedimentary environment, the frequency of co-occurrence, and modern observations can help to infer the most likely reason for co-occurrence.

Other organisms construct their own domiciles in a variety of hard substrates by embedment or boring (e.g., Tapanila, 2005; Taylor and Wilson, 2003), and, consequently, are fairly well protected against predators. Organisms that create such domiciles include some sponges (e.g., Bromley, 1970; Bromley et al., 1984), bivalves (e.g., Savazzi, 1999), decapods (e.g., Klompmaker et al., 2016b), annelids (e.g., Ishikawa and Kase, 2007; Voigt, 1975), and bryozoans (e.g., Pohowsky, 1978).

Various cryptic habitats provide opportunities to hide from predators. Submarine caves are known from the fossil record, particularly in the Jurassic (Reolid and Molina, 2010; Taylor and Palmer, 1994; Wilson, 1998). Reefs (Kiessling, 2009; Wood, 1999) and seagrasses (e.g., Ivany et al., 1990; Moissette et al., 2007; Reich et al., 2015) are other habitats with an ancient origin in which organisms are likely to seek shelter from predators.

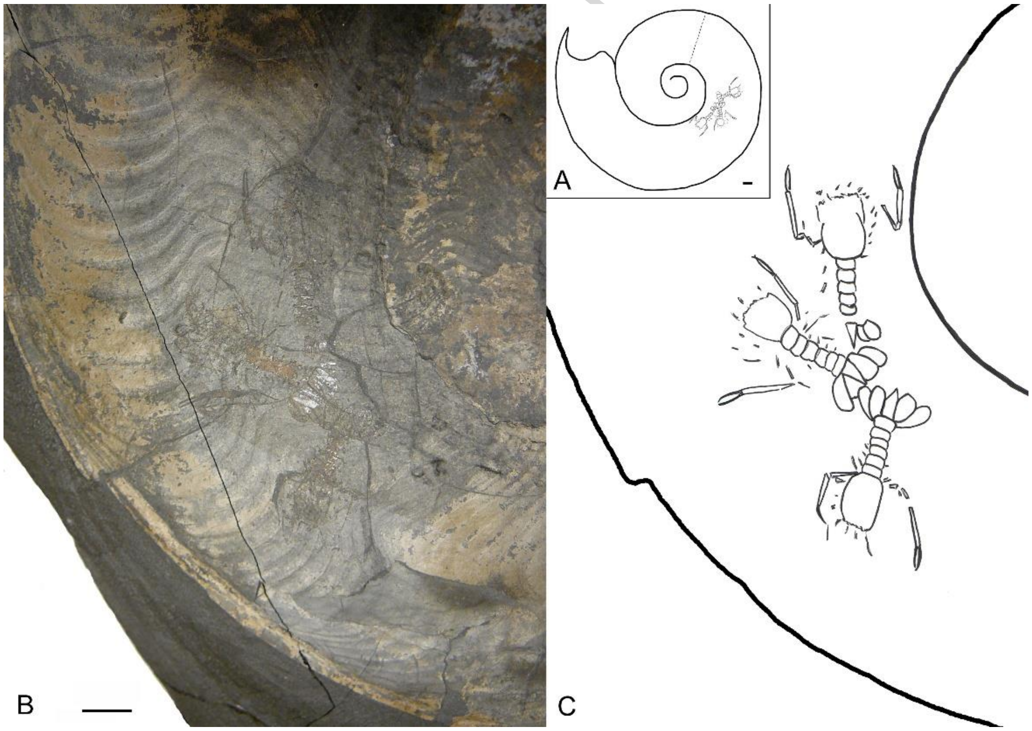

Fig. 14. A compressed specimen of the Early Jurassic (Toarcian) ammonite *Harpoceras falciferum* from Germany with only the translucent periostracum preserved shows three eryonid lobsters within the body chamber. (A) Drawing of entire ammonite specimen with the position of lobsters. (B, C) Photo and drawing of part of the body chamber containing the three lobsters. Scale bar widths: 10 mm. Modified from Klompmaker and Fraaije (2012: figs 3B, 4).

6.2. Passive defenses

Passive defenses are common among shelled organisms and include sculptural features such as ornamentation, thick shells, large size, cementation, certain shell microstructures, shell curvature and shape, size and shape of the aperture, tight shell closure, mimicry of more difficult or dangerous prey (Kohn, 1999), clumping (Casey and Chattopadhyay, 2008; Okamura, 1986), and toxicity/unpalatability (e.g., Thayer, 1985; Thayer and Allmon, 1990; Tyler et al., 2013). In contrast to more active methods of defense, most of the passive defense strategies have been studied to some extent in the fossil record (except for mimicry, clumping, and toxicity/unpalatability, which are not discussed further here).

Shell sculpture includes spines, ribs, nodes, varices, corrugations, and buttresses. The effectiveness against predation varies among features and with the type and strength of the predator. Paleontological studies have evaluated the effectiveness of ornamentation in deterring predators for some prey and time intervals. For example, moderate ribs of Cenozoic bivalves were most effective against drilling predation by naticid gastropods (Klompmaker and Kelley, 2015), Late Cretaceous ribbed oysters have a higher repair scar frequency from unsuccessful attacks by shell-breaking predators than unornamented ones (Dietl et al., 2000), and drill holes were less common in ornamented gastropods from the Eocene (Arua and Hoque, 1987). For cephalopods, Jurassic ammonites that are smooth have more incised injuries than ornamented ones (Kröger, 2002), whereas more ornamented Jurassic and Cretaceous ammonites showed fewer repair scars (Kerr and Kelley, 2015). Brachiopods with lamellae were less frequently drilled than smooth congenerics in the Devonian (Leighton, 2003b) and drill holes in a Devonian brachiopod with spines had a lower success rate than those in a morphologically similar taxon without spines (Leighton, 2001). Finally, for arthropods, Santonian and Paleocene ornamented ostracods were suggested to have a lower drilling percentage than smooth ones (Reyment et al., 1987, but see Villegas-Martín et al., 2019) and enlarged thoracic spines in Cambrian trilobites may have served as a protection against durophagous predators (Pates and Bicknell, 2019).

Although the effectiveness of ornamentation against several types of predation has been demonstrated in deep time, few studies have addressed whether ornamentation evolved in response to predators (evolutionary adaptation), whether it was co-opted (exaptation sensu Gould and Vrba, 1982), or whether it is due to phenotypic plasticity / inducible defense (e.g., Appleton and Palmer, 1988; Sherker et al., 2017). For example, exaptation to drilling was inferred for ribs in astartid bivalves because ribs appeared within the lineage before drilling became common (Klompmaker and Kelley, 2015). The same reasoning was applied to spines in some bivalves (Stone, 1998) and ribs in Jurassic–Cretaceous nautiloids (Bardhan and Halder, 2000). Conversely, ribbing was suggested to be adaptive within lineages of gryphaeid oysters (Dietl et al., 2000).

Various paleontological studies have suggested an increase in ornamentation through geological time for gastropods (Alexander and Dietl, 2003; Dietl and Alexander, 1998; Vermeij, 1987), ammonites (Ward, 1981, but see Kerr and Kelley, 2015), nautiloids (Bardhan and Halder, 2000), brachiopods (Alexander, 1990), some crinoids (Syverson et al., 2018), and Paleozoic invertebrates in general (Signor and Brett, 1984). Often, predation pressure has been hypothesized to be the causal mechanism for such trends, but much testing remains to be done on other groups, on different time intervals, and within specific lineages. An important caveat is that shell sculpture may not necessarily be defensive but serve other functions. For example, Tyler et al. (2014) demonstrated in laboratory experiments that limpet prey with stronger sculpture experienced higher mortality from crabs and suggested that enhanced sculpture primarily served to mitigate against thermal stress, and not as anti-predatory defense. Another study suggested that large spines on the epifaunal bivalve *Spondylus* promote epibiont coverage and not necessarily deter predators (Carlson Jones, 2003). Thus, it is important that we do not automatically assume that all ribs, spines, and other ornamental structures perform an anti-predator function. Fossil prey taxa should be tested on a case-by-case basis without making any *a priori* assumptions about the role of ornamentation.

Shell thickness is positively correlated with shell strength, and thicker shells are more difficult and/or time-consuming to break or drill (Alexander, 1990; Carriker, 1951; Kelley and Hansen, 2003; Kitchell et al., 1981; Kohn, 1999; Zuschin et al., 2003). Thus, an increase in shell thickness is one of the most effective ways to deter predators. Drilling is indeed more likely for thinner shells for infaunal reef bivalves (Martinelli et al., 2016). Several studies have suggested an active role for predation in shell thickening. A Plio-Pleistocene increase in thickness of a single species of bivalve in Florida was suggested to be in response to predators and/or warmer temperature (Roopnarine and Beussink, 1999). In more detailed studies, Miocene bivalves that suffered the highest drilling frequencies experienced the largest increase in shell thickness over the course of 3 million years, leading to a reduction in drilling (Kelley, 1989, 1991b). Similarly, shell thickness increases in other Neogene bivalves were accompanied by an increase in incomplete drilling (Kent cited by Vermeij, 1987, p. 311). Furthermore, some bivalve prey increased in thickness during the Eocene-Oligocene, while naticid drillers did not respond with offensive adaptations (Kelley and Hansen, 2001). Longer-term trends in shell thickness through time are difficult to obtain due to diagenetic processes dissolving all or part of the shell layers (Harper and Skelton, 1993a).

As specimens grow, shell thickness typically increases, but specimens also may reach a size beyond which they become too difficult to manipulate by a given-sized predator (a size refugium, also termed size refuge or escape size; see Kelley, 1991b; Leighton, 2002) (Fig. 15). Size refugia have been demonstrated in the fossil record, as shown for repair scars in Late Ordovician and Devonian brachiopods (Alexander, 1986a; Johnsen et al., 2013; Richards and Leighton, 2012), drill holes in Devonian brachiopods (Sheehan and Lesperance, 1978), repair scars in Middle Ordovician endocerid cephalopods (Kröger, 2011), drill holes in Neogene bivalves (Grey et al., 2006; Leonard-Pingel and Jackson, 2013), and drill holes in Cretaceous and Cenozoic turritellid gastropods (Allmon et al., 1990; Mallick et al., 2013). Another type of proposed size refuge is an increase in the proportion of failed drilling attempts for larger size classes, which was documented for Eocene brachiopods (Schimmel et al., 2012) and Pliocene gastropods (Martinell et al., 2010). However, this lower success rate does not necessarily imply increased safety from predators, because successful predation intensity for large specimens may still be comparable to or greater than that for smaller size classes when larger specimens are attacked more frequently (see for example Schimmel et al., 2012). Additionally, a prey that has reached a size refuge from one type of predator may become more attractive to a different predator.

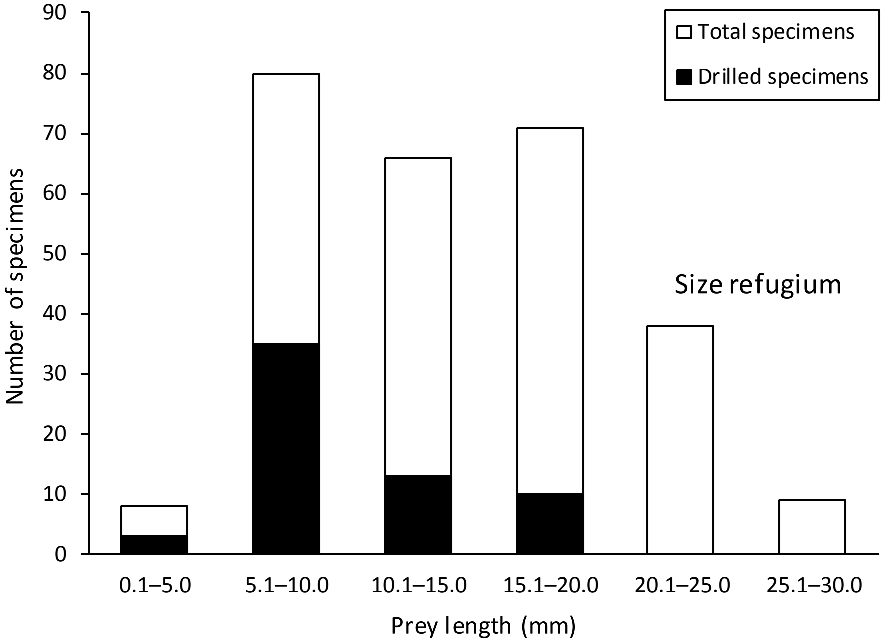

Fig. 15. Example of a size refugium against drilling predation reached at 20 mm shell length by the late Maastrichtian gastropod *Bellifusus* aff. *indicus* from India. Data from Mallick et al. (2014).

Cementation of bivalves has been shown experimentally to be effective against predation by crabs and starfish, as it inhibits manipulation (Harper, 1991). The same paper suggested a causal link between the rise of cementing bivalves and increased predation pressure in the Mesozoic. Conversely, cementation is not effective against drilling by epifaunal drillers that do not manipulate their prey (such as Muricidae), as shown by the higher drilling frequencies in modern and Neogene cementing bivalves (Leonard-Pingel and Jackson, 2013; Sawyer and Zuschin, 2010). Another group of cementing organisms, barnacles, is also drilled primarily by muricids in the Cretaceous–Cenozoic, albeit at assemblage-level percentages of < 10%

(Klompmaker et al., 2015). Cementation also occurred among fossil brachiopods and annelids (Alexander, 2001; Walker and Brett, 2002), but the extent to which it was effective against predation is unknown.

Shell microstructure greatly influences shell strength against predation (Alexander and Dietl, 2003; Zuschin et al., 2003, and references). Of all microstructural types, a nacreous microstructure with an organic matrix appears to be the strongest structure and one of the oldest (Furuhashi et al., 2009; Vendrasco et al., 2010; Zuschin et al., 2003). Indeed, organic content enhances shell strength, but the metabolic cost to produce organics can be 20 times greater than for calcium carbonate (Palmer, 1992). Several examples show the importance of organic material in deterring predation. Epifaunal mussels with a thick periostracum are less prone to drilling by muricids than are mussels from which this organic layer was removed (Harper and Skelton, 1993b), but whether the periostracum evolved as an adaptation to drilling remains unclear as periostraca do not preserve well in the fossil record. So-called conchiolin (organic) sheets or layers, present within some bivalves, are effective against drilling in modern and fossil corbulids (De Cauwer, 1985; Harper, 1994; Kardon, 1998; Kelley, 1988; Klompmaker, 2009; Lewy and Samtleben, 1979) and fossil lucinids (Ishikawa and Kase, 2007). Such layers are also thought to inhibit crack propagation (Kardon, 1998). Whether conchiolin layers are an adaptation (Harper, 1994), an exaptation (Ishikawa and Kase, 2007; Kardon, 1998), serve a function other than anti-predatory (Anderson, 1992; Anderson et al., 1991), or are an artifact of construction (Walker and Brett, 2002) requires further testing.

Shell curvature and general shape affect predation success (e.g., Alexander and Dietl, 2003; Kohn, 1999; Vermeij, 1978; Zuschin et al., 2003). Examples of anti-predatory functions are known from the fossil record: biconvex brachiopods show lower repair scar frequencies than concavo-convex shells (Alexander, 1986a; Forcino et al., 2017); Jurassic ammonites with rounded whorls are suggested to be less susceptible to predatory attacks (Kröger, 2002); and open and planispiral coiling and the presence of umbilica in gastropods decreased through time, trends that were linked to increased predation (e.g., Signor and Brett, 1984; Vermeij, 1987).

Various strategies are used to protect the shell openings of coiled taxa such as gastropods and cephalopods. Apertures have narrowed through time for gastropods (Vermeij, 1987). For serpenticone ammonites, common in the Mesozoic (Parent et al., 2010), small apertures relative to the total body size provided better protection against apertural attacks than relatively large apertures (Kröger, 2002). Some gastropods developed an operculum that closes the aperture (e.g., Bandel, 2008; Kaim and Sztajner, 2005; Norton, 1988) (Fig. 16). Opercula or opercula-like structures apparently evolved independently at least thirteen times in gastropods (Vermeij and Williams, 2007) and are known from the Early Ordovician onward (Yochelson, 1979). Gastropod opercula are effective against predators; 40% of gastropods with an operculum that were ingested whole by fishes survived the digestive tract (Norton, 1988). Opercular thickness of turbinid gastropods is greater in the tropics, where predation pressure is thought to be higher (Vermeij and Williams, 2007). Opercula are also known from Cambrian Mobergellidae (Topper and Skovsted, 2017) and fossil nautiloids (e.g., Dzik, 1981; Edgecombe and Chatterton, 1987). Considerable debate has arisen about the function of ammonite aptychi and anaptychi (summarized in Parent et al., 2014). Although aptychi are considered to have functioned mainly as lower jaws, many workers have suggested an anti-predatory function as well (e.g., Keupp et al., 2016; Lehmann and Kulicki, 1990; Parent et al., 2014; Seilacher, 1993; Tanabe et al., 2015).

Tight closure of bivalved animals (ostracods, bivalves, and brachiopods) is one of the main defense mechanisms to avoid leakage of chemical cues for predators, to remain intact when ingested, and to avoid breakage of the shell margin (Vermeij, 1983, 1987). A globose shell, as seen in some bivalves and brachiopods, helps prevent shell breakage at the commissure (Vermeij, 1983). Vermeij (1987: table 11.3) showed that the incidence of crenulated and overlapping valve margins of bivalves increased throughout the Phanerozoic, and crenulated margins occur more frequently in the more dangerous tropics. Alexander (1986a) hypothesized that a commissural ridge in some Ordovician brachiopods evolved in response to predation. Counterintuitively, the proportion of bivalves with vulnerable gaping margins has increased through time, but most such bivalves burrow deeply and thus are well protected from most predators (Alexander and Dietl, 2003; Vermeij, 1987).

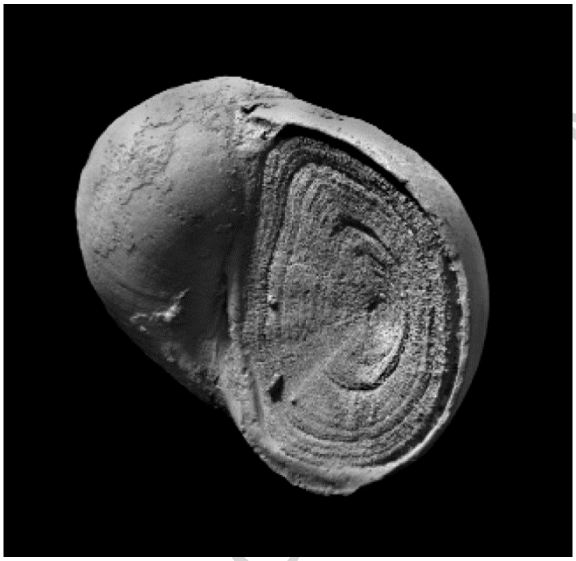

Fig. 16. An operculum still in situ in the Late Triassic gastropod *Fedaiella neritacea* from Italy. Shell height ~22 mm. From Bandel (2008: pl. 1.12).

7. Conclusions and future directions

Research on predation in the marine fossil record started around the mid-19th century, but the topic did not receive much attention until the 1960s, after which a substantial increase in literature is recorded that continues to date. Studies that have contributed to this field include neontological experiments, ecological observations, and paleontological analyses of predation. In addition to documenting some predation traces from less commonly studied prey types, localities, and geologic periods, recent studies also focused on testing hypotheses or validating specific predictions of evolutionary paleoecology. The fossil record of predation in ancient marine ecosystems is dominated by trace fossils, particularly drill holes and, to a lesser extent, repair scars. Mollusks are the clade most often studied as prey and inferred predators, with most data thus far deriving from the Cenozoic of Europe and North America. More work is needed on types of predation other than drilling and shell crushing, taxa other than mollusks, and evidence of predation from understudied regions and pre-Cretaceous times. Additionally, documentation of whole assemblages for which predation intensity appears low is important to better assess temporal trends in predation intensity.

Any analysis of predator-prey interactions requires proper recognition of these interactions. Correcting for abiotic damage is necessary to calculate predatory breakage intensity more accurately; we propose 12 criteria for distinguishing between biotic and abiotic shell damage. We further identify 16 criteria to differentiate predatory from parasitic traces, particularly for drill holes. When a predatory event has been confirmed, the identity of the predator can be pursued. We find that studies focused on gut contents and predatory attacks preserved in place identify predators to the genus- or species-levels more frequently than is the case for other indicators of predation. Taphonomic and other factors can distort the recognition of patterns of predation and should be evaluated cautiously before drawing conclusions about the occurrence and intensity of predator-prey interactions. Many such factors can be identified and accounted for by following specific protocols, but more research is needed.

More work is also required to develop general principles for understanding how predation varies among environments. Factors that affect predation, including taxonomic composition of communities, prey life modes, and predator foraging strategies, vary with water depth and depositional environment, but patterns are not straightforward. Studies of predation in the marine fossil record must take habitat into account. Oxygen, temperature, and ocean acidification are known to affect predator-prey interactions in modern marine ecosystems, but their role in shaping predator-prey interactions through geologic time is currently understudied. The relationship between predation intensity and primary production in today's oceans is still unresolved.

The behavior of predators and prey defense have been studied more thoroughly. The marine fossil record preserves evidence of subjugation, and to a lesser extent search and pursuit, behaviors of predators, including prey selectivity and handling behaviors. Changes in prey behavioral stereotypy and efficiency have occurred through time. Two broad categories of prey defense, active and passive defenses, have been studied in the fossil record with varying levels of detail. These defenses include mobility, burrowing/hiding, enrollment, ornamentation, shell thickness, size, cementation, shell microstructure, shell curvature and shape, size and shape of the aperture, and shell closure. Future research could investigate whether these defenses evolved in response to predation (adaptation) or whether they developed for a different purpose but were subsequently co-opted to serve as anti-predatory features (exaptation).

Acknowledgments

We are very grateful to reviewers Carlton Brett (University of Cincinnati) and Martin Zuschin (University of Vienna) for their useful comments, and managing editor André Strasser (Université de Fribourg) for editorial input. We thank Seth Finnegan (University of California, Berkeley) for discussing outlines of review papers and publishers/editors for permission to reuse of images. The Paleobiology Database (https://paleobiodb.org) was consulted for some age ranges in Table 2; we acknowledge all contributors. This is Paleobiology Database publication #....

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