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# Seals, whales and the Cenozoic decline of nautiloid cephalopods

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## Abstract

**Aim:** *Nautilus* and *Allonautilus*, last members of the once widespread nautiloid cephalopods, are today restricted to the deep central Indo-West Pacific Ocean, for reasons that remain unclear. Cephalopod evolution is generally considered as being driven by vertebrate predation; therefore, we investigated the role of whales and seals in the decline of nautiloids through the Cenozoic.

**Location:** Global.

**Taxon:** Nautiloids, pinnipeds, cetaceans.

**Methods:** Distribution data for nautiloids, pinnipeds and cetaceans through the Cenozoic were compiled and plotted on a series of paleogeographic maps. Nautiloid shell sizes were compiled and plotted against the first appearance of pinnipeds and cetaceans in key regions.

**Results:** From the Oligocene onward, nautiloids became extinct in areas where pinnipeds appeared. The exception is the agile nautiloid *Aturia*, extinct globally at the end of the Miocene. A major role of odontocetes in the demise of nautiloids is not apparent, except for a few brevirostrine Oligocene taxa from the North American Atlantic and Pacific coasts, which appeared in these areas at the same time as nautilids disappeared. The Oligocene disappearance of nautiloids (except *Aturia*) from the American Pacific coasts coincides with the development of oxygen minimum zones (OMZs) in this region.

**Main conclusions:** We hypothesize that the Cenozoic spread of pinnipeds drove nautiloids into their present-day central Indo-West Pacific refuge. Additional factors for the local extinction of nautiloids in the Oligocene include predation by short-snouted whales and the development of OMZs, preventing nautiloids from retreating into deeper water.

**KEYWORDS**
deep-sea, extinction, living fossils, marine mammals, *Nautilus*, oxygen minimum zones, predator-driven evolution

## 1 | INTRODUCTION

Cephalopods are a prime example of predator-driven evolution. The coiling of their shells was considered an adaptation by Paleozoic nautiloids and ammonoids to avoid predation by other large cephalopods and early gnathostome fishes (Kröger, 2005; Mapes & Chaffin, 2003, and references therein), and strong sculpture with a deep living chamber in Mesozoic ammonites were seen as adaptations against shell-breaking predators (Keupp, 2006; Kröger, 2002). The internalization of the shell, high mobility and ink sack of Mesozoic belemnites and modern coleoid cephalopods are regarded as a means to avoid predation by fast-swimming ray-finned fishes (Klug et al., 2016, 2019; Tanner et al., 2017). Other than human fisheries and octopods, surprisingly little is known about potential predators of nautilids, but the present-day restriction of nautilids to deeper water is considered as an escape from predatory teleosts (Ward, 1987; Ward, Dooley, et al., 2016). *Nautilus* and *Allonautilus* are regarded as "Living Fossils" (but see [Casane & Laurenti, 2013; Ward, 1984] for discussions of this term) because they are the last survivors of the entire cephalopod order Nautilida, which had its heyday in the Ordovician and has since shown a steady decline in diversity (Combosch et al., 2017; Kummel, 1956; Simpson, 1953). Although the fossil history of the genus *Nautilus* and the number of its extant species are still a matter of debate (Goedert et al., 2022), they seem to have a large population size and even show signs of an ongoing diversification (Bonacum et al., 2011; Combosch et al., 2017; Huang et al., 2022). However, the restriction of nautilids to the central Indo-West Pacific Ocean remains unexplained. Here, we hypothesize that the radiation of pinnipeds (walruses, seals and sea lions) during the Neogene played a major role in shaping the present-day distribution of nautilids (Figure 1) and their demise everywhere else.

## 2 | MATERIALS AND METHODS

Basic stratigraphic and geographic distribution data for the Nautiloidea are from the Paleobiology Database (https://paleobiodb.org/). They were updated with new records and with improved taxonomic and



**FIGURE 1** Approximate present-day distributions of nautilids (red; data from Saunders et al., 2017) and pinnipeds (blue; data from Würsig et al., 2018). Mollweide projection.

**SIGNIFICANCE STATEMENT**
The iconic 'living fossil' Nautilus occurs mainly in the deep tropical Indo-West Pacific Ocean. The fossil record indicates that this restriction from a once worldwide distribution was largely driven by the Cenozoic spread of seals, highlighting the role of vertebrate predation in the evolution of cephalopods.

stratigraphic information through a comprehensive literature survey, particularly for regions and time intervals where nautiloid and pinniped occurrences overlapped. Among nautiloid data, we separated the genus *Aturia* (Table S1) from the remaining nautiloids (Table S2), because it stands out with its compressed, thin shell, complex suture line, and distinct reproductive strategy (Laptikhovsky et al., 2013; Miller, 1949). In contrast, the remaining nautiloids share more globular, thick shells with simple suture lines, and furthermore, the assignment of Cenozoic nautiloid specimens to the various genera remains contentious (Goedert et al., 2022; Ward, Flannery, et al., 2016). Nautiloid size data are taken from the original publications (and should be considered minimum if specimens are lacking the living chamber [see Miller, 1949]). Basic stratigraphic and geographic distribution data for pinnipeds are from Deméré et al. (2003) and were updated through a comprehensive literature survey (Table S3). The regional first occurrences of cetaceans are listed in Table S4.

## 3 | RESULTS

Late Eocene to Pleistocene distributions of nautiloids (nautilids: N = 46, *Aturia*: N = 203) and pinnipeds (N = 185) are shown in Figure 2. By Oligocene time, nautiloids (except *Aturia*) had disappeared completely from the shores of the American continents. From the late Oligocene onward, nautiloids (except *Aturia*) became extinct locally when pinnipeds appeared in that region. *Aturia* was common and widespread until the middle Miocene, but in the late Miocene it was less common and largely restricted to extra-tropical, mid-latitude areas (Figure 2). The Oligocene appearance of brevirostrine, or short-snouted, odontocetes on the Atlantic and Pacific coasts of North America coincides with the disappearance of nautiloids (except *Aturia*) from these regions.

The only exception to the regional extirpation of nautiloids with the appearance of pinnipeds is the eastern North Atlantic/ Mediterranean Region in the early to middle Miocene, with the coeval, early Miocene records of the pinniped *Noriphoca gaudini* from Italy and the nautilid *Eutrephoceras dubaleni* from Saubrigues on the Atlantic coast of southwestern France. However, the two records are from rather different environments and subregions: Saubrigues hosts deep-water deposits from a deeply incised paleocanyon open to the Atlantic Ocean (Cahuzac & Poignant, 2002), the pinniped is from shallow-marine carbonates in the Mediterranean Sea (Dewaele et al., 2018). This leaves the possibility that encounters between the two taxa were unlikely. Likewise, the other potential
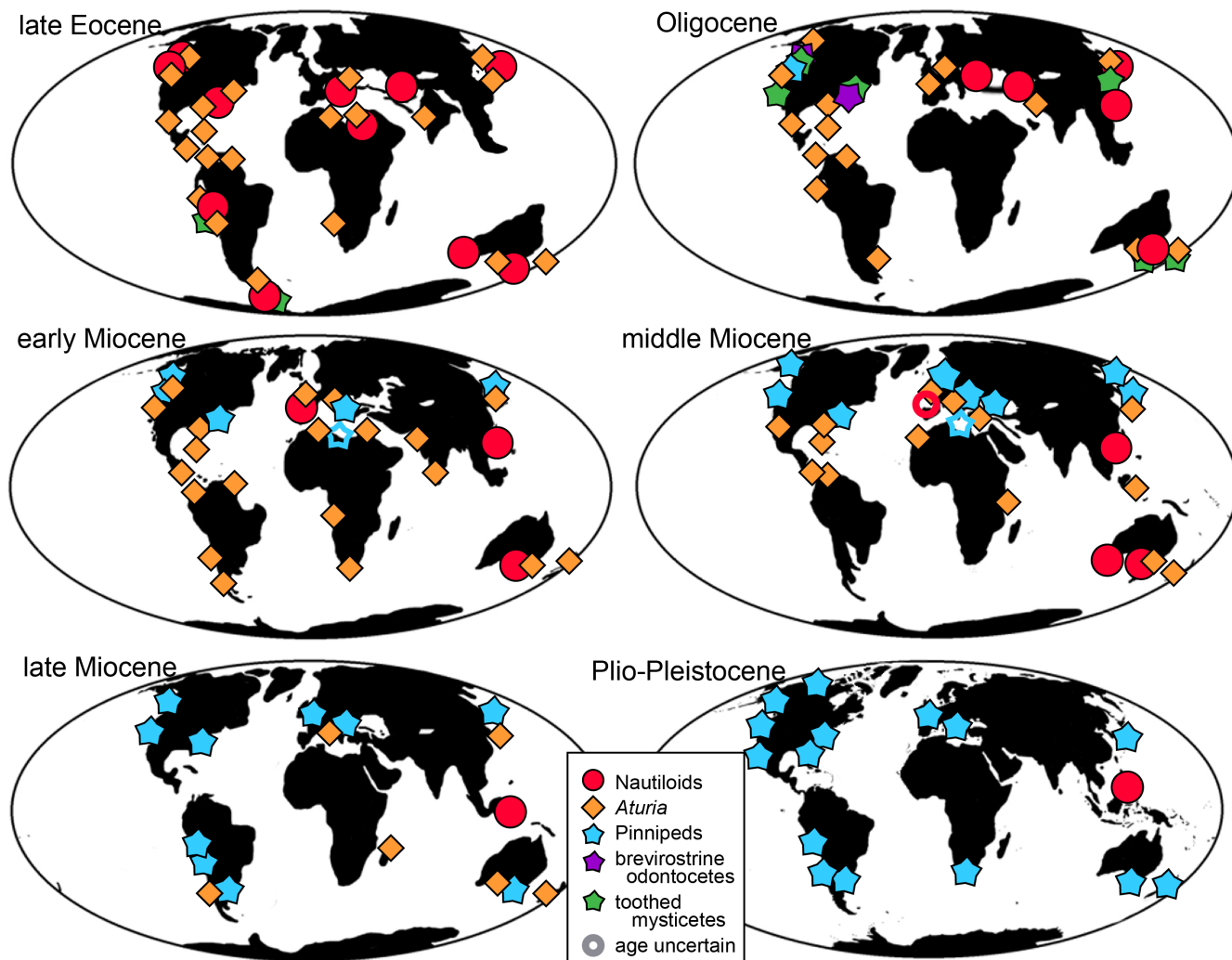
**FIGURE 2** The global late Eocene to Pleistocene distributions of nautilids, *Aturia*, pinnipeds, brevirostrine odontocetes and toothed mysticetes. See the text for the explanation of uncertain ages. Maps (Mollweide projections) updated from Deméré et al. (2003).

early Miocene pinniped record (*Afrophoca libyca* Koretsky and Domning (2014) from Libya) was reported from shallow-marine strata of the Mediterranean Sea, and furthermore, its stratigraphic age is uncertain. It has a provisional age from Burdigalian to Langhian (ca. 19–14 Ma, Koretsky & Domning, 2014), but the actual fossil-bearing strata (Jabal Zaltan deposits) were not dated; the age is based on nearby outcrops of the same formation, and it was noted that those "deposits differ in facies and possibly in age" from the deposits containing the pinniped (Koretsky & Domning, 2014, p. 224). Also uncertain is the age of the potential middle Miocene nautilid from Saubrigues that was originally considered as late Miocene (Peyrot, 1933). But those strata are now dated as early to middle Miocene (Cahuzac & Poignant, 2002) and the species is thus recorded in the PBDB as being present in the middle Miocene. However, the exact locality, and hence age, for the specimen that Peyrot (1933) referred to is unknown.

Nautiloid maximum shell sizes and geochronologic ranges of cetaceans and pinnipeds from the Paleocene to the Pleistocene are shown in Figure 3. The maximum shell size of nautiloids (except *Aturia*) often decreases with the appearance of the earliest whales, archaeocetes,

specifically Basilosauridae, although this pattern is not global; in some regions the size decrease is neither immediate nor particularly large. In contrast, the appearance of toothed mysticetes often coincides with a notable decrease in maximum shell size among nautiloids (except *Aturia*) to 100 mm or smaller. *Aturia* reached its maximum shell size at different times in different ocean basins: in the late Eocene in the Atlantic Ocean and the Indo-West Pacific region, and in the Oligocene in the western Pacific region. The latter includes the largest Cenozoic nautiloid: *Aturia yokoyamai* from the early Oligocene of Japan, which exceeded 700 mm diameter (Nishida & Aoki, 1984). The maximum shell size of *Aturia* typically decreased with the appearance of pinnipeds, but it does not become locally extinct (Figures 2 and 3). Prior to its extinction, late Miocene *Aturia* rarely exceeded 75 mm in maximum diameter.

## 4 | DISCUSSION

Our interpretations and hypotheses focus on the disappearance/absence of nautilids from certain areas, raising the question whether the observed lack of nautilid fossils is real or potentially a taphonomic
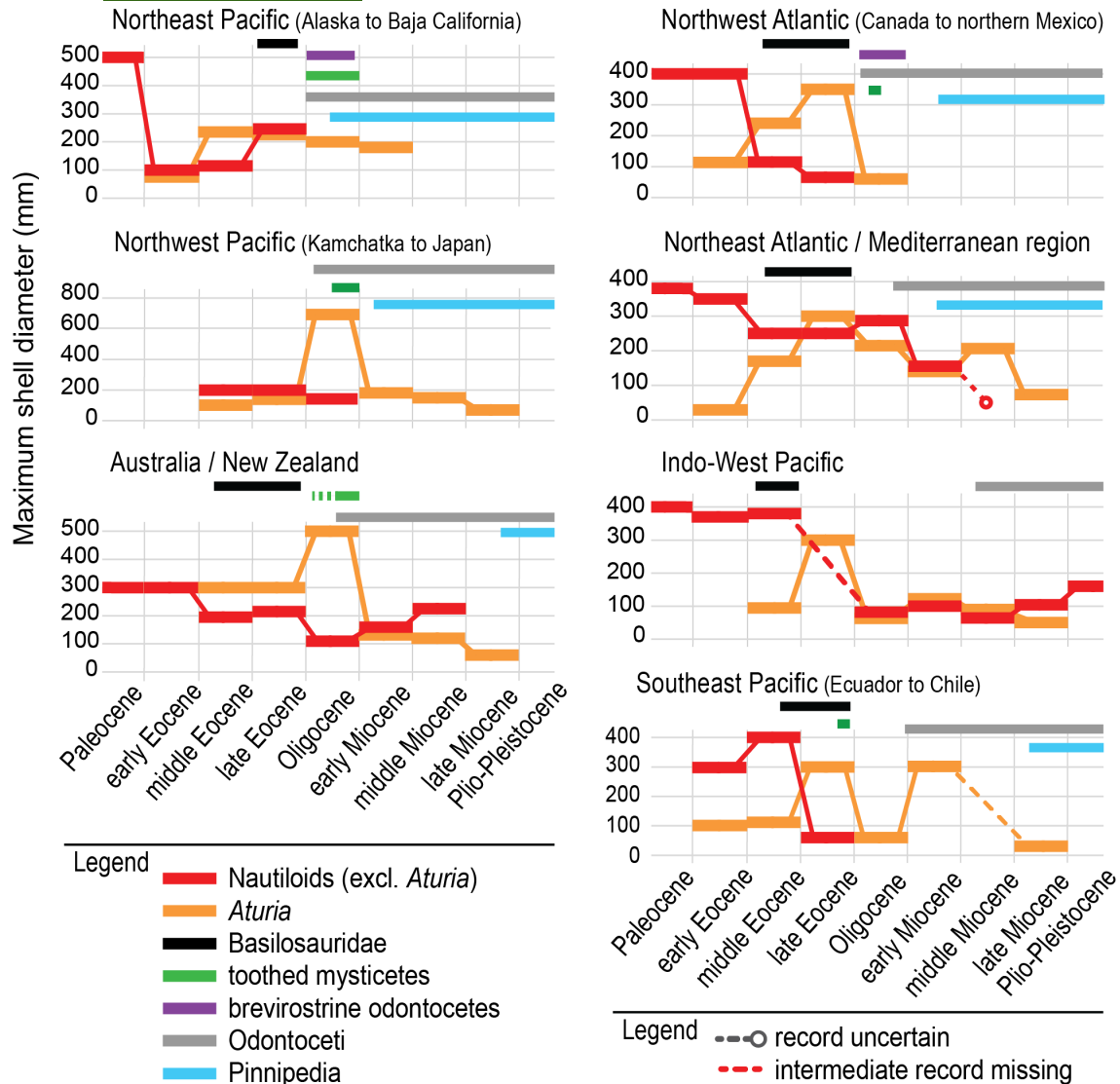
**FIGURE 3** Eocene to Pleistocene maximum shell sizes of nautilids and *Aturia*, and the geologic ranges of pinnipeds and cetaceans, in key regions.

bias. As Figure 2 shows, *Aturia* was still present in the areas from which nautilids had disappeared. This argues against a taphonomic bias because the shells of nautilids and *Aturia* have basically identical properties such as form, function and mineralogy.

Nektonic marine vertebrates are regarded as key antagonists towards cephalopods throughout their evolution (Tajika et al., 2018; Tanner et al., 2017). The first fully marine mammalian predators to evolve in the Cenozoic were cetaceans, with the basilosaurids being the most widespread (Uhen, 2018). Dental enamel microwear indicates that the basilosaurid diet resembled that of pinnipeds and included shelled molluscs (Fahlke et al., 2013). Thus, basilosaurids may have preyed on shelled cephalopods, but this did not affect nautiloid evolution. Odontocetes, which hunt using echolocation, were considered well-suited for preying on nautiloids because the solid, gas-filled nautiloid shells should reflect sound better than soft-bodied cephalopods (Lindberg & Pyenson, 2007); however, some early odontocetes could not echolocate (Racicot et al., 2019). Others were macrophagous predators

that likely would not prey upon something as small as a contemporary nautiloid (Boessenecker et al., 2020), or had long, slender rostra with numerous teeth (Boessenecker et al., 2020; Geisler et al., 2014; Lambert et al., 2019) and we find it unlikely that they could extract a nautiloid from its shell or crush a nautiloid conch effectively. Indeed, our compilation indicates that the appearance of odontocetes did not lead to the immediate local extinction of nautilids or *Aturia* (Figure 3).

Remarkable exceptions include brevirostrine Oligocene odontocetes, simocetids in the northeast Pacific Ocean (Fordyce, 2002; Vélez-Juarbe, 2017) and perhaps agorophiids (Godfrey et al., 2016) in the northwest Atlantic Ocean. Their relatively short rostra are typically seen as an adaptation to suction-feeding (Fordyce, 2002; Werth, 2006). Although nautilids and odontocetes co-occur in the present-day tropical West-Pacific, there is thus far no evidence that odontocetes feed on nautilids (Würsig et al., 2018). However, simocetid and agorophiid odontocetes had heterodont dentitions that included robust, strongly serrated teeth that could have been

well-suited for preying on shelled nautiloids by snapping at their arms, crushing the living chamber, and perhaps subsequent vigorous shaking on the sea surface. The appearance of simocetids in the northeast Pacific and agorophiids in the northwest Atlantic Oceans coincides with the disappearance of nautiloids (except *Aturia*) in these regions and could thus have contributed to their local extinction.

The appearance of toothed mysticetes coincides with the local extinction of nautilids only in areas where brevirostrine odontocetes have been found; in the other areas it coincides with a notable size decrease among nautilids. Some toothed mysticetes were of relatively large size, with heterodont dentitions comprised of large serrate molars, premolars and incisors coupled with wide rostra, but these have been assumed to be adaptations for filter feeding (Geisler et al., 2017; and references therein), implying less selectivity in choice of individual prey items. Consequently, they probably did not process captured prey to any great degree, which would be necessary for larger nautiloids. However, we cannot exclude that some small-bodied toothed mysticetes, like Aetiocetidae in the late Oligocene of the North Pacific, may have specialized in small-sized *Aturia* which sometimes abound in the same strata. Some Mesozoic nautiloid and ammonite shells have punctures made by the teeth of marine reptiles (Kauffman & Sawdo, 2013; and references therein). We have not found any descriptions or illustrations of such traces of predation in the many reports of Cenozoic nautiloids that we surveyed during this study. This could indicate that despite their similar dentition, the early cetaceans did not employ this kind of durophagous predation, supporting our assumption that cetaceans had only a minor impact on nautiloid evolution.

A potential implication of these observations is that the broader disparity of cranial morphologies among early odontocetes (Churchill et al., 2018) might have resulted from niche partitioning that exploited a broader diversity of prey, similar to the early toothed mysticete whales (Tsai & Ando, 2016). Given the wide spectrum of skull morphology (including brevirostrine and longirostrine or toothed and toothless) and feeding strategies (such as raptorial, bottom-feeding, suction-feeding and filter-feeding) during the explosive radiation of early odontocetes and mysticetes (Churchill et al., 2018), the intense competition should have driven the possibility of feeding on shelled cephalopods, but extant cetaceans are not known to prey on nautilids. Feeding on shelled cephalopods seems to require the more elaborate prey processing ability that pinnipeds, not cetaceans, possess. Still, our compilation shows that odontocetes or mysticetes (especially brevirostrine morphotypes), while expanding their ecological niches and exploring evolutionary possibilities at the early stage, possibly caused some regional extinctions of shelled cephalopods.

From the Oligocene onward and thus coincident with the rise of pinnipeds, the nautiloids went extinct locally when pinnipeds appeared in that region (Figures 2 and 3). Most extant pinnipeds are generalist feeders employing a "pierce-feeding" technique that involves catching prey using sharp, homodont teeth (Jones et al., 2013), but some employ suction or process prey more completely at the water surface by vigorous shaking (Hocking et al., 2021; Marshall et al., 2015). An analogous feeding strategy is inferred for basal

Oligocene and Miocene pinnipeds based on their cranial and dental morphology (Adam & Berta, 2001; Churchill & Clementz, 2015; Jones et al., 2013). Slow-moving and largely defenceless nautilids such as extant *Nautilus* (Saunders et al., 1987) would have been easy targets for predators like the agile early pinnipeds. Furthermore, pinnipeds have more complex prey processing habits than odontocetes (Würsig et al., 2018) and hence we expect their impact on nautiloid evolution and survival to be greater than that of odontocetes. Importantly, once nautiloids were extinct in areas otherwise favourable for their survival, the presence of pinnipeds after Oligocene time would have prevented nautiloids from ever recolonizing those areas.

The impact of mammalian predation was probably more severe for the nautilids than for *Aturia* due to (i) their low reproductive rates compared to *Aturia* and coleoid cephalopods (Laptikhovsky et al., 2013; Rocha et al., 2001), and (ii) their limited lateral dispersal capabilities, because nautilids move only along the seafloor but not across open water (Ward, 1987). Therefore, we consider predation by pinnipeds and brevirostrine odontocetes to have been a major driver of the local extinction of nautilids.

Another factor might have been upwelling. The present-day distribution area of *Nautilus* is remarkably free of upwelling (Kämpf & Chapman, 2016). Upwelling typically results in local oxygen minimum zones (OMZs) in water depths of 50–1500 m (Helly & Levin, 2004). Such OMZs would prevent *Nautilus* from retreating into the depth it requires to escape predation. Thus, the enhanced ocean circulation and associated upwelling around the Eocene–Oligocene transition (Miller et al., 2009) could have led to the local extinction of nautiloids (except *Aturia*), especially along the Pacific Coast of South America.

Somewhat puzzling in this context is the Caribbean region. It appears to offer a setting suitable for nautiloids—tropical archipelagoes with scleractinian reefs in close proximity to deep ocean basins, and lacking pinnipeds save for the late Pleistocene monk seal (Rule et al., 2020)—yet, there are no records of nautiloids (except *Aturia*) from this area after the middle Eocene (Table S2). Notably, the uplift of the core of the present Antilles started after the Middle Eocene and reached its peak during the Eocene–Oligocene transition (Iturralde-Vinent, 2006), so that deep-marine connections from the Caribbean region to the Atlantic Ocean were limited, but open to the Pacific. Thus, nutrient-rich and/or oxygen-limited waters from the deeper Pacific might have entered the Caribbean region and affected the nautilids living there. A similar argument of upwelling-related changes was made about Oligocene to Neogene fish and coral communities in the Caribbean region (Aguilera & de Aguilera, 2001; Edinger & Risk, 1994), but these events post-date the late Eocene disappearance of nautiloids from the Caribbean region. The absence of nautilids from the American Pacific coasts and dispersal barriers between the Caribbean region and the European Tethys, such as temperature and depths (as outlined for cuttlefish, cf., Young et al., 1998), could have prevented nautilids from re-colonizing the Caribbean region after their late Eocene disappearance.

Temperature has been put forward as an important factor controlling nautilid distribution, in particular when explaining their

appearance in the Antarctic Peninsula during the Eocene greenhouse period (Dzik & Gaździcki, 2001). Thus, one might argue that the post-Eocene contraction of the distribution area of nautiloids is largely related to temperature. However, we consider this unlikely because it is inconsistent with their scarcity and early disappearance from the Caribbean region, and with their largely extra-tropical (but warm-temperate) distribution during the Oligocene-middle Miocene, despite the presence of *Aturia* in tropical regions during this time (Figure 2).

If pinnipeds played a role in the demise of *Aturia*, it was initially not as lethal as suggested here for the nautilids. *Aturia* was a fast swimmer with a rapid reproductive cycle (Chirat, 2001; Laptikhovsky et al., 2013; Ward, 1980). This might have enabled *Aturia* to withstand predation pressure by pinnipeds and other predators, at least temporarily. The overall decrease in shell size of *Aturia* from the Oligocene onward (Figure 3) might provide insights in this context. It should be noted, though, that the sizes given here are a mixed bag of juveniles, adults, and specimens with or without living chamber. However, assuming that the overall trend is real (Kobayashi & Inoue, 1961; Miller, 1949), it could also have been a response to increased predation pressure by marine mammals, as suggested here for nautilids and toothed mysticetes. The arms of a large-sized *Aturia* could have been an easy target for a fast-moving marine mammals, especially those with a bite-and-shake feeding strategy. This type of attack was likely more difficult and offered less nutrients in return in the case of small-sized *Aturia*. A potential disadvantage of not reaching larger size might have been that it made *Aturia* more vulnerable to other predators such as fishes.

The extinction of *Aturia* at the end of the Miocene had been attributed the global cooling of surface waters due to intensified circulation around Antarctica (Beu, 1990). This was based on the perception of *Aturia* as a warm-water genus living mostly in tropical-subtropical settings (Beu, 1990; Chirat, 2000). However, that view has been questioned due to findings of juvenile individuals outside the tropical realm (Kurihara, 2019; Schlögl et al., 2011) and of abundant and well-preserved *Aturia* shells in higher, colder latitudes (Kurihara, 2019; Nielsen et al., 2009). Our compilations show that after the middle Miocene, *Aturia* occurred mainly in extra-tropical, mid-latitude areas without upwelling, and consisted of small-sized individuals (Figures 2 and 3). We propose a new hypothesis to explain why *Aturia*—but not *Nautilus*—became extinct by the end of the Miocene. While *Aturia* is typically considered to have lived at around 100 to 350 m water depth (Moore, 1984; Schlögl et al., 2011; Westermann, 1999), *Nautilus* is able to retreat to much greater depth (Dunstan et al., 2011). Thus, the increased predation pressure that that *Nautilus* could escape in deeper water ultimately caused the extinction of *Aturia*, because *Aturia*'s adaptation to a light-weight, thin shell (Miller, 1949) did not allow it to retreat to such great depth.

## 5 | CONCLUSIONS

Our study emphasizes the prominent role of nektonic vertebrates in the evolution of cephalopods (Tanner et al., 2017). It also highlights that quick local extermination of organisms defenceless against the arrival of new predators, as known for example from flightless birds on oceanic islands (Duncan et al., 2013; and references therein), are also possible in the vast marine realm with a perhaps only seemingly broad range of refuges, such as the deep ocean. It was indicated that extant *Nautilus* might have been undergoing a period of evolutionary radiation throughout deeper waters in the western Indo-Pacific region since the Miocene, and therefore a bright future for the coming few million years was predicted (Bonacum et al., 2011; Combosch et al., 2017). Our analysis indicates that nautilids could potentially be driven to extinction if pinnipeds manage to radiate into the tropical Indo-West Pacific Ocean in the coming million years. However, human fisheries (Dunstan et al., 2010) are a more immediate threat to nautilids because of the same factors that made nautilids so vulnerable to predation by pinnipeds—low reproductive rate, limited escape response and slow lateral migration.

## DATA AVAILABILITY STATEMENT

All data related to this article are available in the online supplement (Tables S1–S4).

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**BIOSKETCH**

**Steffen Kiel** is an invertebrate paleontologist with an interest in evolution and its drivers on geologic timescales. He studies mainly marine molluscs, with a focus on deep-sea ecosystems and interactions with the evolution of marine mammals.

**Author contributions:** All authors developed the ideas and interpretations, and assembled the datasets; S.K. wrote most of the manuscript and prepared the illustrations, with input from J.L.G and C.H.T. All authors read and approved the final manuscript, and they declare no conflict of interest.

**SUPPORTING INFORMATION**

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