The influence of reefs on the rise of Mesozoic marine crustaceans

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ABSTRACT

Ecosystems changed dramatically during the Mesozoic marine revolution, including the rise of decapod crustaceans such as lobsters, shrimp, true crabs, and squat lobsters. However, quantitative patterns of decapod biodiversity through geological time are virtually unknown. This hampers our understanding of their importance in past ecosystems and timing and causes of their radiations and extinctions. Based on our compilation of ~1300 Mesozoic decapod species, we document a long-term shift in diversity of dominant groups, marked by the first appearance and increasing presence of true crabs and, to a lesser extent, squat lobsters. By the end of the Mesozoic, true crabs became the primary contributor to decapod diversity, a pattern that has persisted until the present time. This "Mesozoic decapod revolution" was advanced by a major radiation of reef-dwelling crabs, which coincided with a dramatic expansion of reefs in the Late Jurassic. The subsequent collapse of reefs near the end of the Jurassic was mirrored by a sharp (albeit temporary) drop in decapod diversity driven primarily by extinctions of numerous species of crabs. This concurrent decline also suggests that decapods inhabiting reefs, especially obligatory reef dwellers, may face elevated extinction risks today as reef ecosystems continue to deteriorate. The reef-related diversification of Late Jurassic decapods and the significant correlation between decapod diversity and reef abundance throughout the Mesozoic underscore the macroevolutionary importance of biotic interactions and ecosystem engineering.

INTRODUCTION

Today, ~15,000 species of decapods are known (De Grave et al., 2009), representing an important commercial food resource and the most diverse order of crustaceans including crabs, shrimp, crayfish, and lobsters (Martin et al., 2009; Matzen da Silva et al., 2011). The decapod groups that dominate today first became ecologically relevant in the Mesozoic Era (252–66 m.y. ago), when shrimp and lobsters radiated, and Brachyura (true crabs) and Anomura (including hermit crabs and squat lobsters) originated and diversified. Our knowledge of their fossil record has been growing rapidly in recent years. As of 2010, nearly 3300 decapod species have been documented from the Phanerozoic (Schweitzer et al., 2010), providing an opportunity for examining large-scale secular trends in their evolutionary history because robust quantitative studies on decapod diversity are lacking.

We document a major reorganization in dominant decapod groups during the Mesozoic, a process accentuated by a rapid diversification of Brachyura during the Late Jurassic when reef ecosystems expanded. Subsequently, brachyuran diversity dropped in concert with the collapse of reefs. By the end of the Mesozoic, the Brachyura became the most diverse decapod group, a *status quo* that has persisted through today.

METHODS

Literature records of body fossils of marine Mesozoic decapod crustaceans were assembled into a database consisting of stage-level, presence-absence records for 110 families, 378 genera, and 1298 species (Appendix DR1 in the GSA Data Repository[1]). Due to the relatively low fossilization potential of decapods (e.g., Kidwell and Flessa, 1995), singletons (taxa restricted to single time intervals) dominate, and presence-absence data instead of occurrences are recorded for each stratigraphic stage. The compilation also includes assignment of species to preferred sedimentary facies: "siliciclastics," "reef-associated limestones," and "other." The definition of reefs follows Kiessling and Flügel (2002). Previously published estimates of Mesozoic changes in sea level (Golonka and Kiessling, 2002) and reef abundance (Kiessling, 2002) were used to construct comparative multistage time series and assess pairwise Spearman's rank correlations between compared time series for raw and detrended data (first differences). In addition, multiple tallying and corrective strategies were employed to assess methodological volatility of the results, evaluate the impact of singletons, and minimize biases induced by variable sampling intensity, including variation in stage duration and the amount of rock available for sampling. Corresponding genus-level curves were constructed based on the intermediate, species-level data sets (Fig. DR1 in the Data Repository). Diversity curves were corrected (1) for

the unequal duration of stages by standardizing per 5 m.y. per epoch, and (2) by standardizing per 100 formations per epoch to minimize the combined effects of the stage duration, the unequal preservation of rocks, and geographic collecting biases.

RESULTS

Species-level and genus-level diversity curves (Fig. 1), corrected for marine rock outcrop area (number of taxa per 100 formations) or stage duration (number of taxa per 5 m.y.; Fig. DR2), consistently indicate that decapod diversity was relatively low in the Triassic. Shrimp and lobsters dominated then and the first anomurans and caridean shrimp appeared. The earliest brachyurans are known from the Early Jurassic. Diversification accelerated during the Late Jurassic, especially at the species level (Fig. 1). Diversity dropped sharply near the end of the Jurassic, a decline that is more pronounced at the species level than at the genus level. The discrepancies between species- and genus-level results are due to an elevated species-to-genus ratio in the Late Jurassic (Fig. DR3). Of all decapod taxa recorded in the latest Jurassic (Tithonian), 66% (53/80) of genera and 27% (10/37) of families went extinct. In total, 28% (12/43) of the Late Jurassic (Oxfordian–Tithonian) families did not survive into the Cretaceous (in contrast, 21% of the families went extinct during the Late Cretaceous; Schweitzer and Feldmann, 2005). Rediversification took place in the mid- to Late Cretaceous. Over the entire Mesozoic, a long-term shift took place: lobsters and shrimp dominated in the Paleozoic and Triassic, whereas Anomura and especially Brachyura became increasingly diverse starting in the Jurassic (Fig. 1). The trends remain comparable regardless of applied corrections, tallying strategies, and taxonomic level (Fig. 1; Figs. DR1 and DR2; Table DR1).

The Mesozoic changes in decapods occurred during a time of major fluctuations in sea level (e.g., Golonka and Kiessling, 2002) and reef abundance (Kiessling, 2002, 2009). After binning the data into three-stage time intervals to obtain a sufficient sample size of at least 20 taxa per interval, species- and genus-level decapod diversity curves standardized for number of formations correlate significantly with reef abundance, both for raw and detrended data (Fig. 2A; Table 1). In contrast, changes in sea level correlate with decapod diversity for raw data only (Fig. 2B; Table 1). Data standardized using stage durations yield comparable results (Table DR2).
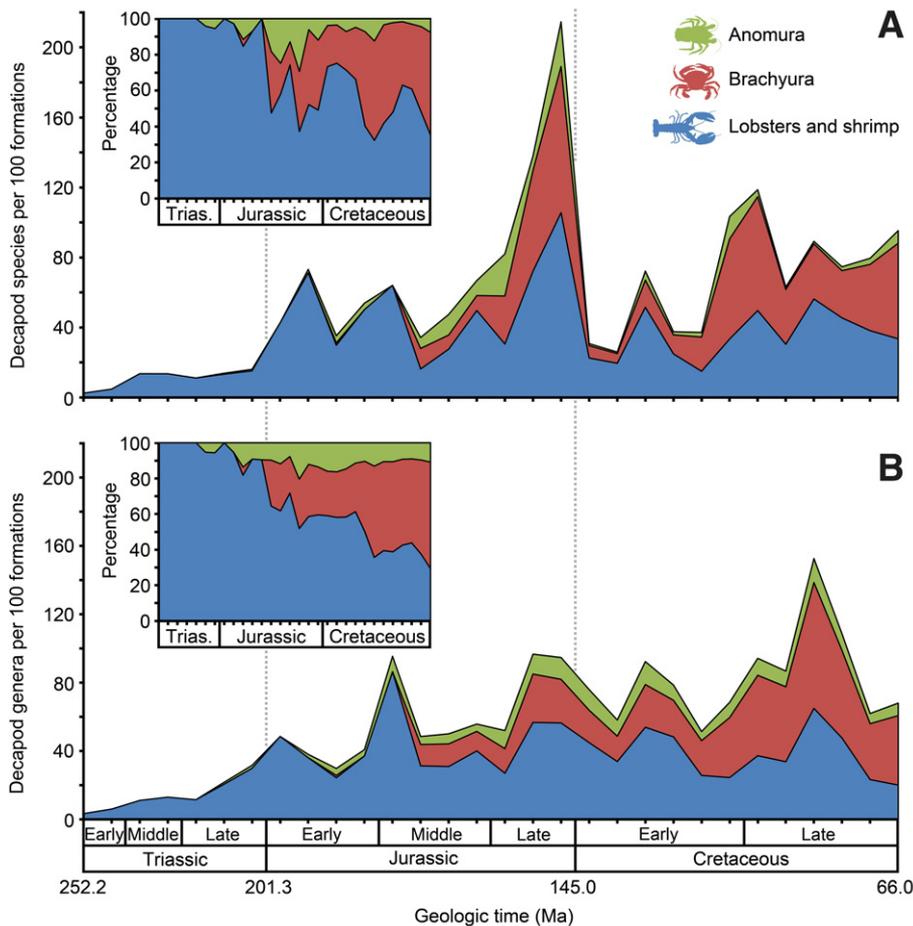
Figure 1. Mesozoic decapod diversity standardized per 100 formations for each stage. A: Species-level diversity. B: Genus-level diversity. Insets highlight proportional changes in relative dominance of different decapod groups through time.

affected the diversity patterns. The effects of time-variant sampling intensity were minimized using two applicable corrective strategies, which yielded congruent results (Table 1; Fig. DR2; Table DR2). Changes in lithification and lithification-related specimen acquisition methods are trivial because the Mesozoic is dominated by lithified rocks (Hendy, 2011), including decapod-bearing strata. Preferential preservation of decapods in Late Jurassic Lagerstätten created a localized diversity anomaly (Fig. 3A). However, correlations between decapod diversity and reef abundance remain significant after excluding these data (Table DR4), and the post-Jurassic diversity loss remains severe as well. Moreover, removal of Lagerstätten decapods eliminates the diversity peak for non-reef dwellers (lobsters and shrimp), but not for brachyurans and anomurans (Fig. 3D). Other decapod-specific biases, including biases due to the incompleteness of the decapod record, differential fossilization potential, and collecting biases (relatively more collecting in Europe and North America) may have affected the data, but they are unlikely to have been responsible for the large-scale trends. For example, shrimp are relatively abundant in reefs today (Abele, 1976), yet are rarely preserved in Mesozoic reefs, suggesting that the Late Jurassic peak might be suppressed. Also, the use of the number of formations is expected to minimize regional variations in collecting efforts (Peters and Foote, 2001). The results are further supported by the fact that disparate metrics (diversity, species-to-genus ratios, and facies distribution patterns), which likely vary in bias sensitivity, all point to

The correlation is congruent with results of local to regional studies in modern (Abele, 1976) and ancient ecosystems (e.g., Krobicki and Zatoń, 2008; Klompmaker, 2013; Klompmaker et al., 2013), which indicate that decapod diversity is elevated in reefs. Our results suggest that this relationship may scale up to evolutionary time scales, as qualitatively hypothesized previously (Glaessner, 1969; Förster, 1985).
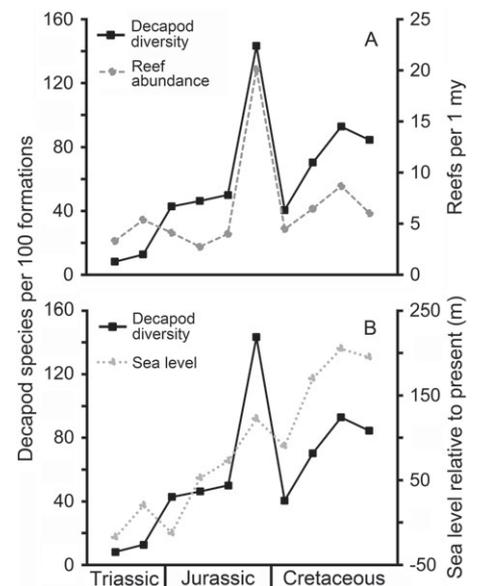
If decapod diversity is causally linked to reef abundance, then many reef-associated decapods should be found in the Late Jurassic when reefs expanded dramatically (Kiessling, 2009). Our analyses indeed indicate that the Late Jurassic decapod radiation was primarily driven by their expansion into reef-associated facies (Fig. 3A), due primarily to diversification of reef-dwelling brachyuran and, to a lesser extent, anomuran species (Figs. 3B and 3C). Genus-level analyses document comparable patterns (Fig. DR4). Moreover, Late Jurassic Brachyura and Anomura are characterized by a high percentage of genus originations in reef settings (27% [46/169] and 42% [18/43], respectively) despite the fact that, even at the time of their Late Jurassic expansion, reefs were unlikely to

represent more than a tiny fraction of marine environments; today, reefs occupy <0.1% of all oceanic habitats (Kiessling and Heiss, 2011). A considerable percentage of other Phanerozoic marine invertebrates also originated in reefs (Kiessling et al., 2010). In contrast to brachyurans and anomurans, lobsters and shrimp are rare in Mesozoic reefs (Fig. 3D) and only 4% (6/153) of their genera originated there. A similar pattern is also observed today: brachyurans and anomurans are diverse in reefs, but lobsters are not (Serène, 1972; Abele, 1976). The high decapod diversity in Mesozoic reefs may have been due to elevated speciation rates as reef-associated decapod genera contained significantly more species than non-reef genera (Fig. DR5; Table DR3). The absence of a Late Triassic peak in decapod diversity (Fig. 1) despite an acme in reef abundance (Kiessling, 2009) is explained by the fact that brachyurans had not evolved yet and anomurans had just originated.

DISCUSSION

Common biases of large-scale patterns in the fossil record (e.g., Raup, 1972; Kowalewski et al., 2006) are unlikely to have substantially

Figure 2. Decapod species-level data plotted at three-stage resolution compared to reef abundance (A) and sea-level changes (B). Data for reefs from Kiessling (2002), and for sea level from Golonka and Kiessling (2002).

	Raw data		First differences	
	Reefs	Sea level	Reefs	Sea level
Species	$r_s = 0.709$	$r_s = 0.830$	$r_s = 0.783$	$r_s = 0.343$
	$p = 0.011*$	$p = 0.001*$	$p = 0.006*$	$p = 0.183$
Genera	$r_s = 0.745$	$r_s = 0.927$	$r_s = 0.683$	$r_s = -0.033$
	$p = 0.007*$	$p = 0.0001*$	$p = 0.021*$	$p = 0.466$

Note: Significant one-tailed tests are also significant when the more conservative two-tailed tests are applied.
*Denotes statistically significant p-values at the 5% level.

a correlation between the evolutionary histories of Mesozoic decapods and reefs.

The results support previous notions, based on either qualitative (Förster, 1985) or limited quantitative (Sepkoski, 2000) data, that the Mesozoic was a pivotal time in decapod evolution. Only four decapod species are known from the pre-Mesozoic record (Bachmayer and Malzahn, 1983; Feldmann and Schweitzer, 2010), compared to ~1300 recorded from the Mesozoic, when species-rich clades populating modern oceans originated (Brachyura, Anomura, and Caridea). Also, Mesozoic decapods invaded new environments such as reefs and deeper waters (Glaessner, 1969), developed a burrowing lifestyle (Förster, 1985), and evolved durophagous predatory strategies (Dietl and Vega, 2008; Schweitzer and Feldmann, 2010). Finally, the diversity partitioning across major groups of modern decapods may have been already established by the end of the Mesozoic. The combined percentage of latest Cretaceous (Maastrichtian)

decapods represented by brachyuran and anomuran species (65%) is nearly identical to, and statistically indistinguishable from, the value for modern oceans (63%; De Grave et al., 2009) ($\chi^2 = 0.09$, p = 0.76). This Mesozoic decapod revolution, an important part of a major reorganization of marine metazoans during the Mesozoic Marine Revolution (Vermeij, 1977), includes the Late Jurassic radiation in reefs, but also the subsequent, less dramatic rediversification in a variety of the Cretaceous habitats (Fig. 3). Quantitative diversity patterns of other marine crustaceans are less resolved, but Sepkoski (2000) suggested that ostracodes rediversified in the Mesozoic and that barnacles radiated in the Late Jurassic.

The correlatives between the evolutionary histories of reefs and decapods highlight the importance of biotic interactions as a macroevolutionary force, which remains a contested issue (e.g., Jablonski, 2008). The decapod radiation may represent an example of "ecosystem engineering" (e.g., Jones et al., 1994; Erwin, 2008): the expansion of reef ecospace enabled decapod diversification dominated by the brachyuran and anomuran newcomers. As is the case today, Mesozoic reefs likely provided an effective habitat for shelter and foraging and may have facilitated decapod speciation (Fig. DR5), as suggested for modern decapods (Malay and Paulay, 2009).

The sharp decline in diversity of brachyuran and anomuran species following the collapse of Late Jurassic reefs foretells extinction vulnerability of present-day reef decapods. Today, a substantial part of their biodiversity is associated with coral reefs, and many species are obligatorily associates (Serène, 1972; Poupin, 2012). Modern reefs are declining due to ocean acidification, diseases, and other natural and anthropogenic causes (e.g., Hoegh-Guldberg et al., 2007; De'ath et al., 2012). By the end of this century many corals may disappear (Hoegh-Guldberg et al., 2007) and as much as 20% of reef habitats may vanish within 20–40 yr (Wilkinson, 2008). The severe diversity loss of decapods following the contraction of Late Jurassic reefs suggests that decapods, especially those obligatorily associated with reefs, face elevated extinction risks as the present-day reefs continue to deteriorate. This underscores the importance of reef conservation.

CONCLUSIONS

The fossil record of decapod crustaceans suggests that a major diversification of these marine arthropods took place in the Mesozoic. Concurrently, dominant decapod groups shifted due to an ascendency of brachyurans and, to a lesser extent, anomurans. These changes were accelerated by the Late Jurassic radiation of reef-dwelling decapods with elevated species-to-genus ratios and increased origination rates. The diversification coincided with reef expansion and was followed by a severe diversity loss
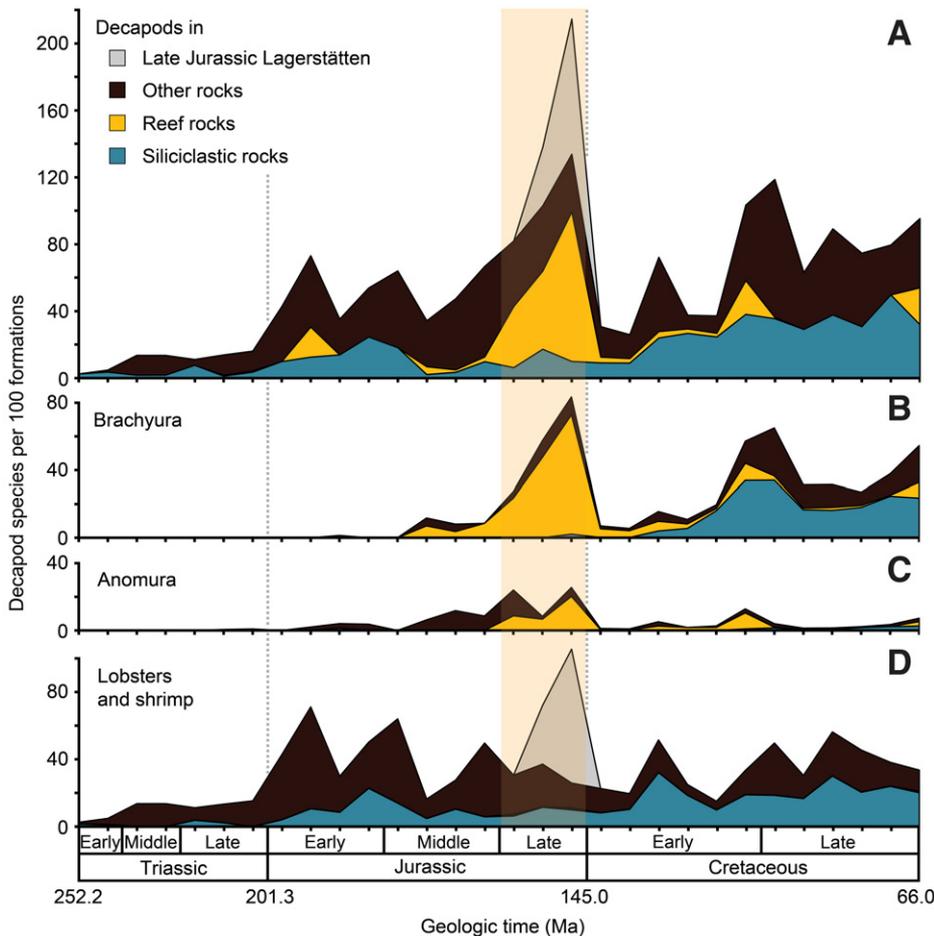

Figure 3. Stage-level decapod species diversity standardized per number of formations with data partitioned by sedimentary facies and different decapod groups (B–D). Orange shaded bar highlights the high diversities in the Late Jurassic. Secondary peaks (in gray) represent inclusion of data from Late Jurassic lithographic limestones.

as reefs contracted, suggesting that reefs may act as ecosystem engineers over evolutionary time scales. The modern reef decline may lead to severe losses in decapod biodiversity, with long-term macroevolutionary consequences.

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