Palaeogeography, Palaeoclimatology, Palaeoecology 374 (2013) 256–273

Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

How to explain a decapod crustacean diversity hotspot in a mid-Cretaceous coral reef

Adiël A. Klompmaker [a,b,*], Joseph D. Ortiz [a], Neil A. Wells [a]

[a] Department of Geology, Kent State University, 221 McGilvrey Hall, Kent, OH 44242, USA
[b] Florida Museum of Natural History, University of Florida, 1659 Museum Road, Gainesville, FL 32611, USA

ARTICLE INFO

Article history:
Received 4 October 2012
Received in revised form 27 January 2013
Accepted 31 January 2013
Available online 8 February 2013

Keywords:
Albian
Cretaceous
Decapoda
Paleoecology
Coral reef
Diversity

ABSTRACT

The mid-Cretaceous (late Albian) decapod crustacean fauna from the Koskobilo quarry in Spain is the most diverse decapod fauna known thus far from the Cretaceous. This may be related to the coral reef environment in which these decapods were found within the Aldoirar patch reef. This diversity hotspot was further investigated by a detailed paleoecological study focusing on variation in lithology throughout the quarry using carbonate rock hand samples, thin sections, and acetate peels; and by studying decapod-rich sites within the quarry. The northern and stratigraphically oldest part of the Koskobilo quarry contained mostly wackestones and biomicrites, the middle to southern part contained floatstones and biosparites or biomicrites with many sponge remains, whereas the southernmost and stratigraphically youngest part consisted of coral-rich boundstones and biolithites. Fossils were more abundant and generally larger in the southern part of the quarry. Decapod-rich sites were restricted to the southern part of the quarry, possibly in part because of an increased possibility for shelter and food in a coral-rich area in the southernmost part of the quarry. Water depth was estimated to be between 20 and 80 m for at least the southern part, with energy levels apparently increasing from the northern to the southern part of the quarry. Systematic collecting was performed at four decapod-rich sites in the quarry to investigate differences in decapod diversity, composition, and size (width). The decapod fauna from the site within the coral-rich boundstones and biolithites appears to be the most diverse based on several diversity measures, has a statistically different faunal composition, contains species that were not found in other parts of the quarry, and consists of smaller decapods compared to other sites. More specimens of species with a smaller maximum width were found here as well as fewer specimens with a large maximum width. Smaller, presumed juvenile specimens of the crab *Goniodromites laevis* were also excavated here. This shows that decapod size can vary within a reef. Paguroids (hermit crabs) were mostly restricted to this coral-rich site. Some of the many decapods at this site may have been obligatory associates with the mostly branching corals. One site within the floatstone and biosparite zone contained hardly any decapods, which may be related to the abundance of hard-to-eat corallinacean red algae. A site in the Olazagutía quarry in the same patch reef consisting of massive colonial corals did not yield any decapods, presumably because of the inaccessible nature of the coral framestone leaving few places as shelter for decapods. The results suggest that different decapod sub- and microenvironments existed within this patch reef, thereby explaining at least in part the high diversity of decapods known from the Koskobilo quarry. This is one of the first times that a detailed paleoecological study has been performed for decapods in a fossilized coral reef. These results concur with modern reefs in that decapod communities also differ among subenvironments. The methodologies introduced herein for studying fossil decapods in reef environments can be used as well to study the paleoecology of decapods as well as other invertebrates from other periods in Earth's history.

1. Introduction

Both extant and fossil decapods have exhibited a preference for reef habitats, showing them to be important coral-reef inhabitants. Examples of decapod-rich faunas associated with corals from the fossil record are known from the Miocene of Malta (Gatt and De Angeli, 2010), the Eocene of Hungary (Müller and Collins, 1991), the Paleocene (Danian) of Denmark (Jakobsen and Collins, 1997), the Late Cretaceous (Maastrichtian) of the Netherlands (Collins et al., 1995; Leloux, 1999), and the Late Jurassic (Tithonian) of the Czech Republic and Austria (e.g., Robins, 2008; Schweitzer and Feldmann, 2008, 2009a,b; Robins et al., 2013). Diverse decapod faunas are also known from the Late Jurassic (Oxfordian) sponge-microbial reefs of Poland (Collins and Wierzbowski, 1985; Müller et al., 2000; Krobicki and Zatoń, 2008) and the Late Jurassic of Germany (Wehner, 1988; Müller et al., 2000), although the number of species is lower compared to faunas found in coral reefs. This link between a high number of decapod taxa and reefs is further supported by Fraaije (2003a) and Müller (2004), who qualitatively suggested that reef-associated fossil decapods show a

---

[*] Corresponding author at: Florida Museum of Natural History, University of Florida, 1659 Museum Road, Gainesville, FL 32611, USA. Tel.: +1 352 273 1942; fax: +1 330 672 7949.

E-mail address: adielklompmaker@gmail.com (A.A. Klompmaker).

0031-0182/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.palaeo.2013.01.024

higher diversity than those living in other habitats. Coral reefs also provide preferred habitats for many extant decapods. Abele (1974, 1976) found that decapods were especially diverse in a subtidal *Pocillopora* coral community and in a rocky intertidal habitat in Panama, part of which consisted of *Porites* corals. In addition, he noted that the number of decapod species increased with increasing complexity of the habitat; that is, with more substrates in a certain habitat (Abele, 1974). Abele (1979) also suggested that 80–96% of all macrofaunal specimens and 76–89% of all species associated with live *Pocillopora* coral heads off the Pacific coast of Panama were decapods. Austin et al. (1980) found similar results for coral heads of *Pocillopora damicornis* in the Great Barrier Reef as Crustacea, predominantly Decapoda, comprised 72% of the species and 86% of the individuals on the coral heads.

Studies on extant decapods have provided a variety of ecological knowledge concerning decapods in coral reef habitats. Decapods use reefs for numerous purposes including as a place of shelter, as a feeding site, and as a source of nutrition (Abele, 1974). A coral reef contains different sub- and microenvironments, such as in between coral branches, on the corals, distal to the corals themselves in unprotected parts of the reef, etc. Grajal and Laughlin (1984) noted that shelters may not only be used as resting places, but the commensal brachyuran *Domecia acanthophora* Desbonne and Schramm, 1867 also uses them for reproduction and brood care. Many of the decapod species associated with the Great Barrier Reef in Australia appear to be obligatory associates with the branching coral *Acropora* by virtue of the fact that they live on the coral (Patton, 1994), whereas facultative associates (ones that can live in other habitats as well) were usually absent from the coral heads. The same author also noted that the spaces between the branches contained decapods.

Decapod communities are known to differ within extant reef environments (e.g., Thomassin, 1974; Martínez Iglesias and García Raso, 1999). Different subenvironments may favor slightly different decapod communities within the reefs, thereby in part explaining the high decapod biodiversity of reefs in general. For example, Martínez Iglesias and García Raso (1999) found that decapod species richness was higher in the lagoon and on the slope than on the reef flat based on three Cuban reefs. This low diversity on the reef flat was explained by higher hydrodynamics and a lower diversity of substrates related to fewer coral species. The decapod communities in these subenvironments consisted of a combination of exclusive species and shared species but differing in abundance per subenvironment. Interestingly, Edwards and Emberton (1980) found that the number of decapod specimens and species on the coral *Stylophora pistillata* was greater in reef flats than in the smaller, deeper water colonies, which was, in part, attributed to the higher openness of the coral branches in deeper waters in the Red Sea. Here, they argued, fishes would be better able to enter the coral complex and prey upon the decapods. These observations are consistent with the ecological "species-sorting hypothesis", which postulates that diversity is related to environmental gradients and thus the density of niches within a given region (e.g., Whittaker, 1962, 1972; Leibold et al., 2004). Similar results have been found for arthropods in tropical rainforest environments relative to adjacent non-rainforest sites (Basset et al., 2012), the only other type of environment known to rival the diversity found in reef environments.

The goal of this paper is to investigate the high decapod crustacean diversity found in the mid-Cretaceous (upper Albian) strata exposed in the Koskobilo quarry (N 42.8823°, W 2.1990°) near Alsasua in northern Spain. The number of decapod species found in the Koskobilo quarry is currently unsurpassed for a single locality in the Cretaceous with 36 species (Klompmaker, 2013). This paper will test the hypothesis that this high diversity in the Koskobilo quarry can at least in part be explained by the presence of multiple sub- and microenvironments that favored different decapod faunas. The systematics and taxonomy of the decapods from this quarry have been investigated in detail recently (Fraaije et al., 2009, 2012a; Klompmaker et al., 2011a,b,c, 2012a,b; Artal et al., 2012; Klompmaker, 2013) and provide the basis for this study.

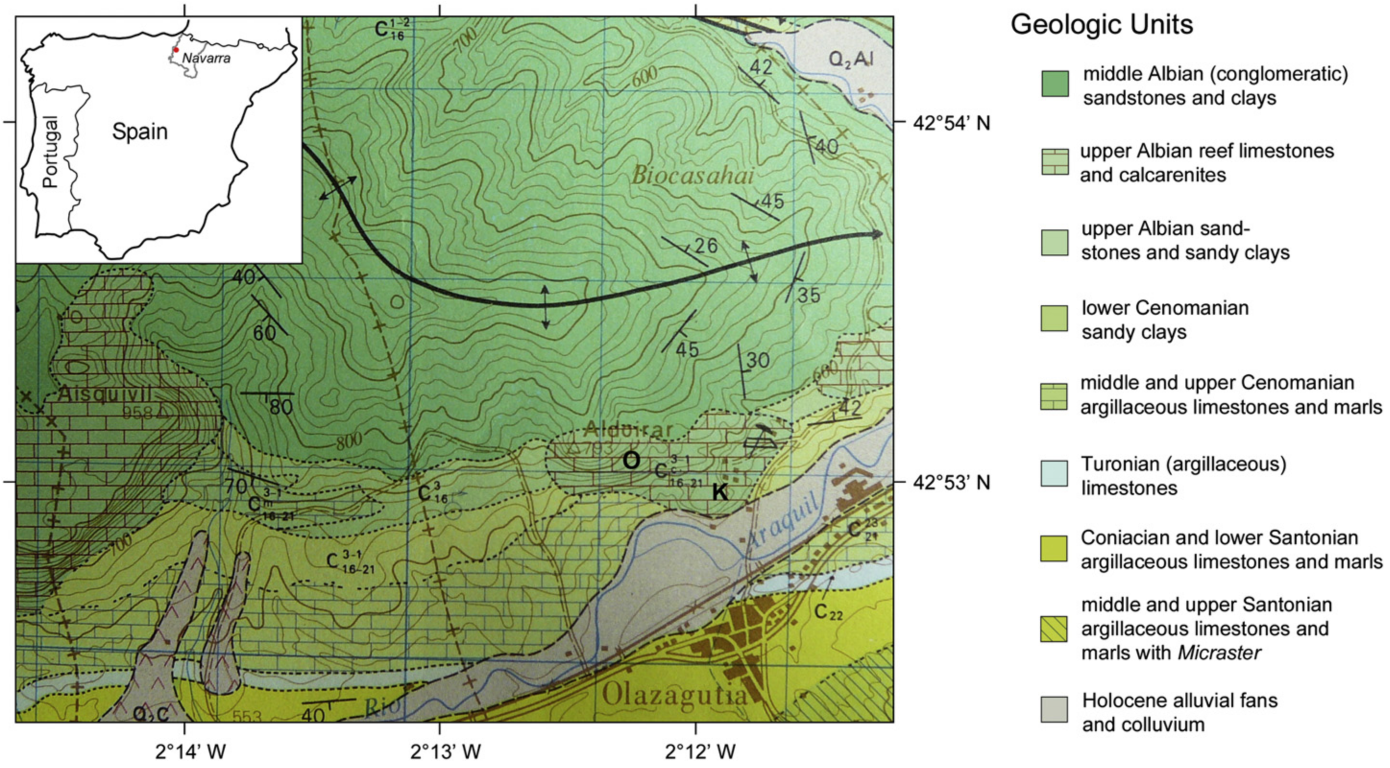

Fig. 1. A geological map of the area north of Olazagutía with an inset showing the location of the study area (red dot) in the Navarra region, northern Spain. The Aldoirar patch reef contains two quarries: the abandoned Koskobilo quarry (K = southern part of this quarry) and the active Olazagutía quarry (O). An anticlinal structure can be found north of the patch reef. The hammer symbol NE of the Koskobilo quarry is not part of this quarry. The distance between 53′ and 54′ is 1853 m.
From: Mapa Geologico de España, E. 1:50,000, Salvatierra, Segunda serie — Primera edición, 1978.

2. Geological setting and age

The Albinez Unit of the mid-Cretaceous Eguino Formation includes six patch reefs that developed in an area of approximately 30 km^2 in what is now western Navarra in northern Spain. The Koskobilo quarry is located at the eastern edge of the Aldoirar patch reef as can be seen on a geological map from the Salvatierra region of Spain (Fig. 1, K is the southern part of the Koskobilo quarry). The Olazagutía quarry (O) is located more centrally in the patch reef, approximately 500 m northwest of the southwestern part of the Koskobilo quarry (Fig. 2). Its northernmost part contains what appears to be the reef core consisting of densely packed colonial coral communities and orbitolinid foraminifera as the dominant fossils.

The Koskobilo quarry is located approximately 1 km south of the axis of an east–west directed anticlinal structure (Fig. 1). Thus, a southerly dipping direction of the layers in the Koskobilo quarry may be inferred. However, the limestones in the Koskobilo quarry could not be used for a strike and dip as the layers were obscured by joints. The southerly dipping orientation of the strata could, however, be confirmed by two geopetal structures within in situ brachiopod shells from the southwestern corner of the Koskobilo quarry. One part of the brachiopod shell typically contained a carbonate mud infill and the rest was hollow surrounded by calcite crystals. The first geopetal structure was found near site 25 (see Fig. 3 for sample numbers) and measured 80°/50°SSE, whereas the second one was found approximately 25 m south of that site in the same quarry and measured 60°/45°SSE. The southerly direction was further confirmed by another geopetal structure with a southerly dip, of which the exact measurements could not be made. This one was found at site 17. Additionally, layers of the reef core consisting of a dense network of colonial corals in the Olazagutía quarry did show a southerly orientation of the layers. Thus, using the average orientation of the two measured geopetal structures, the limestone layers in the Koskobilo quarry are suggested to have a general orientation of 70°/47.5°SSE. Hence, the limestones get progressively younger toward the southern part of the Koskobilo quarry (see Fig. 3).

Turonian (argillaceous) limestones can be found stratigraphically above the top part of the Aldoirar patch reef, followed by, Coniacian–lower Santonian (argillaceous) limestones and marls. Middle Albian sandstones, conglomeratic sandstones, and intercalated clays occur stratigraphically below the Aldoirar patch reefs and other patch reefs in the area (Mapa Geologico de España, E. 1:50,000, Salvatierra, 1978) (Fig. 1). These patch reefs, including the Aldoirar patch reef, in the Albinez Unit of the Eguino Formation were considered to be Albian–Cenomanian in age by López-Horgue et al. (1996), based on ammonites from underlying, overlying, and laterally equivalent strata. However, Klompmaker (2013) argued that all of the decapods were late Albian in age based on a reevaluation of evidence presented by López-Horgue et al. (1996) and an ammonite found in the Koskobilo quarry at site 17, which is the stratigraphically youngest part of the Albinez Unit (see Klompmaker, 2013 for a more thorough discussion on the age assignment). This late Albian age assignment also applies to decapods from Monte Orobe and the Olazagutía quarry (Artal et al., 2012; Klompmaker et al., 2012c).

3. Methods

3.1. Rock samples, thin sections, and acetate peels

To check whether the differences in carapace widths of decapods, decapod diversity, and decapod communities are possibly related to the particular environment in which the decapods were found, in situ ~20-cm^2 samples were taken throughout the quarry and especially from the sites where many decapods were encountered (13, 17, 23, 25, see Fig. 3). The samples were chosen so that they would best represent those particular parts of the quarry. If, upon inspection, some differences existed, two hand samples were collected. All hand samples were classified according to the limestone classification schemes of Folk (1959, 1962) and the modified Dunham (1962) classification (Embry and Klovan, 1971) after hand samples were cut and polished to show the lithologic details. In the case of in situ coral accumulations, the classification methodology of Insalaco (1998) was used to describe the coral fabrics.

Nineteen thin sections were made to study the carbonate microfacies of the decapod-rich sites and the hand samples from other sites within the quarry. The initial criterion used for selecting a hand sample for a thin section was a change in the lithology based on the modified Dunham classification performed on all the hand samples. Two thin

Fig. 2. A Google Earth image of the Koskobilo quarry (K = southern part of this quarry) and the active Olazagutía quarry (O). The extension northeast of the Koskobilo quarry is officially not part of the Koskobilo quarry and was not investigated.

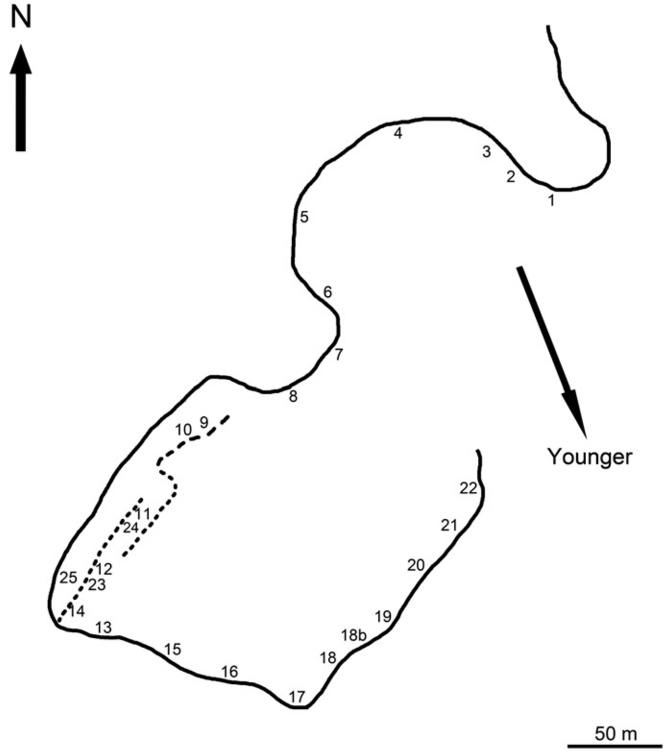

Fig. 3. The Koskobilo quarry showing the locations of the samples. The black solid lines are vertical quarry walls representing the quarry rim, whereas the dashed lines represent shorter vertical walls within the quarry.

sections were made from each of the decapod-rich sites and one other site that contained a significant amount of coarse biogenic material but not many decapods, in order to account for possible lithologic variation and to verify Dunham and Folk classifications (which was particularly necessary for Folk classifications). Two thin sections proved to be sufficient because analyses of the second thin section resulted in the same modified Dunham and Folk classifications in the great majority of cases. One thin section was made for each of the other sites. The glass slides on which the rock thin sections were mounted were 46 × 27 mm long and wide, whereas the actual thin sections of the carbonate rocks somewhat smaller. For each thin section, 100 points were counted with a Leitz Wetzlar point stage counter, under the cross-hairs of a Leitz Laborlux 11 pol microscope for quantitative analysis of the thin sections, following the precedent of Martindale et al. (2010) in their quantitative analysis of reef limestones. The spacing of the points was 2 mm, which allowed counting most of the area of the thin section. Every point was counted regardless of whether one skeletal grain had been counted previously, implying that larger grains will not be underrepresented. If the cross-hairs were exactly on a boundary between two grains or a grain-matrix contact, then the right or upper part was chosen for identification. Spaces enclosed by a skeletal grain (e.g. the open space inside a gastropod) were counted as part of the skeletal grain. To see both fine details and also larger structures that were not always evident under the microscope, points were studied at 4, 10, and 40 times magnification, and, in addition, the thin section as well as the rock slab from which the thin section was sliced were studied with the naked eye and hand lens to avoid misidentification. Acetate peels were made for the remaining hand samples to verify the Folk classification for that particular rock and to identify the abundant fossils.

The results of the thin section, acetate peel, and hand sample study were plotted on maps of the quarry: one map shows modified Dunham classifications, another map shows Folk classifications, the third map shows abundant fossils (here defined as ≥5% based on the thin section, acetate peel, and hand sample study) and the common fossils (<5% but >1%) based on the thin section study, and a last map shows fossils identified via qualitative field observations (see Fig. 4). Quantitative analysis of the fossils in the thin sections proved not to be possible after 100 point counts per thin section as too few fossils could be identified with confidence beyond "fossil indet.". This was partly due to fragmentation of fossils, but also because of their variable degree of recrystallization (see Table 1). Therefore, only a semi-quantitative comparison among thin sections was feasible, as outlined above.

3.2. Systematic collecting at decapod-rich localities

In 2008 and 2009, four localities containing numerous decapods were discovered in the Koskobilo quarry (13, 17, 23, 25, see Fig. 3). In 2010 more systematic collecting was performed at these four sites to investigate: a) decapod diversity and evenness per site, b) which taxa made up most of the fauna on the species and superfamily level, and c) whether decapods were differently sized at these localities. The superfamily level for b) was chosen so that the differences among the sites can be seen most easily as fewer categories are present compared to species rank. Pie graphs were made to illustrate this.

At each site, 9 h of collecting was conducted in an area of a few square meters of the (sub)vertical wall. An equal amount of time was devoted collecting from in situ limestones in the sunshine at the different sites (~4 h); the rest of the time was collected under cloudy conditions. Collecting an equal amount of time in the sunshine was judged to be necessary because decapods can be observed more readily in the sunshine. This ensured an equal possibility of finding decapods at these four sites. To compare the decapods from the sites within the quarry some other standardizations were employed: a) only internal molds and internal molds of carapaces with (part of) the cuticle preserved were used to avoid double counting of specimens if external molds were to be selected; b) only carapaces were used because they are relatively well preserved and this is a morphologically unique part of a decapod specimen in contrast to appendages; c) the specimens were collected by the first author only to avoid biases in collecting strategies; d) because decapods were usually similar in color to the surrounding sediment, the limestones were held as close to the eye as possible and examined under different angles to collect all decapods possible; and e) only those specimens with the axial part of the cervical groove preserved were selected for further analysis to avoid double counting of specimens. This unique landmark of the specimen is located in the central portion of the carapace, thus having a higher chance of preservation. Biases such as potential breakage of larger specimens or specimens with a weaker cuticle are largely circumvented by employing this method. This further ensures that as many as possible specimens were incorporated in the study. In the case of the paguroids *Annuntidiogenes worfi* Fraaije et al., 2009, *Cretatrizocheles olazagutiensis* Fraaije et al., 2012a, and *Mesoparapylocheles michaeljacksoni* Fraaije et al., 2012a, the cervical groove was often not preserved as the posterior portion of paguroids, including the ones found at Koskobilo, is often poorly calcified, which lowers the potential of preserving the axial part of the cervical groove, if present. In this case, specimens were selected only if the axial portion of the anterior carapace was preserved.

In addition to the systematic collecting at the four decapod-rich localities, large biogenic grains were also found at site 24, possibly suggesting the presence of decapods. Therefore, approximately 2 h of collecting was spent at this site to test this hypothesis. Two thin sections were made from samples collected in situ at this site.

To verify the systematic collecting results from 2010 in terms of number of species, genera, families, and superfamilies, all species for which the exact site of collecting in the quarry was noted were included. The additional specimens were collected by several people in 2009, and the exact number of hours collected at each site is not known, but is roughly comparable. This may also validate the question of whether or not 9 h of collecting at each site was sufficient in terms of obtaining the same qualitative results for diversity.

Table 1
Folk and modified Dunham classifications, abundant and common fossils, relative skeletal grain size, and the amount of recrystallization per sample. The bold samples are based on hand samples and thin sections, whereas the others are based on hand samples and acetate peels. Common fossils and the amount of recrystallization could not be determined for the latter.

Sample no.	Folk (1962)	Modified Dunham (1962) by Embry and Klovan (1971)	Abundant (≥5%) fossils (in area)	Common fossils other than abundant fossils	Some fossil grains very large compared to average grain (Y/N)	Recrystallized fossils (rare, common or abundant)
1	Sparse biomicrite	Floatstone			Y	
2	**Sparse or packed biomicrite**	**Wackestone**		Echinoderm	N	Abundant or common
3	Sparse biomicrite	Wackestone			N	
4a	Fossiliferous biomicrite	Wackestone			N	
4b	Sparse biomicrite	Wackestone			Y	
5	**Intraclastic, sparse or packed biomicrite**	**Wackestone**		Bryozoa, red algae, echinoderm	N	Common
6	Fossiliferous biomicrite	Micstone			N	
7	**Fossiliferous biomicrite**	**Micstone**		Small, benthic foraminifera	N	N/A (hardly any fossils)
8	**Fossiliferous intra- or pelsparite**	**Micstone**			N	N/A (hardly any fossils)
9	Packed biomicrite	Floatstone	Sponge		Y	
10	**?Pel- or intraclastic, sparse biomicrite**	**Floatstone**	Sponge		Y	Abundant
11	Sparse biomicrite	Floatstone	Sponge		Y	
11b	**Pelletized, unsorted biosparite**	**Packstone**		Echinoderm and red algae	N	Common
24a	**Intraclastic, unsorted biosparite**	**Floatstone**	Red algae	Sponge	Y	Common
24b	**?Pel- or intraclastic, packed biomicrite**	**Floatstone**	Sponge	Echinoderm and red algae	Y	Abundant
23a	**Intraclastic, unsorted biosparite**	**Floatstone**		Orbitolinid foraminifera, gastropod	N	Common or abundant
23b	**Intraclastic, unsorted biosparite**	**Floatstone**		Orbitolinid foraminifera, echinoderm	N	Abundant
12	Dismicrite or unsorted biosparite	Crystalline carbonate or floatstone			N	
25a	**Intraclastic, poorly washed biosparite**	**Floatstone**	Coral		Y	Rare
25b	**Intraclastic, unsorted biosparite**	**Floatstone**	Coral and red algae	Echinoderm, algae indet.	Y	Rare
13a	**Pel- or intraclastic, unsorted biosparite**	**Floatstone**	Algae indet.	Mollusk or brachiopod	Y	Abundant
13b	**Intraclastic, sorted biosparite**	**Floatstone**		Mollusk or brachiopod	N	Abundant
14	**Pelletized, sparse biomicrite**	**Wackestone**		Echinoderm	N	Common or abundant
15	Biolithite	Baffle- (pillar)stone	Coral		Y	
16a	Biolithite	Framestone	Coral		Y	
16b	Biolithite	Boundstone indet.	Coral		Y	
17a	**Biolithite**	**Baffle- (pillar-) or framestone (latter due to colonial corals)**	Coral		Y	Abundant
17b	**Biolithite**	**Baffle- (pillar)stone**	Coral	Rudist	Y	Abundant
18a	Biolithite	Framestone	Coral		Y	
18b	Biolithite	Framestone	Coral		Y	
19	**Poorly washed biosparite**	**Floatstone**	Sponge	Bryozoa	Y	Abundant
20	Packed biomicrite	Floatstone	Sponge		Y	
21	Intraclastic, packed biomicrite	Wackestone	Sponge		Y	
22	**Pel- or intraclastic, sparse biomicrite**	**Wackestone**			N	Common

3.3. Decapod diversity and evenness

To investigate possible diversity differences per site, multiple measures of diversity were employed. All specimens that could be determined to the species level were included in the analyses.

1. Taxa richness: the number of species, genera, families, and superfamilies found at each site
2. Margalev's $d=(S-1)/\ln(N)$, where S is the number of species and N is the number of specimens found at the site to account for the fact that more specimens yield more species in general.
3. Simpson's Index of Diversity $=1-(\sum n(n-1))/(N(N-1))$, where n is the number of specimens of a species and N again is the total number of specimens found at the site. This measure accounts not only for the number of specimens involved, but also for the number of specimens per species. To discover whether the Shannon–Wiener Indices of all four sites are statistically different from one another, the t-test as described by Magurran (1988) was applied by using the statistical program PAST 2.15 (Hammer et al., 2001).
4. Shannon–Wiener Index or Shannon Index or Shannon–Weaver Index $H=-\sum p_i(\ln(p_i))$, where p_i is the proportion of the ith species, thus additionally taking into account the number of specimen per species.
5. Individual rarefaction curves with 95% confidence intervals were computed for each of the samples using PAST 2.15.
6. The Chao1 Index (Chao, 1984) estimator of the absolute number of species in an assemblage: $S_{Chao1}=S_{obs}+(F_1^2/2\ F_2)$, where S_{obs} is the number of species in the sample, F_1 is the observed number of species represented by one specimen, and F_2 is the observed number of species represented by two specimens. This measure calculates the theoretical number of species if an infinite number of specimens had been collected. This measure and the standard deviation thereof were calculated using EstimateS 8.2.0 (Coldwell, 2009).

Pielou's evenness index was also calculated: $E=H/\ln(S)$, where E is the evenness index and H is the Shannon Index (see above).

3.4. Comparison of decapod fauna compositions

The composition of the decapod faunas of sites 13, 17, 23, and 25 were compared quantitatively at the species level using three types of methods. The first three formulas are only based on the number of species in each sample and all species are weighted equally. Formulas 4–7 also take into account the relative abundance of each species. Fisher's Exact Test was used to compare the species composition statistically with p-values. Once again, all specimens that could be determined to the species level were included in the analyses.

1. Simpson Coefficient = 100k/B, with k = the number of species common to sample A and B, and B = the total number of taxa found in the smaller assemblage ($B \leq A$).
2. Jaccard Coefficient = $k/(A+B-k)$.
3. Dice Coefficient or Sørensen similarity index = $2\,k/(A+B)$.
4. Morisita–Horn Index = $1-2(\sum(S_{A,i}/n)(S_{B,i}/m))/(\sum(S_{A,i}/n)^2+(S_{B,i}/m)^2)$, where $S_{A,i}$ = the number of individuals from assemblage A in the ith species, $S_{B,i}$ = the number of specimens from assemblage B in the ith species, n = the number of specimens in assemblage A, and m = the number of specimens in assemblage B.

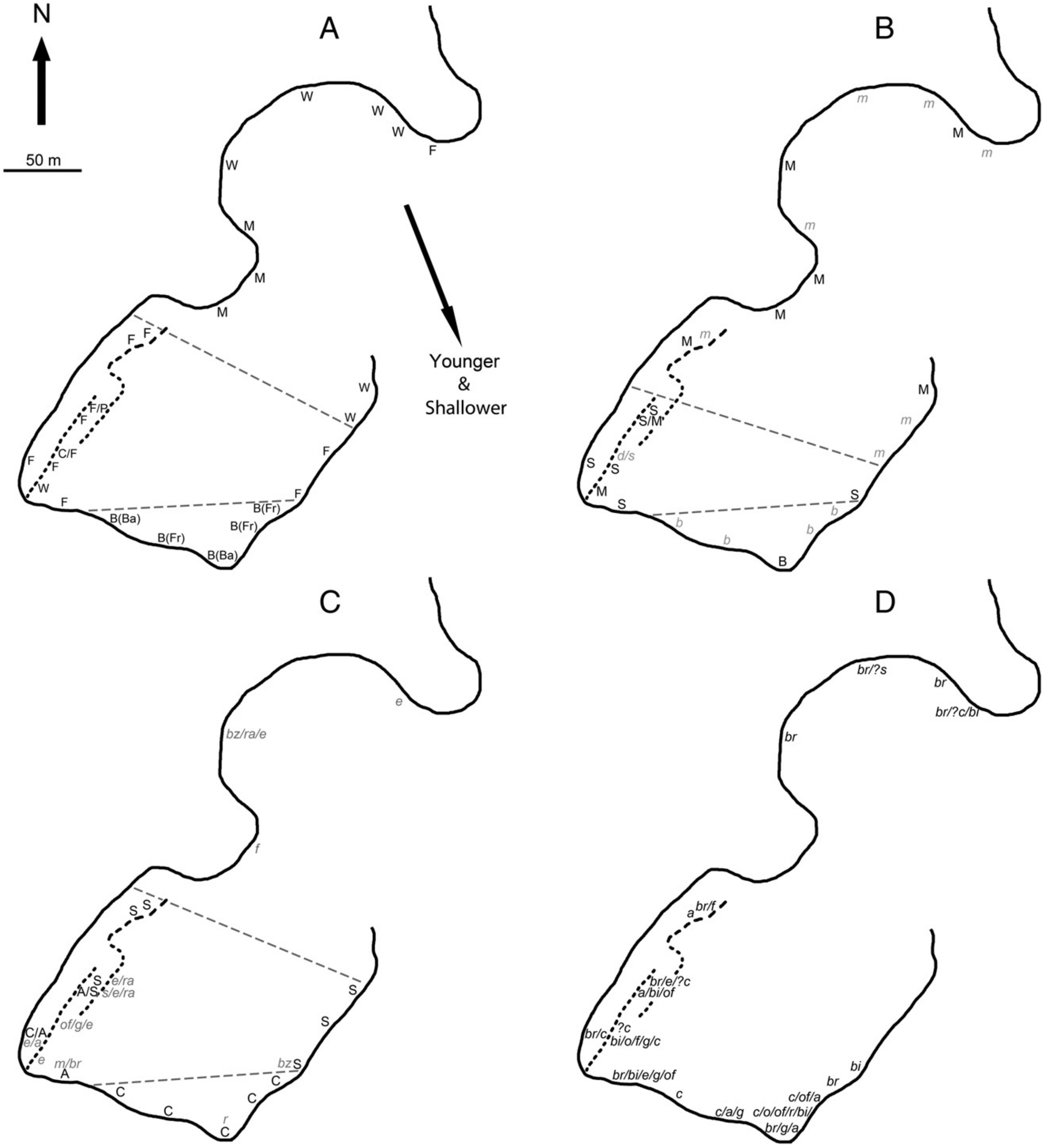

Fig. 4. The Koskobilo quarry with the samples classified according the modified Dunham classification (A), Folk classification (B), fossils present in hand samples, acetate peels, and thin sections (C), and fossils present based on field observations only (D). A) F = Floatstone, W = Wackestone, M = Micstone (= micritic carbonate mud), P = Packstone, C = Crystalline Carbonate, B(Ba) = Boundstone (Bafflestone), and B(Fr) = Boundstone (Framestone); B) M/m = biomicrite, S/s = biosparite, d = dismicrite, and B/b = biolithite. The uppercase, black letters are based on thin sections and hand samples, whereas the gray, lowercase, italicized letters are based on acetate peels and hand samples; C) showing the abundant (<5% in area) fossils in uppercase/black letters based on thin sections, acetate peels, and hand samples, and the common (<5%, but >1%) fossils based on thin sections in gray, lowercase, italicized letters. S/s = sponge, A/a = algae indet., C = coral, e = echinoderm, bz = bryozoan, ra = red algae, f = foraminifera indet., of = orbitolinid foraminifera, g = gastropod, m/br = mollusk/brachiopod, and r = rudist; and D) a non-comprehensive overview of fossils found at the sample localities in the quarry. bi = bivalve, (?)c = coral, br = brachiopod, (?)s = sponge, f = foraminifera, a = algae indet., e = echinoderm, of = orbitolinid foraminifera, o = ostracod, g = gastropod, and r = rudist. The gray dashed lines represent the boundaries between different zones.

5. Relative Abundance Index $= 100(I_c/(I_A + I_B))$, where $I_c =$ number of specimens of the taxa in common, $I_1 =$ number of specimens in assemblage A, and $I_2 =$ number of specimens in assemblage B.
6. Bray–Curtis Dissimilarity Index $= 1 - 2(\sum(\min(S_{A,i}, S_{B,i})/(\sum S_{A,i}) + (\sum S_{B,i})$, where $S_{A,i} =$ the number of specimens in the ith species of assemblage A, $S_{B,i} =$ the number of specimens in the ith species of assemblage B, and where min $(S_{A,i}, S_{B,i})$ means the minimum number of specimens for the species for both assemblages.
7. Yue and Clayton theta similarity coefficient $= 1 - (\sum^{St}_{i=1}(a_i b_i)/((\sum^{St}_{i=1}(a_i - b_i)^2 + (\sum^{St}_{i=1}(a_i b_i)))$, where $S_t =$ the total number of species in assemblages A and B, $a_i =$ the relative abundance of species i in assemblage A, and $b_i =$ the relative abundance of species i in assemblage B.
8. Fisher's Exact Test was used to compare the composition of the decapod faunas statistically. This test was chosen instead of the χ^2 test because many categories contain values of less than 5. The specimens are collected randomly and the samples are independent.

3.5. Decapod size

Based on field observations in 2009 and 2010, the average size of the decapods seemed to differ per site: in particular decapods at site 17 appeared smaller. This was tested using measurements of width instead of length for two reasons: 1) maximum width was more frequently measurable than maximum length, because these decapods are typically longer than wide, and are thus more frequently broken across their length than their width, and 2) their bilateral symmetry means that widths can be calculated for broken specimens as long as the axis and one side are preserved. The length and width are typically highly correlated in decapods, making measurement of both axes redundant. Parametric statistics (One-way ANOVA and the Tukey–Kramer multiple comparisons procedure) could not be used to compare mean widths because the assumption of normal distributions was rejected: the Shapiro–Wilk and the Jarque–Bera tests both returned p-values <0.05 for all four sites. Instead the non-parametric Kruskal–Wallis test was used because the samples are independent and the distributions of the data are similarly scaled and shaped (right-skewed); normal distributions are not required for this test. The null hypothesis was that the samples are taken from populations with equal medians. Subsequently, the Mann–Whitney pairwise comparisons test was used (with and without a Bonferroni correction) to discover which decapod sample widths are different from one another. The statistical program PAST 2.15 was used to perform the computations. A significance level of 5% was used for both tests.

It was also suspected that specimens of *Goniodromites laevis* were relatively small at site 17 compared to the other sites. To test this, we employed the Kruskal–Wallis test and the Mann–Whitney pairwise comparisons test for the specimens collected in 2009 and 2010 to obtain an as high number of specimens per site as possible. Once again, a significance level of 5% was used.

4. Results

4.1. Quarry overview based on rock sample study

The northern (stratigraphically oldest) part of the Koskobilo quarry exposures consists mainly of fine-grained wackestones and micstones (= micritic carbonate mud), the mid-southern part contains floatstones,

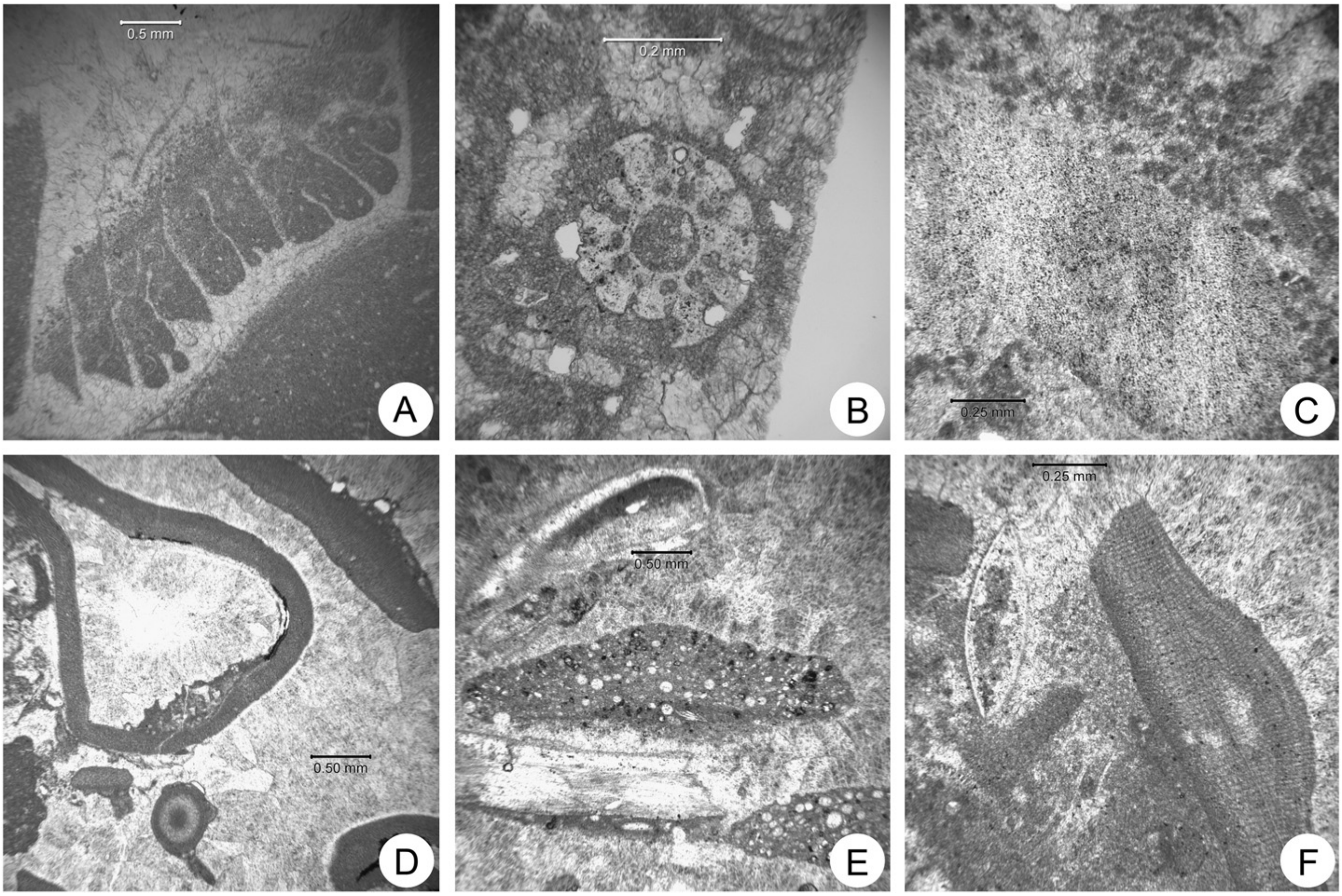

Fig. 5. Fossils commonly found in the thin sections. A) a recrystallized coral from site 17, B) a possible cross-section through an echinoid spine from site 17, C) an echinoderm plate from site 13, D) several red algae from site 24, E) an orbitolinid foraminifer from site 23, and F) a possible ostracod (left) and red algae (right) from site 25.

and the southernmost part of the quarry contains boundstones (bafflestones and framestones) using the modified Dunham classification (Fig. 4A). Using the Folk classification, biomicrites can be most commonly found in the northern part of the quarry, whereas biosparites are more frequently present in the southern half of the southern part with the exception of the southernmost part, where biolithites dominate (Fig. 4B). Based on the thin sections, acetate peels, and the accompanying hand samples, it appears that abundant (≥5% in area) fossils are present mostly in the southern part of the quarry (Fig. 4C, Appendix 1). Corals dominate the southernmost part of the quarry. Algal remains and especially sponges are abundant in the mid-southern part of the quarry where corals do not dominate. Based on the thin sections, common fossils locally include rudists (only at the southernmost part at locality 17), (red) algae (e.g., *Agardhiellopsis cretacea*, ?*Paraphyllum*, ?*Lithophyllum*), echinoderms, bryozoans, sponges, (orbitolinid) foraminifera (*Orbitolina* and *Textularia*), gastropods, and bivalves. Based on field observations (Fig. 4D), brachiopods (?*Cyclothyris*) and bivalves (such as pectinids and *Neithea*) were found in the quarry. Corals (e.g., ?*Calamophyllia*) dominate the southernmost part of the quarry. Fig. 5 shows some of the fossils found in the thin sections, and Table 1 shows the underlying data for Fig. 4.

A network of in situ scleractinian corals was observed only around site 17 in the Koskobilo quarry. The bafflestones at site 17 contain a network of coral branches with an occasional cluster of massive colonial corals. The branching corals produced most of the topography on the sea floor at the time of deposition. Using the work of Insalaco (1998: Fig. 11), the fabrics can be best described as an unbound pillarstone because of the dominant vertical component of the corals that do not rely on binding encrusters. Whether the corals at site 17 can be best classified as a dense or sparse pillarstone cannot be determined as Insalaco (1998) did not provide a quantitative boundary.

4.2. Decapod diversity and evenness

Using the data in Table 2, species, genera, family, and superfamily richness all show that site 17 is most diverse (Table 3). The same result was also obtained for Margalev's d, the Shannon–Wiener Index, and the Chao1 Index, but for the Simpson's Index of Diversity site 17 came in second after site 25 (Table 3). Site 12 was consistently at the bottom of the list, whereas site 13 and site 25 alternated at the second and third place. The t-test on the Shannon–Wiener Index results showed that none of the diversities of the sites were different based on this test (Table 4), although sites 17 and 13, and sites 17 and 23 were close to being different. The results of this test could be influenced by the low number of specimens from each sample as doubling all occurrences results in statistically different Shannon diversities for these two pairs. The standard deviations of the Chao1 Index are given in Fig. 6, and suggest that site 17 may contain more species than at least site 25 with infinite collecting. The slopes of the rarefaction analyses also suggest that site 17 may yield the most species (Fig. 7). Furthermore, Table 5 shows that site 17 contains the most species when the collections of 2009 and 2010 are merged. Thus, based on a variety of diversity measures site 17 can be considered the most diverse, also given the fact that an equal number of hours was spent collecting at each site. In terms of evenness, all sites have a relatively high evenness ranging from 0.76 to 0.87, which implies that more than one species are important contributors to the decapod fauna at each site (Table 3).

Table 2
Data for the number of specimens per species per site after 9 h of collecting in 2010.

	Site 13	Site 17	Site 23	Site 25
Acareprosopon bouveri (Van Straelen, 1944)	0	2	1	2
Annuntidiogenes worfi Fraaije et al., 2009	0	1	0	0
Caloxanthus paraornatus Klompmaker et al., 2011a	3	2	2	2
Cretatrizocheles olazagutiensis Fraaije et al., 2012a	1	2	0	0
Decapoda indet.	0	1	0	0
Distefania incerta (Bell, 1863)	2	1	5	4
Distefania renefraaijei Klompmaker et al., 2012b	3	0	2	0
Distefania sp.	3	0	1	0
Eodromites grandis (von Meyer, 1857)	1	4	0	1
Eodromites grandis or *Navarradromites pedroartali*	0	2	0	0
Eomunidopsis navarrensis (Van Straelen, 1940)	9	24	26	9
Eomunidopsis orobensis (Ruiz de Gaona, 1943)	6	0	1	1
Faksecarcinus koskobiloensis (Klompmaker et al., 2011a)	0	1	1	0
Galatheoid	1	0	0	0
Gastrodorus cretahispanicus Klompmaker et al., 2011b	1	0	0	0
Glyptodynomene alsasuensis Van Straelen, 1944	0	1	0	2
Goniodromites laevis (Van Straelen, 1940)	24	10	6	2
Graptocarcinus texanus Roemer, 1887	3	2	11	10
Hispanigalathea pseudolaevis Klompmaker et al., 2012a	0	1	0	0
Laeviprosopon hispanicum Klompmaker, 2013	1	1	2	1
Laeviprosopon edoi Klompmaker, 2013	0	0	1	0
Laeviprosopon crassum Klompmaker, 2013	0	1	0	0
Laeviprosopon sp.	1	0	0	0
Mesoparapylocheles michaeljacksoni Fraaije et al., 2012a	0	6	0	2
Navarradromites pedroartali Klompmaker et al., 2012b	0	1	0	0
Navarrara betsieae Klompmaker, 2013	1	0	0	0
Navarrahomola hispanica Artal et al., 2012	0	1	0	0
Paragalathea ruizi (Van Straelen, 1940)	2	19	8	4
Rathbunopon obesum (Van Straelen, 1944)	0	2	1	1
Viaia robusta Artal et al., 2012	0	1	0	0

Table 3
Diversity metrics and an evenness index for the four decapod-rich sites (highest values in bold face).

	Site 13	Site 17	Site 23	Site 25
# specimens	57	**86**	67	41
# species	13	**20**	13	13
# genera	11	**19**	10	12
# families	8	**12**	6	7
# superfamilies	7	**9**	5	6
Margalev's d	2.99	**4.30**	2.85	3.23
Simpson's Index of Diversity	0.78	0.85	0.80	**0.88**
Shannon–Wiener Index	1.95	**2.27**	1.96	2.23
Chao1 Index	19.3	**30.0**	17.2	14.6
Pielou's evenness index	0.76	0.76	0.76	**0.87**

Of special note is the low occurrence of decapods at site 24. After approximately 2 h of collecting, only one decapod specimen, *Paragalathea ruizi* Van Straelen, 1940, was found. The thin sections showed that red algae and sponges dominate the fossil content locally.

4.3. Decapod composition per site

As shown in the species-level pie diagram (Fig. 8), species that dominate the fauna are a combination of *Eomunidopsis navarrensis* Van Straelen, 1940, *Paragalathea ruizi*, *Goniodromites laevis* Van Straelen, 1940, and *Graptocarcinus texanus* Roemer, 1887, for all sites. Most notable in comparison to other sites are the presence of the small paguroid *Mesoparapylocheles michaeljacksoni* at site 17, the abundant presence of the galatheid *P. ruizi* at site 17, and the abundant presence of *G. laevis* at site 13. At the superfamily level (Fig. 9), some combination of Galatheoidea, Homolodromioidea, and Dromioidea (only represented by *G. texanus*) compose the majority of the fauna. Of note is the abundance of the Paguroidea at site 17 compared to other sites.

The first seven quantitative analyses comparing the decapod compositions from the four sites indicate that in terms of species, sites 13 and 17 are most dissimilar, whereas sites 23 and 25 are most alike

Table 4
The p-values of the t-tests on the Shannon–Wiener Index results.

	Site 17	Site 23	Site 13	Site 25
Site 17	–	0.12	0.12	0.71
Site 23	–	–	0.90	0.26
Site 13	–	–	–	0.24
Site 25	–	–	–	–

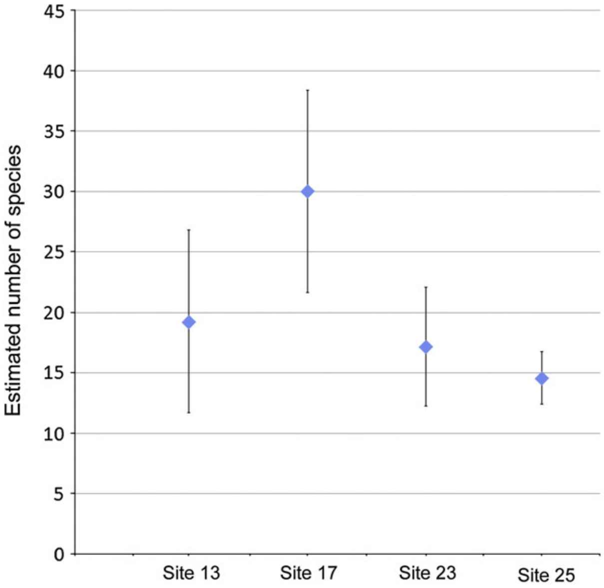

Fig. 6. The Chao1 Index giving the estimated number of species for each site and the standard deviations.

(Table 6). This is also reflected in the pie diagrams (Fig. 8). The eighth test, Fisher's Exact Test, shows that the taxonomic composition of decapods at the species level of all sites are statistically different from one another with the exception of sites 23 and 25 (Table 7), also suggested by the other analyses.

4.4. Decapod widths

The Kruskal–Wallis test based on the decapods collected in 2010 shows that the medians of the decapod widths of the samples are different ($p = 0.0000006$) (Appendix 2). The subsequent Mann–Whitney pairwise comparison tests shows that the decapod widths

Table 5
The species found at each site when the collections of 2009 and 2010 were merged. 'x' means present.

	Decapod taxon	Site 13	Site 17	Site 23	Site 25
1	*Acareprosopon bouvieri* (Van Straelen, 1944)	x	x	x	x
2	*Albenizus minutus* Klompmaker, 2013				
3	*Annuntidiogenes worfi* Fraaije et al., 2009		x	x	
4	*Caloxanthus paraornatus* Klompmaker et al., 2011a	x	x	x	x
5	*Cretatrizocheles olazagutiensis* Fraaije et al., 2012a	x	x		
6	*Cretamaja granulata* Klompmaker, 2013		x		
7	*Distefania incerta* (Bell, 1863)	x	x	x	x
8	*Distefania renefraaijei* Klompmaker et al., 2012b	x	x	x	
9	*Eodromites grandis* (von Meyer, 1857)	x	x		x
10	*Eomunidopsis aldoirarensis* Klompmaker et al., 2012a				x
11	*Eomunidopsis navarrensis* (Van Straelen, 1940)	x	x	x	x
12	*Eomunidopsis orobensis* (Ruiz de Gaona, 1943)	x		x	x
13	*Etyxanthosia fossa* (Wright and Collins, 1972)		x		
14	*Faksecarcinus koskobiloensis* (Klompmaker et al., 2011a)	x	x	x	x
15	galatheoid Klompmaker et al., 2012a				
16	*Gastrodorus cretahispanicus* Klompmaker et al., 2011b	x			x
17	*Glyptodynomene alsasuensis* Van Straelen, 1944		x		x
18	*Goniodromites laevis* (Van Straelen, 1940)	x	x	x	x
19	*Graptocarcinus texanus* Roemer, 1887	x	x	x	x
20	*Hispanigalathea pseudolaevis* Klompmaker et al., 2012a		x		
21	*Hispanigalathea tuberosa* Klompmaker et al., 2012a				
22	*Koskobilius postangustus* Klompmaker, 2013		x		
23	*Laeviprosopon crassum* Klompmaker, 2013		x	x	
24	*Laeviprosopon hispanicum* Klompmaker, 2013	x	x	x	x
25	*Laeviprosopon planum* Klompmaker, 2013		x		
26	*Laeviprosopon edoi* Klompmaker, 2013	x		x	x
27	*Mesoparapylocheles michaeljacksoni* Fraaije et al., 2012a		x	x	x
28	*Navarrara betsieae* Klompmaker, 2013	x		x	
29	*Navarradromites pedroartali* Klompmaker et al., 2012b		x		
30	*Navarrahomola hispanica* Artal et al., 2012		x		
31	*Nykteripteryx rostrata* Klompmaker et al., 2012a		x	x	
32	*Paragalathea multisquamata* Vía Boada, 1981		x		
33	*Paragalathea ruizi* (Van Straelen, 1940)	x	x	x	x
34	*Paragalathea straeleni* (Ruiz de Gaona, 1943)				
35	*Rathbunopon obesum* (Van Straelen, 1944)	x	x	x	x
36	*Viaia robusta* Artal et al., 2012	x	x		
	Total number of species	18	27	18	17

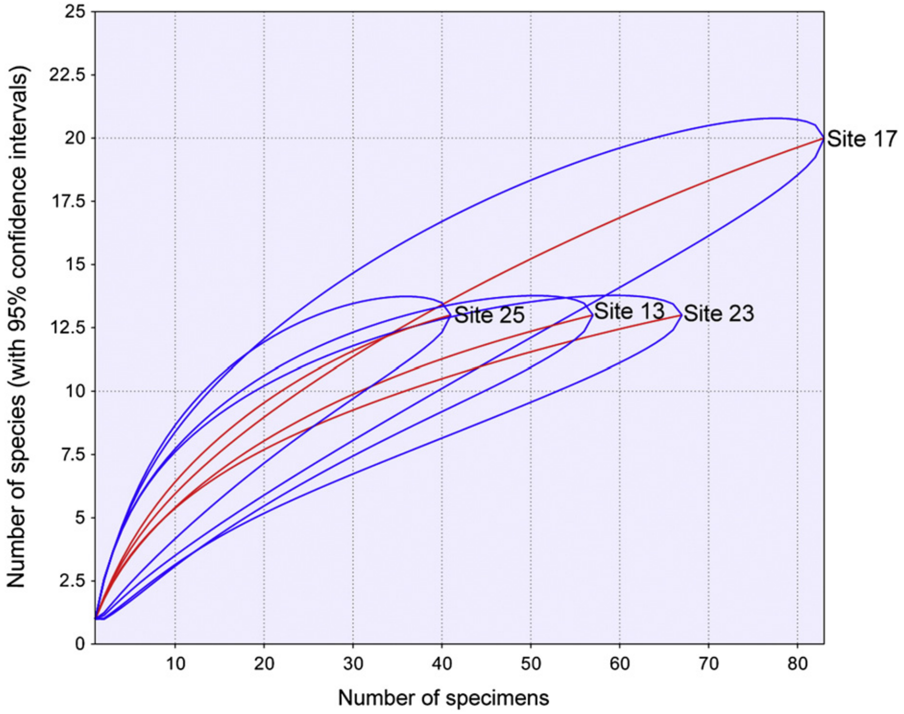

Fig. 7. Rarefaction analyses for each site as well as the 95% confidence intervals as computed using PAST 2.15.

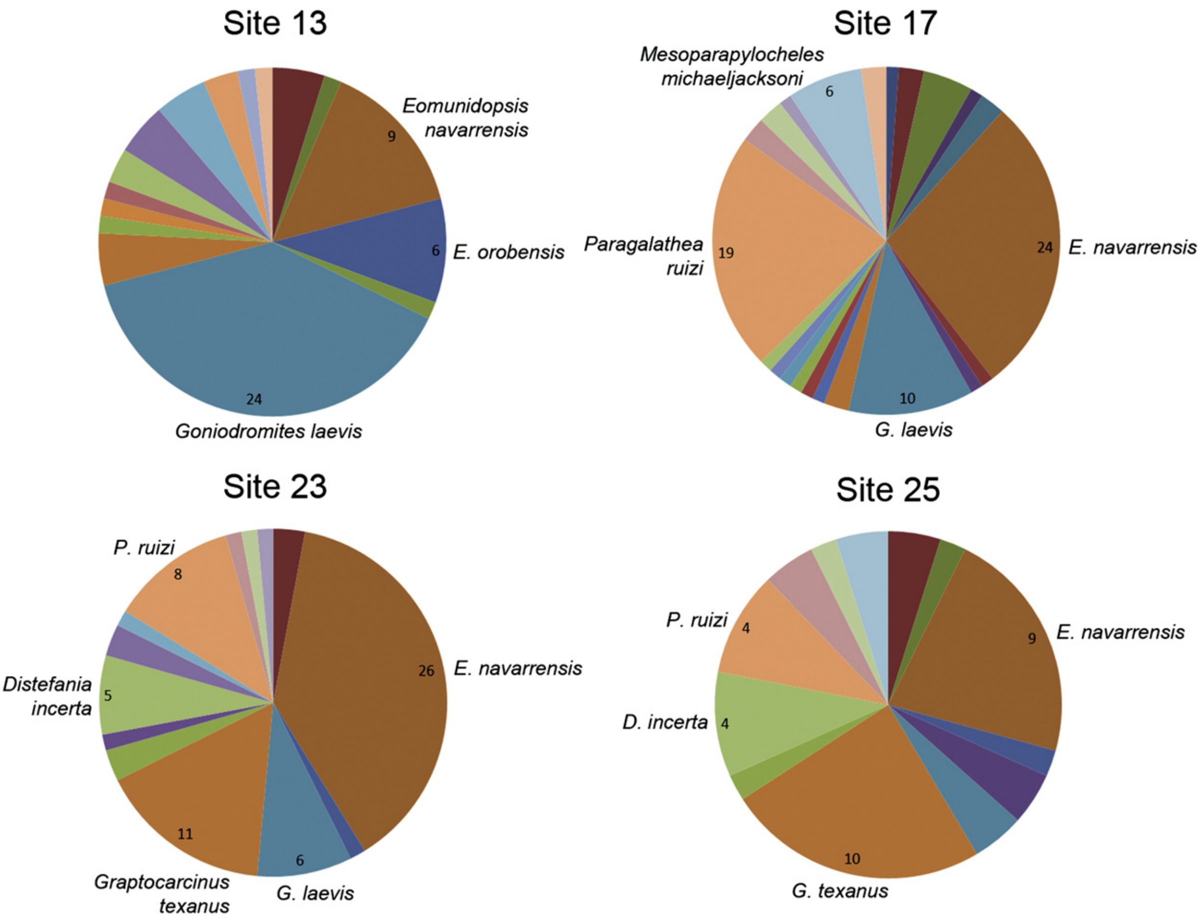

Fig. 8. Pie diagrams of the species compositions per site. The numbers within the diagrams represent the number of specimens from each species.

of all samples are different from one another with the exception of those of sites 23 and 25 without the Bonferroni correction (Table 8). When the Bonferroni correction was applied, site 13 was different from all other sites (Table 8). Site 17 was not statistically different from sites 23 and 25 anymore, although the p-value was close to 0.05 ($p = 0.06$ and $p = 0.12$, respectively). Larger sample sizes may show that the decapod widths are different when comparing site 13 with sites 23 and 25. The medians of sites 17, 23, 13, and 25 are 4.1, 5.4, 7.9, and 4.9 mm, respectively. The results suggest that site 13 contains relatively many large specimens and site 17 relatively small specimens compared to the other sites.

The same tests were performed for specimens of *Goniodromites laevis*, grouping all specimens collected in 2009 and 2010 in this case. This shows that the median of the decapod widths of the samples (Appendix 3) is different ($p = 0.001$). The Mann–Whitney pairwise comparison tests show that sites 17 and 23, and 17 and 13 are statistically different without the Bonferroni correction, but only 17 and 13 with the Bonferroni correction (Table 8). Given the medians for each site (5.5 mm for site 17, 10.7 mm for site 23, 10.2 mm for site 13, and 8.6 mm for site 25), site 17 appears to contain smaller specimens of *G. laevis*. Results should, however, be interpreted with care as the sample sizes are low with only 14 specimens for site 17, 13 for site 23, and 5 for site 25, whereas site 13 yielded 56 specimens (Appendix 3).

5. Discussion

5.1. General water depth, energy regime, salinity, and nutrients

Recently, cold-water corals and their ecosystems have been increasingly investigated (e.g., Freiwald and Roberts, 2005; Hovland, 2008; Roberts et al., 2009). Roberts et al. (2006: p. 545) speculated that “their biodiversity may be comparable to that found on tropical coral reefs”. Turley et al. (2007) showed that these reefs were important at depths usually ranging from 200 to 1000 + m. Deep cold-water corals typically do not exhibit the zooxanthellae that cause the wide variety of colors that typify shallow, warm water corals. In terms of areal extent, the United Nations Environmental Programme website indicates that, “global coverage of cold-water coral reefs could equal, or even exceed, that of warm-water reefs”, which is 284,300 km^2 (http://unep.org/cold_water_reefs/comparison.htm). This, then, begs the question of whether the reef strata of Koskobilo were deposited in shallow, warm waters or in deeper, colder waters. Wendt et al. (1997) and Belka (1998) proposed to answer the question using, among other indicators, the presence or absence of algae, which rely on photosynthesis and can only grow in water depths to ~100 m. In the case of the Koskobilo quarry, numerous algae are found (see Figs. 4 and 5; Table 1), so this reef must have formed in shallow, warm waters. The presence of warm waters (~20 °C) around Spain during the mid-Cretaceous is supported by climate models (e.g., Barron et al., 1995; Fluteau et al., 2007) and isotopic evidence (e.g., Barron and Washington, 1982). Based on a combination of the common presence of scleractinian corals, orbitolinids, and especially corallinacean red algae the general water depth can be estimated as being between 20 and 80 m for at least the decapod-rich localities (see Flügel, 2004: p. 635). The branching scleractinian corals in the stratigraphically youngest part of the reef may been able to live at shallower waters as extant, branching, colonial corals such as *Porites porites* and *Acropora palmata* are known from very shallow waters, but the commonness of corallinacean red algae at site 17 suggests a somewhat deeper environment.

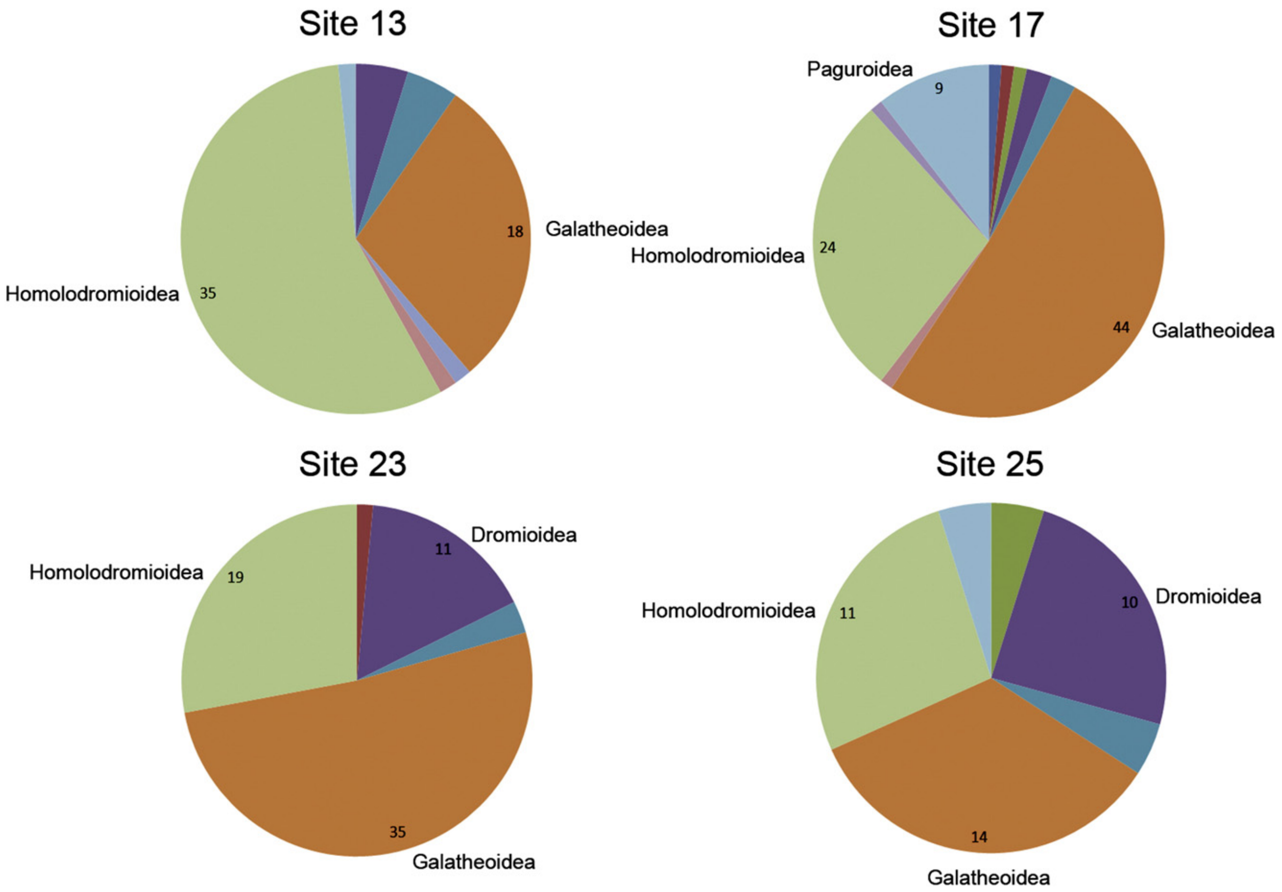

Fig. 9. Pie diagrams of the superfamily compositions per site. The numbers within the diagrams represent the number of specimens from each superfamily.

The environment at the norther, oldest part of the quarry experienced mainly a low intensity of waves or currents given the abundant presence of biomicrites (see Flügel, 2004: Fig. 12.1). A band of mostly biosparites just south (up section) of the biomicrites consists mainly of unsorted biosparites, although a sorted biosparite was encountered at site 13. These biosparites suggest a higher energy regime compared to the biomicrites (see Flügel, 2004: Fig. 12.1), especially for site 13, which contains many similar-sized biogenic fragments. However, decapods from all sizes were not preserved in noticeably different ways from decapods at other sites, suggesting that decapods were not fragmented more due to higher energy levels. This interpretation of higher energy levels assumes that no recrystallization took place from biomicrites to biosparites, but this could have happened as recrystallization of fossils is abundant locally. The combination of frame- and bafflestones in the southernmost part of the Koskobilo quarry points to medium levels of physical disturbance (see Flügel, 2004: Fig. 8.1).

The common to abundant presence of the combination of scleractinian corals, corallinacean red algae, sponges, and echinoderms suggest a normal marine salinity between 30 and 40‰ (see Flügel, 2004: Fig. 12.11). A combination of frame- and bafflestones are found at the southernmost part of the quarry. Using Flügel (2004: Fig. 8.1), this could either mean a low or higher nutrient levels at the time of deposition of these autochthonous carbonates.

5.2. Reef development and decapod abundance

The lithologic gradation from the oldest parts of the reef strata to the youngest parts of the reef may be explained by the evolution of the reef along the reef margin. In the oldest parts, the rocks may have been part of the slope of the reef buildup and, thus, belong to the slightly deeper parts of the patch reef. The abundance of fragmented fossils points to transport. The fact that biomicrites dominate, indicating a low hydrodynamic regime (see Section 5.1), supports a deeper water interpretation. Although this part of the quarry was not studied in detail for its decapod yield per time unit, the number of decapods (mainly galatheoids) that were encountered during a survey in 2009 was limited.

The reef may have become shallower at the floatstone and biosparite dominated part, allowing for more light to penetrate. A higher abundance of organisms that photosynthesize such as red algae is in evidence (Appendix 1). The fragmentary nature of the fossils including

Table 6
Results of the quantitative analyses of the decapod species composition of the four decapod-rich sites. Values in bold indicate the lowest similarity for each test.

	17 vs 13	17 vs 23	17 vs 25	13 vs 23	13 vs 25	23 vs 25
Simpson Coefficient	**69.2**	76.9	92.3	**69.2**	**69.2**	76.9
Jaccard Coefficient	**0.38**	0.43	0.57	0.53	0.53	0.63
Dice Coefficient or Sørensen Similarity Index	**0.55**	0.61	0.73	0.69	0.69	0.77
|Morisita–Horn Index − 1|	0.56	0.82	0.54	0.55	**0.39**	0.71
Relative Abundance Index	**79.9**	84.7	91.9	93.5	86.6	91.7
|Bray–Curtis Dissimilarity Index − |	**0.41**	0.63	0.45	0.45	0.47	0.65
|Yue & Clayton theta similarity coefficient − 1|	0.29	0.57	**0.23**	0.35	0.29	0.77

Table 7
The p-values of the Fisher's Exact Test on the decapod species composition per site. The p-values <0.05 are underlined.

	Site 17	Site 23	Site 13	Site 25
Site 17	–	0.002003	3.88E−07	0.008154
Site 23	–	–	1.30E−05	0.33688
Site 13	–	–	–	1.59E−05
Site 25	–	–	–	–

the sponges and the abundant presence of biosparite, suggest a higher energy regime as mentioned in Section 5.1, which is consistent with a shallower water depth. The wackestones at the eastern end of this mid-part of the quarry may be explained by their location at the reef margin (Fig. 1), where the finer material presumably accumulated, as opposed to the coarser floatstones at the western end of the quarry, which is more centrally located in the patch reef. The latter part of the floatstone and biosparite zone is where decapod-rich localities 13, 23, and 25 were encountered as well as the relatively decapod-poor site 24 (see Section 5.4.3). Overall, this part of the quarry contained more decapods than the northern part, which could be explained by the increased abundance of food for decapods.

The last phase of the reef as exposed in the Koskobilo quarry is dominate by coral biolithites and boundstones. These corals may have become the dominant fossils because they formed in even shallower waters compared to the previous sponge-dominated floatstone and biosparite phase, assuming the sponges formed in situ. The shallower nature of corals compared to sponges is also hinted at by Leinfelder et al. (1996: Fig. 12), who indicated that Late Jurassic siliceous sponges are found at greater water depths than corals based on numerous Late Jurassic reefs across Europe. They also indicated that nutrient levels may play a role as corals facies were said to be found in stable oligo- to mesotrophic conditions, whereas these sponges could withstand fluctuating nutrient levels. Thus, a change in nutrient level cannot be excluded to explain the shift in facies. On the other hand, the presence of corals in shallow, well-lit environments and the presence of sponges in deeper waters is also known for today's reefs (Wood, 1998). This part of the quarry contains the richest decapod site within the quarry, site 17. Thus, it may be concluded that decapods become progressively more abundant going from wacke- and micstones to floatstones and finally to boundstones. Controls on the proposed water depth change may be intrinsic (buildup of the reef itself to shallower depth) as well as extrinsic (sea level change and tectonics) or a combination thereof.

5.3. On differences in taxonomic composition per site

The taxonomic composition per site (see Fig. 8), which appeared statistically different for each site except when sites 23 and 25 are compared, may reflect the composition at the time the decapods were alive. However, some biases may have affected the composition. The degree of fragmentation of similarly sized and shaped decapods may be different for strongly calcified decapods compared to weakly calcified decapods. However, since the axial part of the cervical groove was chosen as the reference point for counting a specimen for all species except for paguroids, this possible bias is considered to be minimal. Another possible bias is caused by a possible different rate of molting of different species. All specimens found at Koskobilo are taken into account including molts and possible corpses. Schäfer (1972) and Bishop (1986a) recognized that molts would bias the fossil record of decapods in that more specimens might be found due to the molting process than actually were present. It would be beneficial to be able to unambiguously determine whether a specimen represents a molt or actual corpse so that all molts can be eliminated from the count. Mertin (1941: p. 251) estimated that the ratio of molts versus corpses was about 5 to 1 based 94 molts and 20 corpses of fossil lobsters. If a distinction were to be possible in Koskobilo, this would result in a lower number of specimens, possibly to the extent that even qualitative comparison may not be possible in this case as decapod ecdysis produces numerous molts per live specimen. Moreover, distinction between molts and corpses is only possible for very well preserved faunas, which is not the case in Koskobilo. Not a single specimen is found with the appendages, abdomen, or venter still attached to the carapace resembling the second taphonomic model in Müller et al. (2000: Fig. 23). Additionally, almost all carapaces are broken to at least some extent, thereby hampering the identification of possible molt indicators on the ventral side of the carapace. Thus, distinction between molts and corpses is not possible here. Hence, for the diversity measures Margalev's d, Simpson's Index of Diversity, Shannon–Weaver Index, Chao1 Index, and the comparisons of decapod widths among sites, it is assumed that the preservation potential across decapod species is similar and that the number of molts per species and per time unit is comparable.

Table 8
The p-values of the Mann–Whitney pairwise comparison test for all decapod widths per site and for specimens of *Goniodromites laevis*. The p-values<0.05 are underlined. The upper right are p-values without the Bonferroni correction, whereas the lower left is with the Bonferroni correction applied.

All decapods	Site 17	Site 23	Site 13	Site 25
Site 17	–	0.01065	2.49E−08	0.01951
Site 23	0.06392	–	0.00484	0.9819
Site 13	1.49E−07	0.02904	–	0.004243
Site 25	0.117	1	0.02546	–
Goniodromites laevis	Site 17	Site 23	Site 13	Site 25
Site 17	–	0.01625	9.36E−05	0.2108
Site 23	0.09753	–	1	0.2369
Site 13	0.000561	1	–	0.1453
Site 25	1	1	0.8717	–

5.4. Decapods per site

5.4.1. Site 17

Based upon the results, the immediate question arises why site 17 yields the most diverse decapod fauna (20 species arranged in 19 genera based on 86 specimens) in comparison to all other sites (Table 3). This is most likely related to the particular subenvironment of this site, which differs from the other sites from which decapod-rich faunas are known in the quarry. General field observations indicate that site 17 consists of a combination of in situ branching scleractinian corals and massive colonial corals, the latter being less common than the branching corals. The diameter of these branches ranges from approximately 5 to 19 mm in cross section, with heights generally >40 mm. The cement, matrix and skeleton percentages varies, but 50–70% matrix and cement is common (Fig. 10 for an example). The decapods were found in between and in proximity of these branches. Corals were less common or absent in other decapod-rich localities and throughout the quarry. The largest bioclastic grains were generally smaller in other sites and throughout the quarry as well. Thus, the corals could have provided a shelter and a feeding site that was not present at other sites within the quarry. The preservation of the decapods at site 17 is similar to that at other sites, indicating that the higher diversity at this site is not caused by a preservational bias within the framework of corals. Also because of this similar preservation, it seems unlikely that decapod remains were preferentially caught in the coral framework during transport, thereby increasing the number of specimens and possibly also the number of species.

From modern occurrences it is known that the spatial separation of the branches of corals and colonies may have an effect on the decapod species richness (Edwards and Emberton, 1980; Lewis and Snelgrove, 1990). Future work on this part of the quarry may test whether this is true for decapods in fossil reefs as well.

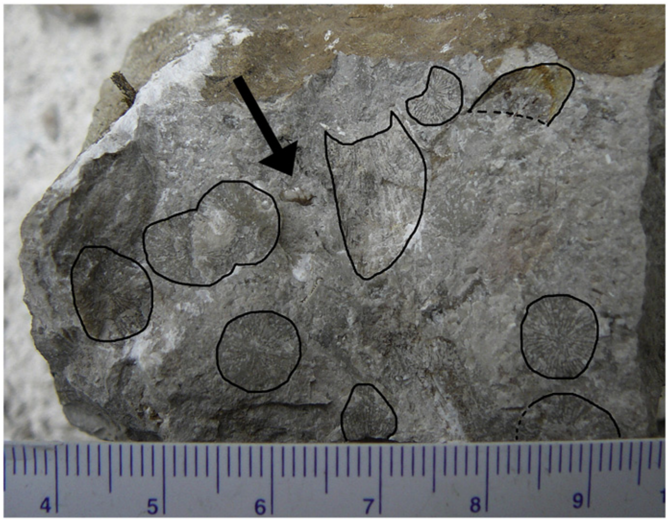

Fig. 10. A typical rock for site 17 of the Koskobilo quarry showing branches of corals, which are outlined here. In between these branches numerous decapods were found including *Acareprosopon bouvieri* (see arrow).

Paguroids were found predominantly at site 17. The posterior part of the carapace and the abdomen are typically not preserved (see Fraaije et al., 2012a), suggesting that they relied on protection for this part of the body by mid-Cretaceous times. This is not surprising given the fact that Late Jurassic paguroids often lack this part as well (e.g., Van Bakel et al., 2008; Fraaije et al., 2012b,c, in press). However, not a single paguroid carapace was associated with a gastropod (as is known from many extant paguroids), or any other type of protection. Thus, these paguroids may not have relied on gastropod shells as a protection, which is supported by the fact that gastropods are rarely found in the Koskobilo quarry. Ammonite shells have been used for protection by Cretaceous paguroids (see Fraaije, 2003b), but are also unlikely in this case, as only one ammonite specimen is known (see Section 2). Instead, these paguroids may have used the abundant bivalve shells, algal remains, rock crevasses, or even parts of decapod molts for additional protection for the posterior part of the carapace and the abdomen (see Ďuriš, 1992: Fig. 9; McLaughlin and Lemaitre, 1997). The corals at site 17 may have offered an additional protection against predators such as fish. Patton (1977) citing Glynn et al. (1972) mentioned that the hermit crabs *Trizopagurus magnificus* (Bouvier, 1898) and *Aniculus elegans* Stimpson, 1858 ate the tissue of the coral *Pocillopora* by scraping of the tips the branches using their chelipeds. The hermit crabs could have used a similar method of feeding since they are most frequently associated with corals in the Koskobilo quarry.

5.4.2. Sites 13, 23, and 25

These decapod-rich sites all yielded the same number of species, but the number of specimens differed. In terms of the species composition, 23 and 25 are much alike (see Fig. 8), which may be related to their close proximity in map view and their similar lithologies as identified by both the Folk and modified Dunham classifications (intraclastic, unsorted biosparite and floatstone, respectively). The preservation in terms of recrystallized fossils and the common to abundant fossils are, however, deviant. The lower number of specimens at site 25 is not easily explained, especially since some corals are present here based on field observations (Fig. 4D) and thin sections (Fig. 4C) because corals can explain the peak diversity of decapods at site 17 (see Section 5.4.1). However, corals are found infrequently here in contrast to the mass occurrence of corals at site 17. The paguroids at site 25 may have been associated with the corals, as for site 17. Site 13 appears different from the other two in that the fossils seem to be better sorted, but not better preserved compared to other sites, which suggest that the decapods were not transported to this site from far away. Moreover, the species composition is different in that galatheoids and *Graptocarcinus texanus* are less common, whereas *Goniodromites laevis* is more common.

5.4.3. Site 24

Even though more collecting took place at decapod-rich sites (9 h) compared to site 24, this still does not explain the relative difference in the number of specimens found. The lowest number of decapod specimens for the decapod-rich localities is 41 specimens, whereas only one specimen was found at site 24 after 2 h of collecting. Assuming the same rate of collecting decapods, only four to five specimens would be expected after 9 h of collecting at site 24. Thus, decapod abundance appears anomalously low at this site, despite the presence of coarse-grained biogenic material at this site, which usually is an indicator for the abundant presence of decapods in the southern part of the Koskobilo quarry. The low abundance of decapods may be related to the abundant presence of red algae. Even though certain red algae are reported to be sources of decapod decoration (e.g., Wicksten, 1978; Mastro, 1981) or food for Crustacea (e.g., Kain and Norton, 1990), Wicksten (1993: p. 320) mentioned that red algae would be “distasteful” and Kain and Norton (1990: p. 394) noted that “many red algae contain a variety of potentially distasteful substances”. Interestingly, the latter authors also mentioned that corallinacean red algae have the most effective physical defense against being punctured and consumed because of the tough outermost part of the thallus, which is why these red algae are very resistant to grazing. These are exactly the types of red algae that are abundantly present at this site. Thus, this particular site may not have provided as much food as did other parts of the reef, possibly explaining why decapods were largely absent here. Fewer possibilities of shelter as a reason for the lack of decapods seems unlikely because a high decapod diversity can be found at site 13 where not many possibilities for shelter were present either.

5.4.4. Decapods in the Olazagutía quarry

In 2009 and 2010, the Olazagutía quarry (Fig. 2) was visited and a reef core consisting mostly of a very dense cover of massive colonial corals and orbitolinid foraminifera was discovered (Fig. 11). Other common fossils were bryozoans and echinoid fragments, whereas bivalves, brachiopods, algae and serpulids were rarer. No decapods were found upon inspection of the surfaces exposed after 1 h, suggesting that decapod abundance is low here. This can be easily explained by the dense, inaccessible nature of the coral framestone, leaving few places as shelter for decapods. The only decapod remains were found adjacent to this framestone in wackestones.

5.5. On sub- and microenvironments

Most diversity measures show that site 17 is more diverse than other sites. Additionally, the taxonomic composition is also different from all other sites, the size of decapod specimens appears smaller, and some species are exclusively found at this site. This suggests that the southernmost part of the quarry containing in situ corals, is a different sub-environment within the reef, at least for decapods, compared to the sites found in the floatstone zone. The taxonomic composition of the decapods at site 13 is also different from all other sites. In addition, the decapods are larger in size. Thus, site 13 might represent a different microenvironment within the floatstone zone sub-environment compared to the decapods found at sites 23 and 25. Site 13 did, however, not yield unique species unknown from other sites, whereas site 17 did. The northern part of the quarry may be considered a separate subenvironment as well given the different lithology and the scarcity of decapods. This applies also to the reef core of the Olazagutía quarry.

Fig. 11. The darker layers in the center represent the reef core of the Aldoirar patch reef as exposed in the Olazagutía quarry. This photo, taken toward the north, is directed approximately perpendicular to the strike of the southerly dipping layers.

5.6. On obligatorily associated decapods

Patton (1994), in a study of decapods from the Great Barrier Reef, referred to taxa found only on living *Acropora* as "obligate associates" of that coral. Furthermore, Bruce (1998) noted that almost all shrimp were obligate associates of scleractinian corals in the Indo-West Pacific. Abele (1976) provided quantitative data on obligatorily associated decapods for a Pacific *Pocillopora damicornis* habitat in Panama. He noted that 15% of the decapod species were obligatory associates with *Pocillopora*. In terms of specimens, 28% of the specimens were obligatory associates including the 4th through 6th most abundant species. Furthermore, 27% of the decapods appeared to be obligatory associates with corals off the coast of West Australia (Black and Prince, 1983, see also their Table 2), and an online database on extant Central Pacific decapods (http://decapoda.free.fr) showed that 76/222 (=34%) of all coral associated decapods were obligatory associates of corals. Patton (1977: p. 16) suggested that decapod–coral associations may have originated with small species feeding on the sediment that settled on the coral and coral mucus, secreted to remove the sediment.

Since many decapods are known to be obligatory associates of corals today, this type of behavior may also be expected to have been present in the past. Therefore, decapod remains of those fossil species should only be found on or in the very close proximity of the corals and be small sized, in accordance with extant decapods that are obligatory associates with corals. This behavior is not well-known from the Mesozoic, but perhaps better from the Cenozoic. Some possible exceptions are known from the Mesozoic. Schweitzer and Feldmann (2009b) noted that one specimen of *Cyclothyreus cardiacus* Schweitzer and Feldmann, (2009b), was closely associated with corals and suggested that it may have lived on or near the coral heads. The specimen from the Late Jurassic (Tithonian) Štramberk Limestone of the Kotouč Quarry in the Czech Republic is 10.4 mm long and 13.4 mm wide. Müller et al. (2000: p. 67) speculated that small, Late Jurassic prosopid crabs from Germany and the Czech Republic may have used the reef as a shelter and possibly would have lived in symbiosis with corals ("commensalism?"). Furthermore, a close association of Late Jurassic (Oxfordian) decapods from Poland with sponge-microbial reefs was postulated by Müller et al. (2000) and Krobicki and Zatoń (2008) as many crabs were discovered in cavities of the reef framework. Cenozoic representatives from the often coral-associated members of the Palaemonidae and Xanthidae are also known (see Schweitzer et al., 2010), but coral-associated examples from the Mesozoic are unknown with the possible exception of the ?xanthid *Cretichlorodius enciensis* Fraaye, 1996, from the Maastrichtian Maastricht Formation (Meerssen Member) of the Netherlands. Members of the coral-associated Trapeziidae have been found in the fossil record dating back to the Eocene (see Schweitzer, 2005; Schweitzer et al., 2010). Unfortunately, members of the coral-inhabiting, millimeter sized Hapalocarcinidae (e.g., Shen, 1936; McCain and Coles, 1979) are not known from the fossil record (see Schweitzer et al., 2010).

Site 17 from the Koskobilo quarry may provide more insight into decapods that are obligatory associates with corals as this site contains a branching framework of in situ corals, unlike other decapod-rich sites from this quarry. Unfortunately, the extant families containing the coral-associated decapod species as mentioned above were not present, which does not exclude the possibility of obligatorily associated decapods at site 17. Diminutive decapods found exclusively at this site may be obligate associates as small sized decapods can more easily access the dense framework of corals and can more easily find a place to retreat into cavities in corals and the branching framework. In terms of size, Patton (1994: Table 2) found that the largest mean length of adult shrimp species was 19 mm and 12 mm for the mean width for the largest adult crab species based on a collection of obligatorily associated decapods from the Great Barrier Reef. Based on all species found at the different sites when collections from 2009 and 2010 are merged (Table 5), *Cretamaja granulata* Klompmaker, 2013, *Koskobilius postangustus* Klompmaker, 2013, *Navarrahomola hispanica* Artal et al., 2012, *Navarradromites pedroartali* Klompmaker et al., 2012b, *Hispanigalathea pseudoleavis* Klompmaker et al., 2012a, and *Etyxanthosia fossa* (Wright and Collins, 1972) were found exclusively at site 17. The majoid *C. granulata* is quite large for an obligatory associate with a maximum width of 11.3 mm (see Klompmaker, 2013). The smaller *K. postangustus* may not be an obligatory associate either as Breton (2009: p. 513) noted that "most living majoids are not known to have a cryptic habitat". Moreover, the first described priscinachid was not mentioned to be associated with corals (Breton, 2009). On the other hand, Black and Prince (1983) noted that the majid *Menaethius monoceros* (Latreille, 1825), is a facultative symbiont on the coral *Pocillopora damicornis* off the coast of West Australia, and Patton (1977: p. 18) mentioned some majid-coral associations. Furthermore, Glynn (1963) noted that the Caribbean majid *Mithrax sculptus* Lamarck, 1818, fed on the polyps of *Porites furcata*. This species can be as large as 5 cm. Thus, the possibility of the obligatory association of the two Spanish priscinachid species with corals cannot be excluded. *Etyxanthosia fossa* was also found in the Cenomanian sands of England (Wright and Collins, 1972), in the calcareous sandstones and chalks of the Cenomanian of France (Breton and Collins, 2011), and in the Albian reef limestones of Monte Orobe in Spain (Fraaije et al., 2008). Therefore, Klompmaker et al. (2011a) concluded that *E. fossa* inhabited a wide variety of environments. Hence, it cannot be considered an obligatory associate with corals. The goniodromitid *N. pedroartali* is represented by some relatively large specimens (width range 2.3–9.0 mm, see Klompmaker et al., 2012b). Members of the goniodromitid family are, however, often associated with coral reef deposits (e.g., Klompmaker et al., 2012b). As for the latter species, the homolid *N. hispanica* is a species with quite a large maximum size (width ranges from 7.7 to 15.1 mm), and, therefore may not have been obligatorily associated with corals. Extant homolids live primarily in deep waters (Guinot and Richer de Forges, 1995: Fig. 76; Schweitzer et al., 2004), and, thus, are unlikely to be associated with corals. Homolids probably moved early on in their evolutionary history into deeper water as Schweitzer et al. (2004) noted that Cenozoic homolids are rare. Indeed, Cretaceous homolids are quite commonly encountered in shallow water sediments, where they inhabited a variety of environments including some coral reef environments (see Collins, 1997). Since specimens of *N. hispanica* were also encountered in other parts of the quarry (P. Artal, pers. comm. January 2012), *N. hispanica* cannot be considered an obligatory associate with corals. *Hispanigalathea pseudolaevis* could be the most likely candidate to be an obligatory associate with corals, as Patton (1977), citing Johnson (1970), noted that at least several extant species of galatheids and porcellanids are obligatory associates with living corals in the Singapore region. Moreover, specimens of *H. pseudolaevis* are small sized (2.0–3.0 mm width range, see Klompmaker et al., 2012a). Even though hermit crabs have been found primarily at site 17, especially *Mesoparapylocheles michaeljacksoni*, they have also been found at other sites that do not contain in situ corals (Table 5). Therefore, they are not likely to have been obligatory associates of corals, but merely species which often occur near or on the corals and were also able to survive in other areas of the reef. In conclusion, only a few, uncommon species found at the Koskobilo quarry (4/36, 11%) may have been obligatorily associated with corals, which could indicate that this behavior had not fully developed yet in the mid-Cretaceous. In turn, this may suggest that decapods in reefs were less vulnerable to extinction at that time.

5.7. Decapod widths

Surprisingly few large decapods were found at site 17 as shown in the results. This is, in part, due to a different decapod species composition of the fauna as a relatively large number of specimens of species with a small maximum width were found at site 17. Examples are *Eomunidopsis navarrensis* (width range based on all sites collected from in 2010 = 2.0–10.5 mm; median (m) = 4.4 mm; n = 68), *Paragalathea ruizi* (width range = 1.9–6.1 mm; m = 3.4 mm; n = 33), and *Mesoparapylocheles michaeljacksoni* (width range = 2.5–5.2 mm; m = 3.5 mm; n = 8). Specimens of species with a large maximum size, such as *Graptocarcinus texanus* (width range = 3.4–27.9 mm; m = 11.5 mm; n = 26) and *Distefania* spp. (width range = 2.4–48.5 mm; m = 14.5 mm; n = 17) comprise only a small part of the fauna at this site.

A special case is *Goniodromites laevis*, specimens of which have a maximum width up to 20.9 mm when all samples are merged. This species is common at site 17 (10 out of 86 specimens). However, the specimens at site 17 seem relatively small compared to other sites (width range site 17 = 4.1–9.7 mm; m = 5.3 mm; n = 9 (10th measurement could not be made due to incomplete preservation of the specimen) versus width range of sites 13, 23, and 25 = 3.9–20.9 mm; m = 10.0 mm; n = 29). This was confirmed by the Kruskal–Wallis test and subsequent Mann–Whitney comparison tests, although sample size was low for all sites with the exception of site 13. With the inclusion of more specimens, the hypothesis that specimens of *G. laevis* are juveniles at site 17, where the protection from the corals be used, could be better supported. If found correct, then this habitat with many branching corals may have served as a nursery for juveniles. This was also suggested for extant fish. Costello et al. (2005: p. 793) indicated that modern deep-water coral reefs "may act as a nursery habitat" for fish, suggesting that juveniles were protected by the corals.

In conclusion, the decapods at site 17 are small because of the abundant presence of species with a small maximum width and the relative rarity of species with a large maximum width, but also because of the common presence of possible juvenile specimens of *G. laevis*. Thus, decapod size can vary within a reef environment.

Decapod size may also vary across environments. A small size of decapods within fossil coral reefs has been suggested qualitatively by other workers. Müller (2004: p. 240) remarked that, "reef-dwelling decapods are generally small sized", which was supported by Gatt and De Angeli (2010). The average size of anomuran and brachyuran decapods in the Maastrichtian type area in the Netherlands is reported to be less than 10 mm (Fraaije, 2003a). Furthermore, Müller et al. (2000: p. 67) mentioned that "for the small forms of prosopids living or finding a shelter in reef cavities was probably a defense mechanism against predators, especially when crabs were losing their carapaces in molt periods". Additionally, Müller et al. (2000: p. 65), referring to Wehner (1988), noted for Late Jurassic (Kimmeridgian) prosopid crabs from southwestern Germany that "small crabs may sometimes be found within the center of massive *Thecosmilia* corals because the small Jurassic prosopids could probably find a refuge". Although the decapod-rich fauna from the Lower Cretaceous (Albian) Glen Rose Limestone (Bishop, 1983) was not directly associated with a dense coral cover, Bishop (1986b) reported the limestones in which the numerous decapods were found to represent back-reef carbonates. He also noted that decapods were small.

The small size is also true for decapods in modern coral reefs. Abele (1976) studied decapod communities of several habitats in Panama including sandy beaches, mangrove swamps, rocky intertidal habitats, and a *Pocillopora damicornis* coral habitat. He (p. 271) noted that "the adult size of species of the coral community is greatly reduced compared to that of other habitats. The mean carapace length of sexually mature adults of 80% of the fauna is 5.4 mm (range 1.7 to 9 mm). This is significantly smaller than the mean size of species in other habitats (11 to 41 mm)". The mean carapace width of specimens found at the coral-rich site 17 of the Koskobilo quarry is 5.1 mm, which is comparable to the results of Abele (1976). A similar size pattern was found by Reaka (1986) for other crustaceans, stomatopods. Reef species had a smaller adult body size than those in level-bottom environments. Further, Reaka-Kudla (1991) suggested that bioeroded holes were an important factor in the evolution of diversity in coral reefs as the cryptofauna that can hide in those holes tends to be of limited size, have a limited dispersal, and, hence, a high rate of evolution. Thus, crustacean size may depend on the habitat today and in the past. Whether the decapods from the Aldoirar patch reef differ in size from decapod faunas collected at other, non-reef environments in the same region is not known due to the scarcity of decapods from these other environments. Future work may elucidate this.

6. Conclusions

This study on mid-Cretaceous (late Albian) decapod crustaceans from the Koskobilo quarry in northern Spain can at least in part explain the occurrence of this highly diverse, coral-associated decapod fauna. Decapod diversity and composition differ among decapod-rich sites. The most diverse decapod fauna was found in the southernmost, stratigraphically youngest part of the quarry consisting of coral-rich boundstones and biolithites and also contained some species unknown from other sites within the quarry. The decapods here could have experienced an increased possibility for shelter and food. The decapods found at this part of the quarry seem to exhibit the smallest width compared to decapod-rich sites found in the floatstones and biosparites. These other decapod-rich sites show lower decapod diversities and different compositions. One site within the floatstone and biosparite zone contained hardly any decapods, which may be related to the abundant presence of hard-to-eat corallinacean red algae. The lowest decapod diversity was found to be present in the northern, stratigraphically oldest part of the quarry consisting of wackestones and biomicrites. This is one of the first times that such a detailed paleoecological study was performed for decapods in a fossilized coral reef. These results concur with results from modern reefs in that decapod communities also differ among subenvironments. The diversity in these decapod faunas is likely greater in reef environments relative to contemporaneous non-reef environments as a result of the greater number of niches present, a result consistent with the ecological “species-sorting hypothesis”. The methodologies introduced herein for studying fossil decapods in reef environments can be used as well to study the paleoecology of decapods and other invertebrates from other periods in Earth's history.

Supplementary data (Appendices A-C) to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2013.01.024.

Acknowledgments

Rodney Feldmann, Carrie Schweitzer, Ferenc de Szalay, and Chris Blackwood (all Kent State University, Kent, Ohio, USA) are all thanked for advice and constructive criticism. The Cementos Portland Valderrivas company is thanked for access to the Koskobilo quarry and for providing maps. For assistance in the field, Pedro Artal (Museo Geológico del Seminario de Barcelona, Barcelona, Spain), Barry van Bakel (Oertijdmuseum De Groene Poort, Boxtel, The Netherlands; and Naturalis Biodiversity Center, Leiden, The Netherlands), Petra van Bakel, Thea van Boom, Yvonne Coole, and René Fraaije (Oertijdmuseum De Groene Poort) are thanked. Thanks also to John Starmer and Alexis Rojas (Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA) for proving useful literature. The comments of two anonymous reviewers are much appreciated. This research was in part supported by a Molengraaff Fonds, an Amoco Alumni Scholarship, a Kent State University Graduate Student Senate research grant, a Sigma Gamma Epsilon (Gamma Zeta Chapter) research grant, and the Jon L. and Beverly A. Thompson Endowment Fund to Klompmaker, and by an NSF grant EF-0531670 to Feldmann and Schweitzer. This is University of Florida Contribution to Paleobiology 654.

References

Abele, L.G., 1974. Species diversity of decapod crustaceans in marine habitats. Ecology 55, 156–161.

Abele, L.G., 1976. Comparative species composition and relative abundance of decapod crustaceans in marine habitats of Panama. Marine Biology 38, 263–278.

Abele, L.G., 1979. The community structure of coral-associated decapod crustaceans in variable environments. In: Livingston, R.J. (Ed.), Ecological Processes in Coastal and Marine Systems. Plenum, New York, pp. 165–187.

Artal, P., Van Bakel, B.W.M., Fraaije, R.H.B., Jagt, J.W.M., Klompmaker, A.A., 2012. New Albian–Cenomanian crabs (Crustacea, Decapoda, Podotremata) from Monte Orobe, Navarra, northern Spain. Revista Mexicana de Ciencias Geológicas 29, 398–410.

Austin, A.D., Austin, S.A., Sale, P.F., 1980. Community structure of the fauna associated with the coral *Pocillopora damicornis* (L.) on the Great Barrier Reef. Australian Journal of Marine & Freshwater Research 31, 163–174.

Barron, E.J., Washington, W.M., 1982. Cretaceous climate: a comparison of atmospheric simulations with the geologic record. Palaeogeography, Palaeoclimatology, Palaeoecology 40, 103–133.

Barron, E.J., Fawcett, P.J., Peterson, W.H., Pollard, D., Thompson, S.L., 1995. A simulation of mid-Cretaceous climate. Paleoceanography 10, 953–962.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R., Guilhaumon, F., Missa, O., Novotny, V., Ødegaard, F., Roslin, T., Schmidl, J., Tishechkin, A., Winchester, N., Roubik, D., Aberlenc, H.-P., Bail, J., Barrios, H., Bridle, J., Castaño-Meneses, G., Corbara, B., Curletti, G., Duarte da Rocha, W., De Bakker, D., Delabie, J., Dejean, A., Fagan, L., Floren, A., Kitching, R., Medianero, E., Miller, S., Gama de Oliveira, E., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S., Roisin, Y., Schmidt, J., Sørensen, L., Leponce, M., 2012. Arthropod diversity in a tropical forest. Science 338, 1481–1484.

Belka, Z., 1998. Early Devonian kess–kess carbonate mud mounds of the eastern Anti-Atlas (Morocco), and their relation to submarine hydrothermal venting. Journal of Sedimentary Research 68, 368–377.

Bell, T., 1863. A monograph of the fossil malacostracous Crustacea of Great Britain, Pt. II, Crustacea of the Gault and Greensand. Palaeontographical Society Monograph, London 1–40 (11 pls).

Bishop, G.A., 1983. Fossil decapod crustaceans from the Lower Cretaceous, Glen Rose Limestone of central Texas. Transactions of the San Diego Society of Natural History 20, 27–55.

Bishop, G.A., 1986a. Taphonomy of the North American decapods. Journal of Crustacean Biology 6, 326–355.

Bishop, G.A., 1986b. Occurrence, preservation, and biogeography of the Cretaceous crabs of North America. In: Gore, R.H., Heck, K.L. (Eds.), Crustacean Biogeography. A. A. Balkema, Rotterdam, The Netherlands, pp. 111–142.

Black, R., Prince, J., 1983. Fauna associated with the coral *Pocillopora damicornis* at the southern limit of its distribution in western Australia. Journal of Biogeography 10, 135–152.

Bouvier, E.L., 1898. Sur quelques Crustaces anomoures et brachyures recueillis par M. Diguet en Basse-Californie. Bulletin du Muséum d'Histoire naturelle Paris 4, 371–384.

Breton, G., 2009. Description of *Priscinachus elongatus* n. gen., n. sp., and Priscinachidae n. fam. for the earliest spider crab (Crustacea, Decapoda, Majoidea), from the French Cretaceous (Cenomanian). Geodiversitas 31, 509–523.

Breton, G., Collins, J.S.H., 2011. New and rare Cenomanian crabs (Crustacea, Decapoda, Brachyura) from the Paris Basin (France), and a comparison with necrocarcinids, etyids and dynomenids from Devon (England). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 260, 141–156.

Bruce, A.J., 1998. New keys for the identification of Indo-West Pacific coral associated pontoniine shrimps, with observations of their ecology (Crustacea: Decapoda: Palaemonidae). Ophelia 49, 29–46.

Chao, A., 1984. Nonparametric estimation of the number of classes in a population. Scandinavian Journal of Statistics 11, 265–270.

Coldwell, R.K., 2009. EstimateS: statistical estimation of species richness and shared species from samples. Version 8.2.0. User's guide and application. Published at: http://purl.oclc.org/estimates.

Collins, J.S.H., 1997. Fossil Homolidae (Crustacea; Decapoda). Bulletin of the Mizunami Fossil Museum 24, 51–71.

Collins, J.S.H., Wierzbowski, A., 1985. Crabs from the Oxfordian sponge megafacies of Poland. Acta Geologica Polonica 35, 73–88.

Collins, J.S.H., Fraaye, R.H.B., Jagt, J.W.M., 1995. Late Cretaceous anomurans and brachyurans from the Maastrichtian type area. Acta Palaeontologica Polonica 40, 165–210.

Costello, M.J., McCrea, M., Freiwald, A., Lundalv, T., Jonsson, L., Brett, B.J., Van Weering, T.C.E., De Haas, H., Roberts, J.M., Allen, D., 2005. Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: Freiwald, A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems. Springer-Verlag, Berlin/Heidelberg, Germany, pp. 771–805.

Desbonne, I., Schramm, A., 1867. Crustaces de la Guadaloupe d'apres un Manuscrit du … I. Desbonne compare avec les Échantillons de Crustaces de sa Collection et les dernifres Publications de M. M. H. de Saussure et W. Stimpson. I. Partie. Brachyures, 1–60.

Dunham, R.J., 1962. Classification of carbonate rocks according to depositional texture. In: Ham, W.E. (Ed.), Classification of Carbonate Rocks. American Association of Petroleum Geologists Memoir 1, 108–121.

Ďuriš, Z., 1992. On a small collection of Crustacea Decapoda from the Bellsund region, Spitsbergen. In: Repelewska-Pekalowa, J., Pekala, K. (Eds.), Wyprawy Geograficzne na Spitsbergen. UMCS, Lubin, Poland, pp. 121–154.

Edwards, A.J., Emberton, H.J., 1980. Crustacea associated with the scleractinian coral, *Stylophora pistillata* (Esper), in the Sudanese Red Sea. Journal of Experimental Marine Biology and Ecology 42, 225–240.

Embry, A.F., Klovan, J.E., 1971. A Late Devonian reef tract on Northeastern Banks Island, NWT. Canadian Petroleum Geology Bulletin 19, 730–781.

Flügel, E., 2004. Microfacies of Carbonate Rocks. Analysis, Interpretation and Application.Springer-Verlag, Berlin/Heidelberg, Germany.

Fluteau, F., Ramstein, G., Besse, J., Guiraud, R., Masse, J.P., 2007. Impacts of palaeogeography and sea level changes on Mid-Cretaceous climate. Palaeogeography, Palaeoclimatology, Palaeoecology 247, 357–381.

Folk, R.L., 1959. Practical petrographic classification of limestones. American Association of Petroleum Geologists Bulletin 43, 1–38.

Folk, R.L., 1962. Spectral subdivision of limestone types. In: Ham, W.E. (Ed.), Classification of Carbonate Rocks. American Association of Petroleum Geologists Memoir 1, pp. 62–84.

Fraaije, R.H.B., 2003a. Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area. Contributions to Zoology 72, 119–130.

Fraaije, R.H.B., 2003b. The oldest in situ hermit crab from the Lower Cretaceous of Speeton, UK. Palaeontology 46, 53–57.

Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M., Artal, P., 2008. New decapod crustaceans (Anomura, Brachyura) from mid-Cretaceous reefal deposits at Monte Orobe (Navarra, northern Spain), and comments on related type-Maastrichtian material. Annie V. Dhondt Memorial Volume: In: Steurbaut, E., Jagt, J.W.M., Jagt-Yazykova, E.A. (Eds.), Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 78, 193–208.

Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M., Klompmaker, A.A., Artal, P., 2009. A new hermit crab (Crustacea, Anomura, Paguroidea) from the mid-Cretaceous of Navarra, northern Spain. Boletín de la Sociedad Geológica Mexicana 61, 13–16.

Fraaije, R.H.B., Klompmaker, A.A., Artal, P., 2012a. New species, genera and a family of hermit crabs (Crustacea, Anomura, Paguroidea) from a mid-Cretaceous reef of Navarra, northern Spain. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 263, 85–92.

Fraaije, R.H.B., Krzemiński, W., Van Bakel, B.W.M., Krzemińska, E., Jagt, J.W.M., 2012b. The earliest record of a diogenid hermit crab from the Late Jurassic of the southern Polish Uplands, with notes on paguroid carapace terminology. Acta Palaeontologica Polonica 57, 655–660.

Fraaije, R.H.B., Krzemiński, W., Van Bakel, B.W.M., Krzemińska, E., Jagt, J.W.M., 2012c. The earliest record of pylochelid hermit crabs from the Late Jurassic of southern Poland, with notes on paguroid carapace terminology. Acta Palaeontologica Polonica 57, 647–654.

Fraaije, R.H.B., Krzemiński, W., Van Bakel, B.W.M., Krzemińska, E., Jagt, J.W.M., in press. New Late Jurassic symmetrical hermit crabs from the southern Polish Uplands and early paguroid diversification. Acta Palaeontologica Polonica.

Fraaye, R.H.B., 1996. A new Tethyan migrant: *Cretachlorodius enciensis* n. gen., n. sp. (Crustacea, Decapoda), from the Maastrichtian type area. Journal of Paleontology 70, 293–296.

Freiwald, A., Roberts, J.M., 2005. Cold-Water Corals and Ecosystems. Springer-Verlag, Berlin/Heidelberg, Germany.

Gatt, M., De Angeli, A., 2010. A new coral-associated decapod assemblage from the Upper Miocene (Messinian) upper coralline limestone of Malta (central Mediterranean). Palaeontology 53, 1315–1348.

Glynn, P.W., 1963. Species composition of *Porites furcata* reefs in Puerto Rico with notes on habitat niches. Association of Island Marine Laboratories of the Caribbean, Fourteenth Meeting, Santo Domingo, 5, pp. 6–7.

Glynn, P.W., Stewart, R.H., McCosker, J.E., 1972. Pacific coral reefs of Panama: structure, distribution and predators. Sonderdruck aus der Geologischen Rundschau 61, 483–519.

Grajal, A.P., Laughlin, R.G., 1984. Decapod crustaceans inhabiting live and dead colonies of three species of *Acropora* in the Roques Archipelago, Venezuela. Bijdragen tot de Dierkunde 54, 220–230.

Guinot, D., Richer de Forges, B., 1962. Crustacea Decapoda Brachyura: révision de la famille des Homolidae De Haan 1839. In: Crosnier, A. (Ed.), Résultats des Campagnes MUSORSTOM 13. Mémoires du Muséum National d'Histoire Naturelle 163, 283–517.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4 (1), 1–9 (art. 4).

Hovland, M., 2008. Deep-Water Coral Reefs: Unique Biodiversity Hot-spots. Springer-Verlag, Berlin, Germany and Praxis, Chichester, Great Britain.

Insalaco, E., 1998. The descriptive nomenclature and classification of growth fabrics in fossil scleractinian reefs. Sedimentary Geology 118, 159–186.

Jakobsen, S.L., Collins, J.S.H., 1997. New Middle Danian species of anomuran and brachyuran crabs from Fakse, Denmark. Bulletin of the Geological Society of Denmark 44, 89–100.

Johnson, D.S., 1970. The Galatheidea (Crustacea: Decapoda) of Singapore and adjacent waters. Bulletin of the National Museum Singapore 35, 1–44.

Kain, J.M., Norton, T.A., 1990. Marine ecology. In: Cole, K.M., Sheath, R.G. (Eds.), Biology of the Red Algae. Cambridge University Press, Cambridge, Great Britain, pp. 377–422.

Klompmaker, A.A., 2013. Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: implications for Cretaceous decapod paleoecology. Cretaceous Research 41, 150–185.

Klompmaker, A.A., Artal, P., Van Bakel, B.W.M., Fraaije, R.H.B., Jagt, J.W.M., 2011a. Etyid crabs (Crustacea, Decapoda) from mid-Cretaceous reefal strata of Navarra, northern Spain. Palaeontology 54, 1199–1212.

Klompmaker, A.A., Artal, P., Fraaije, R.H.B., Jagt, J.W.M., 2011b. Revision of the family Gastrodoridae (Crustacea, Decapoda), with description of the first species from the Cretaceous. Journal of Paleontology 85, 226–233.

Klompmaker, A.A., Artal, P., Gulisano, G., 2011c. The Cretaceous crab *Rathbunopon*: revision, a new species and new localities. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 260, 191–202.

Klompmaker, A.A., Feldmann, R.M., Robins, C.M., Schweitzer, C.E., 2012a. Peak diversity of Cretaceous galatheoids (Crustacea, Decapoda) from northern Spain. Cretaceous Research 36, 125–145.

Klompmaker, A.A., Feldmann, R.M., Schweitzer, C.E., 2012b. A hotspot for Cretaceous goniodromitids (Decapoda, Brachyura) from reef associated strata of Spain. Journal of Crustacean Biology 32, 780–801.

Klompmaker, A.A., Feldmann, R.M., Schweitzer, C.E., 2012c. New European localities for coral-associated, Cretaceous decapod crustaceans. Bulletin of the Mizunami Fossil Museum 38, 69–74.

Krobicki, M., Zatoń, M., 2008. Middle and Late Jurassic roots of brachyuran crabs: palaeoenvironmental distribution during their early evolution. Palaeogeography, Palaeoclimatology, Palaeoecology 263, 30–43.

Latreille, P.A., 1825. Entomologie, ou histoire naturelle des crustaces, des arachnides et des insectes. Volume 10 in Encyclopèdie Méthodique. Histoire Naturelle.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7, 601–613.

Leinfelder, R.R., Werner, W., Nose, M., Schmid, D.U., Krautter, M., Laternser, R., Takacs, M., Hartmann, D., 1996. Paleoecology, growth parameters and dynamics of coral, sponge and microbialite reefs from the Late Jurassic. In: Reitner, J., Neuweiler, F., Gunkel, F. (Eds.), Global and Regional Controls on Biogenic Sedimentation. I. Reef Evolution. Research Reports Göttinger Arbeiten zur Geologie und Paläontologie, Sonderband 2, 227–248.

Leloux, J., 1999. Numerical distribution of Santonian to Danian corals (Scleractinia, Octocorallia) of Southern Limburg, the Netherlands. Geologie en Mijnbouw 78, 191–195.

Lewis, J.B., Snelgrove, P.V.R., 1990. Corallum morphology and composition of crustacean cryptofauna of the hermatypic coral *Madracis mirabilis*. Marine Biology 106, 267–272.

López-Horgue, M.A., Manterola, D.L., Caballero, J.I.B., 1996. Evolución sedimentaria del episodio mixto carbonatado-terrígeno del Albiense Superior-Cenomaniense Inferior entre Altsasu (Nafarroa) y Asparrena (Araba): la unidad Albéniz. Príncipe de Viana, Supplemento de Ciencias 14, 81–96.

Magurran, A., 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, New Jersey, USA.

Mapa Geologico de España, E. 1:50.000, Salvatierra, Segunda serie — Primera edición, 1978. Servicio de publicaciones, Ministerio de Industria, Madrid, Spain.

Martindale, R.C., Zonneveld, J.-P., Bottjer, D.J., 2010. Microbial framework in Upper Triassic (Carnian) patch reefs from Williston Lake, British Columbia, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 297, 609–620.

Martínez Iglesias, J.C., García Raso, J.E., 1999. The crustacean decapod communities of three coral reefs from the southwestern Caribbean Sea of Cuba: species composition, abundance and structure of the communities. Bulletin of Marine Science 65, 539–557.

Mastro, E., 1981. Algal preferences for decoration by the Californian kelp crab, *Pugettia producta* (Randall) (Decapoda, Majidae). Crustaceana 41, 64–70.

McCain, J.C., Coles, S.L., 1979. A new species of crab (Brachyura, Hapalocarcinidae) inhabiting pocilloporid corals in Hawaii. Crustaceana 36, 81–89.

McLaughlin, P.A., Lemaitre, R., 1997. Carcinization in the Anomura — fact or fiction? I. Evidence from adult morphology. Contributions to Zoology 67 (2), 79–123.

Mertin, H., 1941. Decapode Krebse aus dem Subhercynen und Braunschweiger Emscher und Untersenon. Nova Acta Leopoldina, Neue Folge 10, 149–263.

Müller, P., 2004. History of reef-dwelling decapod crustaceans from the Palaeocene to the Miocene with comments about Mesozoic occurrences. Földtani Közlöny 134, 237–255.

Müller, P., Collins, J.S.H., 1991. Late Eocene coral-associated decapods (Crustacea) from Hungary. Contributions to Tertiary and Quaternary Geology 28 (2–3), 47–92 (pls. 1–8).

Müller, P., Krobicki, M., Wehner, G., 2000. Jurassic and Cretaceous primitive crabs of the family Prosopidae (Decapoda: Brachyura) — their taxonomy, ecology and biogeography. Annales Societatis Geologorum Poloniae 70, 49–79.

Patton, W.K., 1977. Animal associates of living reef corals. In: Jones, O.A., Endean, R. (Eds.), Biology and Geology of Coral Reefs 3. Academic Press, New York, USA, pp. 1–36.

Patton, W.K., 1994. Distribution and ecology of animals associated with branching corals (*Acropora* spp.) from the Great-Barrier-Reef Australia. Bulletin of Marine Science 55, 193–211.

Reaka, M.L., 1986. Biogeographic patterns of body size in stomatopod Crustacea: ecological and evolutionary consequences. In: Gore, R.H., Heck, K.L. (Eds.), Biogeography of the Crustacea. Crustacean Issues, 4. Balkema Press, Rotterdam, The Netherlands, pp. 209–235.

Reaka-Kudla, M.L., 1991. Processes regulating biodiversity in coral reef communities on ecological vs. evolutionary time scales. In: Dudley, E.C. (Ed.), The Unity of Evolutionary Biology 1. Dioscorides Press, Portland, Oregon, USA, pp. 61–70.

Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 213, 543–547.

Roberts, J.M., Wheeler, A., Freiwald, A., Cairns, S., 2009. Cold-Water Corals. Cambridge University Press, Cambridge, Great Britain.

Robins, C.M., 2008. Systematics of the Late Jurassic members of the superfamily Galatheoidea Samouelle, 1819, from the Ernstbrunn Limestone of Ernstbrunn, Austria. Unpublished M.Sc. thesis, Kent State University, Kent, Ohio, 164 pp.

Robins, C.M., Feldmann, R.M., Schweitzer, C.E., 2013. Nine new genera and 24 new species of the Munidopsidae (Decapoda: Anomura: Galatheoidea) from the Jurassic Ernstbrunn Limestone of Austria, and notes on fossil munidopsid classification. Annalen des Naturhistorischen Museums in Wien (A) 115, 167–251.

Roemer, F.A., 1887. *Graptocarcinus texanus*, ein Brachyure aus der Kreide von Texas. Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie 1887, 173–176.

Ruiz De Gaona, M., 1943. Nota sobre crustáceos decápodos de la cantera del Monte Orobe (Alsasua). Boletín de la Real Sociedad Española de Historia Natural 40, 425–433.

Schäfer, W., 1972. Ecology and Palaeoecology of Marine Environments. University of Chicago Press, Chicago, USA and Oliver and Boyd, Edinburgh, Great Britain.

Schweitzer, C.E., 2005. The Trapeziidae and Domeciidae (Decapoda: Brachyura: Xanthoidea) in the fossil record and a new Eocene genus from Baja California Sur, Mexico. Journal of Crustacean Biology 25, 625–636.

Schweitzer, C.E., Feldmann, R.M., 2008. Revision of the genus *Laeviprosopon* Glaessner, 1933 (Decapoda: Brachyura: Homolodromioidea: Prosopidae) including two new species. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 250, 273–285.

Schweitzer, C.E., Feldmann, R.M., 2009a. Revision of the Prosopinae sensu Glaessner, 1969 (Crustacea: Decapoda: Brachyura) including 4 new families and 4 new genera. Annalen des Naturhistorischen Museums in Wien (A) 110, 55–121.

Schweitzer, C.E., Feldmann, R.M., 2009b. Revision of the genus *Cyclothyreus* Remĕs, 1895 (Decapoda: Brachyura: Dromioidea). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 253, 357–372.

Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H., Schweigert, G., 2010. Systematic list of fossil decapod crustaceans species. Crustaceana Monographs 10, 1–222.

Schweitzer, C.E., Nyborg, T.G., Feldmann, R.M., Ross, R.L.M., 2004. Homolidae De Haan, 1839 and Homolodromiidae Alcock, 1900 (Crustacea: Decapoda: Brachyura) from the Pacific Northwest of North America and a reassessment of their fossil records. Journal of Paleontology 78, 133–149.

Shen, C.J., 1936. Notes on the family Hapalocarcinidae (coral-infesting crabs) with description of two new species. Hong Kong Naturalist Supplement 5, 21–26.

Stimpson, W., 1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit W. Stimpson. Pars VII. Crustacea Anomura. Proceedings of the Academy of Natural Sciences of Philadelphia 10, 225–252.

Thomassin, B.A., 1974. Soft bottom carcinological fauna sensu lato on Tuléar coral reef complexes (S.W. Madagascar): distribution, importance, roles played in trophic food-chains and in bottom deposits. Proceedings of the Second International Coral Reef Symposium 1, 297–320.

Turley, C.M., Roberts, J.M., Guinotte, J.M., 2007. Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? Coral Reefs 26, 445–448.

Van Bakel, B.W.M., Fraaije, R.H.B., Jagt, J.W.M., Artal, P., 2008. An unexpected diversity of Late Jurassic hermit crabs (Crustacea, Decapoda, Anomura) in Central Europe. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 250, 137–156.

Van Straelen, V., 1940. Crustacés Décapodes nouveaux du Crétacique de la Navarre. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 16 (4), 1–5 (pl. 1).

Van Straelen, V., 1944. Anomure et Brachyures du Cénomanien de la Navarre. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 20 (25), 1–12 (pl. 1).

Vía Boada, L., 1981. Les crustacés décapodes du Cénomanien de Navarra (Espagne): premiers résultats de l'étude des *Galatheidae* [sic]. Geobios 14, 247–251.

von Meyer, H., 1857. Briefliche Mitteilungen. Jahrbuch für Mineralogie, Geologie, Geognosie und Petrefaktenkunde 1857, 556.

Wehner, G., 1988. Über die Prosoponiden (Crustacea, Decapoda) des Jura. Ph.D. Dissertation, Ludwig-Maximilians-Universität, München, 154 p., 8 pls., 1 insert.von Meyer, H., 1857. Briefliche Mitteilungen. Jahrbuch für Mineralogie, Geologie, Geognosie und Petrefaktenkunde 1857: 556.

Wendt, J., Belka, Z., Kaufmann, B., Kostrewa, R., Hayer, J., 1997. The world's most spectacular carbonate mud mounds (Middle Devonian, Algerian Sahara). Journal of Sedimentary Research 67, 424–436.

Whittaker, R.H., 1962. Classification of natural communities. The Botanical Review 28, 1–239.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251.

Wicksten, M.K., 1978. Attachment of decorating materials in *Loxorhynchus crispatus* (Brachyura, Majidae). Transactions of the American Microscopical Society 97, 217–220.

Wicksten, M.K., 1993. Review and a model of decorating behavior in spider crabs (Decapoda, Brachyura, Majidae). Crustaceana 64, 314–325.

Wood, R., 1998. The ecological evolution of reefs. Annual Review of Ecology and Systematics 29, 179–206.

Wright, C.W., Collins, J.S.H., 1972. British Cretaceous crabs. Monograph of the Palaeontographical Society London 126, 1–113.

http://decapoda.free.fr (Accessed 10 July 2012).

Appendix 1. Results counting 100 spots in thin section.

	site 2	5	7	8	10	11	24a	24b	23a	23b	13a	13b	25a	25b	14	17a	17b	19	22
micrite	51	52	46	2	43	12	3	46	6	11	20	3	7	1	61	26	36	40	68
intramicrite or fecal pellets	3	15	23	57		14	3	6	2	3	29	13	7	2	21			1	16
sparite	1	8	8	40	13	40	77	6	56	39	22	53	51	52	4			27	1
intraclast					1	17	3		7	20		14	9	8	2				
vug	2	2	8	1	2	1				5	2	2	1			2	2		
recrystallized calcite or calcite vein	17		1			1									1	43	26		
stylolite	1																		
hematite	1		4																
fossil indet.	21	15	7		21	12	5	28	21	15	14	11	14	3	9	17	17	17	14
foram		1	3																1
mollusk or brachiopod	1										3	2		1					
algae indet.										1	8			4					
rudist																	2		
coral													10	17		9	16		
mollusk											1								
bivalve		1																	
green algae		1										1		1					
sponge		1			19		3	3			1							13	
bryozoa		2						1	1							1		2	
echinoderm	2	1				2	1	2	1	2		1		4	2	1			
brachiopod		1																	
orbitolinid									3	4			1						
red algae						1	5	2						7			1		
gastropod									2										
ostracod																1			
crinoid					1														
sponge or algae								6											
?decapod									1										

Appendix 2. Decapod widths (in mm) per site after systematic collecting in 2010.

	locality 13 (decapod widths in mm)										
Caloxanthus paraornatus	6	5.0	6.1								
Eodromites grandis	6.5										
Eomunidopsis navarrensis	11	10.0	5.5	8.4	3.4	5.2	2.4	1.7	6.2		
Eomunidopsis orobensis	5.6	6.1	7.9	3.8	4.3	4.4					
Gastrodorus cretahispanicus	3.5										
Goniodromites laevis	14	14.0	6.1	13.8	12.8	12.3	8.2	5.3	10.0	14.7	13.4
	5.3	20.9	8.8	9.3	14.4	15.5	9.8	15.6	4.1	9.4	6.9
Graptocarcinus texanus	14	27.9	14.0								
Laeviprosopon hispanicum	4.8										
Laeviprosopon sp.	7.1										
Navarrara betsieae	4.9										
Distefania incerta	32	22.0	10.4	15.1							
Distefania sp.	31										
Paragalathea ruizi	6	4.2									
Galatheoid	5.9										
Cretatrizocheles olazagutiensis	3.6										
AVG	10.0										
STDEV	6.7										
Number of specimens	57										

	locality 17 (decapod widths in mm)											
Annuntidiogenes worfi	1.5											
Caloxanthus paraornatus	4.7	5.2										
Eodromites grandis	2.1	7.1	13.5	4.1								
Navarradromites pedroartali	3.4											
Eodromites grandis or Navarradromites pedroartali	11.0	5.2										
Eomunidopsis navarrensis	4.1	4.8	3.5	5.9	2.4	6.0	2.5	6.1	6.5	2.9	4.0	6.6
	6.2	4.2	3.4	4.3	4.1	6.4	6.7	3.0	3.2	3.6	7.3	2.6
Eomunidopsis orobensis												
Hispanigalathea pseudolaevis	2.5											
Gastrodorus cretahispanicus												
Glyptodynomene alsasuensis	7.8											
Goniodromites laevis	4.1	7.6	5.3	8.2	4.3	4.3	9.7	4.1	8.9			
Graptocarcinus texanus	11.8	10.0										
Viaia robusta	10.5											
Navarrahomola hispanica	10.1											
Laeviprosopon hispanicum	1.4											
Laeviprosopon edoi												
Laeviprosopon crassum	10.4											
Laeviprosopon sp.												
Navarrara betsieae												
Distefania incerta	4.1											
Distefania sp.												
Paragalathea ruizi	2.2	2.5	2.6	4.9	3.8	3.4	3.4	3.7	2.2	4.3	6.1	2.2
	1.9	4.3	3.0	2.7	5.8	2.6	3.0					
Galatheoid												
Acareprosopon bouvieri	3.3	3.4										
Rathbunopon obesum	5.4	6.0										
Faksecarcinus koskobiloensis	20.1											

Mesoparapylocheles michaeljacksoni	4.7	5.2	3.0	2.5	3.7	3.2
Cretatrizocheles olazagutiensis	3.8	2.6				
AVG	5.1					
STDEV	3.0					
Number of specimens	84					

	locality 23 (decapod widths in mm)										
Caloxanthus paraornatus	4.6	6.6									
Eomunidopsis navarrensis	4.0	8.3	3.8	4.5	4.4	5.4	2.6	5.8	3.9	3.2	2.0
	5.3	2.4	2.9	9.4	6.8	3.4	4.9	7.4	6.0	5.6	2.9
	5.1	2.8	3.7	3.7							
Eomunidopsis orobensis	6.5										
Goniodromites laevis	5.4	6.5	13.8	3.9	14.4						
Graptocarcinus texanus	8.7	20.4	21.1	23.8	3.6	6.8	12.4	11.1	9.3	16.1	17.1
Laeviprosopon hispanicum	7.6	2.7									
Laeviprosopon edoi	3.5										
Distefania incerta	49	34.4	14.5	11.6	7.2	8.8					
Distefania sp.	2.4										
Paragalathea ruizi	4.1	4.2	3.5	2.6	5.9	3.4	4.1	2.6			
Acareprosopon bouvieri	3.7										
Rathbunopon obesum	7.1										
AVG	7.9										
STDEV	7.8										
Number of specimens	65										

	locality 25 (decapod widths in mm)									
Caloxanthus paraornatus	5.6									
Eodromites grandis	5	5								
Eomunidopsis navarrensis	5.9	4.4	4.1	6.2	4.2	4.8	4.9	2.3	3.1	
Eomunidopsis orobensis	5.6									
Glyptodynomene alsasuensis	9.8	12								
Goniodromites laevis	12	4.4								
Graptocarcinus texanus	5.2	3.4	4.7	10	21	11	12	4.5	10	19
Laeviprosopon hispanicum	4.1									
Distefania incerta	11	21	23	5						
Paragalathea ruizi	4.5	3.5	2.5	3						
Acareprosopon bouvieri	3.2	3.3								
Rathbunopon obesum	4									
Mesoparapylocheles michaeljacksoni	2.6	4.8								
AVG	7.2									
STDEV	5.4									
Number of specimens	41									

Appendix 3. Decapod widths (in mm) per site for *Goniodromites laevis* after the collections of 2009 and 2010 were merged.

site 13			**site 17**	**site 23**	**site 25**
12.8	7.5	15.6	5.5	10.7	8.6
11.7	11.7	4.1	6.1	11	7.9
13.6	8.9	9.4	4.1	5.4	12
14	10.7	6.9	7.6	6.5	4.4
6.1	15	13.4	5.3	13.8	9.8
13.8	10.8	7.4	8.2	3.9	4.8
12.8	8.2	15.3	4.3	14.4	8.6
12.3	4.3	4.9	4.3	15.7	
8.2	8.3	4.2	9.7	9	
5.3	8.9	10.4	4.1	5	
10	4.9	9.1	8.9	10.7	
14.7	11.1	22.4	5.7	6.4	
13.4	6.7	15	5.1	20.6	
5.3	9.3	17	4.6	17.1	
20.9	15.5	8.1	7.6	14.3	
8.8	9.7	12	5.9		
9.3	15.6	9.8			
14.4	5.7	15			
15.5	18.8				