ABSTRACT
Upper Jurassic coral communities of Portugal (Lusitanian Basin) grew despite high siliciclastic influx. Small, reef-rimmed carbonate platforms existed on basement uplifts over an extended period of time. Other reefs grew when the ambient reef complex changed to a siliciclastic domino reef complex. Various tectonic events caused sea level changes and siliciclastic influx. Reef growth and structure were controlled by tectonic factors and sedimentation. Sedimentation in the central part of the Lusitanian Basin was characterized by deposition of fine-grained sediments during sea level changes. In contrast, siliciclastic influx occurred laterally and simultaneously. Sediment distribution patterns and morphologic changes clearly show that Jurassic hermatypic corals had photosymbionts. However, their frequent occurrence within, or very close to, siliciclastic settings indicates that they could tolerate higher nutrient rates. The high density band ratio of Upper Jurassic reef corals even in very shallow, non-sediment-stressed reef settings.

INTRODUCTION
The Lusitanian Basin is an oceanic basin which heralded the opening of the northern Atlantic. The Upper Jurassic of the Lusitanian Basin is well-known for its fossil coral communities. The basin is characterized by a series of tectonic events that led to the formation of siliciclastic ramps and carbonate platforms. The basin contains a variety of coral communities, including hermatypic and non-hermatypic species. This diversity is due to the complex tectonic and paleoenvironmental processes that occurred during the Late Jurassic. The Lusitanian Basin is a major example of the interaction between tectonic forces and sedimentation processes.

METHODS
The study area is located in the central part of the Lusitanian Basin, where the Arruda sub-basin is situated. The Arruda sub-basin is characterized by a series of tectonic events that led to the formation of siliciclastic ramps and carbonate platforms. The basin contains a variety of coral communities, including hermatypic and non-hermatypic species. This diversity is due to the complex tectonic and paleoenvironmental processes that occurred during the Late Jurassic. The Lusitanian Basin is a major example of the interaction between tectonic forces and sedimentation processes.

![Fig. 1: Sketch map of the central part of the Lusitanian Basin showing the location of Late Jurassic sub-basins.](image-url)
Bioherms and biostromes within massive limestone dominated facies with minor amounts of marl often provided vertical profiles. Here, the reef morphology, faunal density and relationship between sediment and organisms could be studied in detail. Furthermore, the fauna could easily be counted on the exposed surface, perpendicular to the bedding plane.

These semiquantitative faunal collections and descriptions led to the differentiation of several coral communities characterizing the Upper Jurassic coral bearing strata of the Arruda sub-basin (Fig. 3). The Shannon-Wiener evenness-index was used for the evaluation of diversity (cf. Odum 1993). Both terms take into account the twofold character of diversity, species richness and dominance. Furthermore, the Shannon-Wiener index is independent of the sample size, which makes this index very suitable for the variable sized collections in the Arruda sub-basin ranging from 46 to 295 specimens.

THE UPPER JURASSIC CORALS AND CORAL COMMUNITIES OF THE ARRUDA SUB-BASIN

The coral fauna of the Arruda sub-basin is dominated by the following genera: Microsolenia; Calamophyllipsis; Thamnasteria; Convexastera; Comoseris; Ovalastrea; Axsamilla; Dermoaster; Dendroaster. The total number of coral species in the Lusitanian basin, determined and detected by Koby (1904-1905), Geyer (1955) and Noble (1955) is about 130 species. Within the Arruda sub-basin 12 coral communities could be distinguished: Thamnasteria-Ovalastrea; Microsolenia-Trocharea; Calamophyllipsis-Microsolenia; Convexastera-Calamophyllipsis; Convexastera-Dendroaster; Microsolenia-Enallhelia; Microsolenia-Actinastera-Lithophaga; Ovalastrea-Enallhelia; Microsolenia-Convexastera; Ovalastrea-Calamophyllipsis-Calamophyllipsis-community (Fig. 3).

RESPONSE OF UPPER JURASSIC CORALS TO ELEVATED SILICICLASTIC SEDIMENTATION RATES

Changes in sedimentation rate can be deduced from the occurrence and frequency of microbial crusts and other encrusting organisms (e.g. Tubiphytes, bryozoans, oysters, thecideinid brachiopods) and the clay content of reefs and coral communities as well as the nature of growth bands in scleractinian corals. Especially the clay content in combination with the degree of microbial encrustation is a useful tool for the estimation of sedimentation rates.

Reef settings undergoing elevated siliciclastic sedimentation are characterized by a high clay content and the almost lack of slow growing microbial encrustations and other microcrusts as well as borings.

Low siliciclastic sedimentation environments generally show a vigorous development of microbial crusts, leading to a pronounced relief of the reef bodies (Leinfelder et al. 1993b, Noble 1995).

<table>
<thead>
<tr>
<th>communities</th>
<th>diversity</th>
<th>Shannon-Wiener index</th>
<th>evenness</th>
<th>dominant species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thamnasteria-Ovalastrea</td>
<td>1,03±1,87</td>
<td>0,89</td>
<td>Microsolenia</td>
<td>22 %</td>
</tr>
<tr>
<td>Microsolenia-Trocharea</td>
<td>1,06±1,05</td>
<td>0,88</td>
<td>Microsolenia</td>
<td>40 %</td>
</tr>
<tr>
<td>Calamophyllipsis-Microsolenia</td>
<td>1,0</td>
<td>0,83</td>
<td>Microsolenia</td>
<td>30 %</td>
</tr>
<tr>
<td>Convexastera-Calamophyllipsis</td>
<td>1,0</td>
<td>0,95</td>
<td>Convexastera</td>
<td>35 %</td>
</tr>
<tr>
<td>Convexastera-Dendroaster</td>
<td>0,97</td>
<td>0,75</td>
<td>Convexastera</td>
<td>45 %</td>
</tr>
<tr>
<td>Microsolenia-Enallhelia</td>
<td>0,84</td>
<td>0,88</td>
<td>Microsolenia</td>
<td>30 %</td>
</tr>
<tr>
<td>Microsolenia</td>
<td>0,79</td>
<td>0,83</td>
<td>Microsolenia</td>
<td>40 %</td>
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<tr>
<td>Actinastera-Lithophaga</td>
<td>0,64</td>
<td>0,64</td>
<td>Actinastera</td>
<td>46 %</td>
</tr>
<tr>
<td>Ovalastrea-Enallhelia</td>
<td>0,61</td>
<td>0,72</td>
<td>Ovalastrea</td>
<td>58 %</td>
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<tr>
<td>Microsolenia-Convexastera</td>
<td>0,54</td>
<td>0,5</td>
<td>Microsolenia</td>
<td>51 %</td>
</tr>
<tr>
<td>Ovalastrea-Calamophyllipsis</td>
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<td>0,78</td>
<td>Ovalastrea</td>
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</tr>
<tr>
<td>Calamophyllipsis</td>
<td>low diversity</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 3: The coral communities of the Arruda sub-basin (Noble 1995).

Coral morphology

Upper Jurassic coral communities under siliciclastic stress were dominated by branching, phaceloid, dendroid and/or ramose morphotypes (e.g. Ovalastrea-Enallhelia, Microsolenia, Calamophyllipsis-community). The capability of branching forms to cope with elevated sedimentation rates was already described by Wijshman-Best (1972) for modern zevlid corals from New Caledonia and by Pflüger (1980) for Oligocene scleractinians from Italy. Fast growth rates and the ability to reject siliciclastic material make these forms resistant to elevated sedimentation. Among Upper Jurassic scleractinians, the fast growing phaceloid coral Calamophyllipsis (Werner 1986, Noble 1995), and some highly morphovariable forms like Microsolenia agariciformis and Thamnasteria lobata are well adapted to elevated sediment influx (Fig. 4.6).

Another striking feature of corals growing under constant siliciclastic influence is the type of growth banding. According to James and Bourque (1992), non-enveloped growth bands are indicative for elevated sedimentation rates. Under sedimentation stress, Thamnasteria lobata and Microsolenia agariciformis developed branched...
morphologies with distinct non-enveloping growth bands (Fig. 4, 5). Since such a type of stacked growth bands implies that the living coral surface was restricted to the uppermost growth band, the term 'pseudobranch' seems to be more appropriate (Nose 1995). Furthermore, it seems likely that these morphotypes were sticking in the sediment, judging by the non-enveloping character of growth bands and the almost lack of microbial encrustations. Hence, such forms were well adapted to settings characterized by constantly elevated sedimentation with soft bottom substrates.

Coral growth rates
Upper Jurassic scleractinians often show a distinct banding. In polished slabs, bright zones can be distinguished from darker zones. Although the corals are not primarily preserved, the microstructure is often still visible and allows the differentiation between low density bands (thinner septa, loosely spaced dissepiments or synaptycles) and high density bands (thicker septa, closer spaced horizontal elements) comparable to modern zoanthellate scleractinians. Therefore it is assumed that the banding in fossil scleractinians is due to annual growth increments, so that growth rates of Upper Jurassic scleractinians can be measured by the use of growth bands (cf. Ali 1984, Geister 1986, Insalaco 1996). Sometimes diagenetic alteration even emphasizes the band distinctness due to the more intensive recrystallization of the more porous low density band (cf. Ali 1984). Upper Jurassic growth rate data from Portugal were deduced from the following species: Thamnasteria lobata, Ph. concinna, Microsolen a agariciformis, Actinasteria crasso-ramosa (cf. Fig. 6). In accordance with the morphological strategy of Upper Jurassic scleractinians to cope with elevated sedimentation rates, the highest linear growth rate values were obtained by the branched and 'pseudobranch' morphotypes (up to 12 mm/year) growing under elevated siliciclastic influx, whereas the lowest growth rate values (ca. 1-2 mm/year) were shown by foliose and flat morphologies, which dominantly occur only under reduced sedimentation (Fig. 6).

Diversity
The Upper Jurassic shallowing upward succession from the Arruda sub-basin and the character of the accompanying fauna allow the bathymetric interpretation of reefs and even coral communities (Leinfelder et al. 1993, Werner et al. 1994, Nose 1995). Hence, also the diversities of the coral communities can be linked to certain bathymetric levels. In plotting the communities and diversities against water depth, it can be stated that within the euphotic zone the bathymetric position of the reefs and the coral communities is of no relevance for the diversity of the communities. High diversity communities occurred both in shallow inner ramp settings and in the transition of mid- to outer ramp settings (cf. Leinfelder et al. 1996). On the other hand, elevated siliciclastic or carbonate sedimentation rates are obviously the major control on diversity. High clay or carbonate mud content in combination with the almost lack of microbial encrustations indicative of elevated sedimentation rates are rather positively correlated with the occurrence of low diversity coral faunas (Fig. 7).
THE ROLE OF RELATIVE SEA LEVEL CHANGE

Relative sea level change is the major superimposed control on the distribution of the reefs and faunal communities within the Arruda sub-basin. Generally, reef growth in the Upper Jurassic is initiated and intensified during episodes of globally or regionally rising sea level. Episodes of pronounced reef growth are intimately linked to third order sea level rises, which reduced siliciclastic sedimentation and provided large shallow water shelf areas suitable for the widespread growth of moderate to high diversity coral reefs (e.g. Thamnasteria-Ovalastrea, Microsolena-Trocharea-community) (Fig. 8) (Leinfelder 1992a, b; Nose 1995).

In the highstand and early lowstand, siliciclastics and/or skeletal debris may be exported from inner ramp to mid- and outer ramp regions. Reef development is hampered by elevated sedimentation rates and strong skeletal debris accumulation in areas exposed to strong wave action. The fauna mostly exhibits moderate to low diversity coral communities (e.g. Microsolena-, Actinastrea-Lithophaga-, Calamophylophilosophia-community). An elevated sedimentation rate is responsible for both low diversity and the biostrome/meadow geometry of the reefs. Different sea level states are characterized by the growth of different coral communities. Hence, the occurrence and distribution pattern of Upper Jurassic coral communities from Iberia provide a tool for the interpretation of sea level fluctuations (Fig. 8) (Leinfelder et al. 1996).

IMPLICATIONS FOR SYMBIOTIC AND NUTRIENT STRATEGIES OF UPPER JURASSIC SCLERACTINIANS.

Modern scleractinians developed multiple feeding strategies. First, they are able to take up dissolved organic matter (DOM), second they are capable in feeding particulate organic material (POM). Third, they can live from the metabolic products of their symbionts and fourth, modern scleractinians can catch diverse preys with their tentacles and toxic nematocysts (Sorokin 1995). Since paleontologists and paleoecologists can only refer to the skeletal remains of the organisms, direct proofs for the feeding strategies of fossil scleractinians are missing. Nevertheless, out of morphological and microstructural features of fossil scleractinians, the feeding strategies can be indirectly evaluated.

The symbiosis with zooxanthellae, presumably developed in scleractinian corals in the Late Triassic (Norian) (Stanley 1981, 1988), is likely for many of the Upper Jurassic scleractinians. This assumption is based on the following observations:

(a) Shallow marine Upper Jurassic scleractinians mostly comprise highly integrated forms like meandroid and thamnasteriid calical types. High integration is assumed to be indicative for hermatypic zooxanthellate scleractinians in both modern and fossil reefs.
(Geister 1984, Coates and Jackson 1987, Riedel 1991). On the other hand, Stanley and Smart (1995) stated that isotopic measurements that even highly integrated thannasteroid corals from the Upper Jurassic from Poland may be zooxanthellate.

(b) Morphotypes of the Upper Jurassic scleractinians of Portugal exhibit a clear bathymetric zonation. Deeper water reefs, located in the transition of mid- to outer ramp settings show a clear dominance of foliose and flat morphotypes, which indirectly proves the symbiosis with photosymbiotic algae and the adaptation to reduced illumination (Fricke and Schuhmacher 1983, Bertling 1993, Nase 1995, Leinfelder et al. 1996).

(c) Besides the bathymetric zonation of morphotypes, a zonation of some coral species and coral communities is also visible (Nose 1995). Actinastrea cf. furcata, Actinastrea piriformis, Plesiastrea cf. schoepfeli and the Actinastrea-Lithophaga-community frequently only occurred in very shallow high energy waters, whereas Trochareas cf. gregorii and Tricycloseris cf. triangulavis as well as the Microsolenia-Trochareas-community are restricted to deeper mid ramp environments. Similar to the modern example, this bathymetric species and community zonation might be because of different light demands of Upper Jurassic scleractinians.

Growth rates of Upper Jurassic reef building scleractinians are much lower than the growth rates of their modern zooxanthellate counterparts, taking into account not only the reef settings affected by fine silicilastic material, which might show lower growth rates because of higher turbidity, but also the non-turbid, non-sediment stressed shallow marine settings with optimum conditions for reef growth (Fig. 9). Additionally the ratio of low density band thickness to high density band thickness in Upper Jurassic reef building scleractinians is much lower than in modern zooxanthellate scleractinians under comparable environmental parameters (warm shallow non-turbid waters) (Fig. 10). The low density band is considered to represent higher linear growth rates formed during episodes of high light availability. Light availability and hence the low to high density band ratio may decrease with increasing turbidity/sedimentation, latitude and water depth (Highton 1979, Wellington and Glyn 1983, Allison et al. 1996).

Because of both the generally lower growth rates and the lower low to high density band ratio, Upper Jurassic scleractinians apparently could not use light as efficiently as modern scleractinians for supporting skeletal growth (Leinfelder et al. 1996).

On the other hand it is assumed that Upper Jurassic reef building corals demanded more heterotrophic nutrition judging by the frequent occurrence within silicilastic settings with higher detrital nutrient supply. Here, the reefs exhibit the dominance of pennate forms (Microsolenia, Pseudoeris, Comoseris, Trochareas). Pennulae are thought to support a specialized gastrovascular system, like in the modern deeper water coral Leptoosorites fragilis, considerably improving heterotrophic feeding abilities (Insallaco 1996, Leinfelder et al. 1996).

CONCLUSIONS

Upper Jurassic coral reefs and coral communities grew despite a considerable silicilastic influx on a distally steepened mixed carbonate-silicilastic ramp system in the central Lusitanian Basin.

Elevated silicilastic sedimentation rates favour the growth of fast growing branching or 'pseudobranching' corals and considerably reduce diversity of coral communities.

Many highly integrated Upper Jurassic scleractinians presumably have photosymbionts, judging by the dominance of foliose morphotypes in deeper water settings and the bathymetric zonation of coral species and communities. On the other hand, the generally lower linear growth rates and low to high density band ratios in Upper Jurassic scleractinians compared with modern zooxanthellate scleractinians point to a lower efficiency of the symbiosis with zooxanthellae in Upper Jurassic reef building corals. The frequent occurrence within silicilastic settings and the shift to more pennate highly porous forms under silicilastic stress make it likely that a considerable proportion of energy had to be gained by heterotrophic nutrition.

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