Siliciclastic-carbonate ramp, a hostile world for carbonate shelf fauna? The example of the Givetian Ardenne Platform

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LETHAIA

The Givetian platform of the Ardennes Massif records several alternations between a siliciclastic-carbonate ramp and a carbonate shelf. Usually these depositional contexts are considered as a major disruption implying a perturbation of many ecological parameters. We established the impact of these variations on the biodiversity structure through the study of the trophic organisation. Thanks to a previous microfacies analysis, 550 levels of the Mont d'Haurs section in Givet and ten associated environments were precisely defined. Seven palaeotrophic levels are recognized from micropalaeontological data, including benthic, planktonic, heterotroph and autotroph organisms. The spatial and temporal distributions of these levels have been analysed through means of multivariate analyses. The statistic results show that the distribution of the palaeotrophic levels during periods characterized by a mixed ramp is not significantly different than during carbonate shelf influences. These environmental modifications do not affect the community-type. These results support recent studies performed on different benthic communities occurring in the Givetian of the Ardennes Massif. Indeed, trilobite and ostracod faunas of this period appear more affected by global environmental changes as the Kačák (uppermost Eifelian) and Taghanic (late middle Givetian) events. Moreover, along the proximal-distal transect on the platform, the reef constitutes the most singular environment. However, contrary with the Frasnian reefs of the Ardennes Massif, which consist of carbonate mud mounds laying on a deep mixed ramp, there is no trilobite community that appears restricted to Givetian reefs. Thus global bioevents during the Middle Devonian have a more important control on the biodiversity than the platform morphology. These results support the view that at wide scales (spatial and temporal), the biodiversity responds more positively to ecological disturbances. □ *Ardennes Massif, carbonate platforms, ecological dynamics, Middle Devonian, palaeotrophic levels, tropical shallow-water reef.*

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A mixed siliciclastic-carbonate ramp corresponds to a uniform slope from shoreline to the basin whereas a carbonate shelf presents a barrier reef leading to an important break in slope of the platform morphology (Wright & Burchette 1998). Consequently, the erection or the removal of a barrier constitutes a major disruption of the environment that may lead to the raise or the disappearance of communities. Indeed, reefs influence numerous environmental factors (see Harriot & Banks 2002 for a review), with the primary one the hydrodynamic closure since many biophysical parameters are associated to this factor (water residence time, nutrient recycling, turbidity, internal fluxes, nitrogen limitation; see Hatcher 1997). However, the fluctuations observed in community structure are depending of the spatial and temporal scales. Coral communities show a strong sensibility at small scales but they are more stable over broader ones. Indeed, it appeared in analyses considering scale over 10 000 years that reefal communities success to manage shorter ecological chaos (Pandolfi 2002, 2011).

The aim of this work is to evaluate the intensity of palaeoecological modifications between a mixed siliclastic-carbonate ramp and a carbonate shelf during the Middle Devonian. The historic section of the Givetian in the Ardennes Massif, i.e. the Mont d'Haurs section, is considered as example. Multivariate analyses herein are used on the distribution of palaeotrophic levels, as an alternative of the classical taxonomic works, to estimate the palaeoecological modifications.

The diversity of environments recorded during the Devonian of the Ardennes Massif makes this area

a model to study the late Palaeozoic reefal systems. During the Early Devonian, a siliciclastic influx, produced by the dismantling of the Old Red Sandstone continent, is deposited on this passive margin (Averbuch *et al.* 2005). A mixed siliciclastic-carbonate ramp is erected at the beginning of the Middle Devonian (Préat & Kasimi 1995; Kasimi & Préat 1996) due to a sea-level rise (Johnson *et al.* 1985). Reefal buildups are locally developed during the middle Eifelian (Mabille & Boulvain 2007) and a wide carbonate shelf appears at the beginning of the Givetian by a transgression implementation (Préat & Mamet 1989; Kasimi & Préat 1996). During the Frasnian, carbonate mud mounds are fixed on the deep parts of a mixed siliciclastic-carbonate ramp (Boulvain 2001). This wide range of environmental modifications is thus remarkable to understand the parameters leading to the carbonate factory (Boulvain *et al.* 2009).

Evaluating taxonomic variations is a typical method in palaeontology in order to assess the magnitude of environmental modifications. However, it is difficult to compare them directly because a decoupling exists between ecological and taxonomic changes (Droser *et al.* 2000), palaeoecological changes are not necessarily hierarchical and additive (Droser *et al.* 1997). From the guild concept of Root (1967) which 'is a group of species that exploit the same class of environmental resources in a similar way', Bambach (1983) introduces the adaptive strategies renamed thereafter 'Bambachian' megaguilds (Droser *et al.* 1997). Botquelen & Racheboeuf (2008) favour the term palaeotrophic levels because the mode of life of fossilised organisms is not always accessible. Between other characteristic signals, Droser *et al.* (1997) proposed four palaeoecological levels based on palaeotrophic level distributions. Several studies have successfully analysed the fluctuations of these groups in order to appreciate the strength of environmental modifications (Bonuso *et al.* 2002; Fraiser & Bottjer 2005; Botquelen *et al.* 2006; Lebold & Kammer 2006; McGhee *et al.* 2013).

The object of this study is to estimate if the carbonate shelf represents really a disruption for mixed ramp model. Firstly, the relative distribution of the palaeotrophic levels will be described for each environment of a proximal-distal transect, in the purpose to compare the environment organisation along two platform models. Secondly, a multivariate analysis will be used in order to reveal a possible trend in the palaeotrophic level distribution in relation with the platform model type.

Geological setting

The present work focuses on the Mont d'Haurs section at Givet, in the French Ardennes (Bignon & Crônier 2011). This historic section of the Givetian is located on the southwestern border of the Dinant Synclinorium (Fig. 1). Four lithostratigraphical formations are exposed (Fig. 2), restricted to the Lower and Middle Givetian (Bultynck & Dejonghe 2001). The Hanonet Formation is restrained to a Givetian age in this area, represents the last moments of the siliciclastic-carbonate ramp. Its upper limit corresponds to the transition with the carbonate shelf that flourishes during the Trois-Fontaines Formation (Casier *et al.* 2011a). This modification of the platform morphology is led by a local and gradual relative sea-level fall controlled by a tectonic forcing (Préat *et al.* 2007; Mamet & Préat 2009). The passage is not synchronous over the basin because of a structural control from tipped pluri-kilometric blocks (Mamet & Préat 2005). A brief recurrence of the mixed ramp is carried out during the Terres d'Haurs Formation (Casier *et al.* 2010, 2011b), related again to a synsedimentary tectonism and blocks faulting (Kasimi & Préat 1996; Mamet & Préat 2009) and/or to a cessation of the active role of the reefal barrier (Mamet & Préat 2007). A new regression helps to the development of new carbonate shelf facies at the beginning of the Mont d'Haurs Formation (Casier & Préat 2013).

Two platform models are suggested for the Mont d'Haurs section (Fig. 3 and see Sedimentology below), a mixed ramp and a carbonate shelf (Kasimi & Préat 1996; Hubert 2008a). However, many examples of transitional forms between these two models exist in the geological record (e.g. Srinivasan &
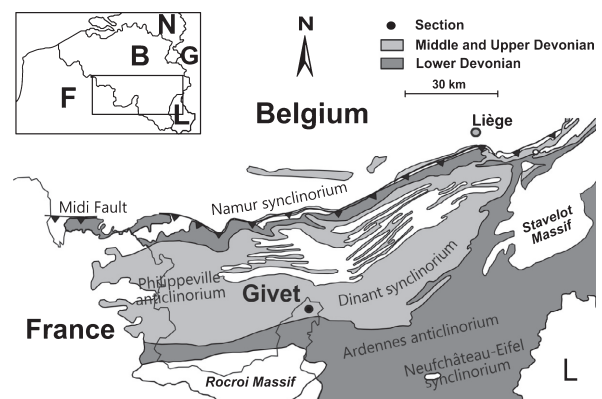

Fig. 1. Geological map of the Ardennes Massif with the location of the Mont d'Haurs section in Givet, modified after Crônier & van Viersen (2007); B, Belgium; F, France; G, Germany; L, Luxembourg; N, Netherlands.
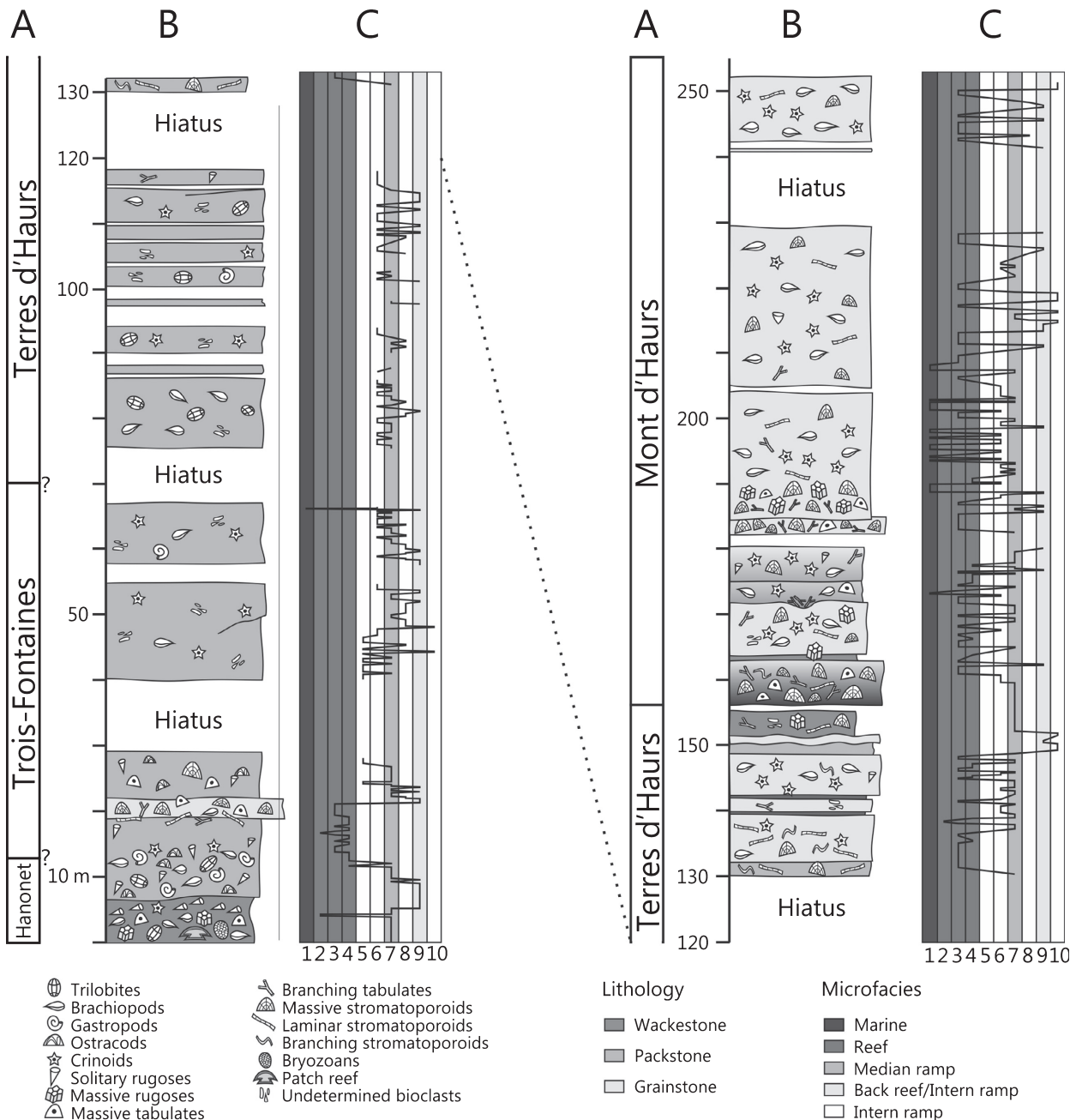
Fig. 2. Lower Givetian Mont d'Haurs section. A, lithostratigraphical formations. B, lithological column. C, microfacies and their deposit environments: (1) open sea, (2) fore-reef, (3) reef crest, (4) reef backside, (5) deep lagoon, (6) biostromal lagoon, (7) median ramp, (8) subtidal lagoon, (9) intern ramp, (10) intertidal pool (see Table 1 for their description). Modified from Hubert (2008a).

Walker 1993; Pomar 2001; Phelps *et al.* 2008). Distinct processes may lead them (sediment influx, space accommodation, biological systems). Consequently, they are difficult to interpret because each evolution recorded in the geological time is unique and the modification of a particular environmental parameter leads easily to the development of another platform model (Pomar 2001; Pomar & Kendall 2008).

The ramp of the Hanonet Formation is submitted to high-energy destroying most of stromatoporoid and coral buildups. In such context, they form a thick biostrome as floatstone and rudstone accumulation (Hubert 2008b). A progressive fall of the sea level leads the development of a carbonate shelf. The shallower environments correspond to lagoonal facies recognized in the middle part of the Trois-Fontaines Formation (Casier *et al.* 2011a). The first
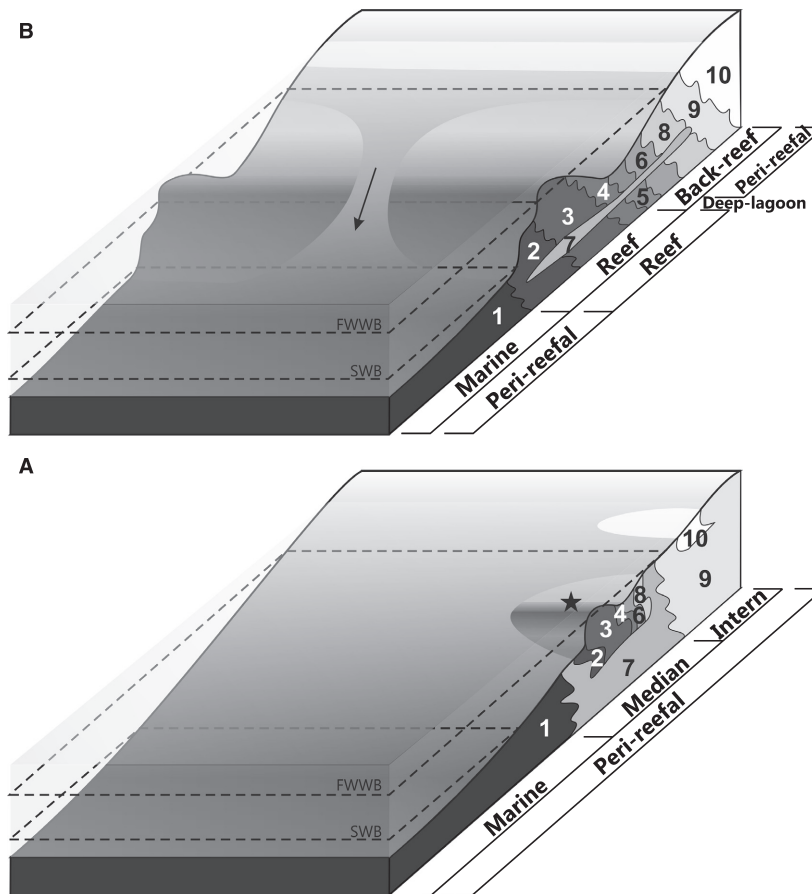
Fig. 3. Two models of marine platforms suggested for the Mont d'Haurs section (after Kasimi & Préat 1996; Hubert 2008a). A, silici-carbonate ramp. B, carbonate shelf, FWWB, Fair Weather Wave Base; SWB, Storm Wave Base; (1) open sea, (2) fore-reef, (3) reef crest, (4) reef backside, (5) deep lagoon, (6) biostromal lagoon, (7) median ramp, (8) subtidal lagoon, (9) intern ramp, (10) intertidal pool, see Table 1 for a more precise description of environments. The arrow represents a reef pass (interpreted as environment 7) and the star local erection of small reefal and lagoonal structures (interpreted as environments 2-3-4-6 and 8).

half of the Terres d'Haurs Formation is interpreted as shallow open lagoons, with several shoals of modest relief. The other part is to be more situated in open-marine facies (Casier *et al.* 2011b). In the carbonate shelf of the Mont d'Haurs Formation, the environments offer data from restricted and shallow lagoon, from the agitated reef and quiet open marine environment (Hubert 2008a,b; Casier & Préat 2013).

Material and methods

Palaeotrophic levels

The distribution of the overall organisms occurring in the Mont d'Haurs section is based on the detailed microfacies analysis and the relative abundance of the biodiversity realised by Hubert (2008a,b). 550 levels were analysed on 269 m of section (Fig. 2). The relative abundance of organisms is interpreted in term of percentages, the 'weak values' are equiva-

lent to 10%, the 'median' 25% and the 'strong' 50%, after the sum of values is returned to 100% for each level. 21 microfacies were described in the section and allocated in 10 environments (Table 1). These environments were mainly interpreted in term of platform type and positioned on a proximal-distal transect (Hubert 2008a). We chose to base this analysis on microscopic data in order to consider all organisms of the environment and so as not to miss a major palaeotrophic level, for example the Planktonic Autotrophs (PA) level would not be identified from macroscopic information. Unfortunately, this kind of data does not allow to define with accuracy the taxonomic position of macro-organisms and consequently to determine precisely their palaeotrophic level.

Thanks to these data, seven palaeotrophic levels are defined in the Givetian of the Mont d'Haurs section (Table 2). From current knowledge on the Algospongia (palaeosiphonocladales), it is not possible to define them more precisely than a group of

Table 1. Description of interpreted environments in the Mont d'Haurs section (after Hubert 2008a).

	Environment	Platform	Environmental belt	Depth	Exchanges	Hydrodynamics
1	Open sea	Ramp and Shelf	Marine	Under or closed SWZ	Opened	Quiet
2	Fore-reef	Shelf	Reef	Under FWWZ	Opened	Strongly agitated
3	Reef crest	Shelf	Reef	Above FWWZ	Opened	Agitated
4	Reef backside	Shelf	Reef	Closed SWZ	Semi-restricted	Moderately Agitated
5	Deep lagoon	Shelf	Back reef	Under SWZ	Restricted	Quiet
6	Biostromal lagoon	Shelf	Back reef	Closed SWZ	Restricted	Quiet
7	Median ramp	Ramp	Median Ramp	Under FWWZ	Opened	Agitated
8	Subtidal lagoon	Shelf	Back reef	Under FWWZ	Restricted or opened	Quiet
9	Intern ramp	Ramp and Shelf	Intern ramp/Back reef	Closed FWWZ	Opened	Agitated
10	Intertidal pool	Shelf	Back reef	Above FWWZ	Semi-restricted	Quiet

Table 2. Palaeotrophic levels recognized in microfacies of the Mont d'Haurs section.

Autotrophs	Benthics	Predators	Fixed	Sessile-Low Autotrophs (SLA)	Algospongia
	Pelagics			Planktonic Autotrophs (PA)	Calcispheres
Heterophs	Sessiles	Suspension Feeders	Fixed-Laid	Sessile-low filter feeders (SLFF)	Bryozoans
					Brachiopods
					Tentaculites
			Fixed	Attached-high filter feeders (AHFF)	Crinoids
					Stromatoporoids
		Carnivores	Fixed	Benthic carnivores (BC)	Rugoses
					Tabulates
	Vagiles	Suspension Feeders		Active filter feeders (AFF)	Ostracods
		Deposits Feeders		Active detritivores (AD)	Trilobites
					Gastropods

protists. The Algospongia are probably photosynthetic (Vachard & Cózar 2010). These organisms, not exceeding a few centimetres in size, are benthic, fixed or not, and consequently they are considered as Sessile-Low Autotrophs (SLA).

Calcispheres refer to spherical calcareous microfossils without established phylogenetic affinities. Thus, this group is probably not monophyletic. Nevertheless, their small size and their single chamber nature indicate phytoplanktonic unicellulars (Versteegh *et al.* 2009). Consequently they are placed within the Planktonic Autotroph level (PA).

Bryozoans, tentaculites and brachiopods are included within the same group, i.e. the Sessile-Low Filter Feeder level (SLFF). Indeed, bryozoans are small organisms living fixed on substrate. If present forms may generate a water flow with their tentacles surrounding the mouth in order to catch wide particles or zooplankton, the filtration is still their main nutrition way (Ruppert *et al.* 2004). Tentaculites are small benthic molluscs and most of them are encrusted (Vinn 2010). They were probably filter feeders (Taylor & Vinn 2006; Vinn & Isakar 2007). Brachiopods are more problematic because it is not possible to differentiate fixed and laid forms from thin sections (Gaspard 1997). Thus, this parameter is not considered in this level and organisms are simply defined as sessile.

The Attached-High Filter Feeder level (AHFF) comprise stromatoporoids and crinoids. This class of echinoderms (crinoids) is mostly provided with a long stalk allowing them to elevate above the substrate and deploy their crown to grasp suspensive particles. Nutrition and phylogenetic position of stromatoporoids are still not clear (Stock 2001). However, since Wood (1987) and Reitner (1992), specialists agree to place them within the Porifera. Demosponge-type spicules have been recently discovered on a specimen, reinforcing this interpretation (Da Silva *et al.* 2014). Consequently, we consider stromatoporoids with a similar nutrition as the present sponges, i.e. filter feeders (Lesser 2006).

Rugosa and tabulata feed probably like the current corals, i.e. heterotrophs catching preys (from bacteria to little fish) with their tentacles and their autotroph capacity thank to symbiotic algae (Pacherres *et al.* 2013). These bioconstructors are grouped in the palaeotrophic level of the Benthic Carnivores (BC).

A variety of feeding habits exist within ostracods. They may be filter feeders, predators, herbivores (Hartmann & Guillaume 1996). Nevertheless, 60–80% of Devonian ostracods are reported as filters feeders (Lethiers & Whatley 1995). S. Maillet (personal communication, 2013) confirmed that close to 80% of Givetian ostracods in the Ardennes Massif

follow this nutrition mode. Consequently we considered the ostracods within the palaeotrophic level of the Active Filter Feeders (AFF), because of thin sections that prevent complete taxonomic identification.

Trilobites and gastropods represent the palaeotrophic level of the Active Detritivores (AD). A great number of nutrition modes are possible within trilobites (Fortey & Owens 1999). The genus *Dechenella* corresponds to more than 90% of the specimens found in the Mont d'Haurs section and they have been reported as detritivores (Bignon & Crônier 2011). Many feeding habits exist within gastropods too, predators, filter feeders, parasites, herbivores (Lecointre & Le Guyader 2006). However, we consider all of them within this trophic group because most of gastropods are detritivore during the Devonian (Botquelen *et al.* 2006).

Sedimentology

The study of the Mont d'Haurs section by Hubert (2008a,b) described 21 microfacies interpreted within 10 depositional environments (main features resumed in Table 1). We provide in the following part a short description of the facies from this work (see these references for more details).

The open sea (Fig. 3A, B; environment 1) corresponds to mudstones and wackestones with few bioclasts (mainly brachiopods and ostracods). Bioturbation is uncommon. These facies are interpreted as an open marine environment under or closed to the storm wave base (SWB) consequently quiet. They are characteristic of ramp and shelf models because situated in front of the reef in the platform.

The fore-reef (Fig. 3A, B; environment 2) is a crinoid rudstone with ossicles poorly deteriorated. Very few brachiopods and ostracods are also described. Situated below the fair weather wave base (FWWB), this open part of the reef is strongly agitated.

The reef crest (Fig. 3A, B; environment 3) is a boundstone with stromatoporoid fragments, colonial or solitary rugosa and tabulata. Crinoid, brachiopod and ostracod bioclasts are observed as well as rare trilobites and algae. This environment, above the FWWB, is open and agitated.

The reef backside (Fig. 3A, B; environment 4) is composed of wackestones and packstones rich in reefal fragments. The bioclasts are mainly stromatoporoids, tabulata, chaetetids and rugosa. Crinoids, brachiopods and ostracods are locally present. This facies is interpreted as a semi-restricted environment closed to SWB and moderately agitated.

The deep lagoon (Fig. 3B; environment 5) corresponds to algal mudstones and wackestones. Calcispheres and Algospongia are abundant, ostracods bioclasts and bioturbations are scarce. It is a restricted environment below the SWB.

The biostromal lagoon (Fig. 3A, B; environment 6) comprises packstones and wackestones with abundant gastropods and ostracods bioclasts, algae are common too. Bioturbation is present. It is a restricted and quiet environment closed to SWB characterized by algal and/or reefal beds.

The median ramp (Fig. 3A, B; environment 7) is recognized through various kinds of facies. These wackestones, packstones and grainstones have abundant bioclasts and are dominated by brachiopods, gastropods, ostracods and algae. These levels are usually bioturbated. This open environment is closed to FWWB and consequently agitated.

The subtidal lagoon (Fig. 3A, B; environment 8) corresponds to packstones rich in peloids and bioclasts, or rich in algae and ostracods. In both facies, ostracods, gastropods and algae are abundant. This part of the lagoon, situated under FWWB, is quiet and may be opened or restricted.

The intern ramp (Fig. 3A, B; environment 9) is a packstone with micropeloids, locally bioturbated and rich in bioclasts. Gastropods, brachiopods, crinoids and ostracods are relatively abundant. The bioturbations are vertical. This part of the ramp is opened, closed to FWWZ and agitated.

Intertidal pools (Fig. 3A, B; environment 10) are identified thanks to laminated wackestones and mudstones. The bioclasts are rare but algal encrustings are frequent. This environment is above FWWB (sometimes emerged), semi-restricted and quiet.

Reefal and lagoonal levels (Fig. 3B; environments 2, 3, 4, 6, 8 and 10) have been recognized on the ramp model, although they are characteristic facies of carbonate shelf model. They correspond probably to small areas where the local conditions allow the development of such structures (Fig. 3B; represented by the star). They appear as patch-reefs, biostromal units and shoals in the Hanonet and Terres d'Haurs formations (Hubert 2008b; Casier *et al.* 2011a,b). Similarly, environments typical of the ramp model (Fig. 3A; environments 7 and 9) are described in the carbonate shelf. This is interpreted as a local opening of the reef (Fig. 3A; reef passes represented by the arrow) or rivers mouth where hydrodynamic conditions and siliciclastic inputs are more important (Rogers 1990; Bianchi *et al.* 1997; Schrimm *et al.* 2002; McNeill *et al.* 2004; Ogston *et al.* 2004; Devlina & Brodie 2005; Hernández-Arana & Ameneyro-Angeles 2011).

Taphonomy

A summary of the deposit environments is proposed in the Figure 2C. The Hanonet Formation corresponds to an intern/median-ramp facies. The transport is substantial in the median-ramp, destroying bioconstructions and accumulating them as floatstones and rudstones. The energy is moderate in the intern-ramp with preserved crinoid stems (Casier *et al.* 2011a). A biostrome, composed of reworked organisms, at the base of the Trois-Fontaines Formation marks a transition to more restricted environments. Above the biostrome, the facies change to a restricted and calm shelf (Hubert 2008a; Casier *et al.* 2011a). The Terres d'Haurs Formation represents an evolution from the carbonate shelf to open-marine facies in a ramp system. The first part of the formation corresponds to an open lagoon in the intern-ramp and the second to a shoal settlement at the limit intern/median-ramp (Hubert 2008a; Casier *et al.* 2011b). This environment is characterized by a mixing of several biocenosis. The outer and median-ramp seafloor of the Terres d'Haurs Formation, below FWWB, is only affected by storms. The main part of bioclasts consists of reworked autochthonous organisms. The intern-ramp facies are characterized by a low energy or a reworking of the shallower environments with low energy (Casier *et al.* 2011b). The two-first decade metres of the Mont d'Haurs Formation correspond to the settling of a reef and the last part of the formation correspond to a lagoon with periods of opening (Hubert 2008a). The energy is variable with a bioclast transport from proximal to more distal facies (Casier & Préat 2013). The rest of the formation suggests mostly restricted environments. However, episodic and more agitated openings are recorded as deep and distal facies (Hubert 2008a).

The taphonomy reveals distinct levels of energy along the section. Some of them correspond to reworked material from more proximal environments. If these conditions imply to consider with caution the comparisons between environments of the same formation, they do not affect the results of the palaeotrophic level distribution between the various formations.

Analytical procedures

We analysed the palaeotrophic level occurrence by means of multivariate analyses. Detrended Correspondance Analyses (DCA) were performed to identify, firstly, the gradient between environments along proximal-distal transect, and secondly, to highlight the relationships between the formations in each environment. DCA compresses the horseshoe effect, caused when extreme values of samples on the first axis have only a little overlap as it is often the case with taxonomic compositions. Consequently, DCA is particularly recommended in palaeoecological studies where the first axis often reflects palaeoenvironmental gradients (Holland *et al.* 2001; Botquelen *et al.* 2006; Botquelen & Racheboeuf 2008; Crônier & François 2014). DCA maximises the correspondence between taxa and samples and provides ordination scores for both taxa and samples according to the relative abundance of taxa. In DCA, the horseshoe effect is divided into a series of segments and the second axis mean for each segment is subtracted from each score within that segment. To finish, the scores near the extremities of the first axis are rescaled for removing unwanted compression (Holland *et al.* 2001; Botquelen & Racheboeuf 2008).

To complete DCA, analyses of Similarities (ANOSIM) were applied to recognize significant differences, respectively, between environments and between formations. Dissimilarity values are based on the Bray-Curtis index (Clarke 1993; Hammer & Harper 2006). This non-parametric test compares differences within each group and between the groups. R-value of 1 notifies that similarity within groups is higher than that between groups. Consequently the groups are different and reciprocally for R-value close to 0. The significance of the results is tested with a permutation test (5000 replicates).

DCA and ANOSIM analyses were performed using the data-analysis software PAST 2.15 (Hammer *et al.* 2001).

Results

Palaeotrophic level distribution

The mean distribution of palaeotrophic levels in each environment and each formation is represented in Figure 4 (see Table 1 for their main characteristics).

The open-sea (Fig. 4; environment 1) is mostly represented in the Mont d'Haurs Formation (MH) with 22 levels (Fig. 4; MH-1) on a total of 24 for the complete Mont d'Haurs section. Filter feeders are dominating (75%) of which the Active Filter Feeder level (AFF) represents the half of the palaeotrophic levels. The palaeotrophic distribution within this quiet environment (Table 1) is probably poorly contaminated. Indeed, below SWB, only the strongest storms may have influenced these results by more proximal material.
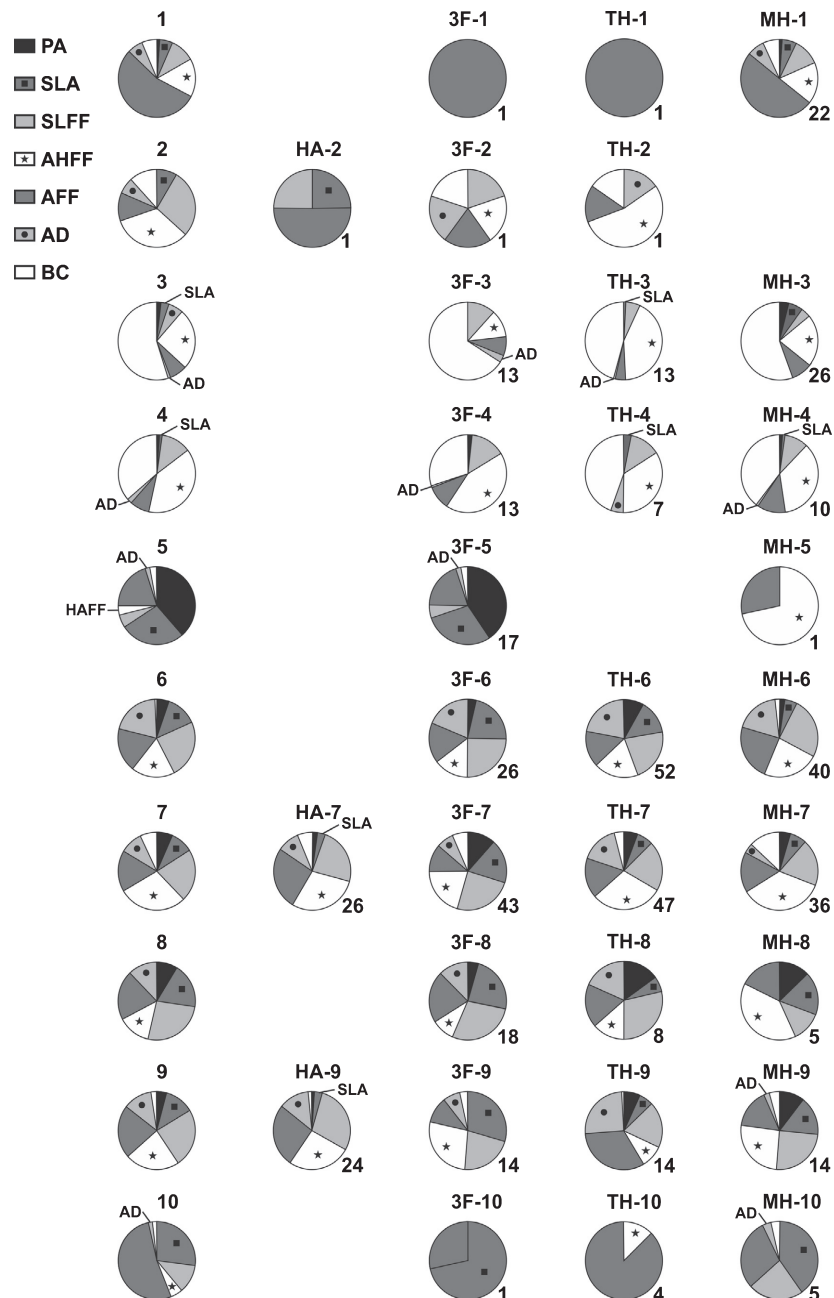
Fig. 4. Relative abundance of palaeotrophic levels along a proximal-distal transect of the Mont d'Haurs section. Environments: (1) open sea, (2) fore-reef, (3) reef crest, (4) reef backside, (5) deep lagoon, (6) biostromal lagoon, (7) median ramp, (8) subtidal lagoon, (9) intern ramp, (10) intertidal pool (see Table 1 for their description). Palaeotrophic levels: SLA, Sessile-Low Autotrophs; PA, Planktonic Autotrophs; SLFF, Sessile-Low Filter Feeders; AHFF, Attached-High Filter Feeders; BC, Benthic Carnivores; AFF, Active Filter Feeders; AD, Active Detritivores (see Table 2 for their description). Formations: HA, Hanonet Formation; 3F, Trois-Fontaines Formation; TH, Terres d'Haurs Formation; MH, Mont d'Haurs Formation; number under each circular chart represents the number of considered levels.

Few levels of the fore-reef (Fig. 4; environment noted 2) occur in the Mont d'Haurs section. Each of the following formations, Hanonet (HA), Trois-Fontaines (3F) and Terres d'Haurs (TH) include only one level of this environment (Fig. 4; HA-2, 3F-2 and TH-2). There is a substantial fluctuation of the palaeotrophic distribution between these three levels, probably a result of the strong hydrodynamic

in front of the reef (Table 1). Consequently it is not possible to discuss these results.

The reef crest and the reef backside (Fig. 4; environments 3 and 4) are dominated by Benthic Carnivores (BC) and AFF levels corresponding to bioconstructors (more than 75%). BC level appears more important in the reef crest and AFF is more abundant in the reef backside. This is particularly

obvious for the 3F and MH formations (Fig. 4; 3F-3, MH-3, 3F-4 and MH-4), but these palaeotrophic levels appeared more equilibrated in the Terres d'Haurs Formation (Fig. 4; TH-3 and TH-4). These environments are strongly agitated (Table 1) and a mix between them occurred probably. However, a contamination of these results from more proximal bioconstructors appears poorly credible because they are very distinct to proximal environments.

The deep lagoon (Fig. 4; environment 5) is mostly represented within the 3F Formation. In this time-slice, photosynthetic organisms represent nearly 75% of the palaeotrophic levels, Planctonic Autotroph (PA) and Sessile-Low Autotroph (SLA) levels being close (Fig. 4; 3F-5). AFF is also significant (around 20%) in this environment. The lagoon is a closed and quiet environment (Table 1) contamination from other environments is implausible from the autotroph dominance, unique on the platform.

The biostromal lagoon (Fig. 4; environment 6) is well-represented by all the palaeotrophic levels. Except the BC level that is nearly absent, the distribution of other palaeotrophic levels is rather similar. Between the formations, the main difference is a strong decrease of autotrophs (PA and SLA) levels in the Mont d'Haurs Formation (Fig. 4; MH-6).

The palaeotrophic level distribution on the median ramp (Fig. 4; environment 7) is similar as in the biostromal lagoon, except that BC is more significant. The two autotroph levels (PA and SLA) are more developed in the 3F Formation than in the other three and BC is more abundant in the MH Formation (Fig. 4; 3F-7 and MH-7).

The distribution in the subtidal lagoon (Fig. 4; environment 8) shows the same tendency than the biostromal lagoon. However, no decrease of autotroph levels (PA and SLA) appears in the MH Formation (Fig. 4; MH-8), the Active Detritivore level (AD) disappeared entirely during this period and the Attached-high Filter Feeder level (AHFF) is more abundant. The distribution in the 3F and the TH formations is very similar except a swap between the two autotroph levels (Fig. 4; 3F-8 and TH-8).

The intern ramp (Fig. 4; environment 9) is also similar to the distribution within the biostromal lagoon. However, there are important fluctuations between the different formations. The autotroph levels (PA and SLA) are nearly absent of the HA Formation; whereas the SLA dominates the 3F Formation (Fig. 4; HA-9 and 3F-9). AD level is abundant (more than 25%) in the TH Formation whereas they are very few in the MH Formation (Fig. 4; TH-9 and MH-9;).

The environments 6–9 present a tendency rather similar in the distribution of their palaeotrophic levels. These environments have distinct hydrodynamic conditions from quiet (in the lagoon) to agitate (ramp facies). A contamination of the material exists most probably between them or some of them. The multivariate analysis allows to better estimate this issue by the dispersion of the levels of each environment (Fig. 5).
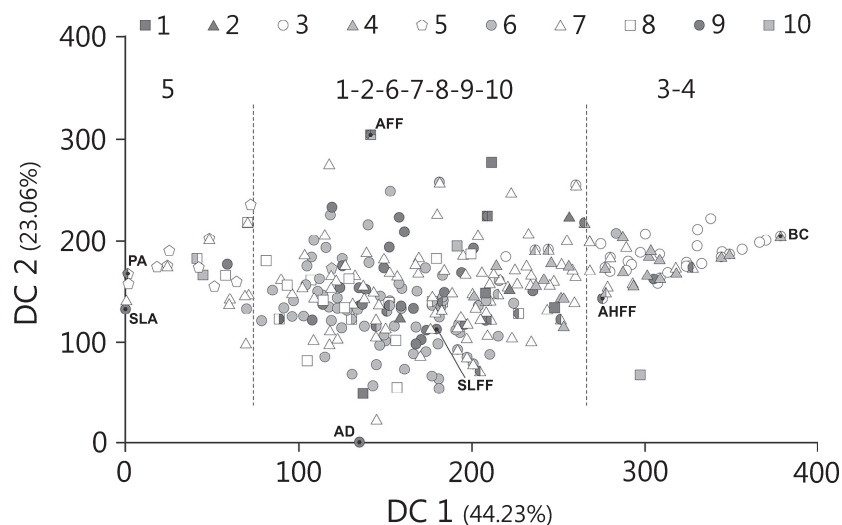

Fig. 5. Scatter plot of the palaeotrophic levels following their environment, according to DCA (representing 67.29% of the total variance). White dot represents 100% of a palaeotrophic level. Environments: (1) open sea, (2) fore-reef, (3) reef crest, (4) reef backside, (5) deep lagoon, (6) biostromal lagoon, (7) median ramp, (8) subtidal lagoon, (9) intern ramp, (10) intertidal pool (see Table 1 for their description). Palaeotrophic levels: SLA, Sessile-Low Autotrophs; PA, Planktonic Autotrophs; SLFF, Sessile-Low Filter Feeders; AHFF, Attached-High Filter Feeders; BC, Benthic Carnivores; AFF, Active Filter Feeders; AD, Active Detritivores (see Table 2 for their description).

Huge fluctuations are recorded in the intertidal pool (Fig. 4; environment 10) between the different formations. Few levels have been recorded but SLA and AFF groups seem to be more abundant in this kind of environment (Fig. 4; TH-10 and MH-10). As a quiet and restricted environment, mixing material from other ones is not probable (Table 1).

Spatial distribution

As the palaeotrophic level distribution shows no radical differences between the formations, these are grouped within only one DCA analysis (Fig. 5). The results of DCA are significant (eigenvalues for DC1 and DC2 axes are, respectively, 0.59 and 0.31). The environments are sorted along DC1 axis, which clearly reveals a main faunal gradient.

The low values on DC1 correspond to a high percentage of both autotrophic levels (PA and SLA). High values on DC1 reveal a strong portion of constructor organisms with BC and AHFF (in a slightly weaker proportion) levels. The remaining three palaeotrophic levels (AFF, SLFF and AD) have average values on the first axis (Fig. 5). They are mainly distributed on the second but no correlation with the environments can be recognized.

DC1 axis reveals three groups of environments (Fig. 5). The deep lagoon levels (environment 5) are characterized by a high proportion of both autotrophic groups. In the opposite side along the first axis, the reefal facies (environments 3 and 4) are characterized by a high proportion of BC and AHFF levels. It should be noted that BC level is favoured in the reef crest (environment 3) and AHFF more in the reef backside (environment 4). All other environments, i.e. distal (environments 1 and 2), back-reef (environments 6, 8, 9 and 10) and ramp (environments 7 and 9), are grouped in median values on DC1 axis. ANOSIM supports a separation of the environments in these three groups (Table 3A).

Temporal and platform morphology distributions

Each environment is compared depending on formations (environments 1, 2 and 5 are not analysed

Table 3. Statistical results of ANOSIM differences between: A, three groups of environments (i.e. 1-2, 6-10; 3-4; 5); B, formations within seven environments; C, two models of marine platforms, i.e. ramp (represented by HA-TH) *versus* shelf (represented by 3F-MH) within seven environments; D, Hanonet Formation and the three younger formations; E, HA-3F and TH-MH; F, the three older formations and Mont d'Haurs Formation.

	A		
	R-value		*P* (same)
Environments	0.343		**<0.001*****

	B		C		D	
Environments	*R*-value	*P* (same)	*R*-value	*P* (same)	*R*-value	*P* (same)
3	0.012	0.526	0.004	0.428	–	–
4	0.119	**0.034***	0.145	0.111	–	–
6	0.206	**<0.001*****	0.038	**0.023***	–	–
7	0.087	**<0.001*****	0.067	**<0.001*****	0.136	0.999
8	0.057	0.234	0.049	0.634	–	–
9	0.124	**0.024***	0.030	0.131	0.057	0.952
10	0.121	0.235	0.128	0.200	–	–

	E		F	
Environments	*R*-value	*P* (same)	*R*-value	*P* (same)
3	0.077	**0.012***	0.110	0.937
4	0.039	0.271	0.036	0.220
6	0.100	**0.005****	0.264	**<0.001*****
7	0.027	**0.021***	0.113	**0.007****
8	0.050	0.156	0.133	0.169
9	0.013	0.274	0.049	0.158
10	0.196	0.087	0.157	0.610

Environments: (1) open sea, (2) fore-reef, (3) reef crest, (4) reef backside, (5) deep lagoon, (6) biostromal lagoon, (7) median ramp, (8) subtidal lagoon, (9) intern ramp, (10) intertidal pool (see Table 1 for their description). Formations; HA, Hanonet Formation; 3F, Trois-Fontaines Formation; TH, Terres d'Haurs Formation; MH, Mont d'Haurs Formation. The bolded values indicate significative difference between the groups. Confidence interval lower: * than 0.05%, ** than 0.01% and *** than 0.001%.

because of a lack of data between several formations) in order to highlight a temporal modifications and/or a distinction between carbonate shelf and mixed ramp. Thus, in Table 3 we applied ANOSIM to examine differences in the structure of palaeotrophic levels according to the following considerations:

A, between three groups of environments.
B, between the formations.
C, between the two models of marine platforms, i.e. the ramp (represented by the Hanonet-HA and the Terres d'Haurs-TH formations) *versus* the shelf (represented by the Trois-Fontaines-3F and the Mont d'Haurs-MH formations).
D, between the HA Formation and the three younger formations.
E, between the two older (HA and 3F formations) and the two younger formations (TH and MH formations).
F, between the three older formations and the MH Formation.

First of all, the *R*-values do not exceed 0.25 (except one reaching 0.26), which reveals that the
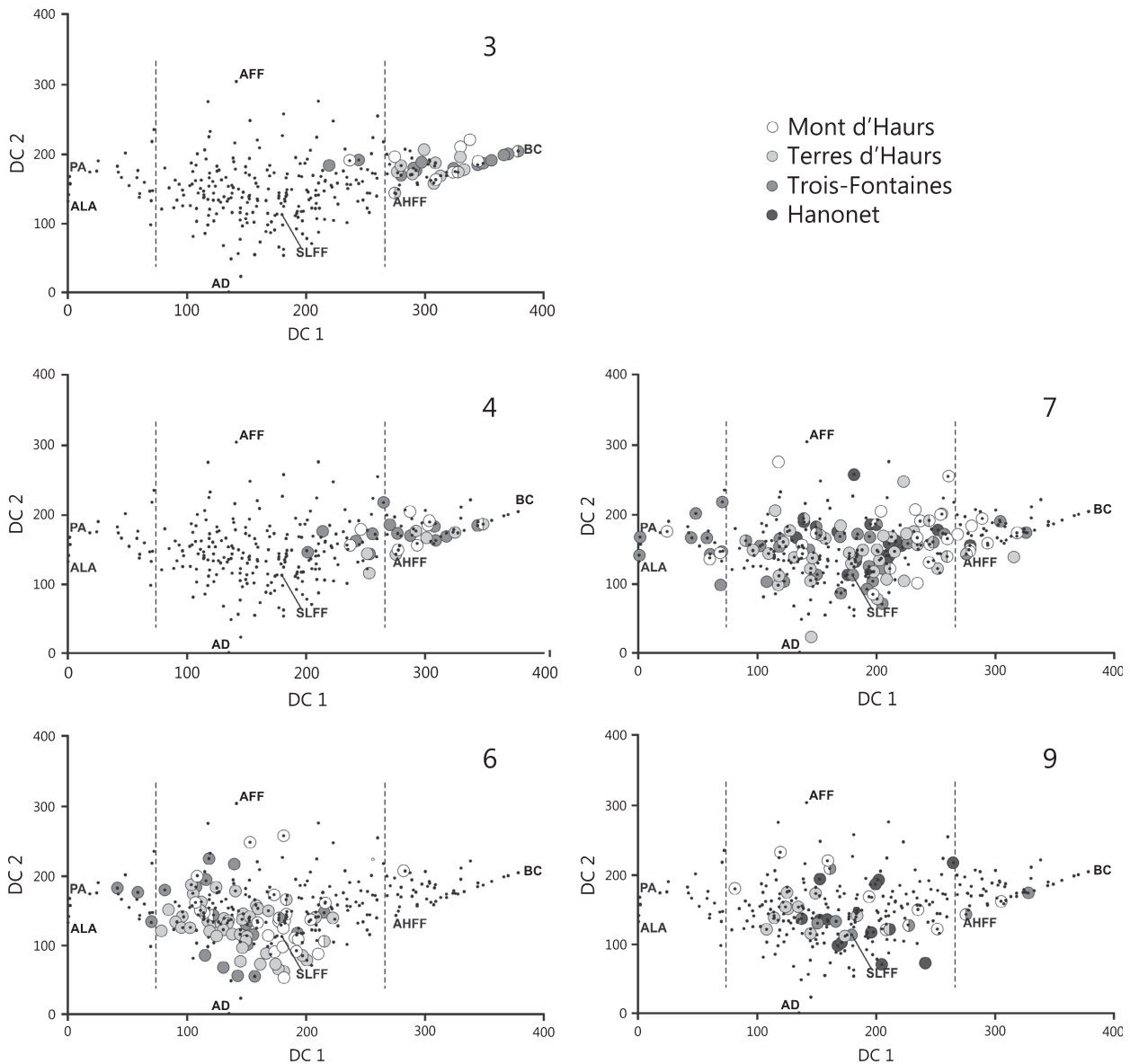

Fig. 6. Scatter plot of the palaeotrophic levels following their formation for the environments 3, 4, 6, 7 and 9. Environments: (3) reef crest, (4) reef backside, (6) biostromal lagoon, (7) median ramp, (9) intern ramp (see Table 1 for their description). Palaeotrophic levels: SLA, Sessile-Low Autotrophs; PA, Planktonic Autotrophs; SLFF, Sessile-Low Filter Feeders; AHFF, Attached-High Filter Feeders; BC, Benthic Carnivores; AFF, Active Filter Feeders; AD, Active Detritivores (see Table 2 for their description).

groups are barely distinguishable (Clarke & Gorley 2001).

ANOSIM recognizes that a significant differentiation exists between the formations for environments 6 and 7, with a *P* value inferior to 0.001% (Table 3B). These environmental differences between the formations may come from the palaeotrophic level distribution developed on either a carbonate shelf or a mixed ramp: a significant difference appears between the two models of marine platforms (Table 3C). However, ANOSIM also highlights a significant difference during the time between the two older formations and the two younger on the one hand, between the three older formations and the MH Formation on the other hand (Table 3E, F). Consequently, it is not possible to rely the differences identified by ANOSIM with a model of marine platform. These results are confirmed in DCA (Fig. 6, environments 6 and 7) where the formations developed in a ramp (HA and TH formations) or a shelf (3F and MH formations) are not particularly associated.

The environments 4 and 9 have a significant difference between the formations but only at a confidence level (*P* value) inferior to 0,05% (Table 3B). However, ANOSIM is not able to show a significant difference of these environments between the two models of marine platforms or over time (Table 3C–F). These results are corroborated by DCA (Fig. 6; environments 4 and 9).

ANOSIM recognizes a weak difference (*P* value inferior to 0.05%) of the environment 3, between the 3F Formation and the two younger formations (Table 3E; TH and MH formations). In this case, the overlapping of the palaeotrophic level distributions is so important between these formations, that it is difficult to recognize a tendency (Fig. 6; environment 3).

Discussion

Biodiversity organisation along the platform

Carbonate shelves are traditionally split in three morphological zones: the fore-reef, the reef crest and the back-reef. The latter can be subdivided in three other zones: the reef flat, the back-reef and the lagoon (Hopley *et al.* 2007). The palaeotrophic level distribution in the Mont d'Haurs section reveals only three environmental sets where differences of their relative distribution are significant: the reef, the deep lagoon and the peri-reefal (Fig. 5). In the Mont d'Haurs section, the reef constitutes a structurally

distinct environment within the carbonate shelf ecosystem (Droser *et al.* 1997). This is revealed by the almost total absence of various palaeotrophic levels (Fig. 4; PA, SLA and AD). As well, the deep lagoon is marked by the overabundance of the autotroph levels (SLA and DA) in comparison with other environments of the distal proximal transect. We distinguished inside the peri-reefal environments the open-sea (Table 1; environments 1 and 2) from the back-reef environments (Table 1; environments 6, 7, 8, 9 and 10), here a fluctuation of the relative distribution of the palaeotrophic level exist with a dominance of AD (Fig. 4). Such a difference in the distribution highlights a shift in the community level within an established ecological structure (Droser *et al.* 1997).

The reef includes the reef crest and backside (Table 1; environments 3 and 4) mainly dominated by BC and AHFF levels, and an absence (or nearly) of the autotrophic and AD levels (Fig. 4). These environments are highly agitated and some mixings and contaminations may exist between them and from proximal environments. However, the reef is mainly composed of bioconstructor organisms that are not so dominant in proximal environments. Thus, the ex-situ material is probably too weak to influence strongly the palaeotrophic level distribution.

The autotrophs prevail in the deep lagoon (Table 1; environment 5). The environment is quiet (below SWZ) and protected from marine influences by the reef. The more proximal environments of the lagoon are as well quiet. Consequently, such concentration of autotrophs is most probably a true representation of the bioceonosis.

The peri-reefal zone includes all other environments of the shelf, in front (Table 1; environments 1 and 2) and in the back of the reef (Table 1; environments 6, 8, 9 and 10). The data of the fore-reef (Fig. 4; environment 2) are too sparse to identify truly a tendency. Although, the lagoon is overall a quiet environment, it is difficult to estimate the mixing part between the distinct sub-environments. Indeed, it may increase the similarity of the palaeotrophic level distributions. However, studies on current benthic foraminifera show that sedimental redeposition did not alter significantly the taxonomic composition of distinct lagoonal environments (Bicchi *et al.* 2002; Gischler *et al.* 2003). The front-reef is slightly more distinct than the lagoonal environments because of a substantial presence of the AFF palaeotrophic level. Here, a mixing from proximal environments is excluded because of the reef presence preventing communication between them. Indeed the high occurrence of this level (Fig. 4; environment 1) could not be explained only

by a contamination because the lagoonal environments (Fig. 4; environments 6, 8 9 and 10) do not have such a percentage in their distribution. As well, a supply for AHFF and BC from the reef may exist but is reduced in comparison of the part of these levels in the reef (Fig. 4; environments 3 and 4). The present results meet analyses based on the biodiversity and trophic levels in current lagoons (Gischler *et al.* 2003; Hauser *et al.* 2007; Parker & Gischler 2011). It appears that benthic assemblages are more homogeneous in spite of the environmental differences within the lagoon, in contrast with the reef. In the same way, the fore reef assemblage has its own characteristics but shares similarities with the lagoon.

Concerning the mixed ramp model (Table 1; environments 1, 7 and 9), the open sea could not be analysed because only one level occurred in a formation where the ramp is developed. The median and intern ramps have a similar distribution (Fig. 4; environments 7 and 9) and the scatter plots of these levels (Fig. 5) are strongly overlapping. An open environment as the ramp favours important hydrodynamic conditions and thus the median ramp was probably alimented in material inputs from the proximal part. It is difficult to estimate the part of this contamination because it is not possible to recognize a tendency between their distributions (Figs 4, 5; environments 7 and 9). Consequently, we cannot conclude from these results that there is no difference between the median and inter ramps.

It is interesting to note that the typical environments of the ramp in carbonate shelf models (Fig. 4; 3F-7, 9 and MH-7, 9) contain more autotroph levels (PA and SLA) than the other environments of this morphology (Fig. 4; 3F-6; 3F-8; MH-6 and MH-8;). However, we cannot estimate if it represents a bioceonosis or a contamination from adjacent environments.

Concerning typical lagoonal and reefal environments (Table 1; environments 3, 4, 6, 8 and 10) that have been identified in ramp model formations (Fig. 4; TH-3, TH-4, TH-6, TH-8, TH-10), no particular distribution of the palaeotrophic levels appears.

Alternation between the mixed ramp and the carbonate shelf

The scatter plot of the relative distribution of palaeotrophic levels presents an important superposition between environments belonging to the mixed ramp and those of the carbonate shelf models (Fig. 6). Such results signify that there is no difference of the community-type between the two morphologies of

platform (Droser *et al.* 1997). The community-type is an aggregate of local communities that are very similar in terms of taxonomic composition and that are recorded in similar environments (Bambach & Bennington 1995). From the present results, these morphologies of platform appear uniform enough not involve a modification of the community-type. It is important to note that similar distributions of the palaeotrophic levels do not imply identical communities.

Studies on the biodiversity or trophic levels organisation on present lagoonal facies (e.g. Schlacher *et al.* 1998; Bazaïri *et al.* 2003; Gischler *et al.* 2003; Hauser *et al.* 2007; Semprucci *et al.* 2010) or ramps facies (e.g. Jayaraj *et al.* 2008; Manokaran *et al.* 2013; Negri *et al.* 2014; Parker & Gischler 2015) facies show a high level of variability in communities depending of environments. The present results show a more intermediate level of variability. Indeed, the fossils record the state of ecosystems during repetitive time periods and under various combinations of environmental factors (Pandolfi 2011). A single stratigraphic horizon may represent decades to 1000 years of time averaging (Jackson & Erwin 2006). Thanks to this mixing, the fossil communities are more complete and representative than living ones because species are commonly rare and make detailed surveys incomplete (Kidwell 2002). Palaeocology is consequently a suitable tool to describe the environment evolution in order to provide insights for predicting the potential future of modern ecosystems (Jackson 2010; Pandolfi 2011; Dietl & Flessa 2013).

Mixed ramps and carbonate shelves are two distinct and complex environments but how estimate this difference? The relative distribution of palaeotrophic levels in the Mont d'Haurs section reveals that the evolution of one platform model to another does not constitute a complete disruption for the biodiversity. Indeed, the community-type is not affected by such changes. Refuges in similar environments, ecophenotypic plasticity and genetic component may explain this observation (Pandolfi 2011). Thus, the 'mixed ramp' organisms may take shelter in the parts of the carbonate shelf where similar conditions exist as reefal channels, with stronger hydrodynamism and turbidity, more siliciclastic and nutrient inputs (Rogers 1990; Bianchi *et al.* 1997; Schrimm *et al.* 2002; McNeill *et al.* 2004; Ogston *et al.* 2004; Devlina & Brodie 2005; Hernández-Arana & Ameneyro-Angeles 2011). Likewise, limited reefal structures are developed on mixed ramp creating locally similar conditions of carbonate shelves (Hubert 2008b; Casier *et al.* 2011a,b). Ecophenotypic plasticity may be also a plausible explanation.

For example the trilobite species *Dechenella ziegleri* Struve, 1992 of the Terres d'Haurs formation (Hubert 2008a; Bignon & Crônier 2011) is encountered both in the biostromal lagoon (Table 1; environment 6), and the median (Table 1; environment 7) and internal ramps (Table 1; environment 9) or the ostracod *Polonellia tertia* Krömmelbein, 1953 mostly found in open marine environments may occur in the algal euphotic zone (Casier *et al.* 2011a, b). Likewise, the genetic component may explain these results. Indeed, environmental changes have led to the emergence of new taxa, more adapted to new platform morphology. In the present case, it is hazardous to analyse how the community-type is maintained in both platform models, but each of these three parameters may have acted on the preservation of the community-type and on the biodiversity dynamics based on environmental changes. Nevertheless, the part of each of these parameters differs likely for each taxon. Whatever the action of these parameters, they may act only because the change of one platform model to another does not constitute a major disruption allowing the necessary time to develop this biodiversity dynamics.

Fluctuations of the benthic biodiversity in the Ardennes Massif during the Givetian

Our results of the palaeotrophic level analysis do not show profound modifications of the palaeotrophic levels during time and between mixed ramps and carbonate shelves. These alternations of the platform morphology represent weak environmental changes affecting only the biodiversity at the community-level (Droser *et al.* 1997). These results support the biodiversity fluctuations of trilobites observed in the Ardennes Massif during the Middle and the Late Devonian (Crônier & van Viersen 2007; Bignon & Crônier 2015). Indeed, only one association (*Dechenella* Association) is identified during the Givetian whether in the mixed ramp or in the carbonate shelf. The same trend is observed during the Eifelian in local attempts of barrier erection (corresponding to the Couvin Formation) and the typical mixed ramp recorded the same trilobite community (Mixed Association). Nevertheless, two new trilobite communities occurred in the Frasnian. One is restricted to the carbonate mud mounds (Scutelluinae association) and the other lives in the adjacent environments of the deep mixed ramp (*Bradocryphaeus* Association). The associative succession of trilobite fauna occurring during the Middle and the Late Devonian seems to be more correlated with global events than to environmental changes recognized in the Ardennes Massif (Crônier

& van Viersen 2007; Bignon & Crônier 2015). Indeed, at the end of the Eifelian, the Kačák bioevent (House 1985) during the *ensensis* conodont biozone (House 2002; Marshall *et al.* 2007), is correlated with the succession of the trilobite faunas (from the Mixed to the *Dechenella* associations). There is no signal of this event in our data because only the *hemiansiatus* conodont biozone is recorded in the Mont d'Haurs that begin at the early Givetian (Hubert 2008a,b; Casier *et al.* 2011a,b). Again, the replacement of the *Dechenella* Association by the two frasnian faunas appears correlated with the Taghanic event (House 1985). This middle Givetian event dated from the middle and upper *varcus* (*timorensis*) conodont biozone (House 2002; Marshall *et al.* 2011) is not indexed in the Mont d'Haurs section. The last formation of this section corresponds to the Lower *varcus* conodont biozone (Bultynck & Dejonghe 2001; Hubert 2008a,b) that is much younger than this event.

Lower and middle Givetian ostracod benthic fauna of the Ardennes Massif (from the Hanonet to the Mont d'Haurs formations) appears to be rather stable. Only a progressive diversification over time can be observed (Maillet 2013, p. 175) but no significant distinction exists between ramp and shelf facies. The same tendency is observed at a more precise level, in the Mont d'Haurs section. The ostracod fauna is progressively replaced, more driven by the environmental fluctuations along the proximal/distal transect than modifications of the platform morphology (Casier *et al.* 2011a,b; Casier & Préat 2013). A faunal replacement, similar as for trilobites, is associated with the Taghanic global event. This signal is described in France, Germany, Poland and Algeria (Maillet *et al.* 2013).

Nevertheless, as constructor organisms, the stromatoporoids show distinct communities between formations characterising a carbonate shelf (represented by 3F and MH formations) than those corresponding to a ramp (HA and TH formations). Firstly, peaks of biodiversity in the Ardennes are observed (Wolniewicz 2012) in the carbonate shelf formations (59 species in 3F and 76 in MH) compared to the mixed ramp (9 in HA and 11 in TH). Moreover, in the Mont d'Haurs section, a significant portion of species from the Trois-Fontaines Formation is present in the Mont d'Haurs Formation too, although several new species occur in the latter formation. On the contrary, the Terres d'Haurs Formation shares only few species with its adjacent formations (Hubert 2008a, p. 143). Unfortunately, no statistical study has been performed to confirm the relationships between stromatoporoid communities and the formations.

Conclusions

The main aim of this work is to analyse if a modification of the platform morphology, between a mixed ramp and a carbonated shelf, constitutes a major environmental disruption. In this way, the study of the relative distribution of palaeotrophic levels is effective to estimate the biodiversity perturbation. Our results show that the community-type is not affected by such environmental modifications. At least, the imbalance is rather weak to allow an adjustment of the biodiversity thanks to environmental refuges, ecophenotypic plasticity and/or organism adaptation. These results are important in the present period of high stress for reefal ecosystems from climate deregulations and influences of the terrestrial discharge linked to human activity. Studies on living communities provide information of causes and consequences of this environmental perturbation. However, only the large temporal scale of the fossil record supplies clues to allow making predictions on the survival of these ecosystems, nurseries of the marine biodiversity. In fact, the profound modifications of the biodiversity, in term of community-type and organization on the platform, seem more correlated with global events. Indeed, at the end of the Eifelian corresponding to the Kačák event, the Ardennes Massif and globally the surrounded parts of the Old Red Sandstone continent know a complete renewal of the benthic fauna. It is important to remark that during the Eifelian, local outbreaks of carbonated shelf appear on the typical mixed ramp without affecting the community-type. Likewise, the Givetian community-type is replaced in concomitance with the Taghanic global event. After this global event, the platform is flooded leading to the development of a siliciclastic ramp associated with deep carbonate mud mounds. Not only, a replacement of the benthic biodiversity is recorded but also several community-types appeared inside this platform morphology.

The Frasnian deep ramp of the Ardennes Massif seems to correspond to a more remarkable environmental change rather than alternations between the mixed ramp and the carbonate shelf of the Givetian. In order to better estimate this environmental disruption it should be important to apply the same analytical procedure, as the present study, on the palaeothrophic levels of this period. Indeed, as distinct benthic community-types are identified in this platform morphology, the palaeotrophic level distribution should be more complex and provide information to compare it within the mixed ramp and the carbonate shelf.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Distribution of palaeotrophic levels in each level of the Mont d'Haurs section (modified after Hubert 2008a).