
Distribution and temporal variation of mega-fauna at the Regab pockmark (Northern Congo Fan), based on a comparison of videomosaics and geographic information systems analyses

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Abstract:

The Regab pockmark is a large cold seep area located 10 km north of the Congo deep sea channel at about 3160 m water depth. The associated ecosystem hosts abundant fauna, dominated by chemosynthetic species such as the mussel *Bathymodiolus* aff. *boomerang*, vestimentiferan tubeworm *Escarpia southwardae*, and vesicomid clams *Laubiericoncha chuni* and *Christineconcha regab*. The pockmark was visited during the West African Cold Seeps (WACS) cruise with RV *Pourquoi Pas?* in February 2011, and a 14,000-m² high-resolution videomosaic was constructed to map the most populated area and to describe the distribution of the dominant megafauna (mussels, tubeworms and clams). The results are compared with previous published works, which also included a videomosaic in the same area of the pockmark, based on images of the BIOZAIRE cruise in 2001. The 10-year variation of the faunal distribution is described and reveals that the visible abundance and distribution of the dominant megafaunal populations at Regab have not changed significantly, suggesting that the overall methane and sulfide fluxes that reach the faunal communities have been stable. Nevertheless, small and localized distribution changes in the clam community indicate that it is exposed to more transient fluxes than the other communities. Observations suggest that the main megafaunal aggregations at Regab are distributed around focused zones of high flux of methane-enriched fluids likely related to distinct smaller pockmark structures that compose the larger Regab pockmark. Although most results are consistent with the existing successional models for seep communities, some observations in the distribution of the Regab mussel population do not entirely fit into these models. This is likely due to the high heterogeneity of this site formed by the coalescence of several pockmarks. We hypothesize that the mussel distribution at Regab could also be controlled by the occurrence of zones of both intense methane fluxes and reduced efficiency of the anaerobic oxidation of methane possibly limiting tubeworm colonization.

Keywords: Cold seep ; Fauna ; Mosaic ; Pockmark ; Regab ; temporal variation

1 **1. Introduction**

2 Cold-seep ecosystems have been identified along active and passive margins
3 worldwide, and are known to host rich and abundant chemosynthetic communities
4 (Sibuet & Olu-Le Roy 2002). Many studies have described the distribution of the
5 dominant faunal assemblages in relation to their environment in several cold seeps
6 systems (Sibuet & Olu-Le Roy 2002, MacDonald et al. 2003, Olu-Le Roy et al.
7 2007a, Jerosch et al. 2007, Lessard-Pilon et al. 2010), and cold seeps are usually
8 considered to provide more stable environments than hydrothermal vents. Although
9 some decadal-scale stability of vent fauna was sometimes observed (Desbruyères
10 1998, Copley et al. 2007, Cuvelier et al. 2011), several studies about temporal
11 variation of vent communities suggested that hydrothermal vents can be highly
12 dynamic environments (Hessler et al. 1988, Shanks 1995, Shank et al. 1998,
13 Mullineaux et al. 2000), especially when considering smaller spatial and temporal
14 scales (Cuvelier et al. 2011). Existing observations of individual taxonomic groups at
15 cold seeps revealed very slow growth rates and extremely long lifetimes likely related
16 to slow and steady fluxes of reduced compounds (Nix et al. 1995, Fisher et al. 1997,
17 Smith et al. 2000, Bergquist et al. 2000). For instance, some tubeworm aggregations
18 were estimated to be at least 250 years old (Fisher et al. 1997, Bergquist et al. 2000),
19 and ages of several hundreds of years have been assessed for *Bathymodiolus*
20 *childressi* (Smith et al. 2000).

21 Up to now, very few works focused on the temporal variation of the faunal
22 distribution (Lessard-Pilon et al. 2010) in a cold seep environment. Such information
23 is not only important to increase our knowledge about the community dynamics, but it
24 also allows better understanding the dynamics of the venting activity. Indeed,
25 chemosynthetic communities are highly dependent on their environment, primarily

1 because distribution patterns of the dominant symbiont-bearing, habitat-creating taxa
2 are linked to methane and sulfide levels and fluxes, and substrata (Sahling et al. 2002,
3 MacDonald et al. 2003, Levin et al. 2003, Bergquist et al. 2005, Mau et al. 2006, Olu-
4 Le Roy et al. 2007a). Distribution changes therefore could also reflect changes in the
5 venting activity.

6 Bergquist et al. (2003b) and Cordes et al. (2005b) suggested that community changes
7 could be also time-related, and proposed a succession model for Gulf of Mexico seep
8 communities, in which mussel beds become replaced by tubeworm communities as
9 carbonate precipitates in the sediments. With time, tubeworm communities then
10 contribute to reducing methane and sulfide availability at the sediment/water
11 interface, thus leading to changes in the associated communities, by allowing non-
12 endemic species to venture and compete with chemosynthetic species.

13 Whatever the cause of flux change, mussel population mortality and movements are
14 considered to reflect changes in seepage flow or chemistry (Roberts et al. 1990,
15 Lessard-Pilon et al. 2010), while tubeworms tend to increase their dominance when
16 fluid flow declines and can persist for years (Bergquist et al. 2003a, b, Cordes et al.
17 2005b). Finally, Lessard-Pilon et al. (2010) attributed a 15 year succession pattern
18 between tubeworm and mussel populations to renewed or redirected active seepage.

19 During the West African Cold Seeps (WACS) cruise in February 2011, the Regab
20 pockmark was intensively surveyed and a 14,000 m²-large video-mosaic was
21 assembled to map the main populated area of the pockmark. A subset of this same
22 area had already been described by Olu-Le Roy et al. (2007a), who provided a
23 detailed description of the spatial patterns of the faunal assemblages, highlighting
24 high degree of spatial heterogeneity. This work was based on imagery data, and in
25 particular on video-mosaics, taken in 2001 during the Biozaire cruise.

1 Using geo-referenced mosaics and geographic information systems (GIS), we provide
2 a description of the current distribution of the dominant megafauna (mussels,
3 tubeworms, clams) and its ten-year development in one of the most densely populated
4 areas of the Regab pockmark. We identify vestimentiferan tubeworms, bathymodiolid
5 mussels and vesicomysids that create the dominant habitats of the pockmark. To our
6 knowledge this is the first study of the temporal variation of the distribution of
7 chemosynthetic fauna at this scale and including such diverse habitats.

8

9 **2. Site description**

10 The Regab pockmark is located on the passive Congo-Angola margin at 3160 m water
11 depth, about 10 km to the north of the Congo deep-sea canyon. The pockmark is a
12 circular-shaped depression on the seafloor that is less than 20 m deep and about 800 m
13 wide (Charlou et al. 2004, Ondréas et al. 2005) (Figure 1). Regab has been described
14 as a ‘pockmark cluster’ since it is considered to be composed of several smaller
15 pockmarks (Ondréas et al. 2005). These features are believed to result from seafloor
16 collapses following the release of over-pressured interstitial fluids. This was
17 suggested after seismic profiles showed the presence of a 300 m-deep subsurface pipe
18 rooted in a palaeo-channel that acts as a reservoir for the accumulating fluids
19 (Ondréas et al. 2005, Gay et al. 2006). Trapped fluids are mostly enriched in methane
20 and are believed to be produced in deeper layers of sediment by microbial activity
21 (Charlou et al. 2004). The presence of gas hydrates was observed both in hydrate
22 outcrops at the sediment surface and in gravity cores down to a depth of 6 m (Charlou
23 et al. 2004, Ondréas et al. 2005). Sulfide is produced from methane and sea-water
24 sulfate in the subsurface sediment by anaerobic methane oxidation, which has been
25 identified in the different habitats (Cambon-Bonavita et al. 2009).

1 The most active area in terms of fluid escape is a 600 m-long and 200 m-wide N70°-
2 directed area located near the middle of the pockmark. This area corresponds to a
3 zone of extensive carbonate crusts and it seems to host most of the fauna that have
4 been identified at the pockmark (Ondréas et al. 2005). The faunal communities
5 present at Regab are dominated by symbiont-bearing species including
6 vestimentiferan tubeworms of the species *Escarpia southwardae* (Andersen et al.
7 2004), two species of Vesicomidae bivalves, *Laubiericoncha chuni* and
8 *Christineconcha regab* (Cosel & Olu 2008, 2009, Krylova & Cosel 2011), and one
9 species of the mussel *Bathymodiolus* aff. *boomerang* (Olu-Le Roy et al. 2007b).
10 These foundation species create habitats that support associated heterotrophic macro-
11 and meio-faunal communities which vary in biomass and diversity among habitats
12 (Gaever et al. 2009, Menot et al. 2009, Olu et al. 2009).

13

14 **3. Methods**

15 3.1 WACS mosaic

16 3.1.1 Acquisition

17 Imagery used for the production of mosaics was acquired with a high-definition color
18 video camera over two ROV dives during the WACS cruise with RV Pourquoi Pas?.
19 The camera is mounted vertically on the ROV Victor 6000 and is dedicated to high-
20 resolution mosaicking applications. The surveys were carried out in a structured way
21 by performing parallel line surveys separated by 3-meter intervals, from an average
22 altitude of 3 meters, so as to ensure overlap between the mosaic lines. The total
23 surveyed area covers a rectangular surface of about 65×220 m² (Figure 2). The limits
24 of this surface correspond to the limits of the 'mosaic 2' produced by Olu-Le Roy et al.

1 (2007a) from images acquired during the BIOZAIRE cruise in 2001. The reason for
2 this is to enable later comparison of the two mosaics. To minimize drift-induced
3 positioning errors, the survey area was split into two equal subareas of $65 \times 115 \text{ m}^2$
4 each (Figure 2). The survey required a total of twenty-one lines per subarea to cover
5 the entire surface. Each line was 115 m long in order to ensure overlap between the
6 two subareas. Moreover, the ROV position was regularly reset onto markers at the
7 beginning of lines in order to eliminate any drifting error before starting a new line.
8 During the survey, the maximum observed drift error at the end of a line was about 3
9 meters. The markers were also used to reset the ROV position when resuming the
10 survey in the second mosaicking dive. Final navigation is therefore a hybrid
11 navigation from USBL and dead-reckoning navigation reset with markers.

12 3.1.2 Construction of the video-mosaic

13 The lines of mosaic were constructed using the Ifremer in-house MATISSE program
14 (Vincent et al. 2003, Allais et al. 2004). The MATISSE program was first designed for
15 online-videomosaicking, i.e. to build the mosaic while the survey is ongoing.
16 However, due to compatibility issues between the program and the new camera and
17 navigation systems of the ROV Victor 6000, building the mosaic involved numerous
18 intermediate data manipulation steps and could not be performed in real-time. For
19 instance, the HD-formatted video files (1920x1080 pixels) had to be converted into
20 DVD-PAL format (720x576 pixels) before they could be read by MATISSE. This
21 involved adding black bands on the video files in order to preserve the 16/9-ratio of
22 HD frames. Conversion to DVD format was done with the ConvertXtoDVD
23 commercial program. Navigation files also had to be rewritten according to an older
24 standard to ensure compatibility with MATISSE. The navigation was then replayed
25 with the Ifremer TRIADE Software, a program that sends navigation entries to

1 MATISSE at a real-time frequency in order to simulate an online mode. Mosaic lines
2 were then constructed at a real-time pace.

3 Each line of mosaic was constructed separately instead of letting Matisse run straight
4 from the beginning to the end of the survey. The reason was to keep size of files
5 small, and to allow more flexibility in the construction of the final areal mosaic.

6 3.1.3 GIS and spatial analyses

7 The separate lines were imported and geo-referenced into ArcGIS. Geo-referencing
8 was done with the ROV navigation data, but caution was taken that corresponding
9 features between overlapping segments match on the same points.

10 For all mosaics, surficial features were manually delineated and polygons were
11 created in ArcGIS to map the spatial distribution of each feature. Mapped features are
12 similar to those used for the Biozaire mosaic (Olu-Le Roy et al. 2007a), and the main
13 categories are: dense *Mytilidae*, sparse *Mytilidae*, dead *Mytilidae*, *Escarpia-Mytilidae*
14 co-occurrence, dense *E. southwardae*, sparse *E. southwardae*, juvenile *E.*
15 *southwardae*, recumbent *E. southwardae*, senescent *E. southwardae*, living
16 *Vesicomidae*, mixed (living and dead) *Vesicomidae*, dead *Vesicomidae*, carbonate
17 concretions (Figure 3). Areas of coverage were computed for each non-sparse
18 category in ArcGIS, using the Mollweide equal-area projection.

19 The dense *Mytilidae* category refers to areas where the living mussel distribution is
20 almost continuous and where the substratum is rarely visible. Conversely, sparse
21 *Mytilidae* applies to areas where the substratum is clearly visible between the
22 individuals. Such distinction was not made for the dead *Mytilidae* category. The dense
23 *E. southwardae* category refers both to single large bushes of adult tubeworms, and to
24 fields of bushes of adult tubeworms, whereas the sparse *E. southwardae* category

1 corresponds to areas where bushes of adult tubeworms are not closely distributed and
2 contain relatively few tubes (roughly 10 or less). The juvenile *E. southwardae*
3 category refers to bushes where tubeworms are of strikingly small size in comparison
4 to the adult community. The recumbent *E. southwardae* category designates bushes
5 where tubes are disposed horizontally, and the senescent category refers to dead
6 individuals and individuals in poor condition whose tubes lie on the seafloor. Patches
7 of vesicomid clams are categorized either as living, mixed (dead and living) or dead.
8 Living clams are normally half buried and stand upright in the sediments, whereas
9 dead clam shells are generally open and lying in the sediments. The 'mixed' category
10 refers to patches that contain both living and dead clams. Carbonate crusts were
11 mapped only where concretions could clearly be seen on the images, and the mapped
12 areas often do not include the carbonated crusts that underlie the tubeworm
13 population, the dense mussel beds, or thin sediment covers.

14 The delineation process was supported by the use of the full HD resolution video files,
15 particularly for differentiating clams from mussels and living bivalves from dead
16 bivalves. Vesicomid clams comprehend two species, *Laubiericoncha chuni* and
17 *Christineconcha regab*, that cannot be separated based on the images. However, both
18 in 2001 and in 2011, *Christineconcha regab* was largely dominant in samples and on
19 close-up views (Cosel & Olu 2009, Decker et al. 2012).

20

21 3.2 BIOZAIRE mosaic

22 The BIOZAIRE mosaic corresponds to the 'mosaic 2' described in the literature (Olu-
23 Le Roy et al. 2007a). Due to the absence of navigation data, the BIOZAIRE mosaic
24 was never geo-referenced. But surfaces could be calculated anyway from the altitude

1 of survey and the camera parameters. In this work we used the new WACS mosaic to
2 geo-reference each individual segment (76 segments) of the BIOZAIRE mosaic, with
3 an average root-mean-square (RMS) error of 0.03 m (SD = 0.1 m) and a maximum
4 RMS error of 0.4 m. The geo-referencing was done in ArcGIS by registering features
5 common to both mosaics, such as unchanged carbonate concretions, patches of dead
6 shells, detritus and also bushes of tubeworms. The advantage of this technique is that
7 it reduces the discrepancies between both mosaics, no matter how accurate the geo-
8 referencing of the WACS mosaic is. In other words, the same polygon should have the
9 same surface on both mosaics and patch sizes should be directly comparable, with a
10 low relative error. However, differences in angles of perspective, in image quality, in
11 visibility and in precision of delineation process also occur and cause some
12 discrepancies in the computed areas. Digitized polygons for living and dead mussel
13 patches are the most affected by such discrepancies.

14 In order to keep consistency with the published work, BIOZAIRE polygons were not
15 redrawn. Instead, the original polygons, drawn in Photoshop by Olu-Le Roy et al.
16 (2007a), were reused. This implied exporting every polygon layer from Photoshop.
17 Polygons were then imported as polygon features into ArcGIS and geo-referenced
18 over the BIOZAIRE mosaic. The surface areas were recalculated according to the new
19 geo-referencing data.

20 Additionally, qualitative direct visual comparison of the two mosaics allowed for
21 identification of small-scale localized changes, which could not be observed from the
22 digitized polygons.

23

24

1 **4. Results**

2 4.1 WACS mosaic (2011)

3 The surveyed zone almost fully covers a 14,000 m²-large rectangular area directed in
4 a southwest-to-northeast direction (Figure 1). Direct mapping of the main faunal
5 assemblages and visible carbonate concretion areas is available for the entire study
6 area (Figure 4a). It shows that the substratum is composed either of soft sediments or
7 of harder carbonate concretions and that the faunal distribution is spatially non-
8 uniform but instead is divided into areas of high and low fauna presence. Areas of
9 high fauna presence can in turn be categorized based on the dominant type of fauna
10 (Figure 4b).

11 Carbonate concretions were visible over a large portion of the survey area (Figure 4b).
12 The total measured extent exceeds 4400 m². This is however a minimum estimation
13 since it does not include carbonate concretions that were not directly visible at the
14 surface, i.e. concretions covered by sediments or underlying fields of tubeworms and
15 mussels.

16

17 4.1.1 Areas of high fauna presence

18 *Mussel distribution*

19 The map of faunal distribution (Figure 4a) shows that large mussel beds were round-
20 shaped and always adjacent to the tubeworms fields. At the limit between the two
21 aggregations, a transition zone with co-occurrence of mussels and tubeworms was
22 often observed. In these transition zones mussels were present on the substratum
23 between the tubeworms but they were also attached onto the tubeworms themselves.

1 The mosaic and video material from ROV dives also indicated that areas of mussel
2 occurrence tended to coincide with areas of hard substrata, i.e. of carbonate
3 concretions, either bare or with thin sediment cover. Indeed, very few mussels were
4 observed on soft sediment areas; however, because the substratum type cannot be
5 reliably identified from the images under all mussel aggregates, the proportion of
6 mussel aggregates that were located in soft sediments could not be quantified.

7 The dense mussel category within the study area covered a total area of 414 m² (Table
8 1) and was mostly concentrated in two main (M2/M3, M1) and one minor (M4) areas
9 (Figure 4b).

10 The largest mussel area, known from the Biozaire mosaic as “M2/M3”, stretched out
11 over 20 m and 26 m in the SW-NE and NW-SE directions respectively; it had an
12 approximate surface of 450 m², of which at least 300 m² were covered by dense
13 mussels. Observations of video footages showed that a large part of the dense
14 population in this area was located at the bottom of a depression between boulders of
15 carbonate concretions (Figure 4a). This mussel bed stretched out towards the north
16 boundary of the mosaic and likely extended further.

17 The second main mussel area (“M1”) was located at about a hundred meters to the
18 southwest of the first one. It was composed of two beds of dense living mussels, one
19 of about 45 m² and the other of about 30 m². The population was almost entirely
20 surrounded by dense bushes of tubeworms but image material shows that mussels
21 were also present, although at a lower density. Patches of dead mussels seemed to be
22 larger at M1, whereas the abundance of living mussels was visibly lower than at
23 M2/M3.

24 Additionally a minor mussel patch was present at the northeastern limit of the mosaic.

1 In this area, the densest mussel bed covered an area of less than 10 m², but was likely
2 to extend over the limit of the mapped area. This area is referred to as “M4”.

3

4 *Tubeworm distribution*

5 The majority of the tubeworm population within the area of study was concentrated in
6 dense bushes. Bushes of tubeworms were in some places isolated but occurred more
7 commonly in large and dense fields. In either case, living tubeworms seemed to occur
8 only on carbonate concretions and mostly around the main mussel areas. However, the
9 substratum under dense tubeworms was not always visible on the images, and it could
10 not be ascertained whether all living tubeworms in the area of study occurred on
11 carbonate concretions.

12 The largest field with high tubeworms density was up to 1400 m² in area and was
13 located near the middle of the study area, west-northwest of M2/M3. This area was
14 more elevated than in the rest of the study area. This was due to the presence of
15 blocks of hard concretions that gave the relief a rugged surface. A relatively high
16 visible abundance of mussels was observed within the transition zone between mussel
17 and tubeworm populations. In this area the transition zone was up to 7 m wide.

18 The second largest field of tubeworms covered an area of about 600 m² and
19 surrounded M1 almost entirely. In this field, the zone of co-occurrence between
20 tubeworms and mussels was very small and it was not observed all along the
21 mussel/tubeworm limit. The field stretched out farther towards the south-southwest
22 and beyond the limits of the study area.

23 The next largest fields of dense tubeworms were located at the eastern and
24 northeastern end of the mosaic. In this area, two fields of about 130 m² each were

1 separated by a zone of soft sediments and low fauna presence. A 55 m²-large zone of
2 co-occurrence between tubeworms and mussels could be observed in the vicinity of
3 M4.

4 Juvenile tubeworms were mostly observed as isolated bushes or as small fields in the
5 periphery of the large aggregations of dense tubeworms. Observed juveniles also
6 seemed to occur consistently on carbonate concretions, but generally close to or at the
7 limit between concretions and soft sediments (Figure 5). They were never observed
8 more than 3 m away from the limit of the concretions, and never on the most
9 protruding, and likely thicker, concretions. Mussels were also observed within
10 populations of juvenile tubeworms, where those bordered the mussel beds.

11 Senescent and/or recumbent populations were rarely observed, and never within the
12 main tubeworms aggregations. The main occurrences were located in the periphery of
13 larger fields of tubeworms. Additionally, senescent tubeworms were often located
14 over soft sediments (Table 1) and in the immediate vicinity of clam aggregations.

15

16 *Vesicomylid clam distribution*

17 Vesicomylids were observed in aggregates of very variable dimensions, and ranged
18 from very small clusters of about 0.01 m² to large fields of up to 400 m², gathering
19 living, dead or mixed (i.e. dead and living) individuals. However, most aggregates
20 contained mixed individuals, and it was hard to quantify the relative proportion of
21 living and dead individuals from the images. In a few cases, small clusters of living
22 clams could be observed and delineated within larger patches of mixed (dead and
23 living) clams. Dimension of individual aggregates of living clams in the survey area
24 did not exceed 3 m².

1 Clam communities seemed limited to the areas covered by soft sediments (Table 1).
2 For instance, clusters of living vesicomyids were scattered across the mosaic but were
3 almost consistently (273 out of 276 clusters) observed in the areas covered with soft
4 sediments (Table 1). Furthermore, 241 out of 276 clusters of living vesicomyids were
5 located in patches of dark reduced sediments, which correspond to 94% of the total
6 area (88 m²) covered by clusters of living vesicomyids (Table 1). Generally, dead
7 vesicomyids were more commonly observed on carbonate concretions (13%) than
8 living (2%) and mixed (5%) vesicomyids.

9 The vesicomyid population was very patchy and heterogeneously distributed within
10 soft sediment areas (Figure 4a); in particular, it concentrated mostly at the periphery
11 of the main mussel/tubeworm aggregations (Figure 4b). The largest field of
12 vesicomyids occurred in the vicinity of M4; within this field, living and mixed (living
13 + dead) vesicomyids covered respectively 39 m² and 258 m².

14

15 4.1.2 Areas of low fauna presence

16 Areas of low fauna presence exhibited strikingly low numbers of tubeworms, clams,
17 and mussels patches in comparison to the rest of the survey area (Figure 4a). Apart
18 from the highly mobile fauna such as the galatheids, most of the fauna in those areas
19 was composed mainly of sparse patches of tubeworms (≤ 25 m²) or of living and
20 mixed (dead and living) clams (≤ 20 m²). Dead clam shells were also frequently
21 observed.

22 The least-colonized zone was located to the south of the large mussels and tubeworms
23 communities located in the middle of the survey area. It covered an area of about
24 1000 m² and was mostly composed of soft, bioturbated sediments.

1

2 4.2 Comparison with BIOZAIRE mosaic (2001)

3 The Biozaire mosaic (2001) does not provide contiguous areal coverage such as the
4 WACS mosaic (2011), and large gaps occur between individual lines. Both mosaics
5 overlap over a 4605 m²-large area, which correspond to a subset only of the WACS
6 mosaic area. In order to compare the trend in faunal distribution, this overlapping area
7 is shown for the Biozaire and WACS videomosaics (Figure 6). Overall, there were
8 only little changes in the spatial location of the main faunal assemblages.

9 The mussel distribution has remained mostly the same as it was during the Biozaire
10 cruise. Although it is hard to compare the size of the main aggregations due to the
11 smaller coverage of the Biozaire mosaic, there is evidence that M2/M3 contained a
12 larger mussel population on the WACS mosaic than on the Biozaire map, with fewer
13 gaps between the different patches (Figure 7a). Conversely, some small mussel beds at
14 M1 seem to have disappeared and to have been replaced by dead mussel shells
15 (Figure 7b). M4 is not covered by the Biozaire mosaic and cannot be compared.

16 Tubeworm fields showed no change in distribution, the slight difference in polygon
17 sizes being more due to the lower resolution of the Biozaire imagery data than on
18 actual distribution changes. From these results, the tubeworm community is believed
19 to be the one that changed the least across the study area. Most bushes or even single
20 tubeworms were found unchanged and in some cases in the exact same position than
21 in the older mosaic (Figures 7c, 8). Tubeworms were indeed the most reliable features
22 when geo-referencing the Biozaire mosaic onto the WACS mosaic.

23 The vesicomylid clam population is the fauna that changed the most since the Biozaire
24 cruise. Although the main clam fields have remained at the same locations, their sizes

1 seem to have increased. In addition, at least 38 new patches of living clams were
2 observed that did not exist during the Biozaire cruise. Those new patches had a mean
3 size of 0.5 m^2 (SD = 0.6 m^2), and their areas sum up to 17 m^2 . They were often
4 located in the close vicinity of older patches (Figure 8b), but were also in a few cases
5 new settlements farther from previously existing patches (Figure 8a). Conversely, 16
6 patches were identified on the Biozaire mosaic, which did not exist anymore in 2011
7 or at least, which were buried under some sediments (Figure 8c). They had a mean
8 size of 0.3 m^2 (SD = 0.2 m^2), and cover a total area of 4.6 m^2 . About 4 of those 16
9 patches contained dead clams only.

10 Areas of coverage by dense mussels, tubeworms and clams were computed for both
11 the Biozaire and the WACS faunal distribution maps (Table 2). Areas of sparse mussel
12 and sparse tubeworm occurrence are not shown due to too large errors in delineating
13 sparse aggregations. In addition, to keep consistency with previous work on the
14 Biozaire mosaic, areas with co-occurrence of living mussel and tubeworm are given
15 (Table 2). Given a total common area of 4605 m^2 between the Biozaire and the WACS
16 mosaics, areas can be expressed in percentage of cover of the overlap area. According
17 to these calculations, coverage changes were very low and remained below 2% of the
18 total overlap area for every category. Patches of living tubeworms, tubeworms with
19 mussels and mixed (dead and living) clams underwent the largest changes, with
20 coverage increases of up to 1.5, 1.3 and 1.2% of the total overlap area respectively
21 (Table 2). The total areal extent of the other assemblages showed almost no change.

22 Overall, the distribution of the carbonate concretions over the study area did not
23 change between the Biozaire and the WACS cruises. The higher resolution of the new
24 mosaic allowed better definition of the limits of the concretions, especially in areas
25 covered with tubeworms or mussels, and no major new area of occurrence was

1 observed. On the contrary, in many places the carbonate concretions tended to slightly
2 disappear under a thin sediment cover.

3

4 **5. Discussion**

5 5.1 Faunal and carbonate distribution

6 The mosaic and the distribution map of the megafaunal communities give a very
7 detailed view and full coverage of the entire study area. The results show that the
8 megafauna at Regab is concentrated mainly in three distinct areas of high fauna
9 presence, separated by areas of relatively lower presence. Such distribution indicates
10 that the chemical fluxes that are required to sustain these chemosynthetic communities
11 are heterogeneous over the study area. Indeed, the distribution of the main faunal
12 assemblages showed a concentric spatial zonation pattern starting from mussel beds in
13 the middle to tubeworms and finally fields of vesicomys towards the outside. In our
14 study this spatial zonation pattern from mussels to vesicomys clams was observed, to
15 various extents, around the three main mussel areas (M1, M2/M3, M4).

16 A model presenting a concentric pattern has been proposed previously for the Regab
17 pockmark (Gay et al. 2006), but it considered both mussels and tubeworms as
18 methane-dependant species inhabiting the same carbonate-dominated facies (Olu-Le
19 Roy 2006). Although *Bathymodiolus* aff. *boomerang* contains both methanotrophic
20 and thiotrophic symbionts (Duperron et al. 2005) and, for the populations living in the
21 Regab pockmark, is known to rely on methane as dominant energy source (Olu et al.
22 2009, Duperron et al. 2011), tubeworms are known to host sulphur-oxydizing
23 symbionts (Dubilier et al. 2008) and to have very high demands in terms of sulfide
24 supply (Cordes et al. 2003).

1 We postulate that the observed distribution is controlled by the strength of fluid
2 advection and related methane fluxes, and propose a model in which the megafaunal
3 distribution at Regab is structured by the presence of discrete zones of intense fluid
4 advection and methane fluxes under the mussel beds (Figure 9). The distribution of
5 the other communities would therefore be related to decreasing advection rates with
6 distance from the mussel beds. The existence of such localized pathways of high fluid
7 advection rate is compatible with the current understanding that the center of the
8 pockmark is composed of several smaller pockmarks (Ondréas et al. 2005). In this
9 section we discuss the concepts of this model, and confront them to more detailed
10 observations of the faunal distribution and of the presence/absence of carbonate
11 crusts.

12 Our observations show that the main mussel beds occur in areas where carbonates
13 form blocs of indurated sediments and concretions within slight depressions, and that
14 the main tubeworm aggregations occur in areas with extensive, continuous and
15 prominent carbonate crusts. The formation of authigenic carbonates is a byproduct of
16 the anaerobic oxidation of methane (AOM) in the sediment (Boetius et al. 2000,
17 Aloisi et al. 2002) and is an indicator of methane fluxes and microbial activity within
18 the sediments. However, the formation of continuous carbonate crusts impacts the
19 porosity and permeability of the sediments and hence reduces the possible pathways
20 for methane- and sulfide-rich fluid escapes and for sulfate-rich seawater infiltration
21 (Hovland 2002, Luff et al. 2004). Therefore, areas of mussel occurrence are likely to
22 be characterized by higher fluxes between the sediments and the bottom water than
23 the encrusted areas where tubeworms occur.

24 We propose that the three main mussel areas present in our study area are located on
25 focused zones where the seepage activity is the strongest, and where fluid flow is

1 intense enough for the methane fluxes to reach the sediment/water interface. Indeed,
2 the distribution of mussels mainly in dense circular beds suggests the presence of
3 localized areas of intense methane fluxes. This hypothesis was mentioned previously
4 from the results of the Biozaire mosaic (Ondréas et al. 2005, Olu-Le Roy et al.
5 2007a). It also is strongly supported by recent biogeochemical analyses in various
6 Regab habitats, according to which extensive seepage of gaseous and dissolved
7 methane was observed only under the mussel habitat (Pop Ristova et al. 2012). This is
8 also in accordance with previous studies in other areas that showed that release of
9 methane to the water column is indeed facilitated in areas of high flux (Boetius &
10 Suess 2004, de Beer et al. 2006, Niemann et al. 2006).

11 Co-occurrence of mussels and tubeworms is commonly observed at the transition
12 between the two populations. In such zones, numerous mussels are observed onto the
13 tubes of the vestimentiferan aggregations that directly border the mussel beds. This
14 could be the result of space limitations within the mussel beds, which would constrain
15 mussels to invade neighboring tubeworm aggregations. Indeed, the dual symbiosis of
16 *B. aff. boomerang* allows this species to use both methane and sulfide, similarly to
17 several other seep and vent mussels of the *Bathymodiolus* genus (Duperron et al.
18 2005). However, unlike in the gills of *Bathymodiolus azoricus* at Mid-Atlantic
19 hydrothermal vents, symbionts in seep mussel gills at Regab and at Gulf of Mexico
20 seeps are predominantly methanotrophic; the thiotrophic symbionts are likely limited
21 by the absence or low level of sulfide in the seawater (Duperron et al. 2011).
22 Moreover, the fact that mussel/tubeworm co-occurrence zones are mostly close to the
23 main mussel beds may also support the hypothesis that methane fluxes are higher in
24 those areas than in the tubeworms aggregations located farther from the mussel beds.
25 This is in accordance with previous studies, which indicate that mussel beds at Regab

1 are located in areas with the highest concentrations of methane in the water (Charlou
2 et al. 2004, Olu-Le Roy et al. 2007a). Such behavior was also observed for
3 methanotrophic mussel populations in the Southern Barbados prism (Olu et al. 1996b)
4 and along the Costa Rica margin (Mau et al. 2006). In the Gulf of Mexico, mussels
5 associated to brine seeps with high methane concentration grow faster and are in
6 better physiological condition than those from petroleum sites with low methane but
7 high sulfide concentrations (Bergquist et al. 2004).

8 The distribution of the tubeworms aggregations around the mussel beds could reflect
9 lower fluid advection rates than under mussel beds. Niemann et al. (2006) and de Beer
10 et al. (2006) suggested that by preventing downward fluxes of sulfate-rich water into
11 the sediments, intense fluid advection rates can hinder the efficiency of AOM. This is
12 in accordance with results from Pop Ristova et al. (2012), who calculated the
13 proportion of upward diffusing methane that is removed by AOM at Regab to be only
14 6-20% under a mussel habitat compared to 47-97% in lower flux areas such as under
15 clam habitats. Such processes could result in different environmental conditions inside
16 and outside the mussel beds, and partly control the relative distribution of tubeworms
17 and mussels. Biotic interactions are known to occur between mussels and tubeworms
18 at hydrothermal vents (Johnson et al. 1994, Desbruyères 1998, Lenihan et al. 2008).
19 For instance, mussels of the species *Bathymodiolus thermophilus* are able to disperse
20 fluids laterally (Johnson et al. 1994), which could make fluids unavailable for
21 tubeworms, and to inhibit recruitment of other vent species (Lenihan et al. 2008).
22 Such interactions could also apply in dense *B. aff. boomerang* aggregations. However,
23 unlike vent tubeworms, which take up sulfide from the seawater (Arp et al. 1985),
24 seep tubeworms such as *E. southwardae* take up sulfide directly from the sediments
25 through their roots (Julian et al. 1999, Andersen et al. 2004), and are likely unaffected

1 by fluid dispersion by the mussels. Furthermore, sulfide is almost absent of the
2 seawater overlying mussel beds at Regab (Olu-Le Roy et al. 2007a, Duperron et al.
3 2011). Therefore, the absence of tubeworms in mussel beds is more likely due to
4 competition for space or to reduced AOM efficiency rather than biotic interactions.

5 Our observations show that large tubeworm aggregations around the main mussel
6 beds correspond to areas where the carbonate crusts are most prominent, and likely
7 the thickest. Carbonate precipitation likely reduced methane flux, thus enhancing
8 AOM and sulfide production, and favoring tubeworm settlement and dominance over
9 mussels. Moreover, as observed at Gulf of Mexico seeps, tubeworms of the species
10 *Lamellibrachia luymesii* were shown to release sulfate through their roots into the
11 sediments (Cordes et al. 2005a), thus preventing a potential sulfate-depletion of the
12 sediments. This characteristic is believed to allow adult *L. luymesii* to fuel or even
13 enhance the AOM (Cordes et al. 2005a, Dattagupta et al. 2008) in order to maintain
14 their supply in sulfide. As a result, the vestimentiferan population contributes to the
15 formation of carbonates, which is supported by our observations that tubeworms are
16 present where concretions form continuous and prominent crusts.

17 Juvenile tubeworms consistently occur near or at the limit between carbonate crusts
18 and bare sediments. Sulfide fluxes and concentrations are likely to be higher in such
19 areas with unsealed sediment/water interface than in areas covered by thick crusts,
20 and thus to provide a suitable environment for the larvae to settle until they can self-
21 maintain their supply of sulfide. According to Bergquist et al. (2002), the recruitment
22 of new tubeworms of the species *Lamellibrachia luymesii* and *Seepiophila jonesii* is
23 time-constrained and stops in older aggregations, due to the presence of thick
24 carbonate pavements and low concentrations of sulfide in the water (Bergquist et al.
25 2003a). Sulfide concentrations have indeed been reported to be higher around

1 aggregations of juvenile than within older aggregations (Bergquist et al. 2003b).

2 This interpretation is further supported by the occurrence of bands of black reduced
3 sediments along the limits of the vestimentiferan-hosting carbonate concretions
4 (Figure 5), indicating that AOM and sulfide release occur in those areas. These
5 features also suggest that part of the methane fluxes trapped beneath the carbonates
6 could be redirected toward the sides of the carbonate crusts.

7 The distribution of the vesicomid population is likely related to even lower advection
8 rates than the tubeworm aggregations. Vesicomid clams require soft substrata to
9 access sulfide through their foot and, thus, are generally excluded from encrusted
10 areas. Results show indeed that the living vesicomid clams are mainly located in the
11 soft sediment areas surrounding the tubeworms and mussel aggregations. However,
12 according to our interpretation, those areas are also where methane and sulfide fluxes
13 are lower. In particular, Olu-Le Roy et al. (2007a) observed that vesicomid clams at
14 Regab are located in areas with relatively low methane concentrations, in comparison
15 to tubeworm and mussel habitats. This is consistent with the current understanding
16 that methane/sulfide availability shapes the structure of the microbial and megafaunal
17 communities (Olu et al. 1996a, b, 1997, Sahling et al. 2002, Sibuet & Olu-Le Roy
18 2002, Levin et al. 2003, Levin 2005, Ritt et al. 2011, Pop Ristova et al. 2012).

19 The vesicomid clam environment is sometimes proposed as being a precursor stage
20 towards a tubeworms/carbonate environment (Sahling et al. 2008). This is partly
21 supported by our observations of dead shells occurrences on some bare carbonate
22 concretions. Also, the presence of dead shells within the concretions has been reported
23 previously (Pierre & Fouquet 2007). These observations suggest that areas with
24 vesicomids transfer to the formation of carbonated crusts, either with or without
25 vestimentiferans. However, we have also observed large patches of dead vesicomid

1 shells within the sediments, sometimes almost buried, that would suggest that seepage
2 activity in these areas decreased or stopped and that living populations either died or
3 moved away. Such areas might never turn into tubeworms/carbonate environments
4 due to too low or too transient fluxes. Thus, vesicomid populations might not be
5 restricted to one particular successional stage of colonization, but be present in a
6 range of areas representing different development stages of the seeping activity and
7 the observed patterns of distribution reflect the spatial heterogeneity of fluid flux.

8 Bergquist et al. (2003b) and Cordes et al. (2005b) suggested that the relative
9 distribution of mussels (*Bathymodiolus childressi*) and tubeworms (*L. luymesii* and *S.*
10 *jonesii*) could be related to different stages of succession, and explain that mussel beds
11 indicate an earlier stage of colonization that would later be replaced by tubeworms,
12 when the formation of carbonate concretions reduces the methane supply to the water
13 column.

14 However, we propose that the situation at Regab is more complex, as the observed
15 patterns of fauna distribution could also be partly related to spatial heterogeneity of
16 the fluid advection regime. Indeed, the particularity of this site is the coalescence of
17 several pockmarks within the Regab site that may differ by their fluid flow regime or
18 their evolution stage (Ondreas et al. 2005; Gay et al. 2006). If the relative
19 mussel/tubeworm distribution was solely related to different colonization stages, the
20 mussel population would expectedly be observed mainly together with, or in the
21 vicinity of, juvenile tubeworm aggregations. Although we do observe juveniles
22 around some small mussel clusters, the larger mussel beds present in the study area
23 are predominantly bordered by large adult tubeworm aggregations. Considering the
24 extreme slow growth rate of tubeworms (Fisher et al. 1997, Bergquist et al. 2000), this
25 indicates that fluid advection in those areas has been going on for a relatively long

1 time, but that recruitment of juvenile has not occurred or has been hindered.

2

3 5.2 Temporal comparison

4 The comparison of the maps of faunal distribution and of the computed areas reveals
5 that the size of the areas of faunal occurrence has remained globally the same between
6 the Biozaire (2001) and the WACS (2011) cruises. We consider the discrepancies in
7 computed values and mapped areas to be largely caused by uncertainties in the
8 method. First, images for each mosaic have been taken with different camera and
9 lighting setups, which results in different resolutions and visibilities between the
10 Biozaire and WACS mosaics. Furthermore, small perspective distortions can, in
11 places, impact the precision of the relative geo-referencing of the mosaics, or make a
12 same feature look larger on one mosaic than on the other. Finally, the delineation
13 process is a manual step that highly depends on the interpretation and precision of the
14 observer. For all these reasons, mapped features may look different and discrepancies
15 in the computed areas may arise that are difficult to evaluate. Nevertheless,
16 considering all these possible sources of uncertainty and the large size of the study
17 area, the computed areas are remarkably consistent between the two mosaics. Indeed,
18 quantitative results showed that the changes in coverage per category are lower than
19 2% of the overlap area, which suggest very little change between the two mosaics.
20 However, based on qualitative observations described below, we consider that the
21 calculated areas are impacted by errors of the method and cannot be used to analyze
22 further such small variations in the areas of faunal cover.

23 For instance, our observations of the mosaics confirm that no change occurred in the
24 population of tubeworms within the overlap area over the past 10 years. Indeed, an

1 increase of the area covered by tubeworms would signify that recruitment occurred.
2 However, we did not observe new juvenile aggregations, possibly because the
3 observation period was too short and that juveniles are still too small to be seen, or
4 that the recruitment in the area covered by the mosaics was somehow limited. Overall,
5 the absence of changes in the vestimentiferan population is in accordance with the
6 findings that some tubeworms (*L. luymesii* and *S. jonesii*) may be very slow-growing
7 and long-living (Fisher et al. 1997, Bergquist et al. 2000). Nevertheless, Lessard-Pilon
8 et al. (2010) did observe evidences of tubeworm recruitment (*Lamellibrachia* spp. or
9 *Escarpia laminata*) within discrete seep communities in the Gulf of Mexico after a 15
10 year period, thus confirming that changes within tubeworms communities could be
11 observed on such time-scales. Their work was based on a comparatively small study
12 area (23.4 m²) and observations were likely more detailed than in our study (4605
13 m²); indeed, they used photo datasets, which provided higher definition images and
14 closer views of the seafloor. Hence, tubeworm recruitment may have occurred within
15 our study area, but it is not evident from our data.

16 Conversely, some changes in size of individual beds of living and dead mussels were
17 observed, which suggest that localized variations of methane fluxes or carbonate
18 precipitation may have occurred. For instance, small scale visual observations suggest
19 that the dense mussel bed in M2/M3 could contain, in the overlap area, a greater
20 abundance of mussels in 2011 than in 2001, and that some minor mussel beds at M1
21 disappeared. This could indicate that the intensity of fluxes increased in M2/M3 and
22 decreased in M1. A decrease in activity in M1 would be consistent with the findings
23 of Olu-Le Roy et al. (2007a), who also hypothesized that a decreasing methane flux
24 occurs in this area, based on the lower density of the mussel beds. Alternatively, the
25 mussel abundance might have been stable and the observed changes could reflect a

1 rearrangement of the mussels. In either case, distribution changes are likely the result
2 of local variations in environmental conditions.

3 However, the observed changes were localized and, overall, the mussel population
4 showed very little variation. Despite the scale difference between the two studies,
5 these findings are consistent with observations of Lessard-Pilon et al. (2010). Both
6 studies agree that only little change was observed on the total area covered by
7 foundation fauna. However, Lessard-Pilon et al. (2010) observed significant small-
8 scale changes in the distribution of mussel populations (*Bathymodiolus brooksi* and
9 *Bathymodiolus heckeriae*), and reported that about 50% of the area originally covered
10 by living mussels at one site had been, after a period of 15 years, either replaced by
11 dead mussel shells or colonized by tubeworms (*Lamellibrachia* spp. or *Escarpia*
12 *laminata*). Interestingly, as we observed at Regab, the hydrothermal vent mussel
13 population of *Bathymodiolus azoricus*, was described to be stable on a decadal scale
14 in terms of overall percentage of colonization (Cuvelier et al. 2011), while small
15 fluctuations occurred on shorter time scales and on smaller spatial scales for seep
16 mussels of the Gulf of Mexico (Lessard-Pilon et al. 2010).

17 In our study, no change was observed in the tubeworm aggregations surrounding these
18 areas where mussel distribution varied. Mussel populations are expected to be more
19 dynamic and to respond faster to environmental changes than tubeworms (Lessard-
20 Pilon et al. 2010), which may be insensitive to small variations of seepage activity.

21 Alternatively, the increased dead mussels occurrence in M1 could reflect a late stage
22 of the successional model developed by Bergquist et al. (2003b), characterized by a
23 decrease of mussel population due to a decrease of methane and maybe of sulfide in
24 the water column. Indeed mussels are associated to areas of vigorous seepages and
25 high methane concentrations (Nix et al. 1995, Bergquist et al. 2005). However, the

1 model proposed by Bergquist et al. (2003b) is true for long time-scales and it is
2 uncertain whether such trend is detectable within a 10-year period.

3 Changes in the population of vesicomimid clams were more frequently observed than
4 for the mussel population. Although we cannot conclude if the total living population
5 globally did change, the location of the aggregates of living individuals shows
6 relatively more differences in comparison to the other populations studied. Indeed,
7 several patches of living individuals observed in the 2011 mosaic did not exist in
8 2001. Conversely some patches of vesicomimid clams that existed in 2001 did not exist
9 anymore in 2011. Also, in some cases, old patches of dead clams were re-colonized by
10 living clams. However, changes in the distribution of patches of living/dead clams are
11 difficult to apprehend since the relative proportion of living and dead clams cannot be
12 estimated from the images. Overall, the distribution of living vesicomimid clams is
13 very patchy and is difficult to understand.

14 Sahling et al. (2008) proposed a model for pockmarks of the Congo fan (100 km north
15 of Regab), in which the distribution of tubeworm (*E. southwardae*) and clam (of
16 similar species than at Regab) assemblages is controlled by the depth of the gas
17 hydrate deposits. The model considers that gas hydrates deposits act as “capacitors”
18 (Dickens 2003) that buffer the transient influxes of methane from below and that
19 ensure a more stable diffusion of methane into the pore water above, thus sustaining
20 long-living seep communities. We think that a similar control mechanism occurs at
21 Regab. Indeed, the presence of gas hydrates at Regab is known both from direct
22 observation of outcrops on the sediment surface and from sediment cores (Charlou et
23 al. 2004, Ondréas et al. 2005).

24 However, although this model is supported by the presence of such large populations
25 of long-living seep communities and by their spatial patterns of distribution, it does

1 not fully explain the temporal changes observed within the clam populations. At
2 Regab, most aggregates of living individuals are indeed located within patches of
3 black sediments, indicating the occurrence of AOM; clams are mobile fauna, hence
4 changes in areas of distribution must somehow reflect changes of sulfide availability.
5 One possible explanation could be that gas hydrate deposits under clam communities
6 are either absent or too thin to buffer the transient methane fluxes over such a time
7 period. The observed changes in clam distribution would therefore be the response to
8 the transient release of methane and subsequent transient sulfide production. Clearly,
9 some monitoring of sulfide concentrations and some geological sampling under the
10 clam aggregates would be required to further refine this interpretation. However, this
11 is in accordance with other studies that suggest that vesicomid clams are supported
12 by diffuse or transient fluxes (Olu et al. 1996a, b).

13

14 **6. Conclusion**

15 In this study, mosaic-based mapping of the faunal distribution over an area of 14,000
16 m² shows that the distribution of dominant megafaunal species (mussels, tubeworms,
17 clams) at Regab is mostly concentrated within three main megafaunal aggregations.
18 Within these three main aggregations, the faunal arrangement follows the same spatial
19 pattern with the methanotrophic mussels in the middle, then the vestimentiferans and
20 finally the vesicomid clams on the outer zone. We interpret that each of these
21 patterns is centered on a zone of high flux of methane-enriched fluids. Such zones of
22 high fluid flow are responsible for the spatial variation of intensity of the fluxes
23 reaching the upper sediments and, hence, structure the distribution of the
24 chemosynthetic megafauna in the pockmark.

1 In addition, this study is the first to describe the 10-year variation of the megafauna
2 distribution in a cold seep environment over a 4600 m²-large area. Through
3 quantitative comparison of the two mosaics, it reveals that the overall size of the
4 dominant megafaunal populations of Regab did not change significantly (< 2% of the
5 comparison area), which indicates that the intensity of the methane and sulfide fluxes
6 that reach the faunal communities has been globally stable at the scale of the
7 comparison area. We interpret that such continuity could be related to the presence in
8 the sediments of gas hydrate deposits acting as “capacitors” for the methane fluxes.

9 Nevertheless, this study also shows that small-scale and discrete distribution changes
10 have occurred, as already observed at other seep and vent sites, but were too small to
11 be reliably quantified with our methodology. Those changes occurred mainly within
12 the living population of vesicomid clams; this suggests that the clam community was
13 exposed to more transient fluxes than the mussel and tubeworm communities.

14

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9

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1 Table 1: Areas of coverage of the different assemblages calculated from the WACS
 2 (2011) mosaic. Information about the distribution in soft sediments is given only for
 3 faunal categories, in which the substratum type could always be identified on the
 4 mosaic.

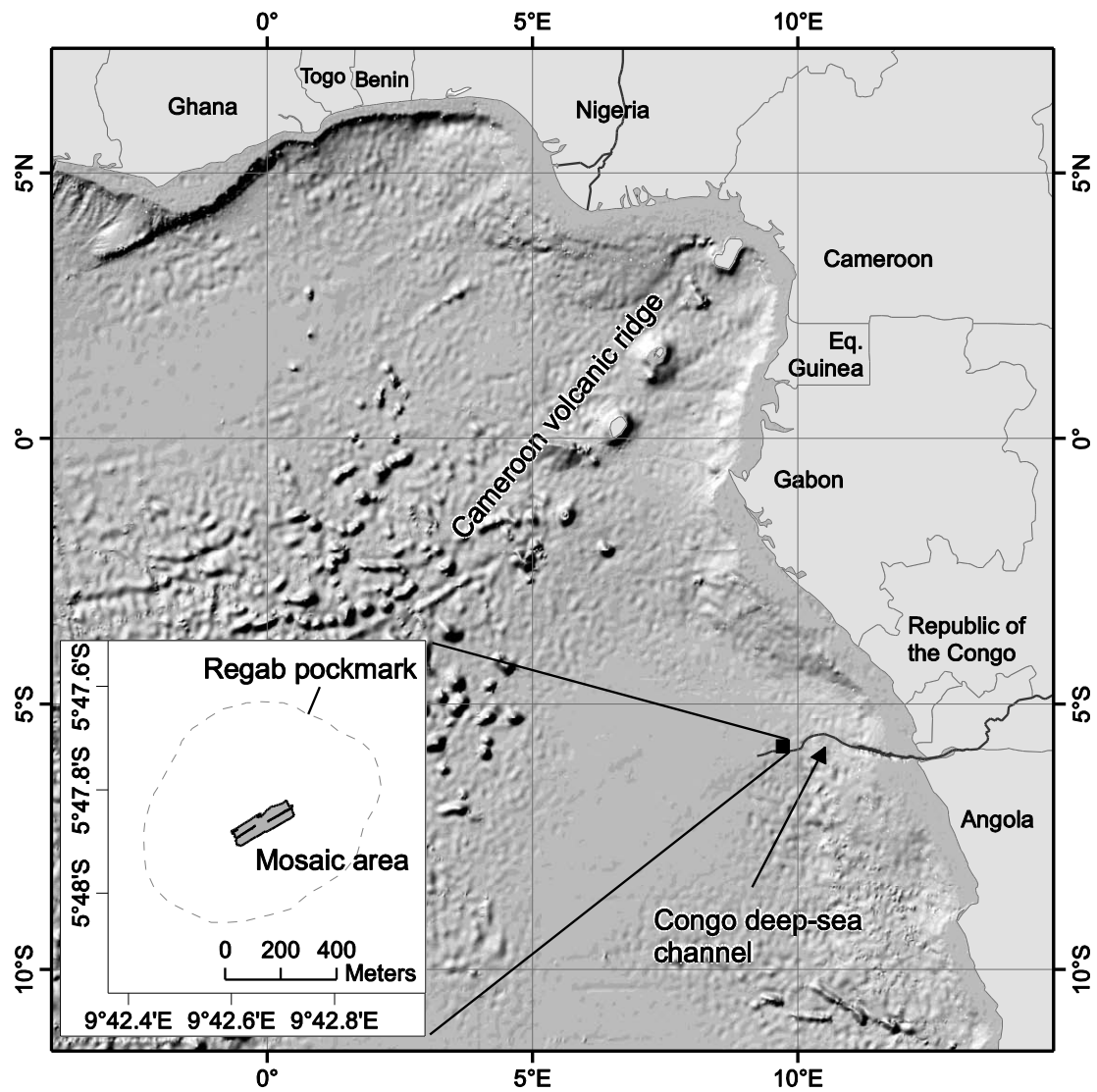
Assemblage	Total Area (m ²)	Within soft sediments (m ²)	Within soft sediments (%)
<i>Escarpia</i> , living	2573	-	-
<i>Escarpia/Bathymodiolus</i> co- occurrence	560	-	-
<i>Escarpia</i> , juveniles	97	-	-
<i>Escarpia</i> , recumbent	70	-	-
<i>Escarpia</i> , senescent	57	56.4	99%
<i>Mytilidae</i> , living	414	-	-
<i>Mytilidae</i> , shells	67	-	-
<i>Vesicomidae</i> , living	88	86.2	98%
<i>Vesicomidae</i> , mixed	534	508.3	95%
<i>Vesicomidae</i> , shells	633	549.9	87%

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1 Table 2: Areas of coverage of the different assemblages in the overlap area between
 2 the Biozaire (2001) and WACS (2011) mosaics. The percentages are relative to the
 3 total area (4605 m²) covered by both mosaics.

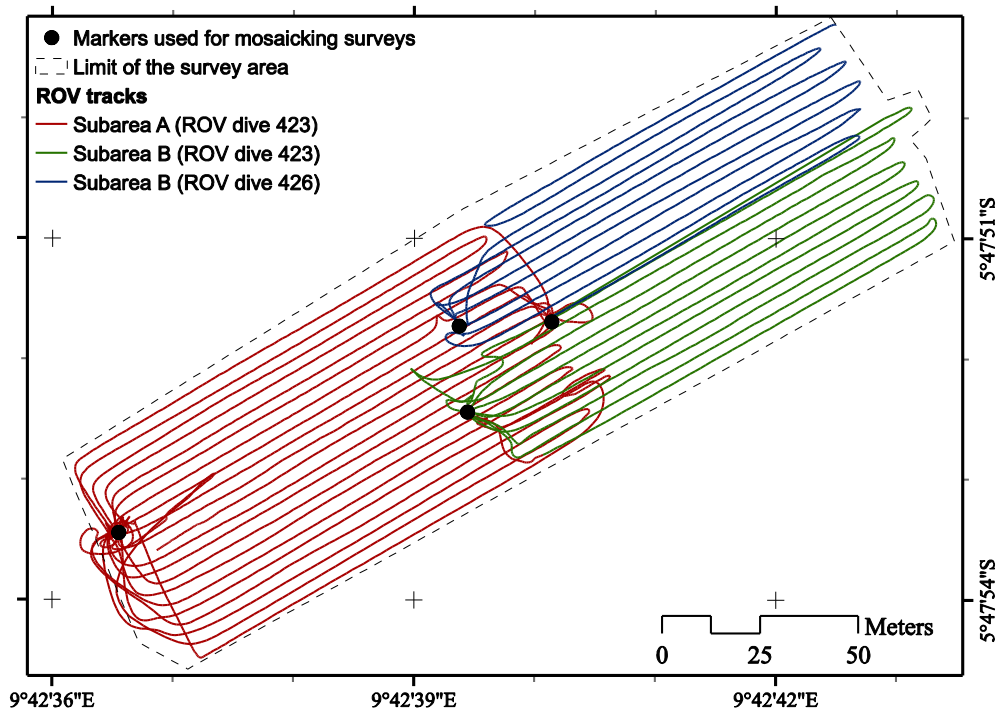
Assemblage	Biozaire (m ²)	Biozaire (%)	WACS (m ²)	WACS (%)	Trend
<i>Escarpia</i> , living	716	15.5%	782	17.0%	+1.5%
<i>Escarpia/Bathymodiolus</i> <i>co-occurrence</i>	207	4.5%	268	5.8%	+1.3%
<i>Escarpia</i> , juveniles	25	0.5%	28	0.6%	+0.1%
<i>Escarpia</i> , recumbent	79	1.7%	60	1.3%	-0.4%
<i>Escarpia</i> , senescent	70	1.5%	95	2.1%	+0.6%
<i>Mytilidae</i> , living	194	4.2%	207	4.5%	+0.3%
<i>Mytilidae</i> , shells	2	0.04%	14	0.3%	+0.3%
<i>Vesicomidae</i> , living	23	0.5%	27	0.6%	+0.1%
<i>Vesicomidae</i> , mixed	141	3.1%	199	4.3%	+1.2%
<i>Vesicomidae</i> , shells	112	2.4%	125	2.7%	+0.3%

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 2 Fig 1: Location of the Regab pockmark; the insert map shows the approximate outline
 3 of the pockmark and the mosaic area.
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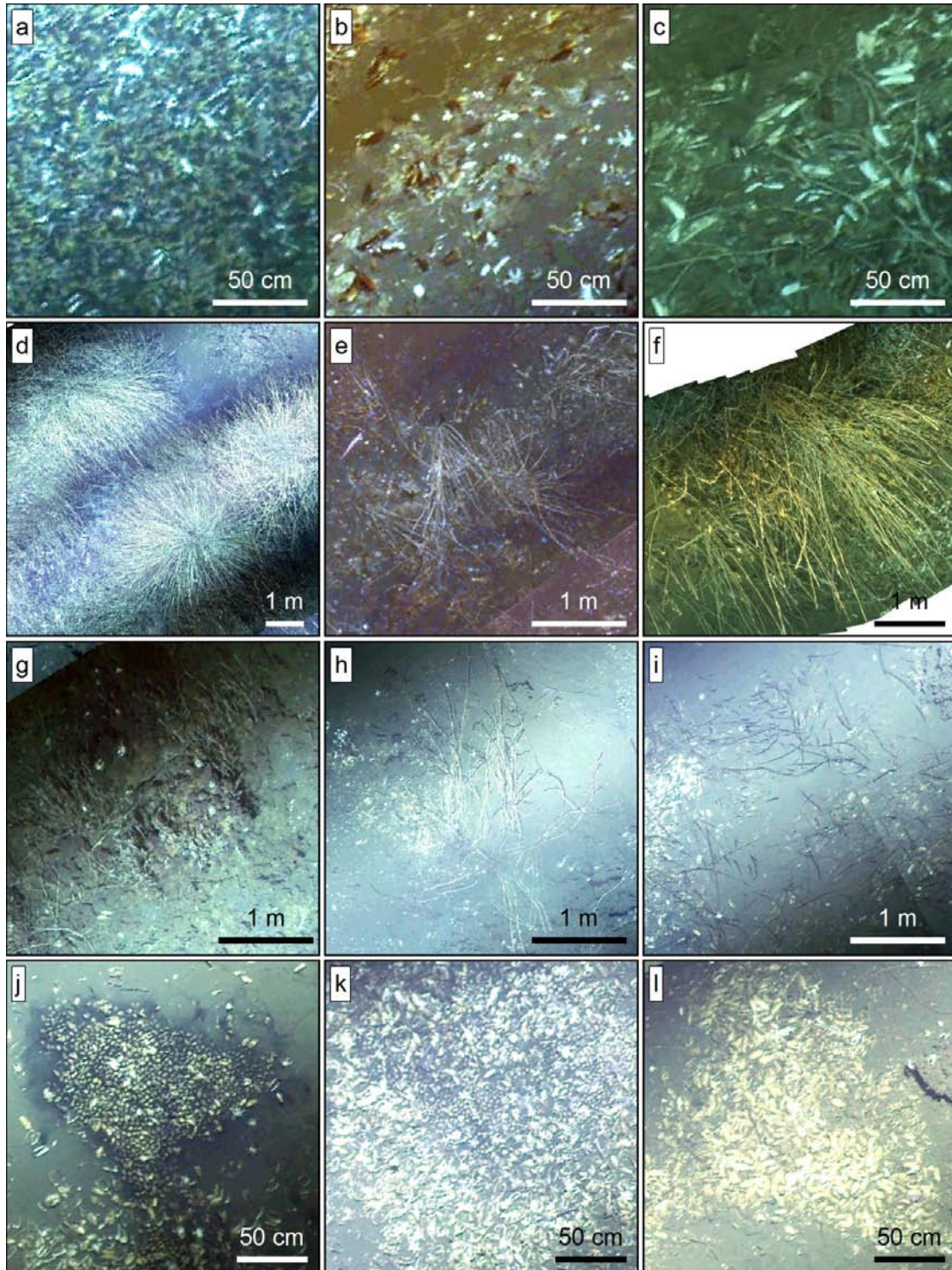


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3 Fig 2: ROV navigation of the WACS mosaicking survey showing the distribution and
4 the overlap of the two subareas (A and B), as well as which areas were surveyed
5 during the two mosaicking dives (423 and 426). The navigation data was regularly
6 reset onto known markers (black dots) to constrain global drifting error.

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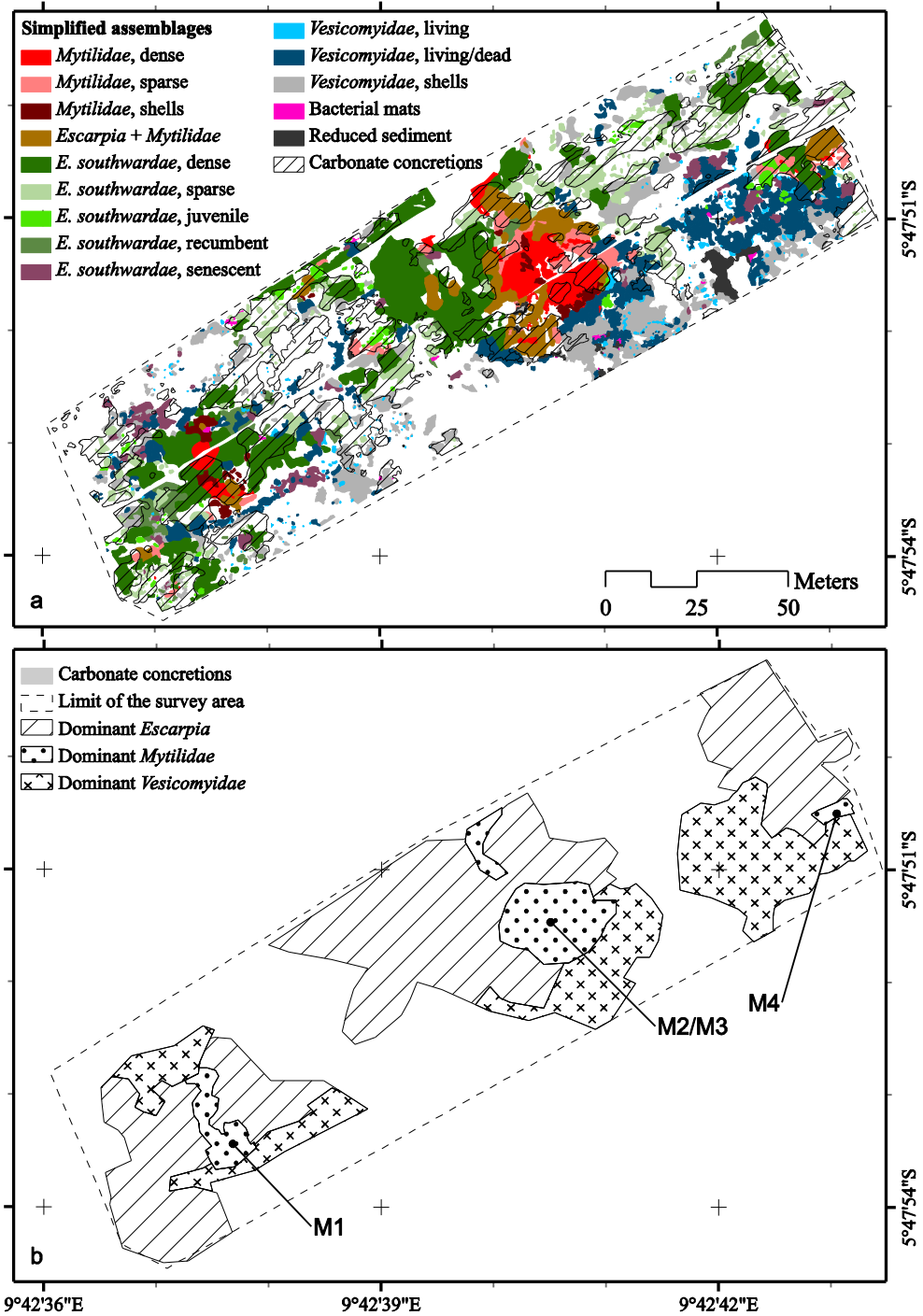
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Fig 3: Excerpts of the WACS mosaic illustrating the different faunal categories; (a) *Mytilidae*, dense; (b) *Mytilidae*, sparse; (c) *Mytilidae*, shells; (d) *E. southwardae*, dense; (e) *E. southwardae*, sparse; (f) *E. southwardae*-*Mytilidae* co-occurrence; (g) *E. southwardae*, juvenile; (h) *E. southwardae*, recumbent; (i) *E. southwardae*, senescent; (j) *Vesicomidae*, living (in the black sediments); (k) *Vesicomidae*, living/dead (mixed); (l) *Vesicomidae*, shells. Images taken by ROV Victor 6000 (© Ifremer, 2011).

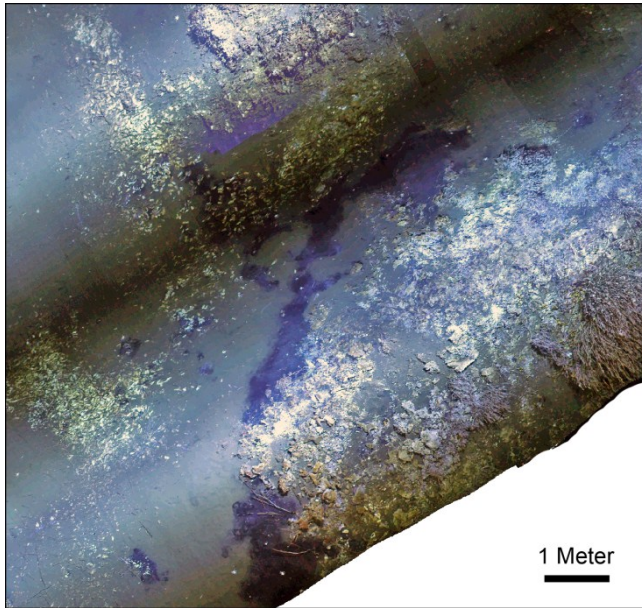
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3 Fig 4: (a) Distribution of the main faunal categories and carbonate concretions based
4 on the WACS mosaic; (b) Simplified areas of distribution of the main types of fauna
5 according to the WACS mosaic; the remaining 'blank' part of the survey area
6 corresponds to the 'areas of low fauna presence' (see text).

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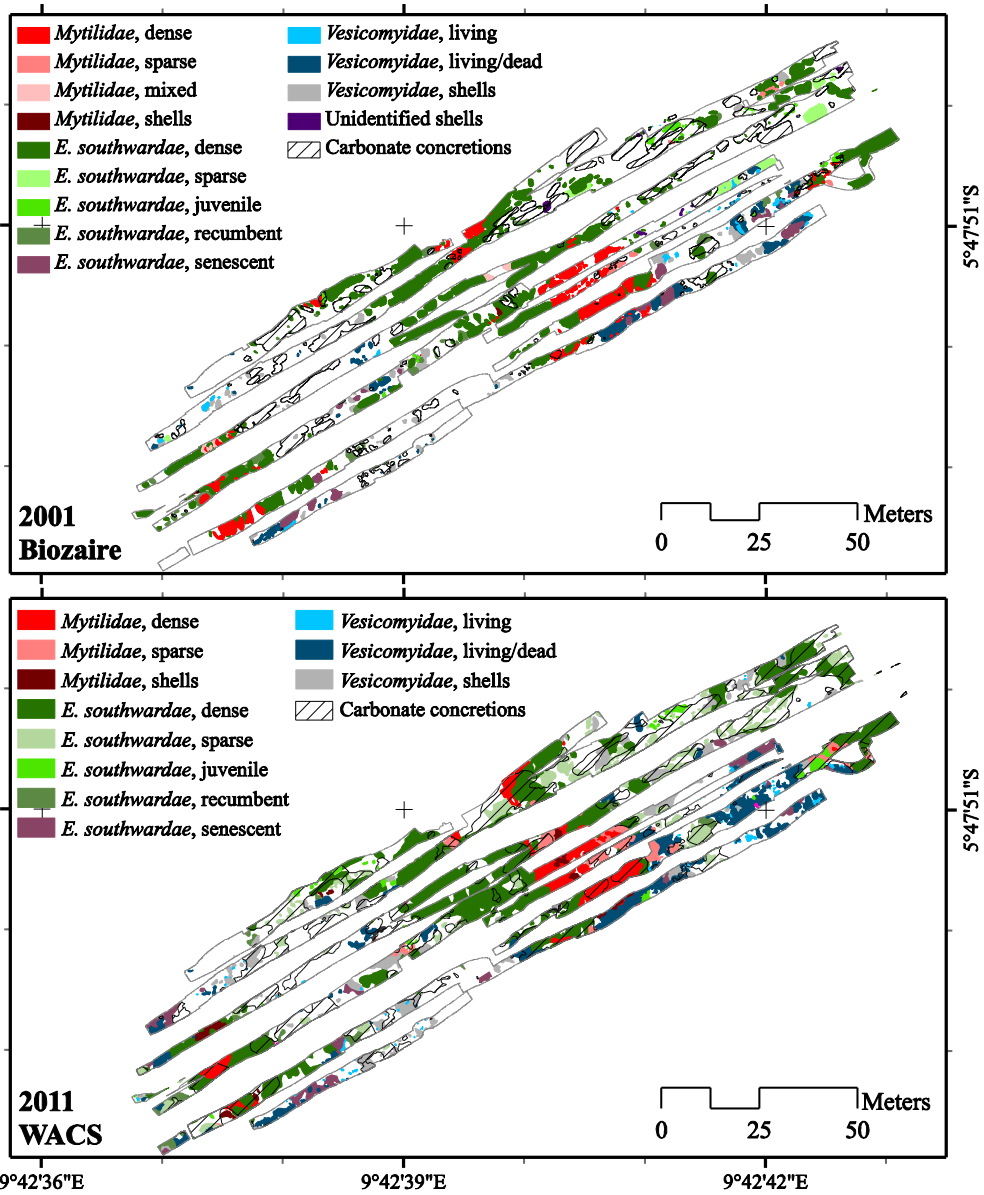


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3 Fig 5: Excerpt from the WACS mosaic showing a limit between carbonate crusts
4 (right) and soft sediments (left); juvenile vestimentiferans are visible on the right and
5 fields of vesicomyid clams can be seen in the sediment on the left. A band of reduced
6 sediments occurs along the border of carbonate crusts. Images taken by ROV Victor
7 6000 (© Ifremer, WACS 2011).

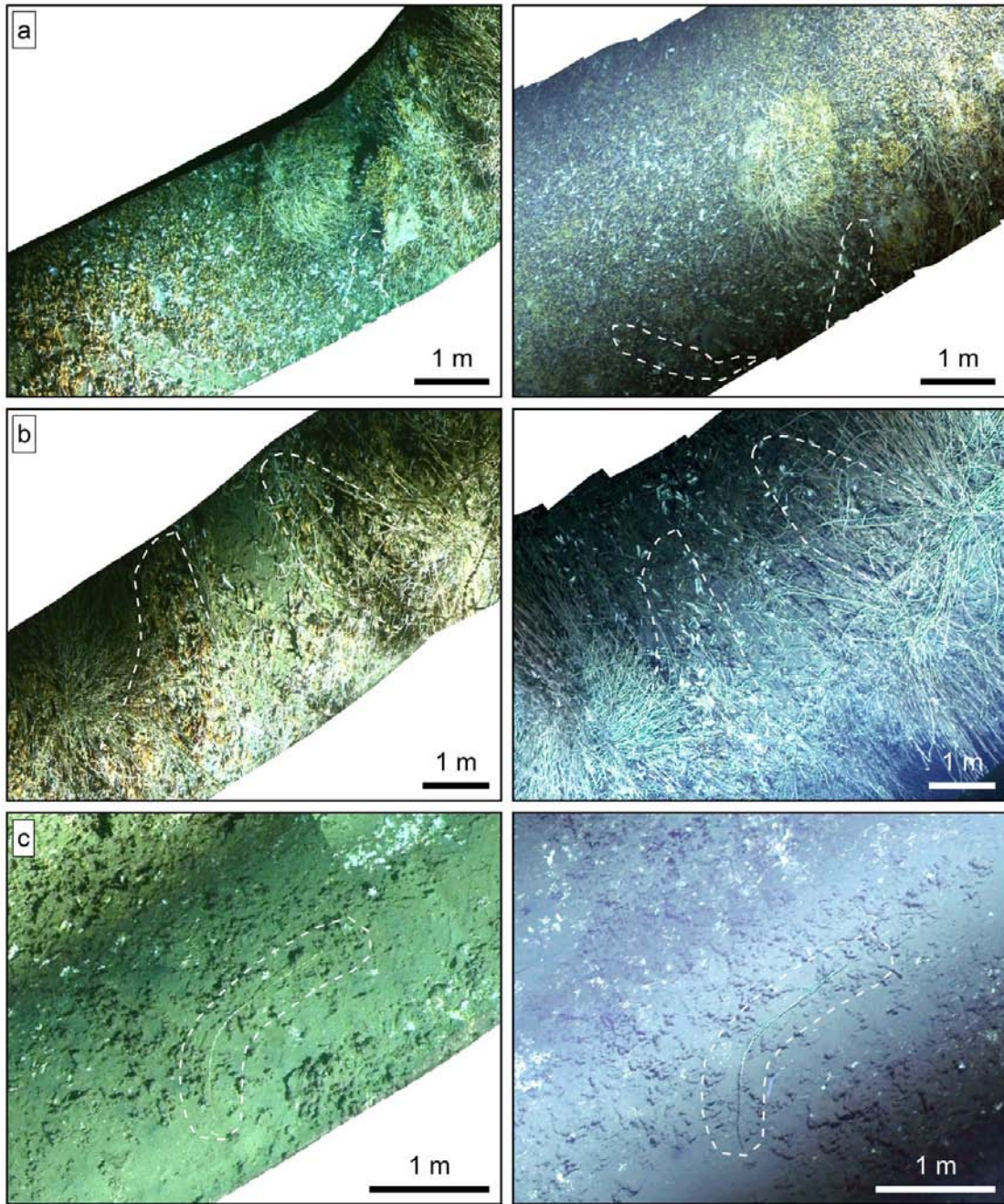
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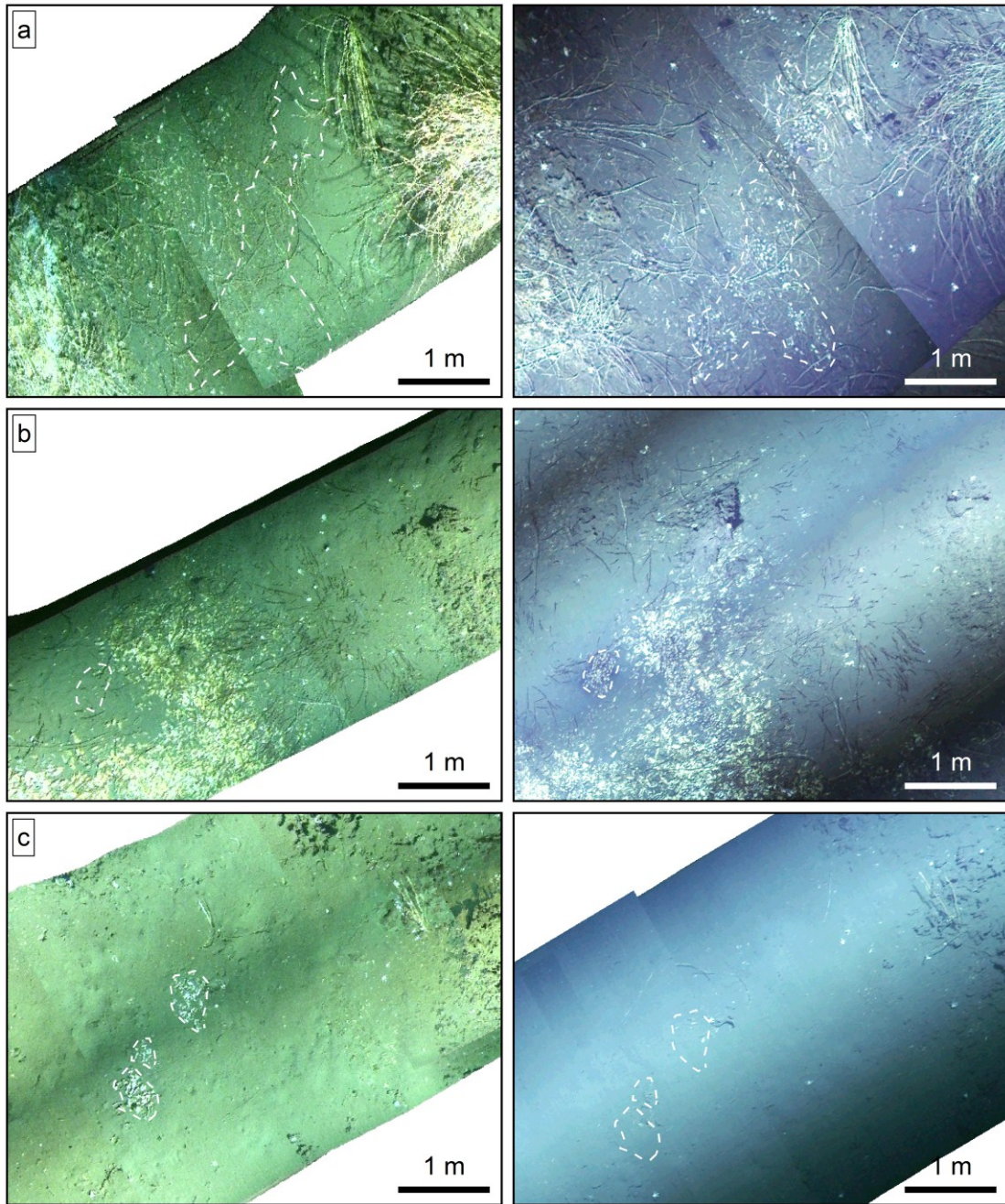


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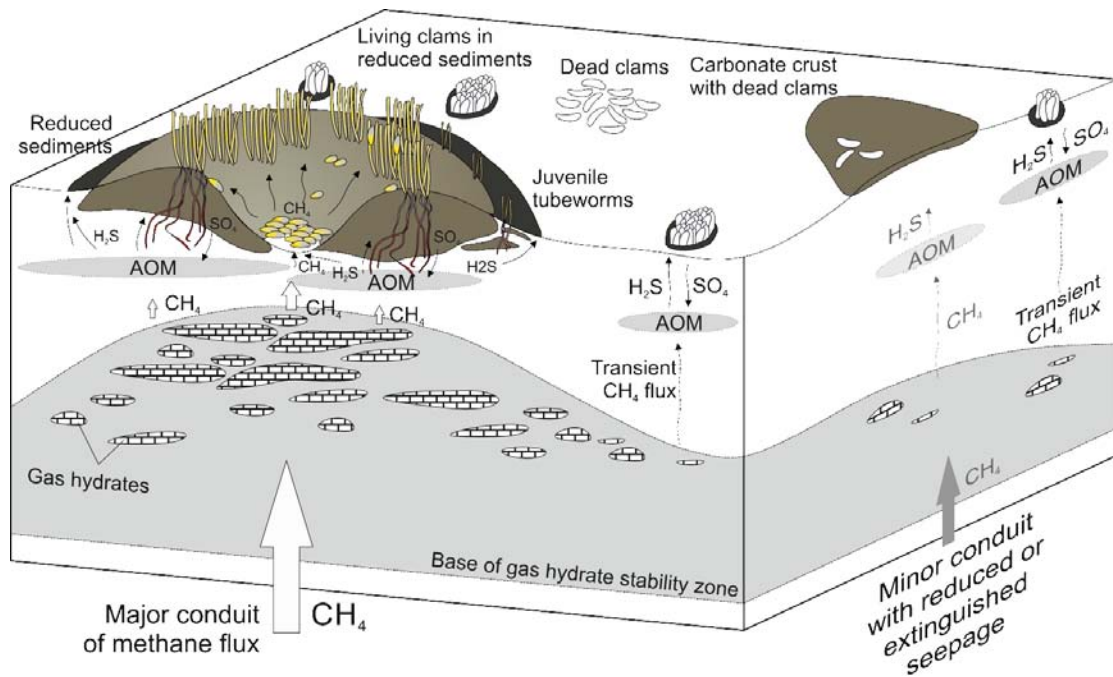
3 Fig 6: Distribution of the main faunal categories and carbonate concretions in the area
4 of overlap between the Biozaire (2001) and the WACS (2011) mosaics.



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 2 Fig 7: Images taken from the Biozaire (left) and WACS (right) mosaics, representing
 3 almost the same areas of the seafloor; (a) at M2, some areas previously devoid of
 4 mussels are now fully colonized by mussels; (b) at M1, small beds of living mussels
 5 on the Biozaire have been replaced by mussel shells on the WACS mosaic; (c) a
 6 recumbent tube of vestimentiferan showed no change in size and position between
 7 2001 and 2011. Images taken by ROV Victor 6000 (© Ifremer, Biozaire 2001 and
 8 WACS 2011).



1
 2 Fig 8: Images taken from the Biozaire (left) and WACS (right) mosaics, representing
 3 almost the same areas of the seafloor; (a,b) new patches of vesicomyids that did not
 4 exist at the time of the Biozaire cruise; b also shows that the patch of dead clams has
 5 been partly re-colonized; (c) a patch of mixed vesicomyids almost disappeared under
 6 sediment cover. Images taken by ROV Victor 6000 (© Ifremer, Biozaire 2001 and
 7 WACS 2011).



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3 Fig 9: Summary schematic model (not to scale). The main aggregations are distributed
 4 in concentric patterns with the mussels in the middle, then the tubeworms on thick
 5 concretions, and finally the vesicomyid clams in the sediments around. Mussels are
 6 present in an area of intense flux with significant release of methane to the water
 7 column. A transition zone is observed where mussels are present at the bottom and on
 8 the tubes of the vestimentiferans. Vestimentiferans are present on carbonate
 9 concretions but reach the sediments with their roots. Through sulfate release, they
 10 maintain the AOM and the sulfide production. Juvenile tubeworms are distributed
 11 near the limit of the crusts where the sulfide fluxes from the sediments are likely
 12 higher. The presence of dark reduced sediments around the concretions indicate that
 13 part of the methane and sulfide fluxes are redirected from under the crusts towards
 14 more sulfate-rich zones where AOM occurs. Populations of vesicomyid clams occur
 15 in the sediments around. Their patchy distribution suggests that it is controlled by
 16 discrete and transient fluxes from below.