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Colonization of coastal environments by foraminifera: insight from shrimp ponds in New Caledonia (sw Pacific)

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Abstract:

The objectives of this study were to observe foraminiferal colonization patterns and behavior in shrimp ponds in New Caledonia during a shrimp-growing (farming) cycle. Weekly collecting at 10 stations in 8 shrimp ponds yielded a total of 170 samples accompanied by environmental data. Seawater pumped from the nearby ocean filled the ponds at the beginning of the growth cycle and its daily renewal maintained salinity at 32–39, and supplied the ponds with influxes of smaller, mostly juvenile, foraminifera. A few days after initial filling, the pioneering species *Ammonia tepida* and *Quinqueloculina seminula* appeared, with *A. tepida* dominant. Their high reproduction rates increased both living and dead assemblage densities during the first 10 weeks. Populations of these two species then stabilized with higher oxygen demand (drop of redox) and consumption of living foraminifera by shrimp. Only a few colonizers subsequently appeared, which was attributed to the isolation of the pond, despite the high rate of water renewal. Only one pond had notably higher species richness, but it could not be distinguished from the others by its physicochemical parameters. The species that appeared in ponds initially barren of foraminifera also survived where there was water seepage between growing cycles, suggesting that the assemblages had already reached equilibrium with the environment. Despite the number of environmental parameters measured, only oxygen and reactive organic matter correlated with the microfauna on a weekly timescale. We assume that other parameters do not significantly affect foraminifera until they reach critical threshold. Consistent with previous studies, *A. tepida* was the species most tolerant of organic influx, but its relative abundance dropped once the organic matter flocculated and settled, leading to disoxic conditions in the sediment. Conversely, *Q. seminula* was able to climb through the floc and reach the oxygenated layer, where its relative abundance increased.

INTRODUCTION

In her review of the colonization of new habitats by benthic foraminifera, Alve (1999) pointed out that a better understanding of dispersal and colonization patterns of foraminifera will enhance paleoenvironmental and biostratigraphic correlations, and evaluation of recovery rates following environmental disturbances. Numerous experiments have been carried out on the colonization of artificial sterile substrates (e.g., Schafer and Young, 1977; Kaminski and others, 1988; Buzas, 1993; Kitazato, 1995; Alve and Olsgard, 1999; Ribes and others, 2000; Wisshak and Rüggeberg, 2006). In addition, field observations have been made of the recolonization of natural environments after major environmental disturbances (Finger and Lipps, 1981; Ellison and Peck, 1983; Schafer, 1983; Kaminski, 1985; Buzas and others, 1989; Coccioni and Galeotti, 1994; Alve, 1995; Hess and Kuhnt, 1996; Speijer and others, 1997; Hess and others, 2001; Galeotti and others, 2002; Hess and others, 2005), and of the colonization of saline environments isolated from the sea (Cann and de Dekker, 1981; Almogi-Labin and others, 1992; Levy and others, 1995; Patterson and others, 1997; Wennrich and others, 2007; Abu-Zied and others, 2007). In these studies, pioneering taxa capable of recolonizing a barren habitat were identified, such as *Stainforthia* in anoxic habitats (Alve, 1994; Elberling and others, 2003), *Reophax* species on experimental colonization trays (Kaminski and others, 1988) and on sterile ash layers (Hess and Kuhnt, 1996), and *Cribroelphidium gunteri* (Cole) in hyposaline lakes (Boudreau and others, 2001). In shallow paralic environments, the most successful colonizer is *Ammonia tepida* (Cushman) in both brackish (Wennrich and others, 2007) and hypersaline (Almogi-Labin and others, 1992) waters. In Croatia, it lives in low-oxygen, slightly hypersaline lagoons, typically in association with *Haynesina depressula* (Walker & Jacob), *Elphidium crispum* (Linné), and *Quinqueloculina* spp. (Vanicek and others, 2000). During interglacial intervals in the Quaternary, *A. tepida* colonized lakes inland from the Dead Sea (Almogi-Labin and others, 1995) and along the Mediterranean (Usera and others, 2002).

Laboratory experiments and field observations do not always yield information about colonization dynamics and the nature of pioneering species. Studies in which sediments were left to be colonized for 32 weeks (Alve and Olsgard, 1999), and artificial leaves retrieved after 3 and 6 months

(Ribes and others, 2000), were colonized by species that were common in the ambient environments at the end of the experiments, but the times required to reach this stage were not determined. Time-series observations provide insight into colonization dynamics in shallow environments. For example, during colonization experiments conducted at a water depth of 1 m in the Indian River, weekly sampling by Buzas (1993) revealed that assemblage density stabilized after three weeks. Shallow-water studies elsewhere suggest that colonization or recolonization of sediments barren of foraminifera needs only days or weeks (Ellison and Peck, 1983; Buzas and others, 1989; Buzas, 1993).

In spite of these recent advances, intensive research is needed to fill the large void in our understanding of the processes governing colonization by foraminifera (Alve, 1999). This study aims to narrow the gap with observations on foraminiferal assemblages in very shallow (60–120 cm) coastal environments. It investigates temporal changes in the assemblages that develop in shrimp ponds that are periodically refilled with sea water after several months of being completely dry, locally wet from seepage, or covered with a layer of organic soil before the beginning of a shrimp growing cycle.

STUDY AREA

Semi-intensive shrimp farming, defined here as non-aerated ponds with moderate shrimp density (15-20 individuals m^{-2}) is common along the west coast of New Caledonia's Main Island, also known as Grande Terre. Most shrimp farms in southeast Asia add chemicals such as copper compounds to eliminate external protozoa and filamentous bacteria in post-larval shrimps, formalin as an antifungal agent and to control ectoparasites, and antibiotics (Gräslund and Bengtsson, 2001). New Caledonian shrimp farms, on the other hand, use none of these additives that could inadvertently affect foraminifera. Because these ponds are ephemeral, they are ideal for studying foraminiferal recolonization in a paralic environment.

The shrimp growing cycle lasts about four months, at which point they are harvested and the ponds are left to dry for several weeks. Once dessicated, the sediments are tilled to enhance oxidation of organic matter and other reduced substances.

Samples were collected from three different shrimp farms (Figs. 1, 2). Two stations were

selected in one of the Saint Vincent shrimp farm (SV) ponds: station SVA had a “clean” bottom with a minor accumulation of readily oxidized material (average EOM = 0.77) and a low sediment oxygen demand (average SOD5 = 1.94) (Table 1), while station SVB had a “dirty” bottom with a moderate accumulation of readily oxidized material (average EOM = 1.77) and a higher sediment oxygen demand (average SOD5 = 5.43). Neither station completely dried up because of saltwater seepage from neighboring basins. Another two stations were selected in a pond of the SeaFarm shrimp farm (SF): SF1 was in an area accumulating fine organic matter resulting from rotating currents driven by a paddle-wheel aerator, whereas SF2 was outside this area. Six stations in six ponds were selected at the Aigue-Marine shrimp farm (AM): ST1 and ST2 were on muddy sand, S1 on a heterometric schist fragments mixed with silt and clay, S2 on schistose bedrock without sedimentary cover (the absence of which impeded the proper tilling of the pond subsoil; in 2008, the bottom of pond S2 was covered with a liner before filling), and TV1 and TV2 were on bottoms fertilized by a layer of organic-rich soil added before filling. Localized seepage prevented stations ST1, ST2, and S1 from complete dessication between growth cycles; hence, their organic matter and other reduced substances were not entirely oxidized.

Water is pumped in daily from the nearby ocean for a partial renewal of the pond water that maintains salinity at 32–39. It flows through the intake canal while the excess pond water drains from the opposite end of the pond to the sea (Fig. 2). The amount of water renewal is adapted to the growing shrimp biomass, gradually increasing daily from 0% at the beginning to 30% at the end of the cycle. Post-larvae were introduced at a density of 18–20 individuals per square meter about two weeks after the ponds were filled. Pelleted food was provided in all ponds at rates ranging from about 6 kg ha^{-1} d^{-1} when the post-larvae were introduced to about 60 kg ha^{-1} d^{-1} before the shrimp were harvested.

MATERIAL AND METHODS

This study was carried out during two successive hot seasons with similar climatic conditions. Sediments were collected weekly at each pond station throughout the growing cycle, resulting in 170 samples. Sampling commenced immediately after filling the ponds with seawater and stopped just

before harvesting. Initial sampling was at stations SV and SF in February 2006; all other stations were first collected in December 2006. At each station, a sediment core was hand-collected with a PVC tube, 25 cm in diameter and 5 cm long. Immediately afterwards, 50 redox measurements were taken in the sediment with a micro-redox electrode (pH/mv meter WTW 315i). For the impending foraminiferal analysis, a sediment sample of ~40 cm^3 was taken from the upper 2 cm of the core and preserved by freezing.

At the time of sampling, temperature, salinity, dissolved oxygen (D.O.), and ammonium (NH_4) were measured 10 cm above the substrate, and redox and pH were measured in the retrieved sediment. Sediment parameters measured in the laboratory were easily oxidized material (EOM, analyzed using the procedure adapted by Della Patrona and others, 2007; from Avnimelech and others, 2004), oxygen demand at 25°C over a period of five days in the dark (SOD5, measured using BODmeter WTW Oxytop apparatus), total organic matter (OM, measured by loss on ignition weekly at stations SV and SF and only once at the other stations), protein to carbohydrate ratio (PRT/CHO), chlorophyll-*a* and phaeopigment concentrations (fluorometric analysis after extraction by methanol), and abundance of bacteria. About 20 cm^3 of each sample were preserved for the bacterial counts by immediate fixing with buffered formaldehyde (2% final concentration) and storage at 4°C. Prior to counting, these subsamples were sonified three times (Bioblock vibro cell 75185; 60 W for 1 min), diluted to 1/2000 with sterile and 0.2-µm pre-filtered formaldehyde (2% final concentration), stained for 30 min with DAPI (4',6-diamidino-2-phenylindole dihydrochloride, 2,500 µg DAPI l^{-1} final concentration), and filtered through black Nuclepore polycarbonate filters (0.2-µm pore size). The filter contents were analyzed using epifluorescence microscopy (Leica DLMN × 1000), as described by Fry (1990) and Epstein and Rossel (1995). For each slide, at least ten microscope fields were observed and a minimum of 300 cells were counted. Bacterial abundance was normalized to dry weight after desiccation (60°C, 24 h). The flocculent layer at the sediment-water interface, composed of dead plankton, uneaten food, and domesticated animal waste, and referred to as lab-lab in aquaculture (Boyd, 1995), was sucked up through micro-pipes and stored in flasks purged with nitrogen for later sulfide analysis.

To allow for weekly comparisons of data, resampling was near but not precisely at the

previous spot because its disturbance the preceding week. This constraint and the collecting of sediment for chemical and bacteria analyses made it impossible to obtain true replicates or to use the pseudoreplication procedure (Hurlbert, 1984) adapted for foraminiferal studies (Debenay and Guillou, 2002). Consequently, the results are prone to bias from the uneven microdistribution of foraminifera, but nonetheless reveal general trends in foraminiferal assemblages. Moreover, these results are well adapted for the interpretation of fossil assemblages in the small samples typically taken from cores. In 2008, the bottom of pond S2 was covered with a liner; at the end of the growing cycle four months later (May), sediment deposited on this liner was collected. For a comparison with the pond fauna, samples were also collected among the mangroves near the farms and one sample was taken from the intake canals feeding the SF and AM ponds (Fig. 2).

In the laboratory, samples were defrosted then washed through sieves with 500-µm and 63-µm openings, and the residue was stained with rose Bengal to distinguish specimens that were alive when sampled (Walton, 1952; Murray and Bowser, 2000). Although this histologic stain has provided reliable results on shelf foraminifera, it is less accurate on coastal and paralic foraminifera, as it has been discussed for a long time (e.g. Le Calvez and Cesana, 1972). The indication that "only bright red individuals are considered as living" is frequently found in the literature, which is quite subjective and may result in false interpretations. During 40 years of researching paralic foraminifera and using rose Rengal, one of us (J.-P. D) has often observed tests devoid of cytoplasm that show red, presumably the stained bacteria that were living inside the test, and living specimens (e.g., *Haynesina germanica* (Ehrenberg) with green cytoplasm) that failed to stain. Thus, we recognize that rose Bengal only provides a general sense of the living assemblages in our study, and the cumulative trend of total (live + dead) assemblages is more useful in studying colonization patterns.

After concentrating the tests by flotation with perchloroethylene (1.622 g cm^3), the dried sediment was scanned for foraminifera. No evidence of significant test breakage from freezing was revealed by comparison with samples that were never frozen. The sample collected in 2008 at station S2 consists of fine organic floc; as recommended by Scott and others (2001), it was examined wet in a Petri dish to avoid the destruction during drying of the fragile species that live in organic-rich sediments. For samples with sufficient numbers, 100–200 specimens were counted, which is

significant for studying the main species (Fatela and Taborda, 2002). They were identified following the generic classification in Loeblich and Tappan (1988) and counted under a Zeiss Stemi 2000-C binocular microscope. Assemblage densities were estimated from specimen counts on a gridded plate and normalized to 50 cm^3 of sediment (D50). The relative frequency of stained specimens in each assemblage was also calculated.

The data set for statistical analysis was restricted to species occurring in more than 20 samples, or in more than 10 samples but making up more than 5% of at least one assemblage. Relationships between species relative abundance and environmental parameters were investigated using a canonical correspondence analysis (CCA), which is appropriate for non-linear data (ter Braak, 1986; ter Braak and Verdonschot, 1995). The multivariate analysis package Ginkgo was used for this CCA. (http://biodiver.bio.ub.es/vegana/index.html; De Cáceres and others, 2003).

RESULTS

PHYSICOCHEMICAL CHARACTERISTICS

Temperatures averaged ~26°C at all stations (Table 1). In the SF and SV ponds, temperatures peaked at the beginning of March, reaching a maximum of 32.4°C in pond SV, then decreased irregularly until the end of the growing cycle. In the Aigue Marine ponds, the highest temperatures were near the middle of the growing cycle in February. The AM ponds were slightly hypersaline with average salinities of 38–39; weekly values were slightly higher than 40 at the beginning of the survey, when a maximum of ~42 was recorded in pond TV1 (Fig. 3). Previous hypersaline conditions resulting from evaporation is evidenced by small gypsum crystals in the first samples from station ST1. Pond SF fluctuated around normal marine salinity (30.9–37.1,, avg. 34.84), whereas pond SV tended to be slightly hyposaline (29.2–35, avg. 32.83). Sediment pH was <7.5 only in ponds ST and TV, but >8 in the overlying water. The highest values were recorded in pond SV (7.66–8.16, avg. 7.92). Higher concentrations of chlorophyll and ammonium in the water, and EOM in the sediment, were detected in the SF and SV ponds. As expected, the highest EOM values were found at the two stations with

notable accumulations of organic matter: SF1 (EOM 0.86–3.53, avg. 2.33) and SVB (EOM 1.15–2.75, avg. 1.77), but station SF2 had the highest number of bacteria (1.99×10^9 to 10.77×10^9, average = 4.85×10^9). Stations SFI and SVB had the lowest average redox (17.68 at SF1, 91.62 at SVB) and the highest SOD5 (9.08 at SF1, 5.43 at SVB), but their overlying waters were high in D.O. Weekly measurements of organic matter (OM) ranged 3.56–7.30% in ponds SV and SF without any discernable trend during the growing cycle. However, SVB sediment became increasingly gelatinous over time. During the growing cycle, the main trends in all AM ponds were increases in EOM and SOD5 with a correlative decrease of redox (including a sudden drop during the second half of January), and an increase in pH before it dropped at the end of the cycle (Fig. 3).

In ponds SV and SF, changes were irregular and no trend was discernable in the time-series data. Redox and EOM values for the beginning and end of the survey are nearly identical, except for a minor decrease of EOM at SVB and a minimal increase at SVA, whereas SOD5 significantly increased at all stations (Fig. 4). Final pH readings were slightly higher at both SV stations but lower in pond SF.

FORAMINIFERAL ASSEMBLAGES

The only foraminiferal assemblages that comprise more than eight species are those of the SV shrimp farm, where maximum species richness was 15. The cumulative number of species identified at the shrimp farms is 47 (Appendix 1). At station TV1, which is in a pond supplied with organic soil, the density of specimens normalized to 50 cm^3 of sediment (D50) increased from 0 at the beginning of the growing cycle in January to 50,000 just before the shrimp harvest in May (Table 2). Dominant taxa were *Ammonia tepida* and *Quinqueloculina seminula* (Linné), the latter being both more abundant and representing of a group of related forms that could not be consistently differentiated because of frequent and severe abnormalities. These two taxa account for 65–100% of each assemblage, except for one weak assemblage (30 specimens) that they are 50% of. Most of the other species are typical of paralic substrates, such as *Brizalina striatula* (Cushman), *Buliminella elegantissima* d'Orbigny, *Cribroelphidium williamsoni* (Haynes), *Haynesina depressula,Caronia exilis* (Cushman and

Brönnimann), and *Glomospira gordialis* (Jones and Parker). Also present but rare are marsh and mangrove species, including *Jadammina macrescens* (Brady) and *Trochammina inflata* (Montagu), as well as a few specimens of shallow-marine species such as *Spiroloculina antillarum* d'Orbigny and *Rosalina bradyi* Cushman.

Density increased during the growing cycle at all stations except SVB, The increase was relatively slow at SVA and S1, where D50 was >1,000 at the beginning of sampling, and very weak at SF1. At station SVB, D50 peaked in April (Fig. 5). Similarly, species richness increased slightly at each station, with the sharpest increase in pond SV, and stabilized by the end of the survey. During the initial stages of the shrimp growth cycle, the number of living foraminifera increased at all stations except dirty stations SVB and SF1. The numbers stabilized after April at stations SVA and SF2, then after February elsewhere (Fig. 6). In all AM ponds, the proportion of living specimens increased irregularly to a maximum at the beginning of February, but then decreased during the latter half of the month (Fig. 6). In ponds SV and SF, the proportion of living specimens increased slightly at the two clean stations (SVA and SF2), but decreased at the two dirty stations (SVB and SF1).

In Figure 7, CCA axes 1 (eigenvalue = 0.19) and 2 (eigenvalue = 0.13) explain 30.6% of the total variance in the foraminiferal data. The arrows on this figure represent explanatory variables and point toward higher values of the corresponding variable. Arrow lengths reflect their relative importance in explaining the variance in the foraminiferal data, and their orientation represents the approximate correlation to the ordination axes as well as to other environmental variables. Here the arrows are short and widely angled with the ordination axes, indicating a weak correlation between foraminiferal assemblages and these parameters.

Intra-set correlations of environmental parameters with axes 1 and 2 (Fig. 7) show a weak negative correlation of OM accumulation in the sediment with axis 1. The OM parameters (EOM, SOD5, NH_4, sulfides and phaeopigments) strongly correlate with each other. The position of species projected perpendicularly onto the environmental arrows approximates their weighted-average optima along each environmental variable. Thus, *Ammonia tepida* is positively correlated and *Quinqueloculina seminula* is negatively correlated, with variables indicating OM accumulation.

In the time-series triplot (Fig. 7c), samples from SVA, SVB, SF1, SF2, and S1 mostly plot

negative (left of axis 1), while those from TV1 and TV2 plot positive (right of axis 1). Samples from S1 are distributed along axis 1 with negative values for those collected at the beginning of the study and positive values for those taken later. This trend evidently is related to the increasing proportion of *Quinqueloculina seminula* (Fig. 8), and it is most obvious for stations S2 and ST2, which show two groups of samples.

When comparing proportions of *Ammonia tepida* and *Quinqueloculina seminula* during the growing cycle (Fig. 8), the general trend detected at all stations was a decrease in *A. tepida* accompanied by an increase in *Q. seminula*, as these two dominant species are prone to autocorrelation when using percentage values. Despite this, *A. tepida* was the dominant species in all samples from ponds SV and SF with the exception of three from the SF2 locality. In the AF ponds, *A. tepida* dominated during the first stages of the shrimp farming cycle, but the situation was drastically reversed at the beginning of February, with the less abrupt dominance inversion at S1 (Fig. 8).

Samples collected at the stand of neighboring mangroves show (1) a high dominance of *Quinqueloculina seminula* in a topographically high talweg filled with seawater concentrated by evaporation at low tide, (2) the presence of the agglutinated species *Trochammina inflata* and *Jadammina macrescens* on a bare supratidal flat, and (3) a higher species richness in the lower *Rhizophora* zone (Table 3). The assemblages in the intake canals of the SF and AM ponds, however, are more diverse than those in the ponds or among the mangroves. Several species that this study found only in these canals are typical of New Caledonian bays, including *Peneroplis* spp., *Monalysidium acicularis* (Batsch), and *Nonionoides grateloupi* (d'Orbigny).

DISCUSSION

PHYSICOCHEMICAL CHARACTERISTICS

Changes in the main physicochemical characteristics of the shrimp pond sediments during a growing cycle are consistent with trends reported in the literature (e.g., Boyd, 1995): redox potential decreased, SOD5 increased, and total organic matter was relatively static. Although EOM values in the

SV and SF ponds were stable or decreased slightly, their increase in the AM ponds indicates an accumulation of native reactive organic matter (Avnimelech and others, 2004). The sample collected on the pond S2 liner had organic matter in the form of lab-lab.

FORAMINIFERAL ASSEMBLAGES

Foraminiferal species richness in the shrimp ponds is small compared to those in New Caledonian bays. Most of the pond species occur in the local paralic environments, but a few are typical of mangrove swamps. Because *Ammonia tepida* and *Quinqueloculina seminula* are considered to be relatively tolerant of environmental stress (Debenay and others, 2000; Debenay and Guillou, 2002), their dominance in the ponds and their proportion of deformed specimens are not surprising (Debenay and others, in press). These two species have been reported as the primary pioneers in other paralic environments. In Lake Qarun (Egypt), for example, they comprise 70% of the total foraminiferal assemblage (Abu-Zied and others, 2007). *Ammonia tepida* is cosmopolitan, colonizing marine and paralic environments and tolerating salinities ranging from 0.2 to to 100 (Bradshaw, 1957; Reddy and Rao, 1984; Debenay, 1990; Almogi-Labin and others, 1992; Wennrich and others, 2007). It also seems to be relatively tolerant of polluted waters (Sharifi and others, 1991; Yanko and others, 1994; Alve, 1995; Coccioni, 2000; Armynot du Châtelet and others, 2004; Vilela and others, 2004; Frontalini and Coccioni, 2008). It can survive very high concentrations of heavy metals (e.g., Ferraro and others, 2006), and might even respond positively to sewage influx (Thomas and others, 2000). In French Guiana, it was one of the dominant hyaline species that, within the first weeks of the dry season, established itself in areas that had been occupied mostly by agglutinated species throughout the rainy season (assemblages passing, at the same station, from zone III to zone II of Horton and others; 2003; Debenay and Guiral, 2006).

In the Araruama lagoon, Brazil, Debenay and others (2001) found *Ammonia tepida* and *Triloculina oblonga* (Montagu) accounting for 56–98% of every assemblage except one (in which they were 30%). Regarding the miliolid identified as *T. oblonga*, they state “the general characteristics of the test, the number of transitional forms and the obviously abnormal morphology of numerous tests

suggest that most of the individuals belong to the same species." They also note that this also applies to *T. oblonga* in New Caledonia. The distinction between small paralic miliolids can be difficult because of their great morphological variability (Schnitker, 1967), including frequent test abnormalities. Upon reexamining the specimens from New Caledonia, however, Debenay and Guillou (2002) decided to ascribe them to *Quinqueloculina seminula*, which is supported by Parker's (2007) remarks about the status of *Q. oblonga*. Their approach that can be applied to the population of the Araruama lagoon is retained in the following discussion.

The shrimp ponds were filled with seawater then stocked with shrimp, and subsequently replenished daily with water pumped from the coastal area in front of the farms. The pumping capacity of ~2,000 m^3 hr^{-1} generated a current strong enough to transport the sediment around the pumping station and into the intake canal (8 m × 1 m in cross-section), where it settled before reaching the pond, as indicated by the very rare mineral particles found in the flocs collected on the liner of pond S2. The absence or extreme rarity of typical bay species other than *A. tepida* and *Q. seminula* suggests that most of the transported adult tests also settled in the intake canals, and this was confirmed in two canal samples.

Unlike larger specimens, embryonic juveniles are easily transported to the ponds because their density is similar to that of seawater and they are capable of enhancing their flotation by extending their pseudopods (Alve, 1999). In the Vilaine estuary in France, Goubert (1997) observed that tidal currents were not able to transport foraminifera coarser than 100 μm, yet embryonic juveniles (<80 μm) of *Cribroelphidium excavatum* (Terquem) were very abundant in tide-transported mud. Thus, we infer that incoming tidal currents and coastal pumping probably introduce many coastal species into the ponds, but most are unable to adapt and multiply in the new environment. Debenay and others (2003, 2006) studied foraminiferal colonization of a man-made basin that was isolated from the sea and filled by pumping the neighboring estuary, and identified *Cribroelphidium gunteri* as the pioneering species, even though it appeared to be very rare in the estuary. They concluded that its undetected juveniles had been dispersed throughout the estuary but the habitat was unsuitable for the species to become established there. As stated by Baas Becking's laws (1934): "everything is everywhere" and "the environment selects." In similar fashion, ponds TV1 and TV2, which were

initially barren of foraminifera, rapidly developed a pioneer fauna strongly dominated by the opportunistic species *Ammonia tepida* and *Quinqueloculina seminula*.

Three general trends consistent with a classic colonization pattern were recorded for most of the shrimp ponds: (1) an increase in number of living specimens of a few species, (2) an increase in the number of empty tests of the same species, and (3) an increase in the number of species. In the initial stage, high reproduction rates of the pioneer species leads to increases in both their living specimens and the accumulation of their empty tests after death or reproduction. Over time, the proportion of living specimens diminishes and their density (normalized to 50 cm^3 of sediment) stabilizes. Before the end of the cycle, species richness also stabilizes, Drainage of the ponds at the end of each 4-month growing cycle precludes any later colonizers or K-strategists from getting established and possibly outnumbering the pioneers. However, assemblage densities stabilized before the end of the cycle, despite the constant supply of juveniles provided by water renewal (Fig. 5 and 6). We attribute this phenomenon to the drop in redox, which was particularly severe in the AM ponds, and possibly to the consumption of foraminifera by shrimp (Thompson and others, 2002; Burford and others, 2004). Although the increase in species richness was much greater in pond SV than in pond SF, the difference could not be related to any of the parameters measured; however, it is concurrent with a significantly better shrimp survival in pond SV (80%) than in pond SF (35%) and in the AM ponds (~40%).

In ponds where localized seawater seepage allows *Ammonia tepida* and *Quinqueloculina seminula* to survive post-harvest drainage (e.g., SVA, S1), the colonization pattern is attenuated but still discernable. The pattern is intensified in ponds TV1 and TV2, which are covered with an organic soil devoid of foraminifera, and in pond S2, where the rock bottom completely dries between growing cycles. The very irregular densities of foraminifera at the beginning of the study probably result from patchy distributions during the initial stages of colonization. The higher density in the first TV2 sample is presumably resulted from preliminary test filling of the pond.

The assemblages that showed a negative trend (i.e., a drop in number and proportion of living individuals), were at the two dirty stations, SVB and SF1. Food availability could not have been a limiting factor because organic matter was plentiful. Considering that foraminifera were abundant when the survey commenced, it is impossible to invoke the adverse impact of OM reported in the

literature (Le Furgey and St Jean, 1976; Setty, 1976; Alve, 1991). The main differences between stations SVA (clean) and SVB (dirty), and between stations SF1 (dirty) and SF2 (clean), are that the dirty stations have higher EOM and SOD5 and lower redox. We can infer, therefore, that lower D.O. is the limiting factor for foraminiferal assemblages in the dirty stations. When the four stations are considered together, however, it is more difficult to come to these conclusions; thus, there could be undetermined environmental parameters influencing the assemblages. This agrees with Murray (2001), who considered that, although oxygen and organic matter might be the prominent controls on foraminiferal distribution, it would be too simplistic to attempt to define all distributions only in terms of these two factors.

The empty ponds were not studied, although small gypsum crystals at station ST1 indicate a hypersaline environment had developed locally as seepage evaporated. When first filled at the beginning of the survey, foraminiferal densities varied among the ponds, possibly because of different amounts of seepage that could have enabled some assemblages to survive between cycles.

The dominance of *Ammonia tepida* at the very beginning of the growing cycle indicates that it was the most successful pioneer species. The general drop in its relative abundance, and the correlative increase a short time later in the relative abundance of *Quinqueloculina seminula* at all stations except SF1, must be related to environmental changes more favorable to this species, but very little is known about its requirements. Its presence in paralic and intertidal environments might be related to evaporation increasing the concentration of calcium and carbonate ions (Greiner, 1974; Murray, 1991; Debenay and others, 2001). Even if AM stations were slightly hypersaline, the higher salinities at the beginning of the cycle cannot explain why *Q. seminula* increased in relative abundance with time. *Ammonia tepida* is one of the species most tolerant of temperature and salinity variations (Bradshaw, 1961; Walton and Sloan, 1990). Culture experiments have provided extensive information on its requirements and have shown that its normal growth occurs in salinities of 20–40 and its generation time of 88 days at 20°C is reduced to 33 days at 30°C (Bradshaw, 1957, 1961). Pascal and others (2008) have found that the rate of uptake of bacteria by *A. tepida* reached an optimum at around 30°C, which is consistent with the results of Bradshaw (1957, 1961). Salinities recorded in the ponds thus appear favorable for the normal growth of *A. tepida*. Whereas less-favorable conditions (i.e., salinity

slightly above 40) occurred at the beginning of the cycle, when the relative abundance of *A. tepida* was the higher, salinity changes do not appear to have caused its decline. Instead, this change might better be related to longer generation times and less-favorable feeding conditions resulting from decreasing temperatures at station SV and ST, but this explanation cannot be applied to the AM ponds where the most favorable temperatures were reached mid-cycle. Consequently, the decrease in *A. tepida* correlative with the increase in *Q. seminula* cannot be attributed to either temperature or salinity.

The weak correlation of environmental parameters with the two first axes of the CCA shows that they have little influence on foraminiferal distributions in the ponds. Strong correlation between EOM, SOD5, NH_4, and sulfides indicates that the organic matter is degraded by the interstitial aerobic microbial pool that consumes oxygen. The negative correlation of *Ammonia tepida* with the first axis, correlated with its almost constant dominance in ponds SV and SF, might be related to the higher EOM contents in these ponds than in the AM ponds (Table 1), and to the degradation of this EOM. This is consistent with observations in Araruama lagoon (Brazil) by Debenay and others (2001), which has a southern margin that is mostly oligotrophic while the northern and eastern margins receive inflows of domestic sewage that raise their levels of organic carbon, phosphorus, and nitrogen. *Ammonia tepida* dominated assemblages in the northeastern part of the lagoon, while *Quinqueloculina seminula* (*Triloculina oblonga*) was dominant along the southern coast. A similar relationship was recorded in the Nile delta by Samir (2000), who found *A. tepida* the species most tolerant of organic pulses.

In Figure 7c, the shift in organic influence of samples from S1, S2, and ST2 from higher (left) to lower (right) is obviously related to the sharp inversion of *Ammonia tepida and Quinqueloculina seminula* dominance. Thus, contradictory to the above discussion, *Q. seminula* becomes dominant under higher organic influence, when EOM content and SOD5 increases (Fig. 3). This could be related to the formation of the lab-lab, which lowers bottom D.O. *Ammonia tepida*, which might be both epipelic and endopelic (Goldstein and others, 1995), is subjected to highly unfavorable hypoxic or anoxic conditions. The coincidence of dominance inversion with a sharp drop of redox is consistent with Wennrich and others (2007), who observed a decrease in abundance of *Ammonia* that they suggested was probably linked to enhanced environmental stress resulting from an extended seasonal

anoxia. Conversely, *Q. seminula* survives in conditions of less stress, yet it was the only species collected in the lab-lab from station S2. As it often climbs through accumulations of microscopic filamentous algae (Debenay, unpublished data), we infer that it is also able to ascend through the lab-lab and into the oxygenated layer, where it becomes dominant. The absence of lab-lab in ponds SV and SF explains why their foraminiferal assemblages differ from that of AM ponds, without dominance inversion.

The ability of *Q. seminula* to sometimes escape adverse conditions and to become dominant in areas that chemical analyses suggest are unfavorable results in odd assemblages and highly heterogeneous relationships between assemblages and sediments. This might explain why correlations between foraminifera and organic matter were so weak in the canonical analysis.

CONCLUSION

This study of foraminiferal colonization patterns in shrimp ponds in New Caledonia during a shrimp-growing (farming) cycle reveals the following:

1. High-energy conditions around the pumping station and short transit time promote rapid colonization (within days) by transporting the smallest foraminifera, primarily embryonic juveniles, to the ponds.
2. The distribution of the dominant species is related to EOM and its degradation with higher oxygen demand. Most of the other parameters measured in this study could not be related to changes in the foraminiferal assemblages on a weekly time scale, presumably because most of parameters have no direct relationship with assemblages until they reach their critical threshold (Murray, 2001). Thus, it is possible to find no statistical correlation even if the parameters that control certain species are known.
3. Filled ponds were populated mostly by the pioneer species *Ammonia tepida* and *Quinqueloculina seminula*, with *A. tepida* initially more abundant. Their high reproduction rates rapidly increased the density of live specimens that, in turn, resulted in a greater accumulation of empty tests. After about 10 weeks, the number of living individuals stabilizes as the result of a drop in redox or their

consumption by the shrimp.

4. Despite a daily supply of seawater containing embryonic juveniles, the rarity of later colonizers and low assemblage diversities show that adverse conditions prevailed. Only one pond seemed more favorable because it increased species richness, but there was no significant difference between the physicochemical conditions of this pond and the others.
5. The dominance of *A. tepida* and *Q. seminula* observed in the shrimp ponds is also seen in restricted bodies of saltwater, including those of an inland saline (16.5–39.7) lake in Egypt and a hypersaline (52–65) lagoon in Brazil.
6. The presence of the same living species in both initially drained dry ponds and drained ponds with seepage suggests that the assemblages reached equilibrium with the environment prior to shrimp harvesting and drainage.
7. Consistent with previous studies, *Ammonia tepida* was the species most tolerant of organic sediments, but its relative abundance dropped when the accumulation of lab-lab resulted in disoxia. Conversely, *Q. seminula* was able to climb through this flocculent layer and flourish in the oxygenated layer above.

On the geologic timescale, foraminiferal colonization by pioneer species is instantaneous, and therefore might be undetectable in the stratigraphic record. But sub-Recent to modern sediments can reveal the subtle changes that occur. In doing so, this study might serve as a template for the recolonization process in coastal environments recovering from natural devastation or being restored after anthropogenic degradation. It sheds light on using foraminifera as bioindicators of environmental changes, including those that involve sea level changes.

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Table Captions

TABLE 1. Average values of physicochemical parameters and bacterial density. Heavy metals were measured only once in 2007, in all ponds except SV.

TABLE 2. Summary of foraminiferal density (expressed as number of individuals per 50 cm^3 of sediment), species richness, and rose Bengal-stained (living) specimens of all taxa; the relative abundance (%) of *Ammonia tepida* and *Quinqueloculina seminula* in total assemblages is given, and the proportion of living individuals is indicated for each of these two species.

TABLE 3. Foraminiferal assemblages in the intake canals of AM and SF ponds and in the neighboring mangrove and salt marshes. NC15 = Small talweg in a *Salicornia* zone, in the vicinity of *Avicennia* trees; NC16 = bare supratidal flat (tanne) between *Avicennia* trees; NC17 = *Rhizophora* zone near LWL; NC18 = *Avicennia* zone near HWL; Ch.AM = intake canal of Aigue-Marine ponds; Ch.SF = intake canal of sea-farm pond.

Figure Captions

FIGURE 1. Location map of the study area.

FIGURE 2. Locations of the sampling stations. Arrows indicate water inputs and outputs during water renewal.

FIGURE 3. Changes in the main physicochemical parameters during the growing cycle at AM stations.

FIGURE 4. Comparison between EOM, redox, and SOD5 values measured at the beginning and the end of the survey.

FIGURE 5. Temporal variations in density and species richness of the total assemblage.

FIGURE 6. Temporal variations in the number and proportion of living specimens in the assemblage.

FIGURE 7. Canonical correspondence analysis (a) triplot with (b) enlargement of the arrows representing explanatory variables, and (c) enlargement of the plots grouped by stations. See text for explanation.

FIGURE 8. Temporal variations in relative abundances of *Ammonia tepida* and *Quinqueloculina seminula* in the total assemblage.

Plate Caption

PLATE 1**. 1** *Quinqueloculina bosciana*. **2** *Q. carinatastriata*. **3** *Q. eburnea*. **4** *Q. seminula*. **5** *Pseudotriloculina subgranulata*. **6** *Q. jugosa*. **7** *Pseudotriloculina lineiana*. **8** *Quinqueloculina* cf. *Q. bosciana* (deformed specimen). **9, 10** *Quinqueloculina* cf. *Q.. seminula* (deformed specimens). (Scale bars = 100 μm)

Debenay et al. Table 1

Stations		Temperature (°C) of the water	Salinity of the water	NH4 (µmol l-1) in the water	Oxygen (mg l-1) in the water	Number of bacteria (number g-1 x 10⁹)	SOD5 (mgO2/g dry sed)	EOM (mgC/g dry sed)	Sulfides (ng-at S/l)	Sediment pH	Redox (mv)	MO (%)	Cu (ppm)	Ni (%)	Zn (ppm)	Mn (%)
SF1	Average	25.32	34.84	2.31	5.88	4.17	9.08	2.33	0.05	7.66	17.68	5.82	24.00	0.05	86.00	0.08
	Stand Dev	2.69	1.80	3.06	1.19	1.25	2.96	0.86	0.03	0.12	46.12	1.05				
SF2	Average	25.37	34.84	2.25	6.85	4.85	5.15	1.33	0.07	7.83	111.77	5.65				
	Stand Dev	2.53	1.80	2.29	0.87	2.22	2.21	0.31	0.04	0.14	56.62	1.38				
SVA	Average	25.55	32.83	1.48	6.94	4.41	1.94	0.77	0.03	7.98	134.45	4.05				
	Stand Dev	3.26	1.61	1.74	0.94	1.18	0.96	0.20	0.04	0.11	25.65	0.76				
SVB	Average	25.81	32.83	2.57	7.13	4.54	5.43	1.77	0.07	7.87	91.62	5.12				
	Stand Dev	3.18	1.61	2.71	1.08	1.41	2.13	0.52	0.03	0.12	38.04	0.97				
S1	Average	26.39	38.10	0.54	4.55	4.30	1.40	0.44	0.01	7.63	132.29	3.56	42.00	0.04	77.00	0.04
	Stand Dev	1.67	1.29	0.86	1.16	1.30	0.90	0.26	0.02	0.22	112.02					
S2	Average	26.45	38.74	0.13	4.84	4.24	1.12	0.39	0.01	7.69	138.51					
	Stand Dev	1.66	1.55	0.18	1.35	3.01	0.91	0.27	0.02	0.44	153.82					
ST1	Average	26.92	38.42	0.56	4.54	3.04	1.33	0.51	0.04	6.95	202.29	7.30	23.00	0.04	344.00	0.05
	Stand Dev	1.63	1.35	1.64	1.07	1.35	0.75	0.22	0.06	0.41	125.06					
ST2	Average	26.93	38.62	0.73	4.69	3.35	1.14	0.43	0.02	7.18	159.43					
	Stand Dev	1.64	1.37	1.62	1.16	1.46	0.77	0.13	0.02	0.47	125.91					
TV1	Average	27.02	38.97	0.54	4.32	2.64	1.03	0.61	0.01	7.27	196.25	5.72	46.00	0.06	99.00	0.15
	Stand Dev	1.67	1.89	1.27	1.06	1.14	0.65	0.18	0.02	0.19	120.45					
TV2	Average	26.88	38.56	0.08	4.42	3.10	1.40	0.66	0.02	6.93	171.31					
	Stand Dev	1.64	1.43	0.15	1.08	1.42	0.85	0.21	0.03	0.29	99.15					

Debenay et al. Table 2

	Dates	Total number of individuals in 50 cm³	Species Richness	% living in total assemblages	% of A. tepida in total assemblage	A. tepida: % of living individuals	% of Q. seminula in total assemblage	Q. seminula: % of living individuals
SV A Saint Vincent	16-Feb	2000	7	32	87	35	10	0
	22-Feb	3000	4	23	95	25	5	0
	3-Mar	8000	4	29	95	31	5	0
	9-Mar	2000	3	17	91	15	8	38
	16-Mar	2500	5	15	86	14	9	33
	30-Mar	2800	9	25	77	28	16	10
	6-Apr	12000	4	25	85	26	12	15
	13-Apr	1000	5	50	81	52	17	41
	21-Apr	15000	11	42	53	42	21	48
	27-Apr	15000	11	42	47	43	28	30
	5-May	12000	11	32	57	31	27	36
	12-May	9000	7	47	66	39	18	61
	18-May	20000	12	41	40	45	24	38
	24-May	6000	6	48	86	49	3	67
	2-Jun	10000	7	36	47	17	18	18
	9-Jun	10000	10	24	38	18	28	31
SV B Saint Vincent	16-Feb	5000	6	55	75	51	18	10
	22-Feb	6000	6	66	83	60	10	30
	3-Mar	4000	8	47	75	42	13	0
	9-Mar	1500	7	28	93	27	4	0
	16-Mar	6000	10	40	70	38	21	9
	24-Mar	12000	8	43	86	43	12	8
	30-Mar	10000	6	43	49	39	45	47
	6-Apr	50000	15	43	56	22	23	43
	13-Apr	20000	12	19	75	14	17	29
	21-Apr	40000	9	26	59	21	23	5
	27-Apr	3000	14	41	60	31	25	24
	5-May	4000	12	38	67	15	13	62
	12-May	3000	9	50	66	32	21	33
	18-May	1500	10	25	55	13	20	42
	24-May	5000	15	24	49	23	33	20
	2-Jun	5000	15	9	47	8	22	9
	9-Jun	3000	15	7	50	8	23	0
SF 1 Sea Farm	14-Feb	1500	3	35	51	45	47	25
	21-Feb	2500	3	53	80	63	19	11
	28-Feb	600	3	51	87	56	12	9
	7-Mar	1500	3	63	95	66	4	0
	14-Mar	1700	2	38	88	43	12	0
	28-Mar	1200	2	35	85	39	15	13
	4-Apr	3000	2	46	71	66	29	0
	11-Apr	400	3	38	94	40	5	0
	19-Apr	3000	2	39	92	43	8	0
	25-Apr	1000	3	25	93	26	6	25
	3-May	3000	4	31	80	39	18	0
	10-May	4000	3	33	61	48	38	10
	16-May	800	4	19	81	20	17	18
	22-May	1500	4	19	67	27	31	3
	30-May	1000	4	14	68	14	28	7
	7-Jun	1500	4	5	70	5	28	3
SF2 Sea Farm	14-Feb	300	3	5	85	1	14	25
	21-Feb	1000	3	19	80	23	19	6
	28-Feb	3000	3	20	72	26	27	4
	7-Mar	1000	3	9	92	10	7	0
	14-Mar	2500	2	5	72	6	28	4
	38067	1200	3	7	74	1	25	24
	28-Mar	4000	2	45	49	23	51	67
	4-Apr	200	3	51	41	52	57	53
	11-Apr	3500	3	27	55	9	44	50
	19-Apr	8000	6	37	64	32	34	47
	3-May	12000	3	24	21	29	79	22
	10-May	8000	2	28	33	33	67	30
	16-May	4000	4	27	60	25	38	28
	22-May	12000	2	34	63	28	37	43
	30-May	6000	5	27	69	21	30	41
	7-Jun	4000	5	25	76	25	21	22

	Dates	Total number of individuals in 50 cm³	Species Richness	% living in total assemblages	% of A. tepida in total assemblage	A. tepida: % of living individuals	% of Q. seminula in total assemblage	Q. seminula: % of living individuals
ST 1 Algue Marine	12-Dec	20	3	0	25	0	50	0
	20-Dec	1500	5	10	65	14	30	3
	27-Dec	1000	5	20	51	8	35	39
	3-Jan	350	3	10	85	9	13	11
	10-Jan	130	2	74	14	0	86	59
	17-Jan	1	1	0			100	0
	24-Jan	1400	3	10	73	9	11	10
	30-Jan	1000	5	35	28	13	68	35
	6-Feb	4000	5	58	12	0	84	67
	20-Feb	1000	2	41	3	0	97	42
	27-Feb	14000	2	28	3	0	97	29
	6-Mar	800	4	13	1	0	97	13
	20-Mar	7000	7	14	1	0	93	11
	27-Mar	11000	3	10	0	0	96	11
	3-Apr	15000	3	5	13	0	86	5
	10-Apr	25000	7	5	5	20	93	4
ST 2 Algue Marine	12-Dec	400	3	22	93	25	5	0
	20-Dec	10	2	0	86	0	14	0
	27-Dec	200	4	31	81	35	14	8
	3-Jan	1200	4	22	75	12	23	52
	10-Jan	25	3	36	29	25	43	67
	17-Jan	1800	3	35	47	13	52	47
	24-Jan	700	5	7	72	7	25	8
	30-Jan	350	4	45	6	40	94	51
	6-Feb	500	3	46	16	0	83	55
	13-Feb	2000	2	39	13	14	87	43
	20-Feb	20000	2	55	0	0	100	54
	27-Feb	15000	5	24	6	0	91	25
	6-Mar	14000	3	9	14	9	85	9
	13-Mar	5500	3	8	12	0	88	9
	20-Mar	24000	3	13	11	42	89	12
	27-Mar	6000	5	20	2	0	94	19
	3-Apr	10000	4	13	16	13	80	12
	10-Apr	20000	4	14	8	25	90	13
S 1 Algue Marine	14-Dec	1800	3	36	76	44	24	10
	22-Dec	1800	3	14	85	15	13	7
	29-Dec	5200	2	12	76	14	24	4
	5-Jan	8000	2	25	82	27	18	13
	12-Jan	3500	3	24	76	20	24	38
	19-Jan	9000	4	29	65	24	34	41
	26-Jan	1500	2	6	62	6	38	5
	1-Feb	7000	3	64	60	62	40	15
	8-Feb	3500	3	19	43	12	53	19
	15-Feb	8000	3	46	44	41	49	45
	21-Feb	8000	4	32	26	50	68	19
	28-Feb	8000	4	40	24	12	72	51
	5-Mar	4500	8	9	30	12	64	9
	12-Mar	20000	3	5	7	0	92	5
	15-Mar	17000	5	13	38	18	62	11
	22-Mar	8000	7	15	23	15	68	10
	29-Mar	15000	2	13	58	10	42	14
	3-Apr	1700	5	5	14	14	84	4
	19-Apr	15000	4	11	41	12	57	9
Average values	SVA	8144	7	33	71	32	16	29
	SVB	10529	10	36	65	29	20	22
	SF1	1763	3	34	79	40	20	8
	SF2	4419	3	24	63	22	36	29
	ST1	5200	4	21	25	5	71	24
	ST2	6760	3	24	33	15	64	26
	S1	7711	4	22	49	22	49	17
	S2	2136	3	23	38	16	65	24
	TV1	647	3	17	13	15	88	11
	TV2	1719	4	17	21	21	72	16

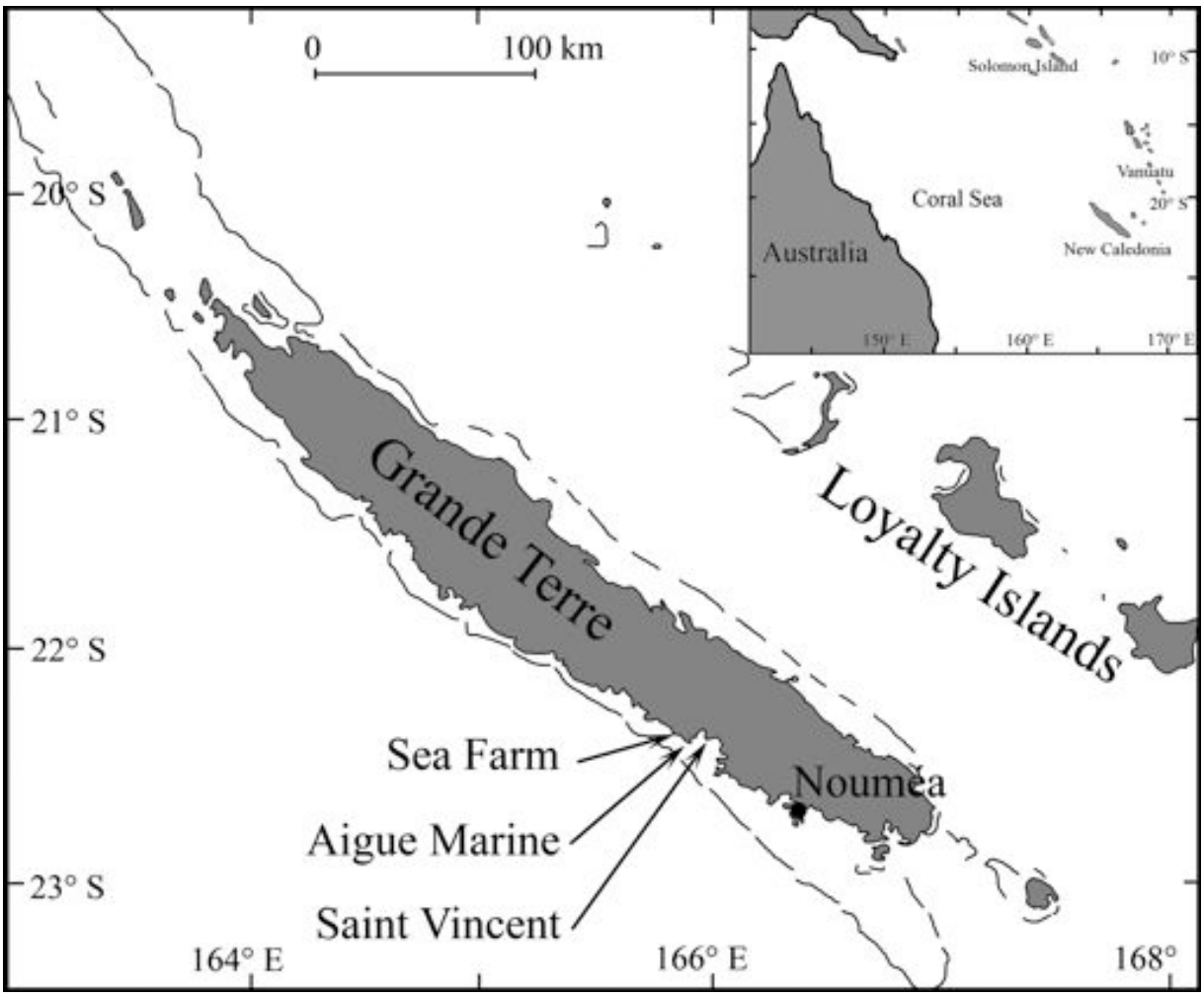
	Dates	Total number of individuals in 50 cm³	Species Richness	% living in total assemblages	% of A. tepida in total assemblage	A. tepida: % of living individuals	% of Q. seminula in total assemblage	Q. seminula: % of living individuals
TV 1 Algue Marine	20-Dec	2	1	0	100	0		
	27-Dec	8	3	50	25	0	50	100
	3-Jan	50	4	74	9	0	83	84
	10-Jan	0	0					
	17-Jan	30	1	0	0		100	0
	24-Jan	20	3	29	9	100	82	11
	30-Jan	120	2	24	24	14	76	27
	13-Feb	1400	3	19	4	25	94	19
	20-Feb	1500	2	1	0		99	1
	27-Feb	2500	3	15	0		97	16
	6-Mar	2000	6	0	1	1	94	0
	13-Mar	350	2	17	0		97	16
	20-Mar	500	2	0	0		98	0
	27-Mar	800	5	9	1	0	94	6
	3-Apr	80	3	13	0		94	13
	10-Apr	1600	4	16	2	50	97	15
	17-Apr	40	3	0	26	0	68	15
TV 2 Algue Marine	12-Dec	100	2	33	19	0	81	41
	20-Dec	25	2	13	88	14	13	0
	27-Dec	30	3	20	30	0	20	0
	3-Jan	120	4	0	52	0	38	0
	10-Jan	200	2	17	31	8	69	21
	17-Jan	180	2	23	27	25	73	23
	24-Jan	140	3	20	50	20	45	11
	30-Jan	1200	5	53	38	49	58	47
	6-Feb	700	4	21	1	0	94	20
	13-Feb	500	2	63	9	80	91	60
	20-Feb	5000	6	12	2	50	94	11
	27-Feb	120	2	9	31	0	69	14
	6-Mar	750	4	1	10	0	83	2
	13-Mar	5000	3	2	0		97	0
	20-Mar	3500	4	5	1	1	95	5
	27-Mar	2000	5	1	0		95	0
	3-Apr	500	5	8	4	50	93	5
	10-Apr	12000	7	22	1	0	79	7
	17-Apr	600	5	0	12	33	83	1
S 2 Algue Marine	14-Dec	20	2	17	67	15	33	25
	22-Dec	100	2	0	67	0	33	0
	29-Dec	100	1	18	100	18		
	5-Jan	150	4	20	84	20	13	13
	12-Jan	30	2	13	88	0	13	100
	19-Jan	75	2	22	72	13	28	44
	26-Jan	50	2	11	61	6	39	18
	1-Feb	250	3	44	4	0	79	37
	8-Feb	5000	4	43	4	25	94	43
	15-Feb	4000	5	35	7	0	87	37
	21-Feb	900	2	35			96	33
	28-Feb	8000	3	32	0		98	35
	5-Mar	7000	6	8	2	0	92	7
	22-Mar	2500	8	13	6	0	88	11
	29-Mar	4500	4	14	3	33	95	13
	19-Apr	1500	4	45	5	75	93	38

Shadows indicate weakly significant samples with less than 100 individuals in 50 cm3

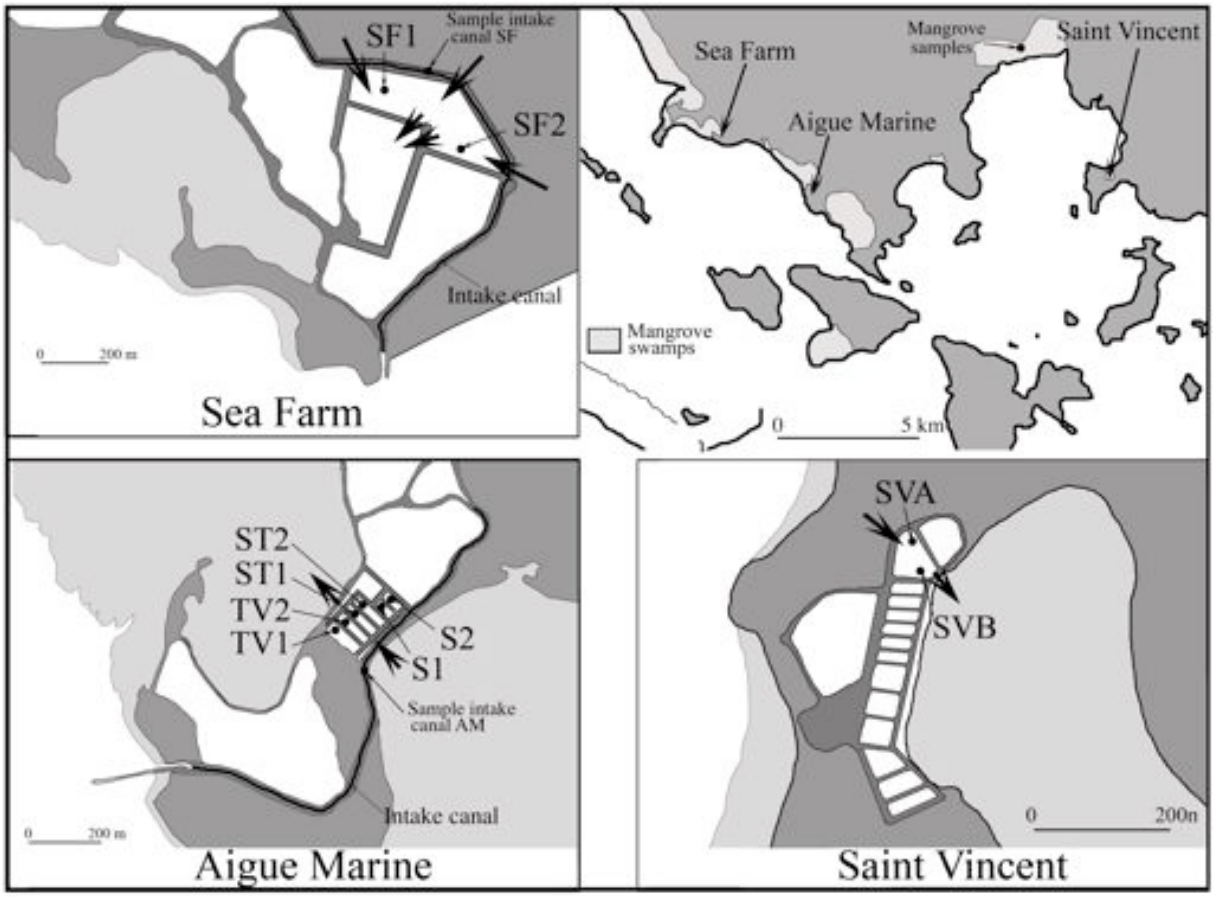
Debenay et al. Table 3

	NC 15	NC 16	NC 17	NC 18	Ic AM	Ic SF
Total number in 50 cm³ (D50)	2500	200	1500	2200	10000	50000
Species richness	2	5	16	10	29	32
Ammobaculites sp.			1		2	0
Ammonia convexa			17			
Ammonia tepida	3	4	31	23	49	47
Ammotium salsum			0		2	
Anomalinula glabrata			33	0		
Arenoparrella mexicana			3			
Bolivina striatula			1	0	11	3
Buliminella elegantissima					1	
Buliminella tenuis					2	1
Cornuspira planorbis					1	8
Edentostomina cultrata					1	0
Elphidium advenum			4	32	6	3
Elphidium excavatum						2
Elphidium simplex				1		
Elphidium oceanicum					2	1
Fissurina lucida					2	4
Gaudryina exilis				1	1	0
Glabratella sp.					1	3
Glomospira gordialis			1		1	0
Haplophragmoides wilberti			1			
Haynesina depressula					3	1
Haynesina germanica			1			
Helonina anderseni			2			
Jadammina macrescens		15	0			
Miliammina fusca			1		2	1

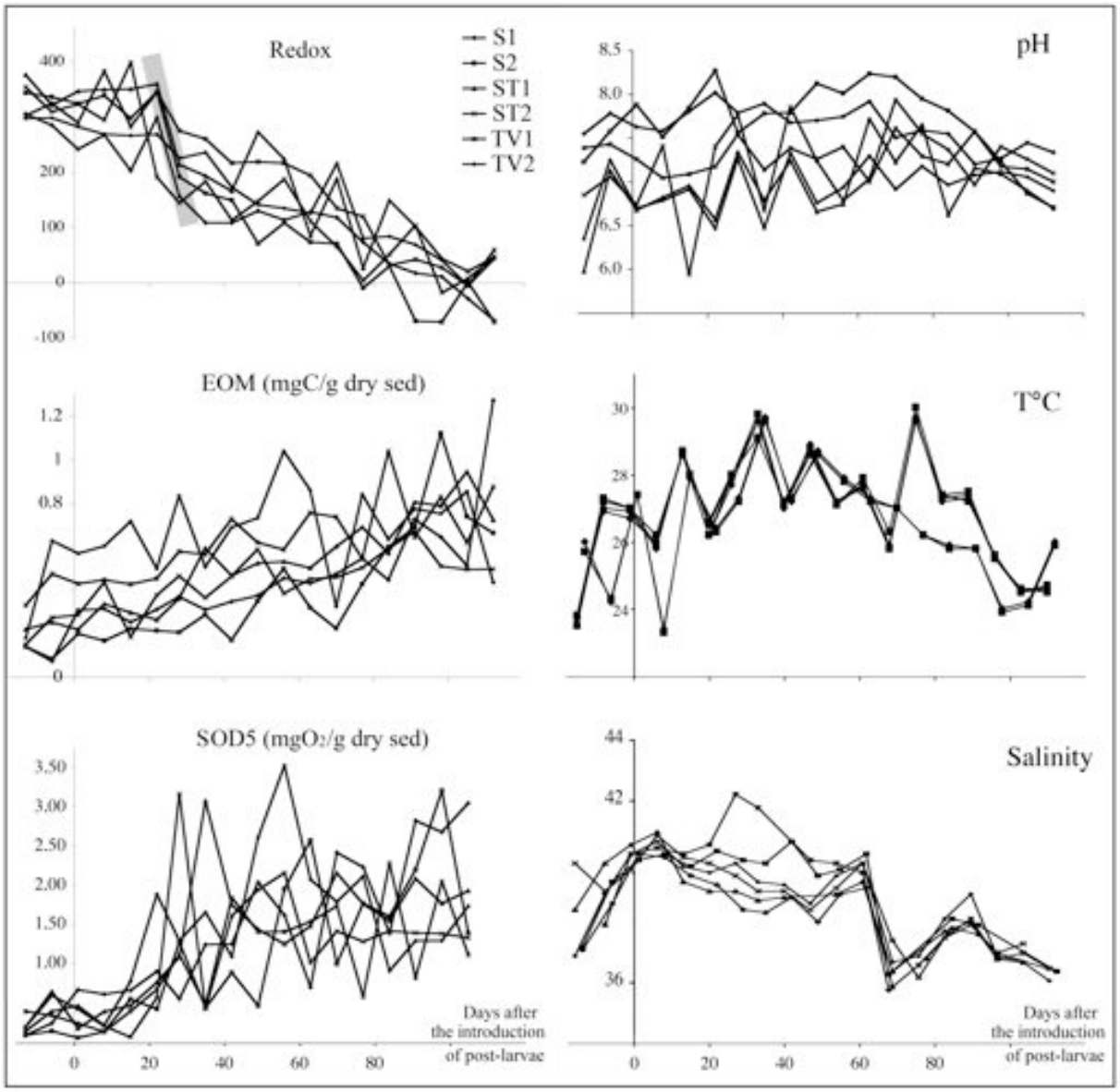
	NC 15	NC 16	NC 17	NC 18	Ic AM	Ic SF
Total number in 50 cm³ (D50)	2500	200	1500	2200	10000	50000
Species richness	2	5	16	10	29	32
Miliola carlandi					2	0
Monalysidium acicularis					0	
Nonion grateloupi					0	1
Parrellina hispidula						3
Peneroplis planatus						0
Planispirillina carlandi					0	
Quinqueloculina carinatastriata					2	3
Quinqueloculina cf. delicatula						0
Quinqueloculina elongata					2	2
Quinqueloculina jugosa					1	
Quinqueloculina lamarckiana					1	
Quinqueloculina poeyana					1	1
Quinqueloculina seminula	97	27	5	39	4	13
Quinqueloculina wiesneri					2	2
Quinqueloculina spp.						4
Reophax nana			1			
Rosalina bradyi					0	0
Schackoinella globosa					1	0
Spirolina arietina						0
Triloculina oblonga				2		
Triloculina tricarinata						0
Trochammina inflata		46		2		0
Trochammina sp.		8		1		
Varidentella neostriatula						1



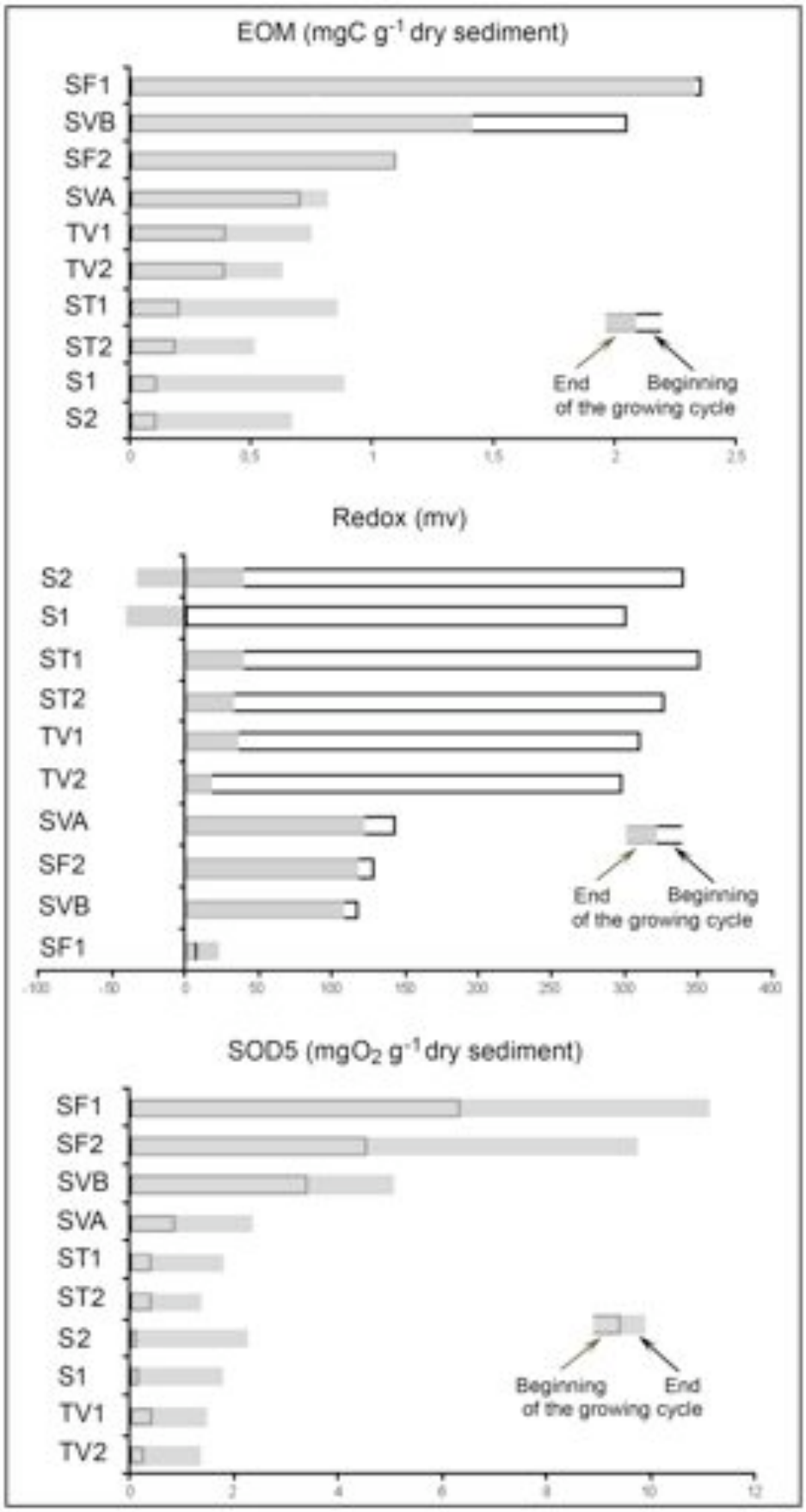
Debenay et al., Figure 1



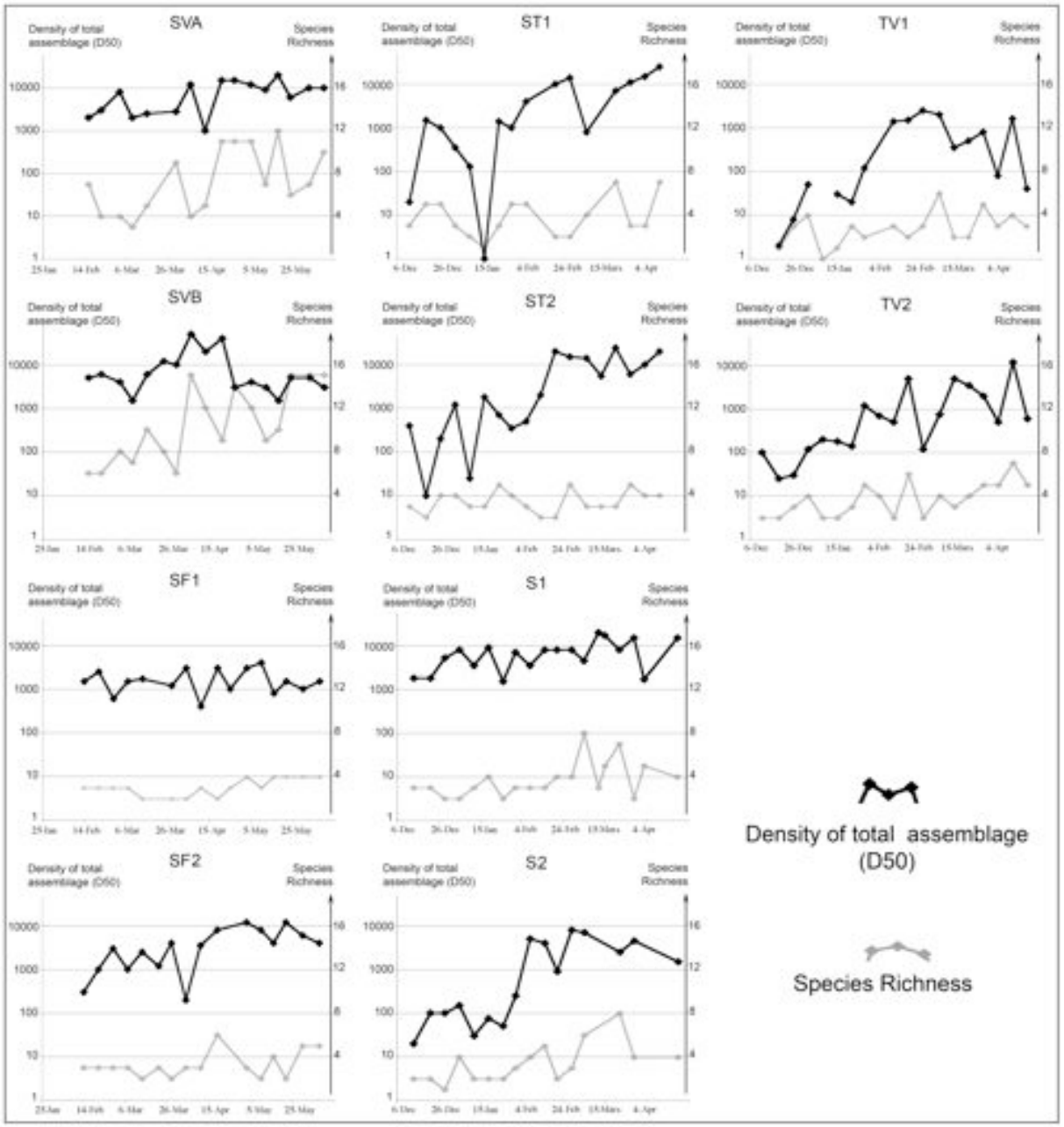
Debenay et al., Figure 2



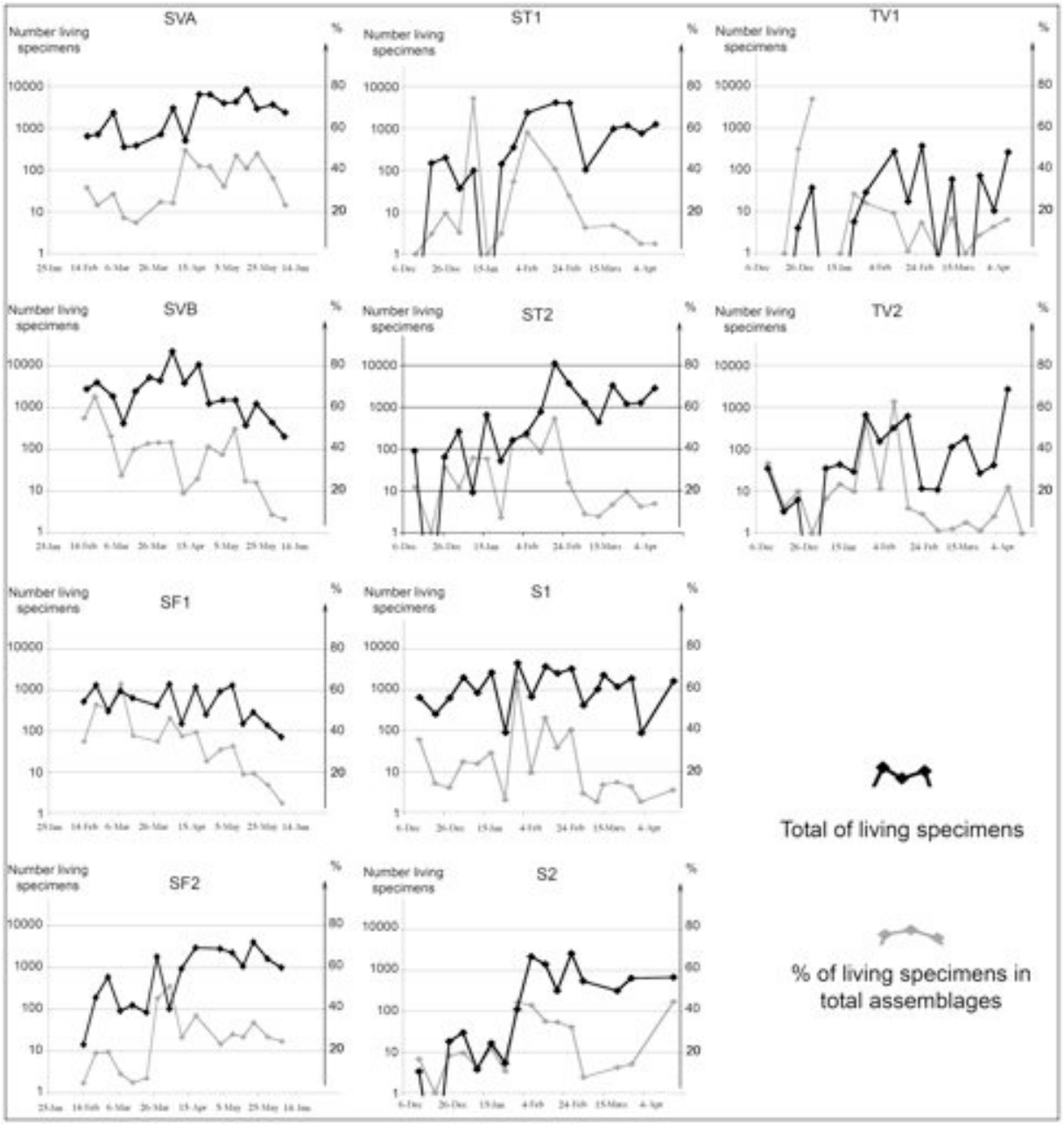
Debenay et al., Figure 3



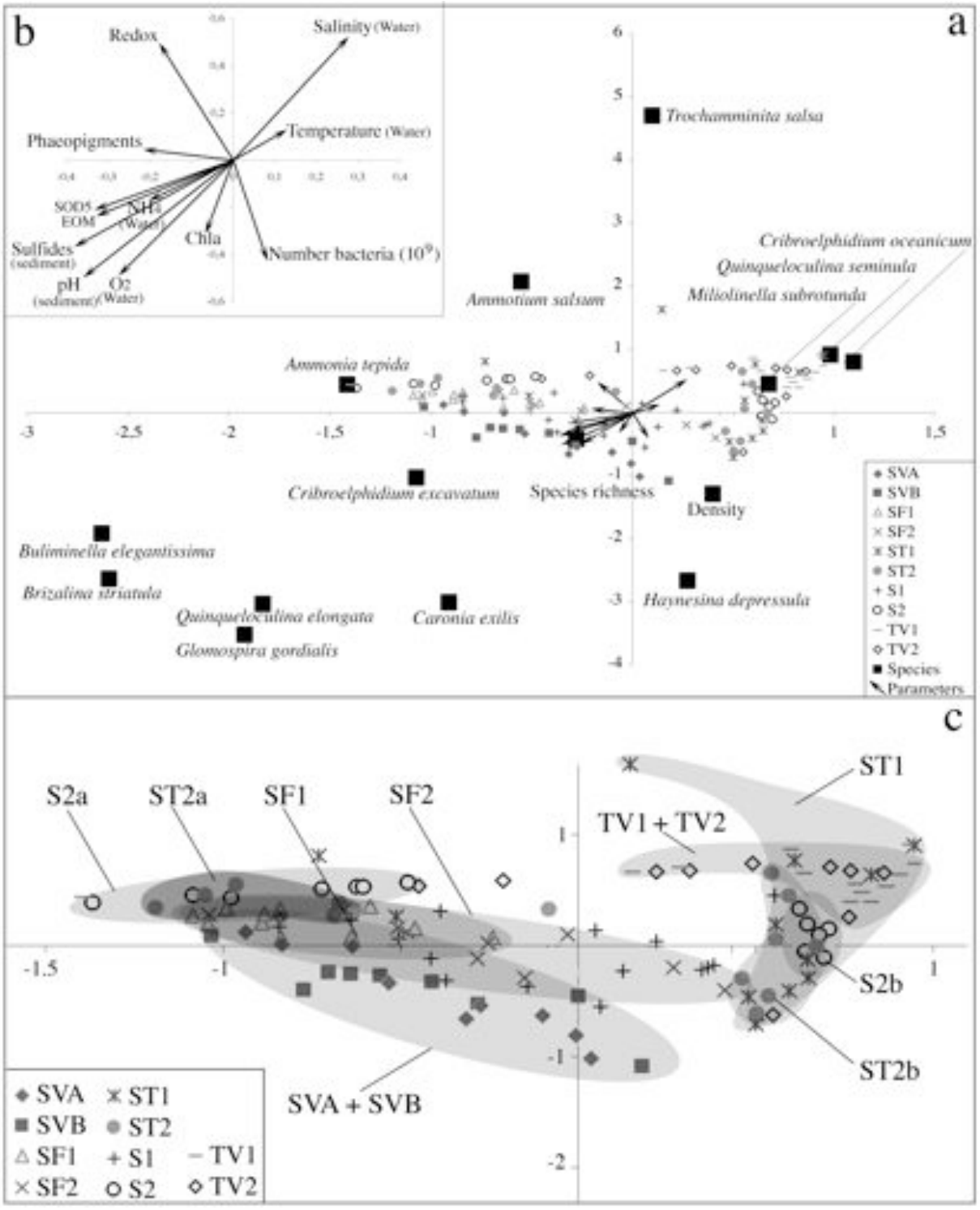
Debenay et al., Figure 4



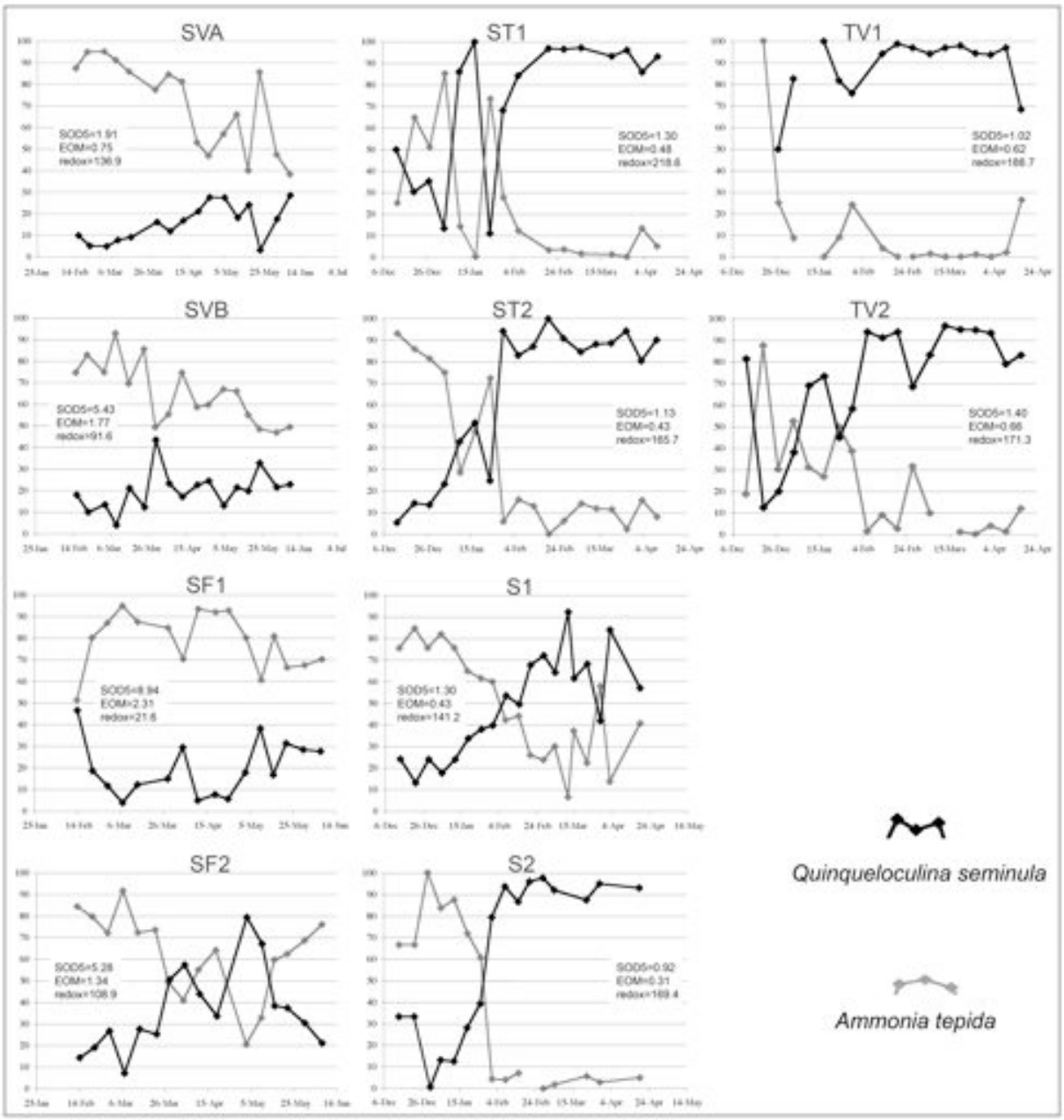
Debenay et al., Figure 5



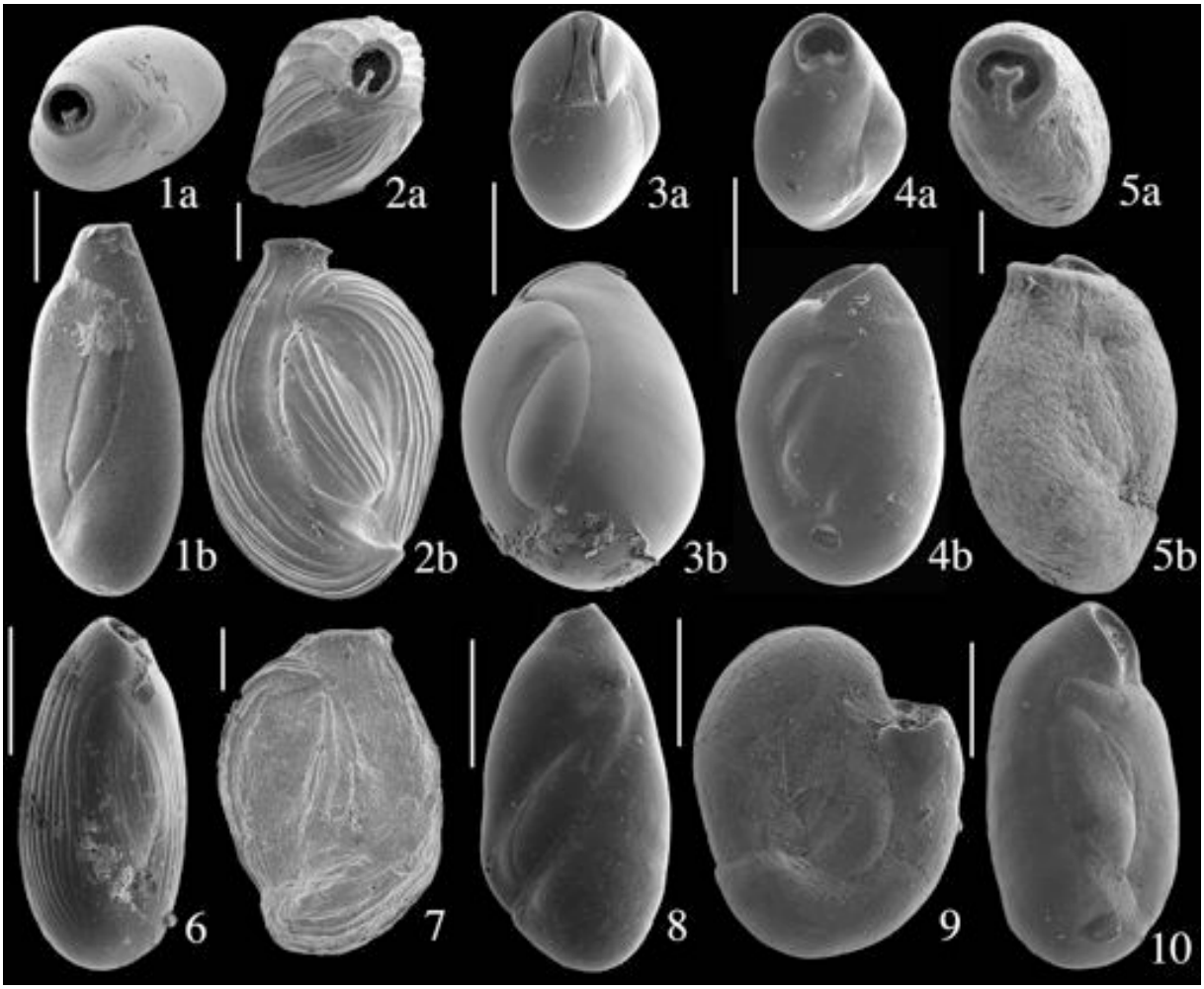
Debenay et al., Figure 6



Debenay et al., Figure 7



Debenay et al., Figure 8



Debenay et al., Plate 1

Species	Number of occurrences	Maximum relative abundance
Ammobaculites exiguus Cushman and Bronnimann	10	5
Ammonia convexa (Collins)	2	2
Ammonia tepida (Cushman)	160	100
Ammotium salsum (Cushman and Bronnimann)	11	29
Aubignyna sp.	1	1
Brizalina cf. *variabilis* (Williamson)	1	2
Brizalina striatula (Cushman)	26	6
Buliminella elegantissima d'Orbigny	23	4
Caronia exilis (Cushman and Bronnimann)	26	3
Cornuspira planorbis Schultze	1	1
Cribroelphidium excavatum (Terquem)	8	1
Cribroelphidium oceanicum (Cushman)	27	5
Cribroelphidium williamsoni (Haynes)	8	3
Cribrononion gerthi (Van Voorthuysen)	1	1
Elphidium advenum (Cushman)	1	2
Fisherinella diversa McCulloch	48	16
Fissurina lucida (Williamson)	5	1
Glabratella sp.	1	0
Globocassidulina cf. *minuta* Cushman	10	2
Glomospira gordialis (Jones and Parker),	2	1
Haynesina depressula (Walker and Jacob)	21	18
Jadammina macrescens (Brady)	44	22
Labrospira jeffreysii (Williamson)	7	12
Miliammina fusca (Brady)	8	50
Miliolinella subrotunda (Montagu)	7	3
Nonion pauperatum (Balkwill and Wright)	16	6
Pseudotriloculina linneiana (d'Orbigny)	8	2
Pseudotriloculina subgranulata (Cushman)	11	2
Quinqueloculina bosciana d'Orbigny	1	0
Quinqueloculina carinatastriata (Wiesner)	19	2
Quinqueloculina eburnea d'Orbigny	8	5
Quinqueloculina elongata Natland	13	5
Quinqueloculina jugosa Cushman,	10	2

Quinqueloculina poeyana d'Orbigny	4	3
Quinqueloculina seminula (Linné)	167	100
Quinqueloculina spp.	8	5
Reophax nana Rhumbler	2	1
Rosalina bradyi Cushman	2	1
Rosalina spp.	2	25
Sigmoilinopsis elliptica (Galloway and Wissler)	10	9
Spiroloculina antillarum d'Orbigny	3	1
Spiroloculina spp.	1	1
Triloculina barnardi Haig	1	0
Triloculina trigonula (Lamarck)	3	1
Trochammina inflata (Montagu)	3	5
Trochammina sp.	1	0
Trochamminita salsa Cushman and Brönnimann	11	25