

Chapter 3

Neoichnology

Since its earliest roots in Renaissance times, trace fossil analysis has relied on actualistic experiences for inspiring and testing theories and models. In fact, each of the major watersheds in the history of ichnology was initiated by advances in neoichnological knowledge, which regards the study of modern ichnological systems.

This section presents a novel method for neoichnological analysis. Similarly to a geographic information system (GIS), the proposed approach integrates hardware, software, and data for capturing, managing, analyzing, and displaying geographically referenced ichnological data. For this reason, the method has been named 'IchnoGIS'.

The IchnoGIS method has been applied to the study of the Grado lagoon (Adriatic Sea, Italy), for which reason this chapter starts with a review of morphology, ecology and ethology of individual traces (section 3.1). Successively, theory and application of the IchnoGIS method are presented (section 3.2). In this context, a question might arise: Is the IchnoGIS method producing realistic results? If the method is working, the predicted scenario will be consistent with the observed one. Based on this hypothesis, the purpose of section 3.3 is to test the validity of the IchnoGIS method by evaluating its prediction performance.

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Chapter 3

3.1 Neoichnology of a barrier-island system: the Mula di Muggia (Grado lagoon, Italy)

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Neoichnology of a barrier-island system: the Mula di Muggia (Grado lagoon, Italy)

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Abstract

Barrier-islands are common landforms and biodiverse habitats, yet they received scarce neoichnological attention. This gap is tackled by studying the Mula di Muggia barrier-island system (Grado lagoon, Italy), focusing on morphology, ecology and ethology of individual traces. The following incipient ichnotaxa are identified: *Archaeonassa*, *Arenicolites*, *Bergaueria*, ‘diverging shafts’, *Helminthoidichnites*, *Lockeia*, *Macanopsis*, *Monocraterion*, *Nereites*, *Parmaichnus*, *Polykladichnus*, *Skolithos*, *Thalassinoides* and ‘squat burrows’. Vertebrate (*Avipeda*-/*Ardeipeda*-like, *Canipeda*) and invertebrate tracks (‘parallel furrows’) are also described.

For each ichnotaxon, tracemaker and behaviour are discussed, together with their position with respect to sediment barriers. Results suggest that sediment barriers impose a sharp contrast in terms of ichnological composition. Back-barrier is dominated by branched burrows (i.e. *Thalassinoides*, *Parmaichnus*), while the fore-barrier presents vertical and U-shaped burrows (*Arenicolites*, *Skolithos*). The environmental conditions of the back-barrier show that low-oxygen substrates favour intense bioturbation, provided that the water column is sufficiently oxygenated.

Keywords: neoichnology, barrier-island, Adriatic Sea, oxygenation

1. Introduction

Barrier-islands are elongate accumulations of unconsolidated sediment that separate the open sea from a landward restricted basin (Schwartz, 2005; Nichols, 2009). At present day, they are important coastal landforms, lining the 10% of the world's shoreline length (Stutz and Pilkey, 2011). Barrier-island systems are also well-represented in the rock record, being documented from the Mesoproterozoic onwards (Köykkä and Lamminen, 2011).

This conspicuous record is not the only reason of importance. In fact, barrier-islands are normally delimiting coastal lagoons, which play a major ecological role. In fact, they commonly provide a collection of habitat types for many species, housing high biodiversity levels and considerable biomass (Pérez-Ruzafa et al., 2011). Historically, barrier-island ecosystems supported numerous human communities, which often posed a threat to these fragile environments (Pérez-Ruzafa et al., 2011). At this regard, barrier-islands are also very sensitive to sea-level rise and storm patterns, thus providing clues to process changes through time (Mallinson et al., 2010).

Despite their inferred importance, barrier-island neoichnology is relatively understudied. In fact, in contrast to the large number of ecological and sedimentological studies, comparatively few barrier-island systems received neoichnological attention: the Wadden Sea (e.g. Cadée and Goldring, 2007; Hertweck et al., 2007), the Georgia Coast (e.g. Howard and Frey, 1985; Martin, 2013) and the New Brunswick Coast (Hauck et al., 2009).

There is therefore a need for neoichnological records of barrier-island systems, in terms of either autecology or synecology of bioturbation. This goes in parallel with another *tenet* of neoichnology, the need of studying tidal depositional systems, which received less ichnological study than wave-dominated environments (Buatois and Mángano, 2011).

The Grado-Marano lagoon (Italy) satisfies both requirements, presenting a vast complex of barrier-islands within a low-energy, tide-influenced regime. Within the Grado lagoon, the area of the Mula di Muggia provides optimal study conditions, given its particularly integer environment. More specifically, the goal of this study is to provide information on morphology, ecology and ethology of individual traces. Knowledge of these aspects is essential for the understanding of the ichnological system as a whole, which will be discussed quantitatively in Baucon and Felletti (2013).

2. Study Area

The Grado-Marano lagoon, located along the Adriatic coast in Northern Italy, is composed of two communicating shallow basins known as the Grado and Marano lagoons. The lagoonal complex started to develop during the transgression that followed the end of the last glacial maximum. The Marano basin is older (5000 years BP), while the Grado lagoon formed in post-Roman times as the result of the diversion of the Isonzo River (Gatto and Marocco, 1992; Triches et al., 2011).

At present day, the Grado-Marano lagoon extends between the Isonzo and Tagliamento rivers, stretching out for about 160 km². The lagoon is connected to the sea through inlets which subdivide barrier islands into six segments (Blasutto et al. 2005; Triches et al. 2011). The tidal magnitude is unusual for the Mediterranean Sea, with semidiurnal mean and spring tidal ranges of 65 and 105 cm respectively (Sconfietti et al., 2003; Covelli et al., 2008). Climate is temperate, influenced by ENE (Bora) and SE (Scirocco) winds (Fontolan et al., 2007).

Although the Grado-Marano system has been subject to significant anthropogenic pressure over the past centuries (Covelli et al., 2008), it remains one of the more pristine wetlands in the Northern Adriatic and Mediterranean Sea as well. In fact the lagoon of Grado and Marano is an important ecological system, both for the habitats of numerous vegetal and animal species (Sconfietti et al., 2003; Ferrarin et al., 2010; Barbone et al., 2011). In particular, the area of the Mula di Muggia Bank (Fig. 1) is recognized for its outstanding biodiversity, for which reason it is receiving environmental protection (i.e. Ramsar Convention, EU Natura 2000 Network; Barbone et al., 2011). Here, a shallow lagoon is fronted by sediment barriers (Fig. 2), which are significantly moderating the effects of waves and currents (Fig. 1). Two geomorphological domains are distinguished on the basis of position with respect to the sediment barriers:

1. the back-barrier (Fig. 3A) is dominated by muddy sand, commonly covered by dense seaweed meadows (Video 1). Laminated and filamentous microbial mats develop on intertidal flats.
2. the fore-barrier (Fig. 3B) present higher-energy conditions and rippled sand. Shell debris is locally abundant (Video 2).

In light of these geological and ecological features, the area of the Mula di Muggia is recognized as an ideal study site for the neoichnology of barrier-island systems.

3. Materials and Methods

The study area was inspected between 2009 and 2010; subtidal areas were explored with a kayak. Major geomorphological features were traced with a GPS unit, which was also used to georeference selected photographic and video documentation (Fig. 1). Burrow architecture was analyzed by resin casting and manual excavation, further refining the morphological description of Baucon (2008).

4. Marginal Marine Ichnology

This section presents the morphological, biological and ethological features of the major ichnotaxa. 16 incipient ichnotaxa were recognized and divided into morphotypes on the basis of burrow morphology and size, after which they are named. A descriptive classification scheme, partly based on Książkiewicz (1977), is adopted to organize the ichnotaxa, to be considered as incipient in conformity with Bromley (1996, p. 164). Trace distribution is qualitatively described in Table 1.

4.1. Branched structures

4.1.1. *Thalassinoides form XL (very large)*

Description: Burrow networks with multiple openings, one of which presents a large sediment mound (diameter: 15–25 cm). Tunnel section cylindrical to elliptical (diameter: 1.5–2 cm); vertical extension usually exceeding 40 cm. This morphotype is confidently assignable to the ichnogenus *Thalassinoides*, consisting of three-dimensional burrow networks connected to surface by vertical shafts (after Häntzschel, 1975).

Tracemaker: *Pestarella candida* (Crustacea: Decapoda).

Ethology: Presence of sediment mounds is indicative of sediment processing, suggesting deposit-feeding (Video 3). This interpretation is supported by different functional classifications of thalassinidean burrows (Griffis and Suchanek, 1991; Nickell and Atkinson, 1995).

4.1.2. *Thalassinoides form L (large)*

Description: Burrow networks characterized by funnel-like openings and chambers characteristically filled by seagrass. Burrow section circular (diameter: 1 cm); vertical extension ranging between 20 and 40 cm. Mounds are small (diameter: 5–10 cm), commonly absent. At a nearby site (Grado Punta Spin), Dworschak et al. (2005) realized complete resin casts of similar forms, revealing spiral shafts from which several debris-filled chambers branched off. Based on the general morphology, these structures are assignable to the ichnogenus *Thalassinoides*.

Tracemaker: *Pestarella tyrrhena* (Crustacea: Decapoda).

Ethology: According to Dworschak et al. (2005), *Pestarella tyrrhena* pulls seagrass debris into the burrow from the funnel-like openings, where it passively accumulates during low tide, for enriching the sediment around the burrow. Indeed, the tracemaker is mainly a sediment feeder (Dworschak et al., 2005).

4.1.3. *Parmaichnus*

Description: Y-shaped burrows consisting of an upper U-shaped section and a lower I-shaped part, both presenting short branches (Fig. 4A). Swellings are present at the base of the U-shaped sections. Tunnels circular in cross section. The same morphology was described by Dworschak (1987a) in adjacent study sites. Although the morphology may be reminiscent of *Psilonichnus*, the presence of swellings at the base of the U-shaped section is diagnostic of *Parmaichnus* (Pervesler and Uchman, 2009).

Tracemaker: *Upogebia pusilla* (Crustacea: Decapoda).

Ethology: Funnel-shaped openings, Y shape and circular tunnel cross section are consistent

with current generation and suspension-feeding (Nickell and Atkinson, 1995). Such interpretation is corroborated by the classification scheme of Griffis and Suchanek (1991). Dworschak (1987a) shown that the main feeding activity of *Upogebia pusilla* occurs in one of the swellings (turning chambers), where the animal intercepts suspended matter with the setae of the pereopods, acting as a basket. Although filter feeding is considered as the primary mechanism of obtaining food, the tracemaker shows also evidences of deposit-feeding and gardening (Dworschak, 1987a; Griffis and Suchanek, 1991). Pervesler and Hohenegger (2006) demonstrated that burrow segments connecting the steep entrance shafts in *Upogebia* are shoreline indicators, being oriented almost parallel to the shoreline.

4.1.4. *Polykladichnus*

Description: I- or U-shaped burrows with Y-shaped bifurcations connecting to the bedding surface (Fig. 4B). This morphology is consistent with the ichnogenus *Polykladichnus*, described by Schlirf and Uchman (2005) as vertical to steeply oblique tubes with single or multiple Y- or U-shaped bifurcation.

Tracemaker: *Nereis* (= *Hediste*) *diversicolor* (Polychaeta: Nereididae)

Ethology: *Polykladichnus* may have multiple functions, as the tracemaker *Nereis diversicolor* (Fig. 4C) uses a wide spectrum of feeding strategies: a) deposit-feeding on the sediment surface and around the burrow; b) suspension-feeding, through the release of a mucus net in the gallery; c) herbivory; d) carnivory (Fidalgo e Costa et al., 2006; Engelsen et al., 2010).

4.2. *U-burrows*

4.2.1. *Arenicolites form XL (very large)*

Description: Vertical U-burrow without spreite. One opening is funnel-shaped, the other is simple and commonly presents a single pile of sediment casts. Tunnel diameter 0.8 cm, burrow penetration 20–40 cm. The morphotype is confidently assigned to the ichnogenus *Arenicolites*, consisting of vertical U-burrows without spreite (Häntzschel, 1975).

Tracemaker: *Sipunculus nudus* (Sipuncula: Sipunculidae)

Ethology: The presence of sediment casts suggest deposit-feeding, which is the typical mode of life of most Sipuncula (Cutler, 1994).

4.2.2. *Arenicolites form L (large)*

Description: Vertical U-burrow without spreite. Simple or funnel-like openings surrounded by radially disposed fecal casts (Fig. 5A). Tunnel diameter 0.5 cm, burrow penetration 20–40 cm. General morphology and the absence of a spreite are consistent with the ichnogenus *Arenicolites* (Häntzschel, 1975).

Tracemaker: *Sipunculus nudus* (Sipuncula: Sipunculidae)

Ethology: According to the presence of sediment casts and to the biology of the tracemaker (Cutler, 1994), these structures are permanent burrows related to deposit-feeding.

4.2.3. *Arenicolites form S (small)*

Description: Simple vertical U-burrow; tunnel diameter 1 mm, limb spacing 1–2 cm (Fig. 5B). Research from other study areas revealed the presence of a spreite between the limbs of similar U-burrows (Bromley, 1996: p.43); apparently, the structures from Grado do not present this feature. Consequently, the described burrow displays all the diagnostic features of the ichnogenus *Arenicolites* (see Häntzschel, 1975).

Tracemaker: *Corophium volutator* (Crustacea: Amphipoda).

Ethology: The tracemaker is predominantly an unselective deposit-feeder, although suspension-feeding and epipsammic browsing may also occur. In particular, diatoms form a consistent part of its diet (Gerdol and Hughes, 1994; Smith et al., 1996). *Corophium* is also known for producing several kinds of trails (Uchman and Pervesler, 2006)

4.3. Chambered burrows

4.3.1. 'Squat burrow'

Description: unbranched burrow with a squat morphology, formally defined by the low depth/diameter ratio (ratio: 1–2.5). Burrow architecture grades from straight (plug- or I-shaped) to variously bending morphologies (L-, J-, U- or banana-shaped). Usually, the lower part of the burrow is occupied by a disc-shaped chamber oriented obliquely or in parallel with respect to the sediment surface. Burrow section sub-circular (diameter: 5–8 cm), with irregular, rounded margins. Piles of loose sediment with crab tracks are commonly present at the burrow entrance.

The broad range of morphological variation poses ichnotaxonomical problems:

- a) Plug-shaped burrows resemble the ichnogenus *Cheiiichnus*, a bowl-shaped trace with scratch marks (Muñiz et al., 2010). Nevertheless, the Grado specimens do not preserve bioglyphs because of the geotechnical properties of the sediment.
- b) The banana-shaped forms closely resembles *Macanopsis plataniformis*, an unbranched J-shaped burrow attributed to brachyurans (Muñiz and Mayoral, 2001).
- c) The larger J- and U-shaped shaped forms reveal similarities to *Psilonichnus*, which comprises simple Y-, J- and U-burrows (Nesbitt and Campbell, 2006). However, it should be noted that the Grado specimens are significantly squatter than the typical occurrences of the ichnogenus.

In conclusion, open nomenclature ('squat burrows') is to be preferred for indicating the broad morphospace that includes these burrows. Similar problems were pointed out by De (2005) for ocypodid crab burrows of the Bengal coast.

Tracemaker: *Carcinus maenas* (Crustacea: Decapoda).

Ethology: In the study area, this burrow is commonly occupied by a crab male holding a female during precopulatory mate guarding. During breeding season, the male of *Carcinus maenas* guards the female several days before mating, defending her against predators and other male competitors (Hardege and Terschak, 2011). For this reason, 'squat burrows' are likely to be mating burrows.

4.3.2. *Macanopsis*

Description: unbranched burrows with a characteristic lower clavate chamber and a convolute, tapered neck (Fig. 6A). Conical piles of sediment (0.5–0.8 cm in diameter) are present in correspondence of the burrow entrance, which is usually concealed. Burrow penetration ranging between 2 and 7 cm.

The presence of a rounded base apparently recalls the ichnofamily Celliformidae (Genise, 2004), but the Grado structures are less regular in shape, present tunnels ('necks'), and do not show spiral closures (Genise, pers. com.). The observed structures are more fitting with the ichnogenus *Macanopsis*, consisting of a straight or slightly bent burrow enlarging to hemispherical hollow (Häntzschel, 1975).

Tracemaker: *Heterocerus flexuosus* (Insecta: Coleoptera).

Ethology: These burrows are linked with the life cycle of heterocerid beetles, as puparia, pupae and adults are commonly found within the burrows (Baucon, 2008). Laminated microbial mats are a source of food, as beetles feed on algae, zooplankton and organic debris (Evans and Hogue, 2006).

4.4. *Plug-shaped structures*

4.4.1. *Bergaueria*

Description: rounded plug-shaped depressions. Diameter 3–5 cm. General morphology is consistent with the ichnogenus *Bergaueria*, consisting of cylindrical or baglike burrows with rounded ends (Häntzschel, 1975).

Tracemaker: sea anemones, including *Cereus* (Cnidaria: Sagartiidae), *Condylactis* and *Anemonia* (Cnidaria: Actiniidae).

Ethology: In the study area, *Bergaueria* is a domichnial structure produced by anemones (Fig. 7). The tracemakers are opportunistic omnivorous suspension feeders (Chintiroglu and Kokouras, 1996).

4.5. *Winding structures*

4.5.1. *Helminthoidichnites*

Description: unbranched horizontal, curved burrows with circular cross-section (diameter: 1 mm). Burrows develop in parallel respect to lamination and maintain a predominantly constant depth. Openings usually concealed, loops very rare. These features are characteristic of the ichnogenus *Helminthoidichnites* (i.e., Uchman et al., 2005).

Tracemaker: Dipteran larvae (Insecta: Diptera).

Ethology: These traces accurately follow the interface between the organic-rich and the mineral-rich layer of microbial mats (Fig. 6B). Consequently, it is likely to assume an undermat mining behaviour, typical of Precambrian to recent microbial mats (Seilacher, 1999; Gerdes, 2003).

4.6. *Simple burrows*

4.6.1. *Skolithos form L (large)*

Description: Open, vertical burrow composed by (1) an upper, short shaft presenting an 8-shaped cross-section and (2) a longer lowermost part, elliptical in section, usually extending for more than 15 cm. Similar bivalve-produced structures include *Siphonichnus* (Gingras et al., 2010) and *Teichichnus* (Bromley, 1996, p. 69), although predominant morphological features are more compatible with the ichnogenus *Skolithos*. In fact the structure is straight, mostly of uniform diameter and do not display evidence of spreite.

Tracemaker: *Solen marginatus*, *Ensis ensis*, *Ensis minor* (Mollusca: Bivalvia).

Ethology: The tracemakers of *Skolithos* L are suspension-feeders, capable of rapid burrowing when threatened (Little, 2000).

4.6.2. *Skolithos form M (medium)*

Description: Straight vertical burrow with constructional lining made of mucus-bound sand grains. Burrow section circular, penetration depth 10 – 15 cm. General morphology is fully consistent with the ichnogenus *Skolithos* (Häntzschel, 1975).

Tracemaker: *Megalomma* sp. (Annelida: Polychaeta).

Ethology: The tracemaker *Megalomma* possesses specialized feeding structures, consisting of ciliated tentacles (radioles) for capturing suspended particles (Dame et al., 2001; Fig. 8). Several compound eyes are present at the tips of the ciliated radioles and serve as a photosensitive alarm. In fact the tracemaker responds to shadows by rapidly retreating inside its domicnial burrow (Video 4).

4.6.3. *Skolithos* form S (small)

Description: simple, vertical burrows with very low diameter/height ratio. Usually, vertical extension ranges between 3 and 7 cm, while burrow diameter is less than 1 mm. General form is strongly reminiscent of the ichnogenus *Trichichnus*, but the studied burrow lacks of the diagnostic walls described by Häntzschel (1975). Consequently, the structure is attributed to the ichnogenus *Skolithos*, although its characteristically small diameter approaches the boundary of the realm of cryptobioturbation.

Tracemaker: worm-like organisms, possibly annelids and nematodes.

Ethology: Vertical burrows are commonly associated to suspension-feeding, but they are produced also by carnivores, deposit and detritus feeders (Bromley, 1996: p. 200).

4.6.4. *Skolithos* form XS (very small)

Description: vertical, unlined cylindrical burrow penetrating for 1–5 cm. Burrow diameter 1 mm. According to the straight, vertical geometry, this trace belongs to the ichnogenus *Skolithos*.

Tracemaker: *Talitrus saltator* (Crustacea: Amphipoda).

Ethology: During the day the tracemaker inhabits its burrow, emerging at night for feeding on

stranded macroalgal detritus (Williams, 1983). Therefore, the burrow may be interpreted as a shelter against desiccation.

4.6.5. *Monocraterion*

Description: vertical, cylindrical tunnels with a funnel-shaped opening at the top of the burrow. Burrow diameter 0.5–1 cm, vertical extension up to 10 cm. These morphological features are diagnostic of the ichnogenus *Monocraterion* (Häntzschel, 1975). It should be noted that this ichnogenus can be potentially confused with the vertical shafts of *Thalassinoides* L, also presenting a characteristic funnel-like opening.

Tracemaker: undetermined annelid.

Ethology: Most probably, this trace is a domiciliary burrow of a suspension-feeder. Nevertheless, it should be noted that vertical morphology is consistent with several trophic functions, including suspension, deposit, detritus and carnivore feeding (Bromley, 1996: p. 200).

4.7. *Tracks and footprints*

4.7.1. *Avipeda*-/*Ardeipeda*-like footprints

Description: broad morphospace including footprints with three digits directed forward; additional features include claw marks, hallux and webbing imprints. Trace width: 5–13 cm. Morphological features resemble known avian ichnotaxa, primarily *Avipeda* and *Ardeipeda*. Nevertheless, avian ichnotaxonomy is still in flux (Lockley et al., 2007), therefore open nomenclature is used.

Tracemaker: *Ardea cinerea*, *Egretta garzetta* (Aves: Ardeidae), *Larus michahellis* (Aves: Laridae).

Ethology: These structures are produced during locomotion.

4.7.2. *Canipeda*

Description: tetradactyl footprints with a distinctive heel pad. Trace width: 5–13 cm.

Tracemaker: *Canis lupus familiaris* (Mammalia: Canidae).

Ethology: These structures are produced during dog locomotion.

4.7.3. 'Parallel furrows'

Description: sets of parallel, elongated furrows. Furrow width: 1–3 mm; trace width: 3–5 cm

Tracemaker: *Carcinus maenas* (Decapoda: Brachyura).

Ethology: These traces are produced by green crabs during sideward locomotion (Video 5).

4.8. Trails

4.8.1. *Archaeonassa*

Description: horizontal trail consisting of a median furrow flanked by two lateral ridges (Fig. 9A). Trace width: 2–3 cm. Based on general morphology, these structures are assigned to the ichnogenus *Archaeonassa* (Häntzschel, 1975).

Tracemaker: *Bolinus brandaris* and *Hexaplex trunculus* (Gastropoda: Muricoidea) are the most conspicuous producers of *Archaeonassa*. Other known tracemakers are *Cerithium vulgatum* (Gastropoda: Cerithiidae), *Pirenella conica* (Gastropoda: Potamididae), *Sphaeronassa mutabilis* and *Nassarius nitidus* (Gastropoda: Nassariidae).

Ethology: In the study site, *Archaeonassa* is related to locomotion behaviour of gastropods, independently of their feeding strategy (Video 6). However, the most representative tracemakers are carnivorous muricids.

4.8.2. *Nereites biserialis*

Description: winding trails constituted by a furrow flanked on both sides by lobes (Fig. 9B). Trail width: 1–3 cm. The presence of a central furrow and lateral reworked zones is characteristic of nereitids (Seilacher, 2007). More specifically, the arrangement of lobes coincides with the ichnospecies *Nereites* (= *Neonereites*) *biserialis* (Mángano et al., 2002; Seilacher, 2007).

Tracemaker: hermit crabs, probably *Pagurus* (Decapoda: Paguridae), inhabiting oblong shells.

Ethology: Traditionally, two models have been proposed for *Nereites*:

1. in the ‘worm model’, *Nereites* is a feeding burrow produced by worm-like organisms, probing and backfilling laterally (Seilacher, 2007)
2. in the ‘arthropod model’, the characteristic lobes are pressure-release structures made by arthropod legs. According to this interpretation, *Nereites* is a locomotion trail (Martin and Rindsberg, 2007).

In the study site, tracemaker identity and behaviour fits with the ‘arthropod model’.

Furthermore, there is a strong relationship between lobe arrangement and shell shape. In fact, biseriate *Nereites* are produced by hermit crabs occupying oblong shells (i.e. *Cerithium*). In contrast to *Nereites biserialis*, the uniseriate form (*Nereites uniserialis*) is related to crabs inhabiting trochiform shells, such as the top shaped *Gibbula* (section 4.8.3). This aspect shows that hermit crab locomotion is affected by shell shape.

4.8.3. *Nereites uniserialis*

Description: winding trails consisting of a furrow flanked by a single row of lobes (Fig. 9C).

Trail width: 0.8–3 cm. General morphology is consistent with nereitids, while the single row of lobes is diagnostic of *Nereites* (= *Neonereites*) *uniserialis* (Mángano et al., 2002; Seilacher, 2007).

Tracemaker: hermit crabs, probably *Pagurus* (Decapoda: Paguridae), inhabiting trochiform shells.

Ethology: The here studied *Nereites uniserialis* is the locomotion trace of a hermit crab, matching the ‘arthropod model’ described by Martin and Rindsberg (2007). In contrast to the roughly symmetric *Nereites biserialis*, *Nereites uniserialis* is produced by hermit crabs occupying trochiform shells. As discussed in section 4.8.2, this ichnological evidence reflects how the locomotion of hermit crabs is affected by shell shape.

4.9. Miscellaneous group

4.9.1. ‘Diverging shafts’

Description: vertical V-shaped tunnels with circular cross-section. Tunnels diverge from a larger structure, usually represented by a curved cylindrical burrow (Fig. 10A). In this case, burrow morphology and tracemaker coincides with *Solecurtus* burrows (Dworschak, 1987b), which are commonly accompanied by *Teichichnus*-like structures (Bromley, 1996). In other cases, tunnels diverge from an almond-shaped burrow, corresponding to the ichnogenus *Lockeia* (sections 4.9.2 and 4.9.3; Fig. 10B).

These V-shaped traces are reminiscent of the ichnogenus *Siphonichnus*, consisting of vertical tubes cutting backfilled laminae (Carmona et al., 2009). Nevertheless, backfilled laminae have never been discerned unequivocally in the study site, therefore open nomenclature is preferred.

Tracemaker: *Abra alba*, *Donax trunculus*, *Solecurtus* sp., *Venus* sp. (Bivalvia: Veneroida)

Ethology: these structures represent siphon traces of suspension-feeding bivalves.

4.9.2. *Lockeia* form S (small)

Description: almond-shaped burrow with smooth, rounded margins. Burrow depth usually ranging between 3 and 5 cm. The almond-shaped part is commonly connected to the surface by a single tapered shaft (diameter: 0.3 – 0.7 cm) or by two thin arcuate branches (diameter: 1–2 mm; Fig. 10B, C). According to Schlirf et al. (2001), the almond-shaped part closely resembles the ichnogenus *Lockeia*. The connections to the surface are reminiscent of the ichnogenus *Siphonichnus*, as illustrated in Gingras et al. (2010, their Figure 5).

Tracemakers: *Mactra corallina*, *Venus* sp., *Venerupsis philippinarum* (Bivalvia: Veneroida)

Ethology: The observed *Lockeia* are resting traces produced by suspension-feeding bivalves, while the *Siphonichnus*-like structures are produced by the siphons of the tracemakers (section 4.9.1).

4.9.3. *Lockeia* form XS (very small)

Description: almond-shaped burrow connected to the surface by two elongate segments.

Branches irregular, very thin (<1 mm) and poorly defined. Burrow depth usually less than 3 cm. The almond-shaped structure is consistent with the ichnogenus *Lockeia*, while the branched segments resemble *Siphonichnus* (Schlirf et al., 2001; Gingras et al., 2010).

Tracemaker: *Abra alba*, *Donax trunculus* (Bivalvia: Veneroidea)

Ethology: *Lockeia* is the resting trace of suspension-feeding bivalves, whose siphons leave the *Siphonichnus*-like structures (section 4.9.1).

4.9.3. Mottling

Description: intense, indistinct bioturbation resulting in a massive lumpy texture, occasionally intersected by convolute patches of varying colour. Physical sedimentary structures not discernible.

Tracemaker: marine phanerogams, primarily *Zostera marina*, *Zostera noltii* and *Cymodocea nodosa* (Magnoliophyta: Najadales), followed by *Posidonia oceanica* in the shallow subtidal. *Nereis diversicolor* (Anellida: Polychaeta), *Echinocardium cordatum* (Echinodermata: Spatangoida), *Asterina gibbosa* (Echinodermata: Asteroidea), *Bolinus brandaris*, *Hexaplex trunculus* (Gastropoda: Muricoidea) and other animal tracemakers may significantly contribute to the amount of biogenic reworking (Fig. 11).

Ethology: general sediment disruption is produced by roots of marine phanerogams, accompanied by polychaetes passing through water-saturated sediments. Polychaete-related mottling resemble the ‘mantle and swirl’ traces described by Lobza and Schieber (1999).

5. Discussion

Overall, the studied ichnofauna is characterized by dominance of boxworks, vertical and U-shaped burrows (i.e. *Thalassinoides*, *Skolithos*, *Arenicolites*). Horizontal trails (*Archaeonassa*, *Nereites*) and chambered burrows (*Macanopsis*) are locally abundant, while ichnodiversity is moderate. These features are consistent with the *Skolithos* and *Cruziana* ichnofacies, and similar

characteristics have been recognized in other tidal (i.e. Garrison et al., 2007) and barrier-island systems (i.e. Hauck et al., 2009).

Although this study is at a qualitative stage, data suggest that characteristic patterns emerge at finer scales of observation. In fact, sediment barriers impose a sharp contrast in terms of environmental variables, feeding strategies and ichnological composition. The sheltered back-barrier is characterized by low-energy conditions, high bioturbation intensity, large deep-tier boxworks (i.e. *Thalassinoides*). Deposit-feeding is the dominant trophic strategy. On the other hand, the fore-barrier exhibit inverse characteristics: higher energy, lower bioturbation intensity, smaller and shallower burrows.

Notably, sediment texture and depth of the redox potential discontinuity show lower oxygen conditions in the fore-barrier. This evidence is contrasting with the majority of the oxygenation models, which suggest that higher oxygen levels support higher bioturbation, larger burrows and deeper tiering (see the reviews in Martin, 2004 and Buatois and Mángano, 2011).

The Mula di Muggia paradox (Fig. 12) is explained by a complex relationship involving hydrodynamics, interstitial oxygen and nutrient availability. Interstitial oxygenation is controlled by sediment permeability, which affects the depth of the redox potential discontinuity. Therefore, interstitial oxygenation depends from grain size which, in turn, is controlled by hydrodynamics (see Raffaelli and Hawkins, 1996: p. 20-23). Sheltered, fine substrates, with their reduced permeability and hence dominating anaerobic chemistry, are optimal for many tracemakers because of their quiet hydrodynamics. Indeed, such low-energy settings offer abundant organic matter and low mechanical stress. Not surprisingly, the major groups of intertidal tracemakers are adapted to dysoxic, sulphide-rich environments: *Corophium* (author of *Arenicolites* S), thalassinidean shrimps (tracemakers of *Thalassinoides* and *Parmaichnus*) and *Nereis diversicolor* (responsible for *Polykladichnus*) (Gamble, 1971; Kristensen, 1983; Johns et al., 1997).

The example from Grado evidences that, if the water column is sufficiently oxygenated, low-oxygen settings favour intense bioturbation with large and deep burrows. This conclusion supports the model of Ekdale and Mason (1988) which considers the relationship between water column and pore-water oxygenation.

In light of these observations, the ichnological contrast between fore- and back-barrier can be considered a signature of barrier-island systems, because it reflects environmental, ecological and sedimentological features proper of these depositional environments. In fact, following Otvos (2012), the essential feature of sediment barriers is their protective function, which impose a shore-parallel boundary between inshore and open marine conditions.

6. Conclusions

This study portrayed the ethological complexity of a barrier-island system through the description of individual ichnotaxa. Consequently, the importance of this research relies in the autecology of bioturbation within a neoichnologically understudied environment. This approach provides a rich source of information for interpreting trace fossils and palaeoenvironments.

In this regard, the studied ichnotaxa allow ‘geological analogies’, such that a fossil evidence can be compared to phenomena already known (Baker, in press). This philosophy is exemplified by the brachyuran-related *Nereites*, serving “not much to provide definitive explanations as to provide a source for hypotheses that move geological research into productive lines of inquiry” (Baker, in press). The same perspective can be applied to other findings of this research, such as the fore-/back-barrier dichotomy and the inverse relation between oxygenation and bioturbation intensity.

Nevertheless, many questions remain unanswered. How are traces distributed in space? What are the mutual relationships between ichnotaxa? What are the environmental mechanisms regulating ichnoassociation patterns?

For these reasons, there is a need for synecological records from the Mula di Muggia system, which will be quantitatively tackled in future studies (i.e. Baucon and Felletti, 2013). To this end, the present autecological perspective is both the prerequisite and the complementary step for understanding the ichnological system as a whole.

Acknowledgments

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Solecurtus burrows.

Figures

Fig. 1. Geographical and geological setting.

Fig. 2. The Mula di Muggia separates the back-barrier from the open sea. Photo location in Fig. 1.

Fig. 3. Main geomorphological domains. (A) The sheltered back-barrier is characterized by muddy sands and biomats. (B) The fore-barrier is characterized by higher hydrodynamics and by numerous subtidal bars, one of which is evidenced by the dashed line. Photo location in Fig. 1.

Fig. 4. Branched structures. (A) Muddy sands with *Parmaichnus* (Pa) and *Arenicolites* (Ar). Profile view. (B) *Polykladichnus* burrow within a laminated microbial mat. The burrow system changes from vertical to horizontal in correspondence of the organic-rich horizon (Or) of the biomat. (C) *Polykladichnus* with its tracemaker, the polychaete *Nereites* (Ne). Note also the amphipod *Corophium* (Co) within a U-burrow. Profile view.

Fig. 5. U-shaped structures. (A) Openings of *Arenicolites* L. Most of the fecal casts have been washed out by waves, but the radial geometry is still manifest. Top view. (B) *Arenicolites* S with its tracemaker (Tr), the amphipod *Corophium*. Sediment-water interface (Sw) colonized by filamentous algae. Profile view.

Fig. 6. Simple and chambered structures. (A) *Macanopsis* (Ma) is commonly associated with intertidal microbial mats, constituted by an upper, organic rich layer (Or) and a lower, mineral rich one. Note the tracemaker of *Macanopsis*, an heterocerid coleopteran (Co). Profile view. (B) *Helminthoidichnites* is produced by dipteran larvae (He) while feeding beneath the organic-rich layer (Or) of intertidal biomats. Profile view.

Fig. 7. Plug-shaped structures. (A) Top view of an actinian anemone, producer of *Bergaueria*. (B) *Cereus* is among the commonest producers of *Bergaueria*. Top view; photo location in Fig. 1.

Fig. 8. *Skolithos* M. The suspension-feeding polychaete *Megalomma* produces vertical burrows, corresponding to the ichnogenus *Skolithos*. Photo location in Fig. 1.

Fig. 9. Trails. (A) An algae-covered gastropod producing *Archaeonassa*. (B) *Nereites biserialis*

produced by hermit crab with oblate shell (*Cerithium*). Furrows (f) and lobed ridges (l) highlighted. (C) Hermit crab with globose shell producing *Nereites uniserialis*. Furrows (f) and lobed ridge (l) highlighted. Photo location in Fig. 1.

Fig. 10. Bivalve traces. (A) Openings of the *Solecurtus* burrow. Following Dworschak (1987a), the larger opening correspond to the inhalant siphon (i), the smaller one to the exhalant siphon (e). Top view. (B) The bivalve *Maetra* produces an almond shaped-burrow (*Lockeia*) connected to the surface by a single shaft. Profile view. (C) The bivalve *Veneropsis* produces *Lockeia* and two ‘diverging shafts’. Profile view.

Fig 11. Sediment disturbance structures. (A) Bioturbating gastropod. (B) A sea star, probably *Asterina gibbosa*, partially buried into the sand.

Fig. 12. Inverse relationship between oxygenation and bioturbation. Maximum tiering depth, bioturbation intensity, burrow size expressed as relative values. Redox potential discontinuity depth (RPD) is shown by the dashed line.

Videos

Video 1. Environmental setting of the back-barrier. Sheltered conditions allow suspension and settling of fine sediment particles. Consequently, the back-barrier is dominated by muddy sands, commonly colonized by seaweed meadows. Note the sediment mound, corresponding to a *Thalassinoides* burrow system.

Video 2. Environmental setting of the fore-barrier. Wave action interacts with the seafloor producing widespread ripples and abundant shell debris.

Video 3. Ichnological features of the back-barrier, filmed at high and low tide. Sediment mounds and a decapod tracemaker (?*Upogebia*) are visible.

Video 4. The polychaete *Megalomma* protrudes from its *Skolithos* burrow for capturing suspended particles. The tracemaker can rapidly retract inside its burrow.

Video 5. Crab locomotion and related tracemaking mechanisms.

Video 6. Intertidal gastropods producing *Archaeonassa*.

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Morphological class	Ichnotaxon	Geomorphological domain	
		Fore-barrier	Back-barrier
BRANCHED STRUCTURES	<i>Thalassinoides XL</i>		***
	<i>Thalassinoides L</i>	*	*
	<i>Parmaichnus</i>	*	**
	<i>Polykladichnus</i>		***
U-BURROWS	<i>Arenicolites XL</i>	**	
	<i>Arenicolites L</i>	***	*
	<i>Arenicolites S</i>	*	**
CHAMBERED BURROWS	'Squat burrow'		**
	<i>Macanopsis</i>		**
PLUG-SHAPED BURROWS	<i>Bergaueria</i>	*	
WINDING STRUCTURES	<i>Helminthoidichnites</i>		*
SIMPLE BURROWS	<i>Skolithos L</i>	**	
	<i>Skolithos M</i>	**	
	<i>Skolithos S</i>	**	*
	<i>Skolithos XS</i>	*	*
	<i>Monocraterion</i>	**	
TRACKS AND FOOTPRINTS	<i>Avipeda-/Ardeipeda-like</i>	*	*
	<i>Canipeda</i>	*	*
	Parallel furrows	*	*
TRAILS	<i>Archaeonassa</i>	**	**
	<i>Nereites biserialis</i>	**	
	<i>Nereites uniserialis</i>	**	
MISCELLANEOUS GROUP	'Diverging shafts'	**	**
	<i>Lockeia S</i>	**	**
	<i>Lockeia XS</i>	*	**
	<i>Mottling</i>		**

Table 1. Qualitative abundance of ichnotaxa with respect to geomorphological domains: *** = very common, ** = common, * = occasional presence

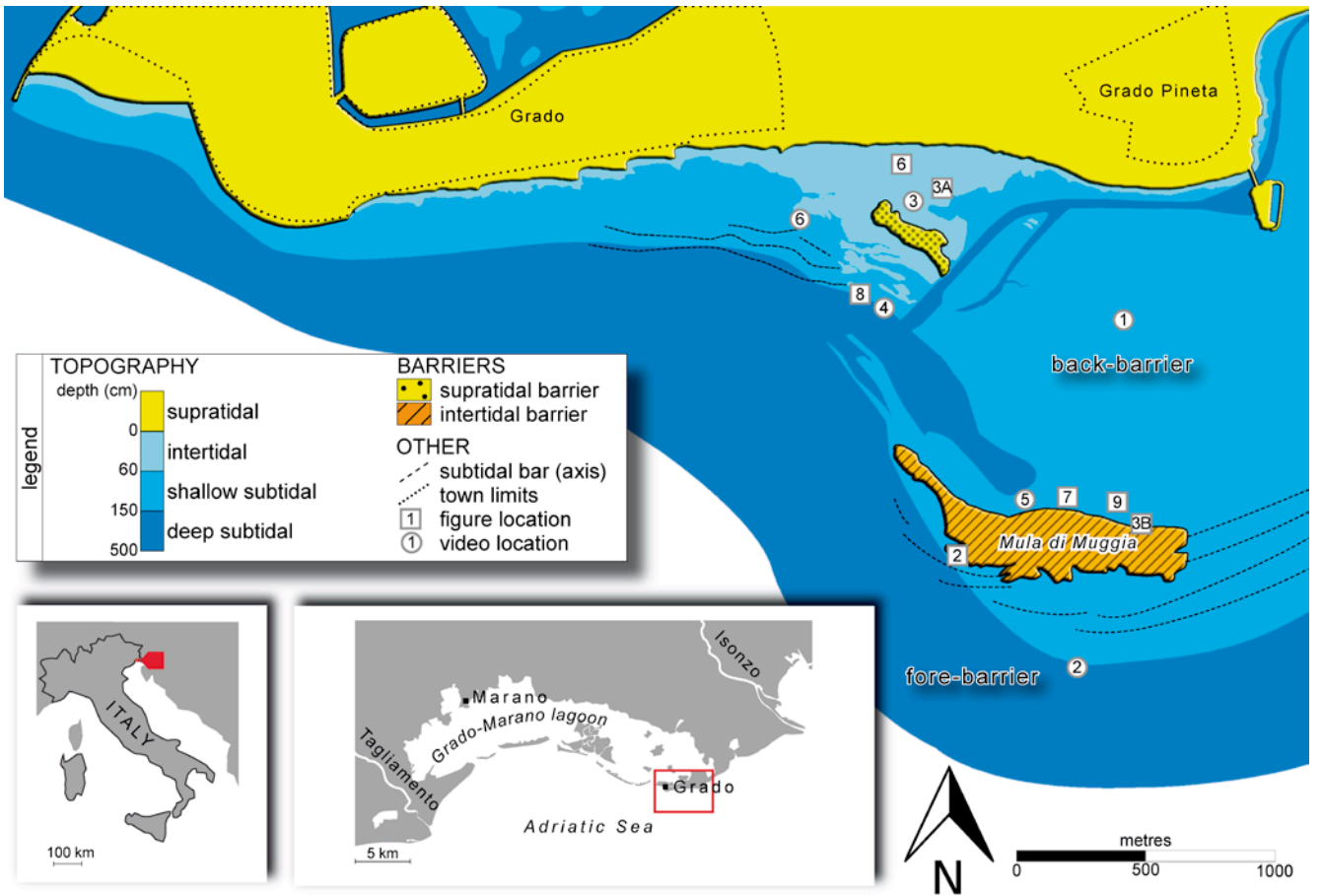


Fig. 1.



Fig. 2.



Fig. 3.

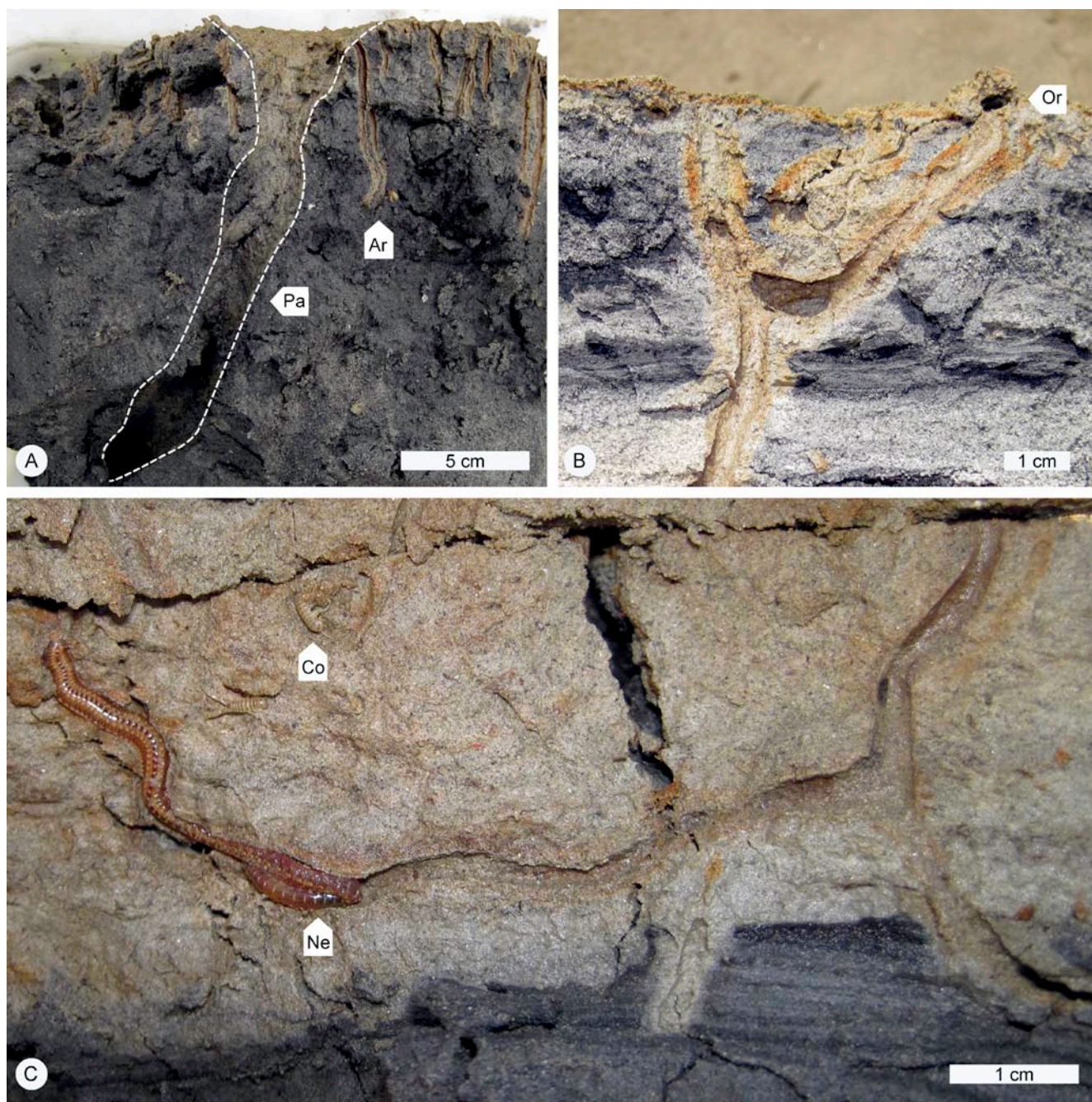


Fig. 4.



Fig. 5.



Fig. 6.

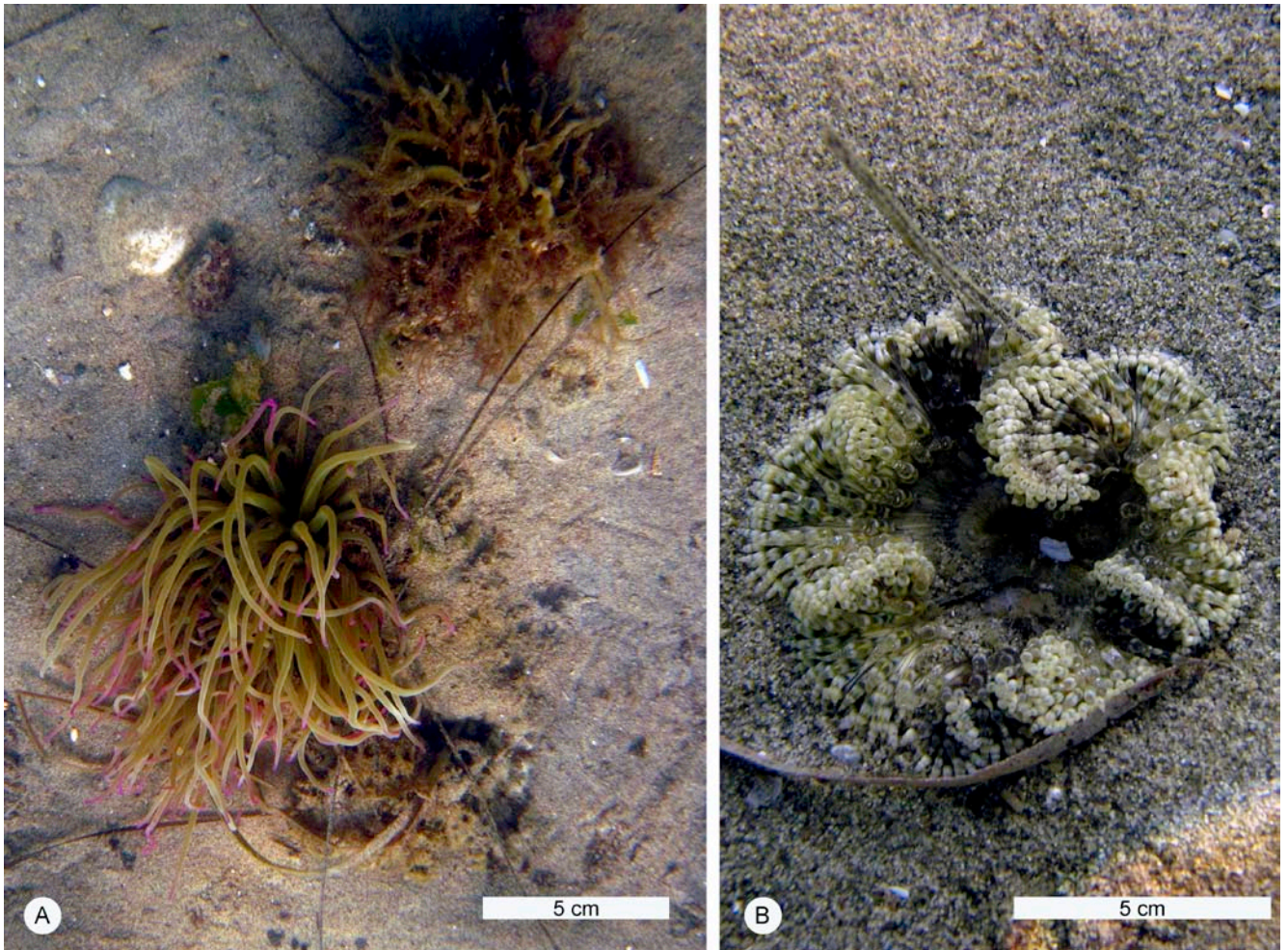


Fig. 7.



Fig. 8.

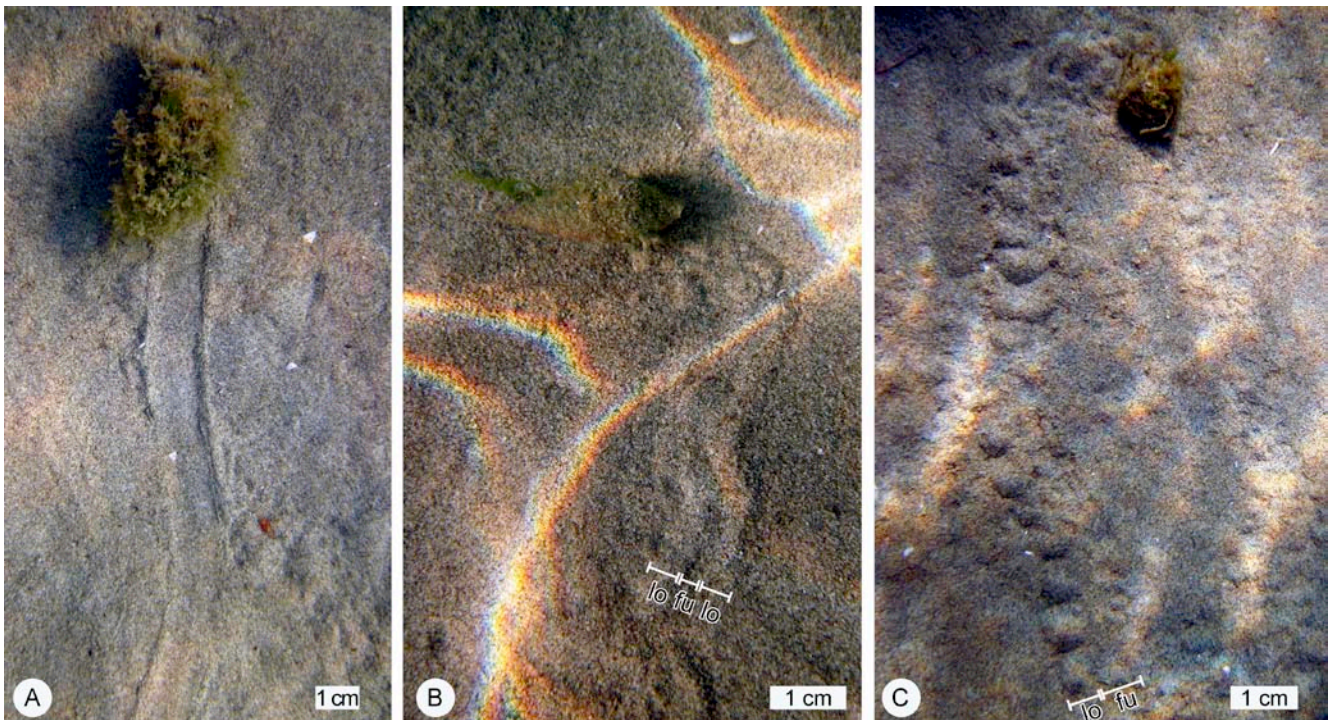


Fig. 9.

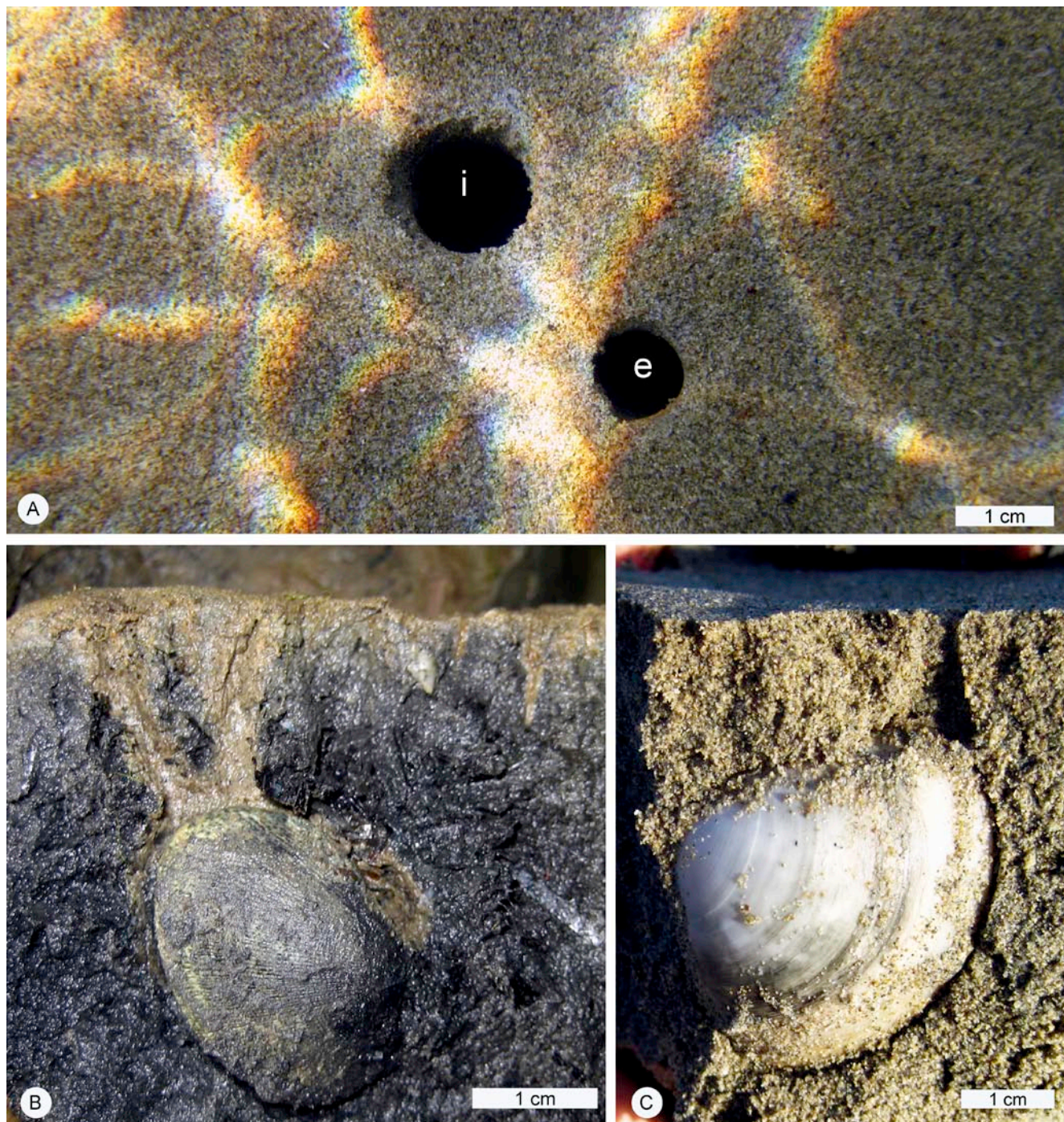


Fig. 10.

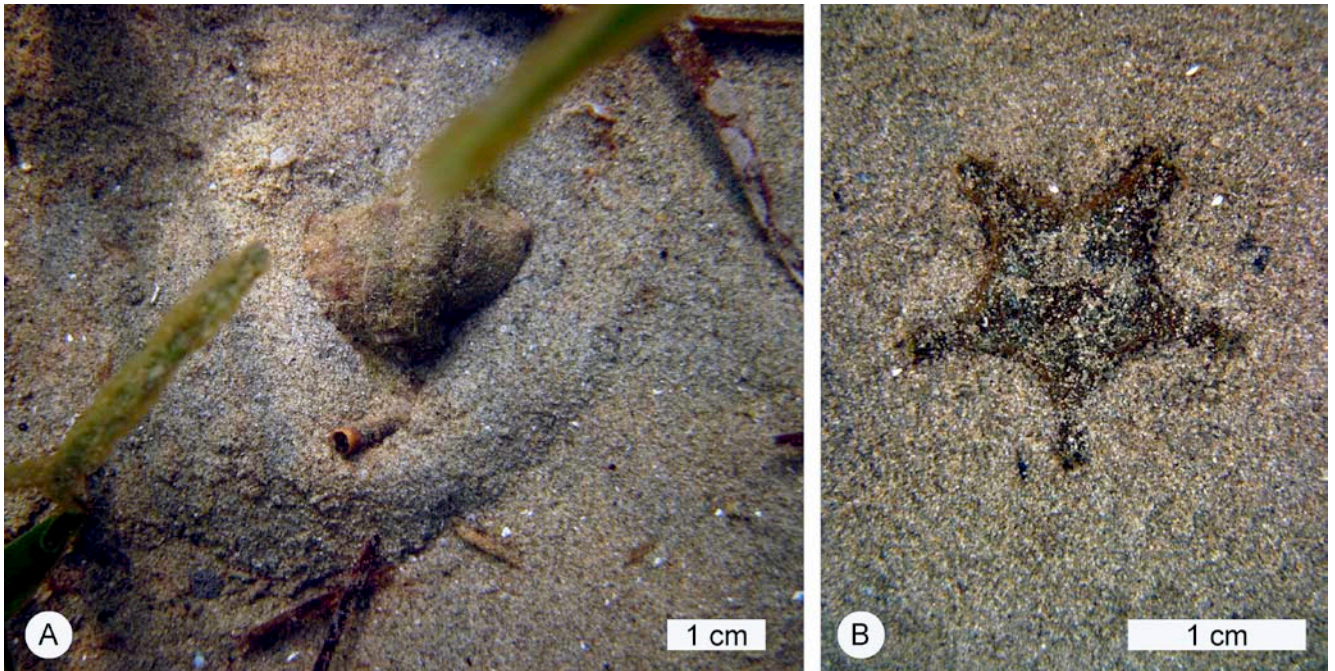


Fig. 11.

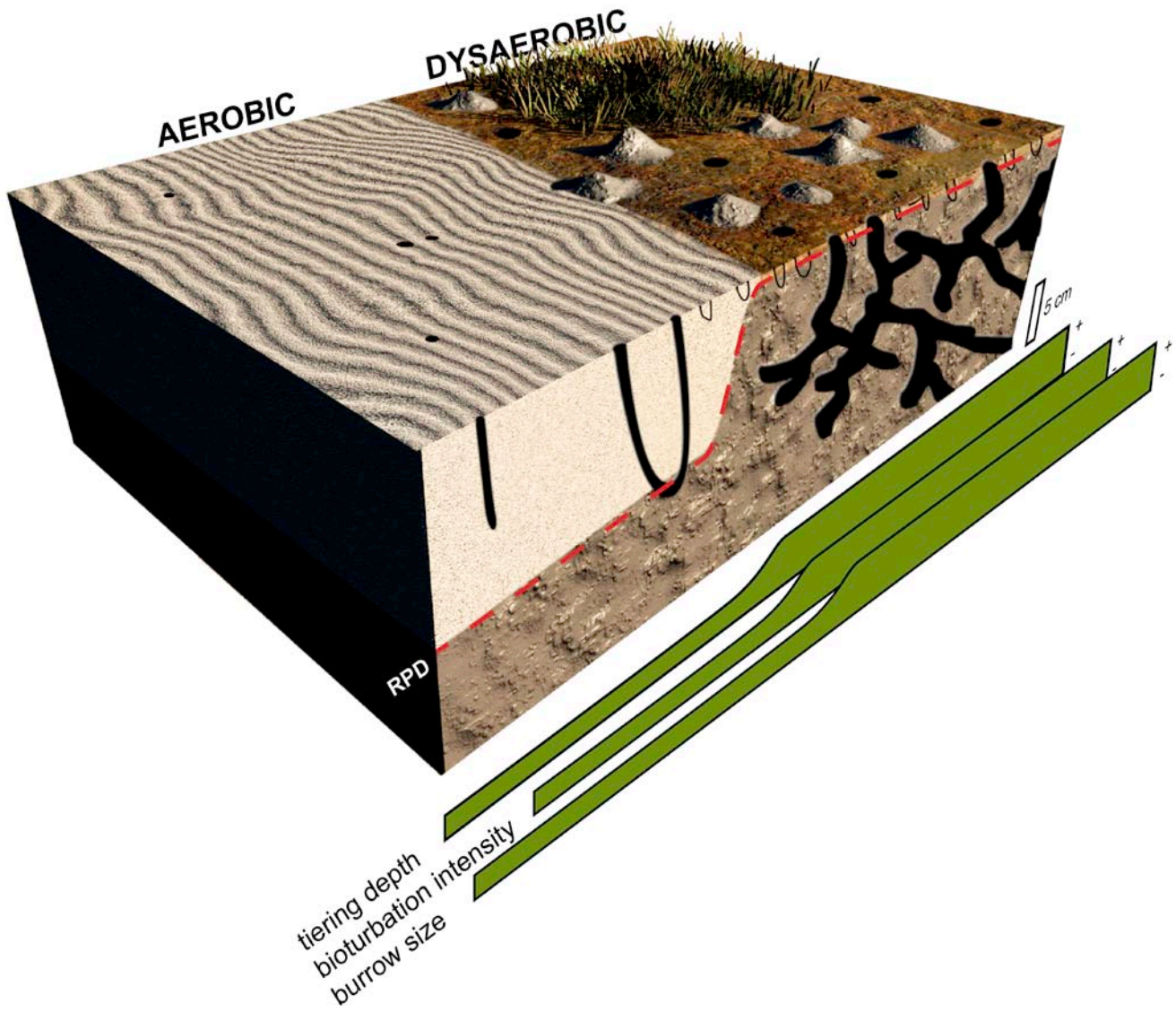


Fig. 12.

Chapter 3

3.2 The IchnoGIS method: Network science and geostatistics in ichnology. Theory and application (Grado lagoon, Italy)

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Full paper in Appendix D

The IchnoGIS method: network science and geostatistics in ichnology. Theory and application (Grado lagoon, Italy)

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ABSTRACT

A new method is proposed for capturing, managing, analyzing, and displaying geographically referenced ichnological data: IchnoGIS. This approach is based on the integration of spatial, geostatistical techniques with network theory, aiming to characterize the environmental significance of recent traces. The efficiency of the IchnoGIS method is tested against a case-study: the Grado lagoon (Italy). The studied site, located within the epeiric Northern Adriatic Sea, consists of a complex mosaic of peritidal environments in a barrier-island context. Here, a diverse ichnofauna includes the following incipient ichnotaxa: *Arenicolites*, *Helminthoidichnites*, *Lockeia*, *Macanopsis*, *Monocraterion*, *Parmaichnus*, *Polykladichnus*, *Skolithos*, *Thalassinoides* and ‘squat burrows’. Ichnofaunal distribution is described by the spatial and geostatistical tools proper of the IchnoGIS approach. Additionally, the application of network theory documents the emergence of organized structures (ichnoassociations) from interactions driven by environmental factors. Our results elucidate the role that environmental processes play in producing the complex ichnological patterns of the Grado site. In particular, emersion time, hydrodynamics, substrate firmness and microbial binding are the major control factors determining the structure and distribution of trace associations. These structuring factors are used to define a predictive model of ichnoassociation composition, providing an immediate tool for future palaeoenvironmental reconstitutions.

Keywords: neoichnology; geostatistics; network theory; Adriatic Sea; geographic information systems; environmental model

1. Introduction

“[a certain species of mollusk] does not swim, but makes a furrow in the sand and proceeds along the furrow’s edges”

- Leonardo da Vinci, Leicester Code, folio 8v

Since its earliest roots in Renaissance times, trace fossil analysis has relied on actualistic experiences for inspiring and testing theories and models. In fact, each of the major watersheds in the history of ichnology was initiated by advances in neoichnological knowledge (Baucon et al., 2012): the palaeoichnological knowledge of Leonardo da Vinci was inspired by modern burrowing and boring organisms (Baucon, 2010), the experiments of Nathorst disproved the botanical interpretation of trace fossils, the Senckenberg Laboratory marked the development of the modern approach in ichnology (Osgood, 1975). In more recent times, Adolf Seilacher’s ethological approach benefited from his studies on modern tidal flats (Cadée and Goldring, 2007), while Robert Frey and the Georgia coast school outlined the palaeoenvironmental significance of trace fossils through the observation of modern ones (Frey and Seilacher, 1980).

Despite these notable landmarks, neoichnology came to a standstill throughout the 1980s and 1990s (Gingras et al., 2011b). With the words of Frey and Seilacher (1980), “the present has been studied considerably less than its importance would dictate”. This scenario is currently exacerbated by the poor integration between marine biology and ichnology, each one with their own nomenclature and literature. As a result, our present models for palaeoenvironmental interpretation still rely on the neoichnological studies of the 1950s, 1960s and 1970s (Gingras et al., 2011b).

With the Internet and GPS among the faster-growing technologies of the decade, the previous historical considerations addresses traditional questions with novel approaches: How are traces distributed in space? What are the association patterns (‘links’) between ichnotaxa? What is the relationship between traces and their environment?

This paper aims to answer to these questions by developing a neoichnological method based on geostatistics and network theory, through which delineate an ichnological model of a mesotidal barrier-island system: the Grado lagoon (Italy) (Fig. 1).

2. Study Area

This study is conducted in the region of the Grado-Marano lagoon, a large transitional system located along the Adriatic coast (Northern Italy; Fig. 1A). In particular, the main target are the intertidal flats of the external margin of the Grado lagoon, located - from west to east - between Grado and Grado Pineta town (Fig. 1B). This area is characterized by significant biodiversity and an integer environment.

Indeed it borders several protected areas recognized by the EU Natura 2000 Network (both habitat and birds directive sites) and the international Ramsar wetland convention (Barbone et al., 2011). The study area is markedly influenced by tides, which are unusually high for the Mediterranean Sea, while climate is temperate (Baucon and Felletti, 2013; Fig. 2).

The sampling area was selected after a preliminary study (Baucon and Felletti, 2013) because it represents widely differing environmental situations, with shoals separating an intertidal back-barrier lagoon from a fore-barrier area (Fig. 1B). Sediments in the back-barrier are dominated by microbial mats and muddy sands, commonly covered by marine phanerogams. Conversely, the fore-barrier shows a dominance of sands and paucity of phanerogams. This configuration, characterized by sediment barriers separating the open sea from a lagoon, makes the area an ideal model for modern and ancient barrier-island systems.

3. The IchnoGIS method

A novel method for neoichnological analysis has been designed for investigating the study area (Fig. 3). Similarly to a geographic information system (GIS), the proposed approach integrates hardware, software, and data for capturing, managing, analyzing, and displaying geographically referenced ichnological data. For this reason, the method has been named 'IchnoGIS'. Its development derived from previous work on the application of GPS and GIS techniques to neoichnology (Baucon, 2008). The present section describes materials and procedures of the IchnoGIS approach through its application to the Grado case study.

3.1. Survey design

The initial step for this study required the definition of the biogenic structures of interest and their correspondence with existing ichnogenera (Table 1). Dominant sedimentary facies were recognized on the basis of texture, colour and sedimentary structures, further refining the classification scheme presented in Baucon (2008) (Table 2). According to practical and logistical considerations, different sampling schemes were adopted for quadrat, trench, environmental and topographical sampling (Table 1).

3.2. *Ichnological and sedimentological sampling*

- Quadrat Sampling: trace abundance is crucial to know how ichnotaxa are distributed in a particular habitat; however, it is usually impossible to count each and every trace present. For this reason, one of the core steps of IchnoGIS is based on quadrat sampling, a method widely used in the interpretation of large ecological data sets with environmental gradients (McIntyre and Eleftheriou, 2005). At each sampling site, a frame of a set size (0.25 m²) was placed on the substrate to determine sedimentological and ichnological attributes occurring within it. In particular, facies type and abundance of each structure of interest (i.e. number of *Arenicolites*) were recorded in conjunction to the spatial coordinates of the sampling site, determined by a GPS unit (Fig. 3). Practical and logistical considerations were unfavourable for adopting a regular sample distribution, therefore nearest neighbour analysis (Borradaile, 2003) was iteratively used to test sampling randomness (section 3.4). A total of 2622 samples were analyzed between June and September 2010 (Table 1).

- Trench sampling: quadrat sampling emphasizes the recognition of distinct structures on the sediment surface, being unsuitable for burrows with poorly visible openings. Consequently, quadrat sampling was complemented by the study of vertical trenches, realized at regularly spaced sites (spacing: 5 m). 13 transects perpendicular to the coast were conducted to obtain sufficient material for analysis (619 sampling sites). Spatial coordinates of each sampling site were recorded, in conjunction with facies type and presence/absence of studied traces (Fig. 3).

3.3. *Environmental and topographical sampling*

- Environmental sampling: representative sampling sites were selected for estimating water and sediment properties. Measured parameters include: pH, Reduction Potential (Eh), nutrients (nitrite, nitrate, phosphate) and salinity. These measurements were conducted both for the water column and interstitial water (Table 1). Sediment properties include depth of the Redox Potential Discontinuity Layer (Fenchel and Riedl, 1970) and substrate firmness, measured with the modified Brinell method (Gingras and Pemberton, 2000). Emersion time was measured by monitoring 19 sites during a complete tidal cycle.

- Topographical sampling: major topographic features were mapped by GPS unit. Bathymetry of 237 sites was obtained by subtracting the tidal influence from the water depth, measured with a metrestick. Tidal influence was derived from the mareograph of ISPRA Venice (recording frequency: 10 minutes).

- Significance test: nearest neighbour analysis was used to test assess the quality of quadrat sampling. This method compares the average site separation with the average separation of randomly distributed sites (Borradaile, 2003). As concerns sampling scheme, nearest neighbour analysis revealed a significant tendency to randomness (nearest neighbour index: 0.78), sufficient for a coherent data analysis.

3.5. *Data visualization and analysis*

In order to explore the relationship between traces and their environment, a defined set of mathematical and graphical techniques were applied for visualizing and analyzing the data collected. This section presents the mentioned techniques, organized according to their target of investigation:

- Spatial organization: point maps were selected for visualizing trench sampling data. As concerns quadrat sampling, a geostatistical approach based on kriging estimation (Matheron, 1962) was applied for interpolating the number of traces at unsampled positions. Among the major interpolation techniques, kriging is well-suited for irregularly distributed sampling sites (Conolly and Lake, 2006; dell’Arciprete et al., 2012) such as our data. This technique uses a

variable to weight the contribution of known values on a given location, based on the assumption that more distant observations have decreasing influence on its estimate (Matheron, 1962; Borradaile, 2003; Conolly and Lake, 2006; Felletti et al., 2006). For this reason, kriging is preceded by an analysis of the spatial structure of the data (variogram analysis; Fig. 4), which is integrated into the weighting procedure (Wackernagel, 2003). More precisely, it is required to define a model variogram (i.e. theoretical variogram) to fit the empirical variogram (i.e. experimental variogram). The variogram analysis of studied variables (i.e. the number of traces per sampling unit) quantifies the lateral correlation length of each sample separated by a distance h (usually called the *lag* distance). Variograms are usually described using two parameters: (a) the *range* is the lag distance at which all successive values are independent from each other; (b) the *sill* is the variogram value corresponding to the range. These parameters constitute one of the strongest constraints in the geostatistical analysis and, depending on their behaviour, they can reveal several spatial characteristics such as continuity, anisotropy, zone of influence, and the trends. Therefore variogram analysis was used as a descriptive tool for discerning the following spatial features (Fig. 4A):

1. **Small scale variability:** a sudden jump at the origin, termed nugget effect, usually mean that the studied variable (i.e. *Arenicolites* density) is characterized by small-scale fluctuations (Matheron, 1962; Caers, 2011).
2. **Spatial correlation:** the presence of a nugget effect does not necessarily correspond to erratic behaviour at all scales. In fact, the rate of increase of the variogram indicates how quickly the influence of a sample drops off with distance (Matheron, 1962; Armstrong, 1998).
3. **Zone of influence:** the mentioned increase could flatten off at a given separation distance, marking the range of the variogram (Matheron, 1962; Caers, 2011). When the variogram stabilizes on a 'plateau' (sill), there is no longer influence (correlation) between samples. Consequently, the range determines the maximum distance of sample-to-sample influence (Zuur et al., 2007).

4. Structure: a variogram can be characterized by other features, such as a bump (corresponding to a hole in the covariance), a ‘peaks-and-valleys’ shape (diagnostic of periodicity) and nested structures (significant of variations at different scales; Matheron, 1962; Sarma, 2009).

- Ichnoassociation composition: network theory (Réka and Barbási, 2002) was used to discern and explore patterns of association. This emerging scientific area, considered as “the new flag of the complexity sciences” (Bascompte, 2007), focuses on systems constituted by interconnected entities. In particular, network theory was applied to ichnoassociation analysis, based on the assumption that ichnotaxa assemble in complex weblike structures (‘ichnological networks’). Despite its vast employ in information science and ecology (May, 2006; Montoya et al., 2006; Bascompte, 2007) network analysis is a new field of application in ichnology and palaeontology as well. For this reason, theory and application of ichnological networks are more thoroughly discussed in section 6.

- Ichnoassociation-environment relationship: one of the crucial goals is to describe the influence of the environment on the numbers and types of traces. In analogy with Legendre (2005), this aim was achieved by finding the ecological requirements common to most or all members of an ichnoassociation. In order to reach this aim, regularities were searched in the environmental parameters coupled to each ichnoassociation, typifying the most recurrent properties. The results were used to define a predictive model based on the major structuring processes of ichnoassociation composition and distribution.

4. Facies and environment

Within the study area, 7 sedimentary facies were recognized and mapped (Fig. 5). These were defined on the basis of texture, colour and primary physical sedimentary structures (Fig. 6). Each facies represents various combinations of environmental parameters that correspond to specific depositional environments. The descriptions of facies and their significance, based on field observations, are

summarized in Table 2.

5. Spatial organization

This section presents the spatial distribution of ichnotaxa, as derived from quadrat and trench sampling. Spatial distribution is outlined with a descriptive approach, based on the geomorphological units distinguished in Fig. 1 and Fig. 5. Ichnotaxonomy is summarized in Table 3 and follows Baucon and Felletti (2013), to which the reader is addressed for a complete description of traces and their ethology. Ichnotaxa, to be considered as incipient (Bromley, 1996: p. 164), are presented with respect to a descriptive classification scheme, partly based on Książkiewicz (1977).

5.1. Branched structures

5.1.1. *Thalassinoides form XL (very large)*

Extensive burrow networks, assigned to the ichnogenus *Thalassinoides*, are commonly produced by the decapod shrimp *Pestarella candida* (Table 3). Sediment mounds, diagnostic of the studied structure, are restricted in environmental and sedimentological range (Figs. 7, 8). In fact, they are more abundant in the back-barrier zone, which is associated to protected conditions and disposability of organic material (Fig. 8). This spatial distribution is well represented by the variogram (Fig. 4A). In fact, the relative low value of the correlation range (~220 m) approximates the average lateral distribution of *Thalassinoides XL*, showing a produced correlation periodicity (a 'peaks-and-valleys' shape). The relative high value of the nugget effect (~ 50% of the sill), indicates a high discontinuity of the variable at short distance (close to the sampling points). The observed distribution is in line with the distribution of the tracemaker, occurring in muddier and more proximal sediments respect to other thalassinidean shrimps (*Pestarella tyrrhena* and *Upogebia pusilla*, authors of *Thalassinoides L* and *Parmaichnus*, respectively; Ngoc-ho, 2003).

Despite its abundance in the middle intertidal, *Thalassinoides XL* is absent in the upper (landward) intertidal (Figs. 7, 9), probably in relation to prolonged subaerial exposure during low tide, which is a stressful condition for the producer.

5.1.2. *Thalassinoides form L (large)*

Burrow networks with funnel-like openings and chambers filled with seagrass (*Thalassinoides* L; Table 3) are particularly abundant in the middle and lower intertidal of the fore-barrier. Similarly to *Thalassinoides* XL, this ichnotaxon is virtually absent from the upper tidal flat, probably because of low-tolerance to desiccation (Figs. 7). This interpretation is consistent with the physiology of the tracemaker, the decapod shrimp *Pestarella tyrrhena*. Variographic analysis indicates complete absence of spatial correlation (*pure nugget effect*), suggesting a highly discontinuous presence of this ichnotaxon or sampling error (*Thalassinoides* L is easily mistaken for *Monocraterion*; Fig. 4B).

5.1.3. *Parmaichnus*

Y-shaped burrows with swellings, assigned to the ichnogenus *Parmaichnus*, are produced by Upogebiid shrimps (Table 3). In the study area, *Parmaichnus* is absent from the landward part of the tidal flat (Fig. 7, 9). More in detail, *Parmaichnus* is related to back-barrier environments with abundant organic debris, corresponding to muddy sand facies (C). The environmental distribution of *Parmaichnus* overlaps with that of *Thalassinoides* XL, although the latter prefers more proximal environments. This observation corroborates the distribution of the respective tracemakers, summarized in Ngoc-ho (2003). *Parmaichnus* is also associated to firmgrounds, which are characterized by dense monoichnospecific assemblages (since a maximum of 25 openings of *Parmaichnus* per sampling unit). This observation is in line with the fossil record of *Parmaichnus* (Pleistocene firmground muds: Pervesler and Uchman, 2009) and with some recent occurrences of Upogebiid burrows (Asgaard et al., 1997; Gingras et al., 2001).

Variographic analysis indicates a correlation range of ~180 m that reflects the smaller lateral continuity of *Parmaichnus* rather than that found in the *Thalassinoides* XL (Fig. 4C). The relative high value of the nugget effect (~ 50% of the sill), indicates small-scale fluctuations of the variable at short distance (close to the sampling points).

5.1.4. *Polykladichnus*

The ichnogenus *Polykladichnus*, consisting of I- or U-shaped burrows with Y-shaped bifurcations

(Table 3), is restricted to the back-barrier area, with high densities associated to algal and microbial facies (facies D and E; Fig. 10). The highest densities correspond to the central area of the tidal flat, which is characterized by high organic content and dysoxic conditions. This phenomenon could be explained by the high sulphide detoxification in the tracemaker *Nereis diversicolor*, which allows it to stay in sulphide-rich patches (Vismann, 1990). Accordingly, Engelsen et al. (2010) provided experimental support that *Nereis diversicolor* can tolerate periods of oxygen depletion and feed on macroalgal mats.

5.2. U-burrows

5.2.1. *Arenicolites* form XL (very large)

In the study area, sipunculan worms inhabit deep U-shaped burrows, corresponding to the ichnogenus *Arenicolites* (Table 3). The largest morphotype, presenting a single pile of sediment casts, is almost exclusively associated to the sandy sediments of the fore-barrier, being particularly abundant on longshore bars at the intertidal-subtidal limit (11). The observed pattern is in accordance with the typical distribution of the tracemaker, common in sandy, unvegetated tidal flats with high and stable salinity. Low emersion times, moderately reducing conditions and moderate hydrodynamics are also typical environmental conditions associated to peanut worms (Ha et al., 2007). In particular, grain size seems to be an important control factor on distribution of Sipuncula, with a preference for sandy sediments (Cutler, 1994; Ferrero-Vicente et al., 2011). Within this depositional environment, *Arenicolites* XL shows a very good lateral continuity (Fig. 4D). This spatial distribution is well represented by the relative high value of the variogram range (~400 m), even though the value of the nugget effect (~ 30% of the sill) indicates a discontinuity of the variable at short distance (close to the sampling points).

5.2.2. *Arenicolites* form L (large)

Large U-shaped burrows surrounded by sediment casts, radially arranged, are produced by deposit-feeding sipunculan worms (Table 3). Quadrat sampling indicates that this form, corresponding to the ichnogenus *Arenicolites*, is particularly abundant in the fore-barrier, whereas it is patchily distributed

in the back-barrier (Fig. 12). Maximum densities (24-36 burrows per m²) are reached at about 80 metres from the shoreline (high tide line). The observed pattern is in line with the environmental requirements of the tracemaker, a sipunculan worm (Cutler, 1994; Ha et al., 2007; Ferrero-Vicente et al., 2011). Variographic analysis indicates a correlation range of ~200 m that reflects the smaller lateral continuity of *Arenicolites* L rather than that found in the *Arenicolites* XL (Fig. 4D-E). The relative low value of the nugget effect (~ 25% of the sill), indicates a good lateral continuity of the variable at short distance (close to the sampling points).

5.2.3. *Arenicolites* form S (small)

The amphipod *Corophium* inhabits small U-shaped burrows, which are distributed either in the fore- or in the back-barrier. More specifically, these structures are corresponding to the ichnogenus *Arenicolites* (Table 3). They are restricted within a belt extending between 40 and 250 metres from the shoreline (Fig. 10). The observed pattern is in line with literature data on the distribution of the tracemaker *Corophium* (Beukema and Flach, 1995).

Within the study area, the highest densities of *Arenicolites* S are concentrated in the middle-upper part of the aforementioned belt, largely but not exclusively dominated by biomats (Fig. 10). This distribution reflects the environmental niche of the tracemaker *Corophium volutator*, which prefers muddy dysoxic sediments respect to well-oxygenated sands (Gamble, 1971). On North Sea tidal flats, microbial mats and other microphytobenthos-rich environments are characteristically associated to U-burrows produced by *Corophium volutator* and *Corophium arenarium*, which feed on diatoms and bacteria (Gerdes et al., 1985; Gerdes, 2003; Andersen et al., 2010).

5.3. Chambered burrows

5.3.1. 'Squat burrow'

During mating season, green crabs (*Carcinus maenas*) build burrows with a low depth/diameter ratio, commonly presenting a terminal disc-shaped chamber (Table 3). These structures, interpreted as mating burrows (Baucon and Felletti, 2013), occur only in the back-barrier, being almost exclusively

associated to filamentous algal mats (facies D; Fig. 13). This pattern is clearly shown by quadrat sampling, which reveals maximum densities (5 openings per sampling unit, 0.25 m²) in the eastward filamentous mats. Moksnes (2002) evidenced the importance of filamentous algal mats for *Carcinus maenas* by showing the habitat selectivity of its megalopae. Possibly, these results confirm the hypothesis that *Carcinus maenas* prefers structured, nutrient-rich habitats during delicate periods of its lifecycle. Indeed filamentous mats provide shelter, nutrients and easy-to-burrow substrates. ‘Squat burrows’ could also trigger a positive feedback in the filamentous mats by influencing the nitrogen cycle (Vopel and Hancock, 2005). It should be noted that, serving as a mating burrow, ‘squat burrows’ are produced only during the breeding season. For this reason, trench sampling – conducted after quadrat sampling – did not reveal specimens of ‘squat burrows’.

Within this depositional environment, this ichnotaxon shows a very good lateral continuity (Fig. 4F). The spatial distribution is well portrayed by the relative high value of the variogram range (~400 m). Moreover, the low value of the nugget effect (~ 25% of the sill) point to a good lateral continuity of the variable at short distance (close to the sampling points).

5.3.2. *Macanopsis*

The biomats of the study area are commonly burrowed by heterocerid beetles, which produce clavate chambers with convolute necks. The distribution of these structures, corresponding to the ichnogenus *Macanopsis* (Table 3), is strongly controlled by biomats (Figs. 14, 15). In fact, 97% of the samples with *Macanopsis* were recovered from laminated mats (facies E). The geotechnical proprieties of the microbial mat provide an explanation for this strict trace distribution pattern, as the biofilm isolates immature forms from predators and physical stress. At the same time, the microbial mat itself constitutes a source of nutrients, readily available to both adults and juveniles (see Evans and Hogue, 2006). Synecological factors are equally important; being submerged during high tide, microbial mats offer a secure protection from terrestrial vertebrates. Few marine invertebrates can compete for space with insects, as the laminated microbial mats are characterized by reducing conditions, noxious phosphate content and moderate to high exposure time (see also Baucon, 2008: p. 198).

These observations support the idea of insect burrows as indicators of biomat-dominated environments (see Gerdes, 2003). In fact, chambered burrows produced by insects are reported from microbial mats of both temperate and arid conditions (Farmer, 1992; Gerdes, 2003). In particular, Gerdes et al. (1985) described heterocerid and staphilinid burrows as typical traces of the Mellum island tidal flats. Finally, insect traces are also associated to lacustrine microbial mats (Scott et al., 2009).

5.4. *Winding structures*

5.4.1. *Helminthoidichnites*

In the study area, unbranched horizontal burrows, consistent with the ichnogenus *Helminthoidichnites*, are strictly related to biofilms (Table 3; Figs. 14, 15). These structures are produced by dipteran larvae, following the interface between the organic-rich and the mineral-rich layer of the microbial mats. More than the 92% of the occurrences are associated to laminated microbial mats, suggesting an undermat mining behaviour *sensu* Seilacher (1999). This strict distribution pattern is explained by the abundant nutrients associated to the microbial mat. Furthermore, the microbial mat offers a significant protection from predators and physical stress. These observations are in line with previous data on dipteran tracemakers (Scott, pers. com.; Seilacher, 1999; Gingras et al., 2011a).

5.5. *Simple burrows*

5.5.1. *Skolithos form L (large)*

Razor clams produce deep vertical burrows with 8-shaped openings, resembling the ichnogenus *Skolithos* (Table 3). Trench sampling revealed the presence of the studied morphotype within the fore-barrier, mostly on sandbars at the intertidal-subtidal limit (Fig. 16). This observation is in line with the suspension-feeding behaviour of razor clams, requiring sufficient turbulence for suspending nutrients. The spatial pattern of *Skolithos* L is also supported by the typical distribution of the tracemakers, which are generally associated to oxygenated sandy bottoms, moderate degree of wave exposure and upper intertidal to lower subtidal conditions (Holme, 1954; Ruppert and Fox, 1988).

5.5.2. *Skolithos form M (medium)*

In the study area, sabellid worms inhabit straight vertical burrows with constructional lining, which are consistent with the ichnogenus *Skolithos* (Fig. 17; Table 3). Trench sampling shows clear evidence of the importance of physical factors in the distribution of this morphotype. In fact, *Skolithos M* is absent in the upper and middle intertidal, while it becomes abundant towards the lower intertidal of the fore-barrier (Fig. 16). Semiquantitative observations recorded its presence in shallow subtidal bottoms, at a maximum depth of 1.5 metres.

The observed distribution suggests a positive correlation with turbulence, which is needed for suspending the nutrients for sabellid feeding (Dame et al., 2001). Such pattern confirms the classical distribution of sabellid worm aggregations, generally found on sandy intertidal and near subtidal zones (Dame et al., 2001).

5.5.3. *Skolithos form S (small)*

Small vertical burrows, resembling the ichnogenus *Skolithos*, are widely distributed on the tidal flat, with the exception of the lowermost intertidal (Table 3). Highest densities are reported from the middle sector of the fore-barrier.

5.5.4. *Skolithos form XS (very small)*

Talitrid amphipods excavate shallow vertical burrows, corresponding to the ichnogenus *Skolithos* (Table 3). In particular, this morphotype marks very precisely the supratidal-intertidal limit (Fig. 16). This zonation is explained by the physiology of its tracemaker, which needs sufficient moisture but suffers from abrupt inundation (Williams, 1983, 1995). Trophic strategy is an additional element of explanation, as stranded algae tend to concentrate in the extreme upper intertidal zone.

For these reasons this morphotype is potentially a very precise environmental indicator, confirmed by similar zonation patterns reported by Williams (1983) and Little (2000). Nevertheless, these burrows present low fossilization potential, although Williams (1983) described deeper talitrid burrows (up to 100 cm) and some fossil examples are known from Cornwall (Scourse, 1996)

5.5.5. *Monocraterion*

Vertical burrows with a funnel-shaped opening (*Monocraterion*; Table 3) are limited to the middle to distal fore-barrier. These structures are easily confused with the vertical shafts of *Thalassinoides* L, also presenting a funnel-like opening.

5.6. *Miscellaneous group*

5.6.1. *Lockeia form S (small)*

Bivalves, among which *Macra corallina* and *Venus* sp., are responsible for almond-shaped burrows resembling the ichnogenus *Lockeia* (Table 3). Trench sampling evidenced high densities of *Lockeia* S on the longshore bars that characterize the fore-barrier sector. Nevertheless, a previous study (Baucon, 2008) reported large specimens from muddier, more protected sectors of the study area. Gingras et al. (in press) interpret *Siphonichnus* as a typical component of tidal deposits.

5.6.2. *Lockeia form XS (very small)*

Small specimens of *Lockeia* are found either in the back-barrier or in the fore-barrier. Nevertheless, higher densities are usually related to the back-barrier lagoon in mat-dominated areas.

5.6.3. *Mottling*

The roots of marine phanerogams are among the major bioturbating agents of the studied site, as they are responsible for intense reworking of the sediment. The resulting mottling is restricted to the back-barrier, where it is usually associated to the middle and lower intertidal. This distribution pattern is explained by the environmental requirements of the major group of tracemakers, marine phanerogams, which suffer severely from desiccation. Indeed, according to recent studies (Koch, 2001; Boese et al., 2003), emersion time and the resulting desiccation stress is the most important factor setting the upper limit of seagrasses. In particular, Koch (2001) defined the minimum depth of seagrass distribution as half the tidal amplitude.

As concerns the association with protected settings, it is difficult to provide a ‘cause-and-effect’

explanation. Indeed seagrasses are ecosystem engineers which attenuate current speed and wave energy, producing a positive feedback on their own growth (Koch, 2001). For instance, currents in seagrass beds can be 2–10 times slower than in adjacent unvegetated areas, while wave attenuation in *Zostera* meadows can reach the 43% (Koch, 2001). According to this interpretation, marine phanerogams are both the cause and the effect of low-energy settings.

In some cases, mottling can be ascribed to the burrowing activity of polychaetes in water-saturated substrates. In such conditions, distinct tunnels cannot be produced, while polychaetes leave convolute structures similar to the ‘mantle and swirl’ traces described by Lobza and Schieber (1999).

6. Ichnological networks

6.1. Quantification of the degree of association

After breaking down the Grado ichnological system into single elements (ichnotaxa), the next logical step is to reassemble them and analyze how they work together. This is a typical task of complexity science, although some aspects have already been introduced in ecology and palaeoecology. For instance, the search for taxa associations is one of the classical problems of community ecology as they provide a conceptual framework to synthesize environmental and ecological characteristics (Legendre, 2005). This philosophy proves to be extremely useful in ichnology, where ichnoassociations are the major building-blocks of (palaeo)environmental analysis. Consequently, a question might arise: what are the recurrent groups of traces in the studied ichnosite?

Life sciences provide several statistical methods for finding associations of taxa, but their major limitation is to assume, for each taxon, within-taxon randomness of the spatial distribution patterns (Roxburgh and Chesson, 1998). On the contrary, the studied trace distribution is characterized by patchy patterns. In fact variogram analysis evidenced that the Grado dataset is characterized by positive spatial autocorrelation, therefore violating the principle of within-taxon randomness.

For overcoming this problem, a method based on probability analysis was followed. In fact ichnoassociation analysis can be approached by measuring the degree to which different ichnotaxa are associated in nature. For instance, a measure of association between *Macanopsis* and *Polykladichnus* is the number of samples presenting both of these ichnogenera (associated occurrences).

Nevertheless, this number of associated occurrences does not provide an immediate description of the likely co-occurrence of two ichnotaxa. This issue is solved by considering the proportion between the number of associated occurrences and the samples with one ichnotaxon (A) or the other (B):

$$J_{A,B} = \text{number of samples with A and B} / \text{number of samples with A or B}$$

This measure of association corresponds to the Jaccard similarity for absence-presence data, a robust index which is widely used in numerical ecology (Wheater et al., 2011) and palaeontology (Hammer and Harper, 2006). It can be seen as a probabilistic measure of association, answering to questions such as: what is the probability of finding both ichnogenera if at least one of them is present in the sample? By calculating the Jaccard index for each pair of ichnotaxa, an association matrix is obtained, where each cell measures the probability of association between two ichnotaxa. This association matrix is conveniently visualized by a heat map, which represents each value in the matrix as a colour (Fig. 18).

6.2. *Ichnonetwork analysis*

6.2.1. *Ichnological systems are networks*

Although the association matrix displays coherently the relationships between ichnotaxa and their strength, patterns are difficultly perceived. This problem emerges from the complex structure of ichnological systems, comparable to webs of mutually associated ichnotaxa. This conceptual image offers an immediate analogy with information networks, typically constituted by blocks of information (nodes) linked by connections (edges) (Brandes and Erlebach, 2005). Typical examples include food webs, neural networks and the Internet (Buchanan, 2003). Similarly, ichnological systems have their nodes (ichnotaxa), some of which are connected to form ichnoassociations. In a network perspective, the association matrix of Figure 18 can be seen as an adjacency matrix, defining which nodes (ichnotaxa) are connected (associated) to which other nodes (Junker and Schreiber, 2008).

The studied ichnological system is conveniently represented by a circular layout graph ('ichnonet graph'; Fig. 19), in which ichnotaxa are placed onto a circumference and each connection is drawn as a line. More in detail, the positive entries of the association matrix (Fig. 18) record the presence of a

connection between node pairs, and its weight (Sporns, 2010). As a result, the ichnonet graph maps which ichnotaxon is associated to which other.

As stated above, the ichnonet graph displays not only the presence of a connection between ichnotaxa, but also records the intensity of each relation. For instance, an intense degree of association is found between *Arenicolites* S and *Thalassinoides* XL+*Parmaichnus* (Fig. 19). Although some weighted metrics exist for valued graphs, concepts, definitions and software are not as well developed as they are for graphs and directed graphs (Wassermann and Faust, 1994; Brede and Boschetti, 2009). For this reason, traditional metrics are adopted for describing the Grado ichnonet, while weights are taken into account when discerning ichnoassociations (section 6.3).

6.2.2. Degree and network density

The most immediate feature of the network is that each ichnotaxon (node) has a varying number of connections (edges) with other ichnotaxa (Fig. 20A). This number, termed degree of connection (Scott, 2000), provide important information about the internal organization of the Grado ichnological system (Table 4):

1. Isolated nodes: *Skolithos* XS and *Lockeia* S have no edges incident to them. This property indicate that these ichnotaxa occur as monoichnospecific assemblages.
2. High-degree nodes: many edges meet *Skolithos* S, *Arenicolites* S, *Lockeia* XS, *Arenicolites* XL+L and *Thalassinoides* XL+*Parmaichnus*. Although these traces co-occur with many others, these nodes are not necessarily environment-crossing ichnogenera. In fact, node degree measures the number of ties only, while environment-crossing ichnogenera are usually appearing in multiple ichnological contexts.

Whereas degree refers to the number of connections incident with each node, it is possible also to consider the number of connections in the network as a whole (Wassermann and Faust, 1994). More in detail, it is useful to measure how close is our network to the full saturation of connections. In the Grado ichnonetwork, the 42.9% of all possible connections are present (network density: 0.429). This measure shows that the Grado ichnonetwork is not a highly-ordered regular graph, but heterogeneities

are present.

6.2.3. Bridge ichnotaxa

Although an ichnotaxon might be associated to others (Fig. 20A), it could be central for a local group of ichnotaxa (Fig. 20B) or, alternatively, it could be central for the whole network (Fig. 20C). For this reason, it is important to take into account those ichnotaxa that act as a bridge between different groups of ichnotaxa, potentially connecting different ichnoassociations and/or subenvironments. In other words, the goal is to find those nodes that lie between many others.

This problem can be solved by considering node betweenness, a centrality measure that examines ‘how between’ a node is (Wassermann and Faust, 1994). More in detail, betweenness is quantified in terms of the number of shortest paths that run through a given node (Wuchty and Stadler, 2003).

Skolithos S, *Arenicolites S*, *Lockeia XS* are characterized by notable betweenness (Table 4; Fig. 20C), meaning that they connect distinct structural entities in the network. If bridge ichnotaxa are removed, parts of the ichnonetwork will be almost disconnected. Therefore bridge ichnotaxa are hubs connecting different structural units, being poor environmental indicators as they are likely to lie between multiple ichnoassociations.

The presence of bridges is an indicator of structure for the whole ichnonetwork: bridge ichnotaxa would not exist in an ichnological system with random co-occurrence patterns. As explained by Barbási (2002), a random system does not support connectors.

6.2.4. Distance and network diameter

Alongside to the centrality of nodes, it is important to look at the degrees of separation between them. This quality is formalized by the geodesic distance, which measures the shortest path of connection between two nodes (Wassermann and Faust, 1994). The Grado network is characterized by the following non-trivial extreme cases:

1. Distance=1 corresponds to directly connected nodes (i.e. *Helminthoidichnites* and *Macanopsis*), which are separated by only one edge. This situation indicates that such ichnotaxa co-occur with a probability proportional to edge weight.
2. Distance=2 corresponds to nodes with two degrees of separation. This is the case of nodes which are only indirectly connected by a common node (i.e. *Skolithos* M and *Thalassinoides* XL+*Parmaichnus*). This topology has an analogue in social networks: a friend shared between people who do not know each other. This configuration is diagnostic of two ichnotaxa with incompatible ecological requirements, which are yet suitable to a more plastic ichnogenus.

Intriguingly, the maximum distance between all pairs of nodes is equal to 2. This measure, known as network diameter (Wassermann and Faust, 1994), indicates a very compact system in which most nodes can be reached from every other by a small number of steps. This phenomenon is also supported by a small average distance (equal to 1.4).

6.2.4. Core ichnotaxa

After considering the distance between an ichnotaxon and a co-occurring one (*neighbour*), a question might arise: how an ichnotaxon is embedded in its neighbourhood? With an example, it is important to know if the ichnotaxa associated to *Macanopsis* are also associated to each other.

In order to solve this question, it is useful to count the number of connections between the ichnotaxa co-occurring with *Macanopsis*. This measure, divided by the maximum number of connections, is the clustering coefficient and quantifies the density of connections between the direct neighbours of a node (Bhadra et al., 2009). In the case of *Macanopsis*, the clustering coefficient is equal to 1 because all of its neighbours are connected to each other. The high degree of clustering, together with the low betweenness (Table 4), implies that *Macanopsis* lies at the core of a group of co-occurring traces.

This interpretation highlights that core ichnotaxa occupy central positions in ichnoassociations and have few connections towards other groups of traces (Fig. 20B). For this reason, core ichnotaxa are potentially the most environment-sensitive traces in a given ichnological system.

This aspect is very evident when comparing core ichnotaxa to bridge ichnotaxa. For instance,

Skolithos S has a clustering coefficient of 0.5 because only some of its neighbours are connected (i.e. *Skolithos S* is associated either to *Macanopsis* or *Skolithos M*, but these ichnotaxa are never occurring together; Fig. 20C). If the traces co-occurring to *Skolithos S* are poorly associated, they are likely to pertain to different domains which are connected by bridge ichnotaxa such as *Skolithos S* itself. In fact clustering depends on the local connectivity pattern, while betweenness reflects the topological structure of the whole graph (Cabana et al., 2008).

6.2.5. *The small-world effect*

As seen for other local measures, the clustering coefficient can be averaged over the whole graph to determine the degree to which ichnotaxa tend to cluster together. The clustering coefficient of the Grado network is significant (0.701) and measures the probability that two ichnotaxa with a common neighbour are connected (Steuer and Zamora López, 2008). The measured clustering coefficient indicates that the network tend to form interconnected clusters of nodes, like a regular lattice; at the same time, the average distance of the Grado ichnonetwork (1.4) is similar to that of a correspondent random graph (1.6, calculated with the algorithm of McSweeney, 2008). These features suggest that the Grado ichnonetwork lies between regular and random networks or, in more formal terms, it represents a small-world network (Watts and Strogatz, 1998). This assumption is confirmed by measuring the small-worldness of the Grado ichnonet with the quantitative index *S* developed by Humphries and Gurney (2008). Indeed the small-worldness *S* of the studied network is equal to 1.736 (1.541 by ignoring isolated nodes).

The small-world property imply that network architecture and its substructures (i.e. ichnoassociations) do not emerge from random assemblage rules. Rather, a small-world is governed by underlying organizing principles (Réka and Barbási, 2002).

6.3. *Ichnoassociations as network communities*

Real-world networks usually display inhomogeneities, consisting of high concentrations of edges within special groups of nodes, and low concentrations between these groups (Fortunato, 2010). In the language of network science, these groups are named communities and their detection has important

implications in understanding network organization. Indeed, communities represent “groups of vertices which probably share common properties and/or play similar roles within the graph” (Fortunato, 2010). Typical examples of communities include groups of web pages dealing with the same topic (in the World Wide Web network), groups of friends (in a social network), compartments (in a food web) (Porter et al., 2009; Fortunato, 2010).

In the context of the ichnonet graph (Fig. 19), communities correspond to groups of ichnotaxa which are highly associated to each other, but weakly associated to other groups of ichnotaxa. According to these assumptions, the communities of network science are ichnoassociations. In light of the neoichnological scenario, each ichnoassociation is likely to represent the work of a group of organisms living in the same space and time, or, an ichnocoenose (also known as ichnocommunity; Buatois and Mángano, 2011; Morin, 2011). Nevertheless, the more neutral term ichnoassociation is here preferred, in the sense of a group of commonly co-occurring traces.

The problem of finding ichnoassociations may be approached graphically, i.e. by looking for groups of strongly interconnected nodes. In the ichnonet graph of our case study (Fig. 19), *Helminthoidichnites-Lockeia XS-Macanopsis-Polykladichnus* form a well-defined group of nodes: an ichnoassociation, or, with the nomenclature of network theory, a community. Nevertheless, the ichnonet graph is too intricate for perceiving other ichnoassociations at first-sight and, consequently, a more analytical approach must be followed.

6.3.1. Infomap method

The Infomap method (Rosvall and Bergstrom, 2008) is one of the most accurate analytical approaches for revealing the organization patterns in networks (Fortunato, 2010). This algorithm is based on finding an efficient description of how information flows on the network under analysis. As expressed by its name, the Infomap method has significant analogies with a geographic map, in which dense clusters of streets are described as towns. Similarly, the Infomap method attempts to simplify the structure of a network by describing groups of well-connected nodes as single, well-connected modules (Rosvall and Bergstrom, 2008). According to this idea, ichnoassociation mining is equivalent to optimally describe the ichnonet graph by using less information than that encoded in

the full similarity matrix (see Fortunato, 2010). In fact, paraphrasing Rosvall and Bergstrom (2008), an ichnoassociation can be regarded as a group of nodes among which information flows easily and, consequently, it can be efficiently represented as a single well-connected region.

The Infomap algorithm uses a random walk as a proxy for finding an optimal coarse-grained description of how information flows on the network; a thorough description of the algorithm is found in Rosvall and Bergstrom (2008). The application of Infomap revealed four ichnoassociations, named after the salient characteristics (Fig. 21A):

1. Low-bioturbation ichnoassociation: The presence of an isolated node (*Skolithos* XS) suggest the existence of a monoichnospecific ichnoassociation; due to its very sparse occurrences, *Lockeia* S has been not considered an ichnoassociation.
2. *Thalassinoides* ichnoassociation: *Thalassinoides* XL+*Parmaichnus*, *Arenicolites* S, Mottling.
3. *Arenicolites/Skolithos* ichnoassociation: *Arenicolites* XL+L, *Thalassinoides* L, *Monocraterion*, *Skolithos* S, M, L.
4. *Macanopsis* ichnoassociation: *Macanopsis*, *Helminthoidichnites*, *Polykladichnus*, *Lockeia* XS.

To ensure that the results of the ichnoassociation analysis were robust, they were tested against other popular methods for community mining.

6.3.1. Cluster analysis

Among the traditional techniques, cluster analysis has the advantage of not requiring a preliminary knowledge on the number and size of the communities (Fortunato, 2010). This technique groups the nodes (ichnotaxa) in a dendrogram with horizontal lines at the levels of similarity between clusters, based on a predefined similarity measure (Hammer and Harper, 2006; Wheater et al., 2011). Keeping with Hammer and Harper (2006), the average linkage algorithm was applied on the association matrix shown in Fig. 18.

The ichnoassociations defined by cluster analysis coincide with those of the Infomap method, with

the only exception of *Skolithos* M (Fig. 21B). It is also interesting to note how *Macanopsis* is slightly separated from the rest of the cluster, reflecting the spatial distribution pattern discussed in section 5.4.2.

6.3.2. Multidimensional scaling

Despite its widespread use, cluster analysis has been commonly criticized because it may recognize groups even when they are not present (Hammer and Harper, 2006). For this reason, the robustness of the recognized clusters was tested against another popular method of network analysis: non-metric multidimensional scaling. This technique aims to spatially represent the similarity between nodes on the basis of a similarity matrix (Wassermann and Faust, 1994). In our case, the target is to position the nodes (ichnotaxa) so that the higher the degree of association, the closer the distance between nodes, and vice versa (Fig. 21C). A stress value gives a measure of the ability to represent the relationships between the ichnotaxa (Hammer and Harper, 2006; Speight and Henderson, 2010). In order to fulfil the recommended stress value (less than 0.3; Wheeler et al., 2011), poorly-represented ichnotaxa (*Skolithos* XS and *Lockeia* S) have not been displayed. A minimal spanning tree has been used to connect the nearest neighbours by respecting the original distances specified in the similarity matrix (Hammer and Harper, 2006).

With respect to Fig. 21, there are striking similarities in the results of multidimensional scaling, cluster analysis and Infomap method. Nevertheless, cluster analysis and multidimensional scaling tend to separate vertical traces from other clusters. This aspect suggest a hierarchical organization of the *Arenicolites/Skolithos* association, composed of a subunit dominated by vertical traces (*Skolithos* S, M, L) and a subunit with prevailing U-shaped burrows (*Arenicolites* XL+L, *Monocraterion*, *Thalassinoides* L).

7. Ichnoassociations and environment

The integration of ichnonetwork and spatial analysis allows an accurate definition of ichnoassociations, which are the fundamental building blocks of environmental analysis. Indeed, taxa associations are better environmental predictors than individual taxa because they are less subject to sampling error

(Legendre, 2005). In line with this principle, this section discusses the results of geostatistical and ichnonetwork analysis, addressing the question of the environmental significance of the observed ichnoassociations through the search for regularities. More in detail, the idea is to find the average environmental conditions related to each ichnoassociation, e.g. the most common hydrodynamic setting of the *Thalassinoides* ichnoassociation. This approach is presented by describing the ichnological and the environmental characteristics of each ichnoassociation, as defined by the IchnoGIS method (Figs. 22, 23):

- The Low-bioturbation ichnoassociation characterizes areas undergoing to prolonged emersion. Such conditions are commonly correlated to sandy sediments with well-developed lamination (facies A), which is a consequence of the low degree of biogenic reworking.
- The *Arenicolites/Skolithos* ichnoassociation develops in energetic, fore-barrier areas, where constant wave action produces widespread ripples (facies B; Fig. 22). In this environmental context, the *Skolithos* ichnoassociation is exposed to higher hydrodynamics, while quieter conditions favour the *Arenicolites* ichnoassociation (Fig. 24).
- The *Thalassinoides* ichnoassociation is largely concentrated on the sheltered flats of the back-barrier, with the exception of those areas with long emersion times (Figs. 9, 24).
- The *Macanopsis* ichnoassociation characterizes sheltered portions of the tidal flats colonized by cohesive microbial mats (Facies E). Significant emersion times and noxious phosphate levels are common (Figs. 22, 24).
- The 'Squat burrows' ichnoassociation is established on the basis of quadrat sampling, because the dominant ichnogenus is produced during breeding season (section 5.3.1). 'Squat burrows' may co-occur with *Thalassinoides* XL, *Parmaichnus*, *Polykladichnus* and *Arenicolites* S. This ichnoassociation characterizes filamentous algal mats, developed in low-energy intertidal flats (Fig. 23).
- The *Parmaichnus* ichnoassociation is established on the basis of quadrat sampling, because of the extreme cohesiveness of sandy firmgrounds. In fact, dense monoichnospecific assemblages of *Parmaichnus* are found in the distal parts of the tidal flat, with high concentrations of burrows within firm, exhumed substrates (Fig. 23).

8. Discussion

8.1. Ichnological modelling of the Grado system

The results of the IchnoGIS method had shown a marked habitat specificity in ichnoassociations, each of which occurs within a restricted range of environmental parameters. Making sense of such heterogeneity is a major goal for providing a predictive model with immediate palaeontological application and, consequently, the definition of structuring forces is of primary importance.

It is widely accepted that organism behaviour can be influenced by a wide variety of environmental factors, including hydrodynamic energy, substrate, oxygenation, salinity, sedimentation rate, bathymetry, among others (Buatois and Mángano, 2011). In order to delineate a defined set of control factors which explain the observed ichnoassociations, two simple principles were followed:

a. Regularity exclusion. Factors exhibiting no significant variation across different ichnoassociations were excluded. For instance, salinity is a major control factor in coastal environments (Buatois and Mángano, 2011), but similar salinities characterize different ichnoassociations (Figs. 22, 23). Therefore salinity cannot explain the observed differences in ichnofaunal composition.

b. Parsimony. If different ichnoassociations exhibit different but correlated environmental parameters, the parameter which explains the other(s) is selected. For instance, the *Thalassinoides* ichnoassociation occurs in fine sediments and quiet environments. As grain size depends on hydrodynamics, the latter is to be considered the major structuring factor.

The application of these simple principles evidenced four major structuring factors (emersion time, hydrodynamics, firmness, microbial binding) synthesized in Fig. 25 and discussed below.

8.2. Emersion

Quadrat and trench sampling showed a sea-land gradient along which bioturbation intensity markedly decrease. The acme of this gradient corresponds to a shore-parallel belt within which only few, small sized ichnotaxa are found (Low-bioturbation ichnoassociation).

The period of emersion (exposure or emersion time) is the most obvious aspect accounting for this

gradient. In fact, more proximal sites generally experience longer period of emersion, which is a fundamental structuring process in intertidal environments (Raffaelli and Hawkins, 1996). This interpretation is proved not only by the low bioturbation index at high intertidal sites, but also by direct comparison of exposure time and burrow abundance (Figs. 7–9). This trend is confirmed for the vast majority of ichnotaxa, with the exception of burrows produced by organisms well-adapted to dry environments (i.e. *Macanopsis* and *Skolithos* XS).

The structuring power of exposure is explained by the numerous types of physical stressors associated to long period of emersion. In particular, desiccation plays a major role as it severely affects the vast majority of marine animals (Raffaelli and Hawkins, 1996). In particular, polychaetes are probably the most sensitive group of tracemakers, being virtually incapable of resisting desiccation (Glasby et al., 2000). Burrowing itself is a strategy to cope with long emersion times, as it allows to reach the water table during low tide. This is particularly true for thalassinidean tracemakers, which rely on water for gas exchange.

In addition, emersion time directly influences important trophic modes. For instance, filter feeders can only feed in water, therefore the time available for feeding dramatically increases towards the sea (Raffaelli and Hawkins, 1996). This phenomenon explains the distribution of the *Skolithos* ichnoassociation, largely dominated by suspension-feeding behaviours and found only at the intertidal-subtidal limit. Furthermore, prolonged emersion time negatively affects seaweed, whose photosynthetic tissues have a poor performance out of water (Raffaelli and Hawkins, 1996).

According to Koch (2001) and Boese et al. (2003), exposure and the resulting desiccation stress are the most important factors setting the upper limit of seagrasses. Therefore, emersion time accounts for the distribution of rhizome-produced mottling, which is a core component of the *Thalassinoides* ichnoassociation. The absence of seagrasses triggers a negative feedback for deposit-feeders, which are favoured by the abundant organic matter deriving from the seagrass meadows. Finally, it should be noted that the areas undergoing to long emersion times are also subject to significant climatic stress. Indeed, air temperature is much more variable than water temperature, therefore proximal areas experience very extreme conditions (Raffaelli and Hawkins, 1996).

These results are supported by numerous ecological studies which recognize a sea-land gradient

(or intertidal gradient), determined by emersion and its directly correlated variables. For instance, Salvat (1964) distinguished four ecological belts on the basis of sand moisture, which is largely a consequence of the shore position and therefore depends on emersion time. At this regard, McLachlan (1990) suggested that the zones of Salvat (1964) correlate with distinct faunal groups characterized by different desiccation tolerance. Salvat's (1964) zonation has a good correspondence with the faunal belts described by Dahl (1952) (Raffaelli and Hawkins, 1996). Furthermore, Swinbanks (1982) subdivided beaches on the basis of emersion time. In geological literature, the exposure index of Ginsburg et al. (1977) confirms the major role of emersion time in structuring habitats. According to these authors, emersion time define similar environments, each with distinct fauna, sedimentology and traces (Ginsburg et al., 1977; see also Rankey and Berkeley, 2012).

In conclusion, emersion time is one of the major structuring factors in intertidal systems, directly affecting bioturbation intensity. Fig. 25 models this phenomenon by mapping decreasing emersion times with the distance from the centre of the scheme.

8.3. Hydrodynamics

While the patterns found along the land-sea gradient are largely attributable to differences in emersion time, other structuring factors are acting in concert along this same gradient. For instance, *Thalassinoides* ichnoassociation and *Arenicolites* ichnoassociation are exposed to the same range of emersion times, but the differences in ichnofaunal composition are striking.

The IchnoGIS analysis shown a well-defined relationship between ichnoassociations and hydrodynamic energy, as expressed by the position with respect to the geomorphological barriers (Fig. 24). In fact, the barrier-island which characterizes the Grado ichnosite acts as a protection against currents and waves, separating a low-energy zone (the back-barrier) from a higher-energy zone (the fore-barrier; Fig. 1). A positive feedback exists between low-energy settings and marine phanerogams, acting as true ecosystem engineers. Indeed seaweeds are favoured by sheltered environments and, at the same time, they induce low-energy environments by extracting momentum from the moving seawater (Koch, 2001).

The pictured scenario is mirrored by facies distribution, characterized by sandy sediments in

the turbulent fore-barrier (i.e. facies B) and finer sediments in the sheltered back-barrier (i.e. facies C; Fig. 3A). Accordingly, fine organic material settles in the lower energy zone, favouring the deposit-feeders responsible of the *Thalassinoides* ichnoassociation. At the contrary, turbulence keep nutritious material in the water column, favouring suspension-feeding strategies (*Skolithos* ichnoassociation) in the fore-barrier. The observed ichnoassociations can be seen in light of the Seilacherian ichnofacies, with the *Skolithos* ichnofacies related to food particles suspended and the *Cruziana* ichnoassociation related to food particles deposited (“food resources paradigm” of Pemberton et al., 2001). It should be noted however that the *Skolithos* ichnofacies occurs seaward of the *Cruziana* ichnofacies, as the energy gradient of the Grado ichnosite is inverted with respect to wave-dominated environments; this aspect has been already highlighted by Mángano et al. (2002) and Buatois and Mángano (2011).

In contrast, food supply does not provide a complete explanation for the *Arenicolites* ichnoassociation, typically occurring within the fore-barrier (Figs. 22, 24). In fact, the dominant ichnotaxa (*Arenicolites* L and XL) are related to deposit-feeding sipunculans, although the fore-barrier provides less organic matter than the adjacent back-barrier. A basic explanation is given by the commonest environmental preferences of sipunculans, which coincide with the conditions of the fore-barrier. In addition, *Thalassinoides*-producing decapods are exploiting the same resource (detritus) of sipunculans, therefore they may compete and trigger spatial resource partitioning.

Although both of these assumptions may be partially true, a deeper level of explanation is required because *Arenicolites*-dominated ichnoassociations are well-documented in similar palaeoenvironments (Bromley and Asgaard, 1991; Bromley, 1996; Pemberton et al., 2001). In this regard, the extended organism perspective (Turner, 2003) have large implications for interpreting U-burrows, which can be regarded as external organs for channelling energy sources. Indeed, when water flows across a surface, its velocity gradient provides a potential source of work and therefore might be employed to induce burrow irrigation (Vogel et al., 1973). U-shaped morphology is very efficient for exploiting such source of energy, which is required by both suspension- and deposit-feeders. In fact suspension-feeders depend on moving water for nutrition and, in some cases, for respiration. The latter aspect is particularly important for intertidal deposit-feeders, which rely on the organic-rich sediments below the redox potential discontinuity. These nutritious but anaerobic sediments can be explored only

by ventilating the burrow with oxygenated water. Therefore, large concentrations of *Arenicolites* are explained by moderate hydrodynamic energy, which is channelled into the U-burrows. Quieter, more hypoxic environments can be inhabited only by very active ventilators such as mud shrimps, which irrigate their large and complex *Thalassinoides* burrows by pleopod beating (Atkinson and Taylor, 2005).

These examples evidence that the studied ichnosite is also affected by the availability of oxygen in the interstitial system. In general, availability of interstitial oxygen could derive (a) from the oxygen concentration in the water column (Weissberger et al., 2009) or (b) from the dynamics of the interstitial system itself (McLachlan and Brown, 2006). The latter hypothesis fits better with the Grado ichnosite because water column presents similar properties in different parts of the tidal flat (Fig. 22, 23). Previous studies (McLachlan and Brown, 2006; Fonseca et al., 2011) evidenced a strong relationship between oxygen availability and grain size, which is ultimately controlled by hydrodynamics. In fact, depth of the redox potential discontinuity reflects how rapidly oxygenating water passes through the sediment (Little, 2000). Therefore, sands deposited in turbulent waters (facies B) are more permeable and consequently are more oxygenated; muddy sediments settle in quiet environments and, being less permeable, display a shallower redox potential boundary. The relationship between hydrodynamics-grain size-interstitial oxygenation is coherently depicted in Raffaelli and Hawkins (1996: fig.1.14). The poor interstitial oxygenation of fine sediments is exacerbated by high demand of oxygen. Indeed, finer grain size means larger surface for bacterial attachment (see McLachlan and Brown, 2006).

Hydrodynamics also represents a source of mechanical stress which is promptly reflected in the ichnological record. For instance, organisms build burrows with constructional lining (*Skolithos* M) in order to face the turbulent waters of the outer fore-barrier, which is also characterized by a low bioturbation intensity (*Skolithos* ichnoassociation). On the other hand, low-energy settings do not favour filter feeders, because their delicate filtering structures may be damaged from an excess of fine particulate material.

In conclusion, data evidence that hydrodynamics influence both ichnofaunal composition

and bioturbation intensity. The structuring effect of hydrodynamics is shown in Fig. 25 through a speedometer-like representation.

8.4. Biomat binding

Quadrat and trench sampling evidenced that matgrounds present very distinctive ichnoassociations (*Macanopsis* and ‘Squat burrows’ ichnoassociation), manifested by abrupt changes in ichnofaunal composition between biostabilized substrates and other facies. For instance, the mat-related *Macanopsis* ichnoassociation passes to the *Thalassinoides* ichnoassociation within few centimetres of space.

In light of these evidences, matgrounds exert an overarching control on ichnofauna, which is the effect of several factors linked to mat metabolism and growth. At this regard, sediment binding is the most obvious effect on substrate characteristics. In fact, the sediment particles of matgrounds are bound by algal filaments (facies D) and extracellular polymeric secretions (EPS; especially in facies E). The predominance of algal or EPS binding severely affects the geotechnical properties of the substrate. The most severe changes are imparted by extracellular polymeric secretions, which form a matrix embedding microbial cells such as diatoms, cyanobacteria and heterophic bacteria (Decho, 2000). EPS strongly characterizes laminated mats (facies E), which are consequently a modern analog of the firm, erosion-resistant biomats typical of Neoproterozoic sea bottoms (Seilacher, 1999; Gingras et al., 2011a). Spatial and ichnonetwork analysis revealed that insect burrows (*Helminthodichnites*, *Macanopsis*) are the most typical burrows within laminated mats (*Macanopsis* ichnoassociation). It may sound surprising that air-breathing insects are the most important tracemakers in periodically submersed environments, but the Grado ichnosite reflects a global trend. Indeed, insect burrows characterizes laminated mats worldwide (Seilacher, 1999; Reise, 2002; Gerdes, 2003). The presence of insects is explained by the geotechnical properties induced by the microbial mat, which seals the underlying sediment from seawater. Consequently, air-breathers may survive within the microbial mat during high tide, exploiting a rich trophic niche.

Both filamentous and laminated mats display a shallow redox boundary discontinuity and

are commonly accompanied by considerable levels of interstitial phosphate (Fig. 22, 23), which is deleterious for marine invertebrates even at low concentrations (Blasiola, 2000). High concentrations of phosphate seems to be a common feature of both modern and fossil microbial mats in consequence of the metabolism of mat-forming organisms (Wilby et al., 1996; Rougerie et al., 1997). The effect of metabolic processes is exacerbated in laminated mats - less permeable than filamentous ones - because they seal upward-diffusing phosphorous (see Wilby et al., 1996).

The mentioned lower permeability is explained by tighter sediment binding in laminated mats. As a consequence, filamentous mats offer less cohesive and more humid substrates, providing more favourable conditions to marine organisms. In accordance with Österling and Pihl (2001), filamentous mats act as a refuge for predation, enhance food levels for detritivores but induce stressful conditions within the sediment (i.e. high phosphate, dysoxic conditions). For these reasons, filamentous mats are selectively burrowed by mating crabs ('squat burrows'), while *Thalassinoides* and *Arenicolites* are usually scarcer than in the correspondent non-microbial facies (muddy sands, facies C).

The role of biomat binding is modelled in Fig. 25, which displays matground-related ichnoassociations in the left hemisphere of the scheme.

8.5. Firmness

The previous section evidenced the role of substrate firmness in structuring the ichnoassociations of matgrounds, with the *Macanopsis* ichnoassociation occurring in firm, laminated mats and the 'Squat burrows' ichnoassociation related to soft, filamentous mats. Firmness is crucial also for sediments without microbial binding, as witnessed by the specific relationships between ichnoassociations and the degree of consolidation. In fact, a large number of ichnoassociations are restricted to softgrounds, while the *Parmaichnus* ichnoassociation is commonly associated to firmgrounds (Figs. 22, 23).

In light of these examples, firm substrates structure ichnoassociations (a) by offering favourable geotechnical characteristics (i.e. pupation chambers require stable substrates) and (b) by excluding tracemakers unable to burrow firm substrates (i.e. the polychaete *Megalomma* is not provided with

strong burrowing appendages). The latter aspect is well-evidenced by the nearly monospecific *Parmaichnus* ichnoassociation, dominated by Y-shaped upogebiid burrows. The importance of substrate firmness is traditionally well-recognized in ichnology, being a primary aspect in the ichnofacies concept (Bromley, 1996; Buatois and Mángano, 2011). At this regard, the *Parmaichnus* ichnoassociation fits very well to the *Glossifungites* ichnofacies.

Fig. 25 model the effect of firmness by displaying firmground-related ichnoassociations in the lower hemisphere of the scheme.

8.6. “Deep time on a tidal flat” or global model?

The above mentioned Grado model (Fig. 25) is consistent with previous ecological studies on tidal flats. Indeed numerous models of ecological zonation recognize a landward belt characterized by scarce biomass and talitrids (see Dahl, 1952; Jaramillo et al., 1993); there is full correspondence with the low bioturbation ichnoassociation, presenting *Skolithos* XS (authored by *Talitrus*) and a low intensity of bioturbation. According to most ecological zonations of temperate to tropical environments, decapod crustaceans start to dominate from the middle tidal flat (see the review in Raffaelli and Hawkins, 1996: pp. 52–61). This observation supports the *Thalassinoides* ichnoassociation. More turbulent, sandy environments commonly present bivalves or polychaetes inhabiting vertical burrows (see the review in Raffaelli and Hawkins, 1996: pp. 52–61). This is consistent with the *Arenicolites/Skolithos* ichnoassociation. These evidences support the global validity of the observed ichnological zonation, at least for similar environmental domains. Indeed, Jaramillo et al. (1993) demonstrated that reflective, intermediate and dissipative beaches display different zonation patterns.

These general features with global validity coexist with peculiar ichnological and environmental aspects. In fact, the Northern Adriatic Sea is an ideal model for past epeiric (epicontinental) seas, being a shallow (average depth: 35 m), semi-enclosed sea lying on continental crust (McKinney, 2003; McKinney, 2007; Zuschin and Stachowitsch, 2009). In addition, recent studies brought an additional analogy, suggesting that the benthic ecosystem of the Northeastern Adriatic Sea closely resembles

Paleozoic-style ecology (McKinney, 2003, 2007; McKinney and Hageman, 2006). According to McKinney (2003), the Adriatic Paleozoic-style is characterized by low-nutrient water, low intensity of grazing predation, and relatively few endobenthic bioturbators. Although some objections were raised on the mentioned ecological aspects (Zuschin and Stachowitsch, 2009), the Northeastern Adriatic is unanimously considered one of the few modern epicontinental seas comparable to some Paleozoic–Mesozoic shelves (McKinney, 2003, 2007; McKinney and Hageman, 2006; Zuschin and Stachowitsch, 2009). Intriguingly, our results show pre-Jurassic styles of bioturbation which are coexisting with more modern, crustacean-dominated ones:

- Laminated microbial mats commonly display a low degree of bioturbation and common *Helminthoidichnites* (*Macanopsis* ichnoassociation). The observed *Helminthoidichnites* reflect the mining of the microbial mat from underneath: ‘undermat mining behaviour’ *sensu* Seilacher (1999). Similar behavioural strategies were particularly common within Proterozoic microbial mats, before of the Agronomic Revolution (Seilacher, 1999).

- The rippled sands of the fore-barrier are dominated by the *Arenicolites/Skolithos* ichnoassociation, consisting of simple, vertical or U-shaped burrows (*Skolithos*, *Arenicolites*) and rarer bivalve structures (*Lockeia*). With the exception of localized clusters with dense *Thalassinoides* L, crustacean burrows are absent. This ichnological expression closely resembles pre-Jurassic shallow marine ichnoassociations, before of the raise of crustacean bioturbators (Buatois and Mángano, 2011).

These remarkable ichnological features, united to the peculiar physiographic and ecological context, make Grado an ideal analogue for past peritidal ichnological systems. Paraphrasing McKinney (2007), the Grado ichnosite allows to study “deep time on a tidal flat”.

This idea is only apparently contrasting with the global validity of the Grado model. Indeed, the background condition is that ancient bioturbation styles are modern equivalents and therefore they may develop nowadays under peculiar environmental conditions. For instance, undermat miners were common in Proterozoic matgrounds, but they are still present in extreme but recurrent conditions (i.e. Seilacher, 1999). Furthermore, ancient styles of bioturbation are relegated to specific areas of the

studied tidal flat, where environmental conditions are unfavourable to decapods and preclude intense bioturbation (Fig. 24).

9. Conclusions

In this paper, a new method for ichnological analysis (IchnoGIS) is presented through its application on a modern case study. Results show that the IchnoGIS method provides unprecedented research opportunities for ichnologists, as it allows to determine accurately spatial distribution, association patterns and environmental significance of traces.

These outcomes encourage future applications of the IchnoGIS method, involving not only other modern environments but also their cross-comparison. In fact, network analysis proved to be particularly efficient in confronting even very different systems, such as wasp colonies and human classrooms (Bhadra et al., 2009), the Internet and food webs (Réka and Bárbasi, 2002), neural systems and power grids (Watts and Strogatz, 1998). At the same time, the geostatistical approach will facilitate spatial recognition of ichnologically-relevant patterns.

The IchnoGIS method also has much to contribute to future debates on palaeoichnology. In fact, the Grado model (Fig. 25) shows that the IchnoGIS method can be used to predict environmental properties from ichnoassociations, being a tool for palaeoenvironmental analysis. In addition, the IchnoGIS procedures are easily applicable to the analysis of the fossil record, thus representing a promising future direction in the study of fossil environments. In fact, this study demonstrates that the structure of an ichnological system can be described by an ichnonetwork, opening the avenues to the quantitative comparison of fossil and modern systems.

These desirable outcomes require usable tools to be provided to the ichnological community. At this regard, the first step has already been done. In fact, IchnoGIS is based on simple survey tasks relying on relatively low-cost tools, while the entire analytical process can be performed with free or open-source software (Table 5). A further step in this direction will be to develop a single software environment dedicated to IchnoGIS analysis.

In light of these assumptions, the IchnoGIS method provides a single template for understanding

quantitatively the relationship between traces and their environment, thus giving prominent grounds for future research in the study of modern and fossil ichnological systems.

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Figures

Fig. 1. Geographical setting. (A) Grado lagoon. (B) The study area is comprised between Grado and Grado Pineta towns. Location markers refer to the ISPRA mareograph (1) and the OSMER meteorological station (2). Images courtesy of Digital Globe.

Fig. 2. Climatological setting. (A) Sea level, measured during the sampling period. Data from ISPRA mareograph (see Fig. 1 for location). (B) Climatic features of the studied area: average of the average daily temperature, precipitation and wind. Data from OSMER meteorological station (see Fig. 1 for location).

Fig. 3. The IchnoGIS method.

Fig. 4. Variogram analysis. (A) Nomenclature used in variogram analysis, superimposed to the variogram of *Thalassinoides* XL. (B) Variogram of *Thalassinoides* L (openings). (C) Variogram of *Thalassinoides*, *Parmaichnus* (openings). (D) Variogram of *Arenicolites* XL. (E) Variogram of *Arenicolites* L. (F) Variogram of the ‘squat burrows’.

Fig. 5. Geological setting. (A) Facies map, drawn after quadrat, trench and topographical sampling. Coordinates indicate eastern and northing, referred to the UTM zone 33; the same convention is adopted throughout the paper. (B) Profile 1: cross-section of the barrier-island system showing facies distribution (colour codes in A). Sea-floor morphology based on 109 bathymetric measurements.

Fig. 6. Sedimentary facies. (A) Rippled sands (facies B). (B) Mat-related facies: algal mat (left, facies D) and microbial mat (right, facies E). (C) Muddy sands (facies C).

Fig. 7. Burrow density and geomorphological gradient. Scatterplots show the number of mounds (*Thalassinoides* XL) and openings (*Thalassinoides*, *Parmaichnus*) against their distance from the coastline. Source area in the inset, centered on the barrier-island; burrow morphology after Dworschak (1987).

Fig. 8. *Thalassinoides* XL, as manifested by sediment mounds. (A) Density map of *Thalassinoides* XL (mounds). (B) A barrier-island (arrowed) separates the turbulent fore-barrier from the quieter back-barrier. Numerous sediment mounds characterize the back-barrier, here photographed at low tide. Quadrat for scale.

Fig. 9. Emergence time and density map of decapod burrows (*Thalassinoides*, *Parmaichnus*). A clear trend is evidenced: the longer the emergence time, the lower the burrow density. Burrow morphology based on Dworschak (1987, 2002).

Fig. 10. Occurrences of *Polykladichnus* and *Arenicolites* S within trench sampling. Both traces are abundant in the back-barrier, usually associated to algal turfs and microbial mats. Coordinates in metres. For graphical clarity, vertical drop lines have not been traced for *Arenicolites* S.

Fig. 11. *Arenicolites* XL. (A) *Arenicolites* XL with its tracemaker, a sipunculan worm. Burrow outlined with dashed line. (B) The typical environment of *Arenicolites* XL: fore-barrier with rippled sands. (C) *Arenicolites* XL, density map.

Fig. 12. *Arenicolites* L, density map.

Fig. 13. 'Squat burrows'. (A) Filamentous algal mat with numerous openings of 'squat burrows' produced by crabs. (B) Close-up of a filamentous mat with the opening of a 'squat burrow'. (C) Density map.

Fig. 14. Insect traces. (A) Top view of the microbial mat with numerous sediment piles, deriving from the burrowing activity of heterocerid coleopterans. The correspondent burrow is *Macanopsis*.

(B) After peeling off the topmost horizons of the microbial mat, numerous insect burrows are visible: *Helminthoidichnites* (He) and *Macanopsis* (Ma). (C) Profile view of two specimens of *Macanopsis*, produced by heterocerid coleopterans (arrowed).

Fig. 15. Microbial mats and their ichnofauna. (A) Stitched panorama of the tidal flat during lowering tide. Laminated microbial mats (fE: facies E) constitute topographical highs with respect to filamentous mats (fD: facies D) and muddy sands (fC: facies C). (B) *Macanopsis* colonizes the laminated microbial mats of the high intertidal, while *Helminthoidichnites* is more distal.

Fig. 16. *Skolithos* M. (A) The polychaete *Megalomma*, emerging from its burrow (*Skolithos* M) for suspension-feeding. (B) *Skolithos* M, profile view. Note the constructional lining.

Fig. 17. Distribution of the major morphotypes of *Skolithos* according to trench sampling. Base map from Fig. 1B.

Fig. 18. Association matrix. Each cell measures the probability of co-occurrence of two ichnotaxa, as expressed by the Jaccard similarity.

Fig. 19. The Ichnonetwork graph consists of a set of nodes (ichnotaxa) linked by a set of connections, each of which record the association between pairs of ichnotaxa. Edge colour and thickness proportional to the degree of association.

Fig. 20. Network topology. The illustrated graphs are fully equivalent to the ichnonetwork graph; layout has been adjusted to evidence topological patterns. (A) In the ichnonetwork context, node degree measures the number of ichnotaxa co-occurring with a given one. Detail of the network. (B) The ichnotaxa associated to a core ichnotaxon tend to be associated to each other. Detail of the network. (C) Bridge ichnotaxa tend to connect otherwise disconnected areas of the network.

Fig. 21. Methods for ichnoassociation mining. (A) The Infomap algorithm finds ichnoassociations by mapping the information flow. (B) Cluster analysis groups ichnotaxa into sets based on their degree of association. Note the correspondence with the groups evidenced in A. (C) Multidimensional scaling positions the nodes so that more associated ichnotaxa are closer in space; edges are not represented for graphical clarity. Circles are used to highlight the proximity, while a minimum spanning tree connects nearest neighbours.

Fig. 22. Environmental setting of the ichnoassociations derived from ichnonetwork analysis.

Fig. 23. Environmental setting of the ichnoassociations derived from quadrat sampling.

Fig. 24. Distribution of ichnoassociations along a land-sea transect. Bridge ichnotaxa not shown; transect corresponding to profile 2 in Fig. 1B.

Fig. 25. The Grado ichnological model. Each ichnoassociation is explained by the combination of four environmental factors: emersion time, hydrodynamics, substrate firmness and microbial binding.

Object of interest	Notes	Number of samples	Sample unit	Sampling scheme	Type of survey
Surface sediment mound	Corresponding to <i>Thalassinoides</i> XL	2622	0.25 m ²	Random	QUADRAT SAMPLING
Simple opening	Corresponding to <i>Thalassinoides</i> and <i>Parmaichnus</i>				
Paired openings with single fecal cast	Corresponding to <i>Arenicolites</i> XL				
Paired openings with radial fecal casts	Corresponding to <i>Arenicolites</i> L				
Large opening	Corresponding to 'squat burrow'				
Facies					
<i>Thalassinoides</i> <i>Parmaichnus</i> <i>Arenicolites</i> <i>Polykladichnus</i> <i>Macanopsis</i> <i>Monocraterion</i> <i>Skolithos</i> Mottling	Different morphotypes were distinguished when sampling	621	3 trenches within a 0.25 m ² area	Systematic sample traverse	TRENCH SAMPLING
Facies					
pH	SERA art .04310 FT11	10	0.25 m ²	Selected sites	ENVIRONMENTAL SAMPLING
NO ₂	Askoll nitrite test	10			
NO ₃	Askoll nitrate test	10			
PO ₄	Askoll phosphate test	10			
Salinity	D&D Seawater Refractometer	10			
Redox Potential	HANNA	10			
Redox Potential Boundary Layer depth		7			
Modified Brinell test		14 x 3 measures			
Emersion time		19			
Facies boundaries		5856	0.25 m ²	Geomorphologically controlled site distribution Selected sites	TOPOGRAPHICAL SAMPLING
Bathymetry		237			

Table 1. Sampling features.

Facies	Description	Environment
A – laminated sand	Tabular sand with parallel lamination, occasionally grading to homogeneous shelly sand with faint lamination. Small ripple patches may be found. Shell fragments often common.	Upper intertidal flats
B – rippled sand	Medium- to fine-grained sand with subordinate contributions of silt. Diagnostic presence of wave ripples with straight to sinuous crests.	Moderate-energy intertidal and subtidal
C – muddy sand	Grey-coloured sand with significant contributions of mud and vegetal debris. Sparse shelly bioclasts.	Protected lagoonal environment, intertidal to subtidal
D – filamentous mat	Muddy sand to sandy mud pervasively colonized by filamentous algae. Dispersed bioclasts.	Low-energy intertidal flats
E – laminated mat	Microbial mat represented by laminated sediments with an upper, organic-rich layer and a lower mineral-rich one. Very common structures related to growth (stabilized surfaces, biostabilized and levelled ripples), physical mat destruction (chips, erosional fringed edges, upcurled shrinkage cracks); presence of features linked with the metabolic activity (green and dark horizons).	Intertidal microbial mats
F – sandy firmground	Sandy firmgrounds with occasionally abundant bioclasts. Such deposits are often organized in decimetric layers.	Exhumation of dewatered sediments
G - gravel	Pebble-sized gravels with well-rounded clasts. Variable contribution of sands.	Exhumation of fluvial deposits; anthropic deposits

Table 2. Facies and depositional environments.

	Ichnotaxon	Amended description	Tiering depth	Dominant behaviour	Tracemaker
Branched structures	<i>Thalassinoides</i> XL	Burrow network with multiple openings	40 cm	Deposit feeding	<i>Pestarella candida</i> (Crustacea: Decapoda)
	<i>Thalassinoides</i> L	Burrow network with chambers filled by seagrass	20–40 cm	Deposit feeding	<i>Pestarella tyrrhena</i> (Crustacea: Decapoda)
	<i>Parmaichnus</i>	Y shaped burrow with swellings	20–40 cm	Suspension feeding, ?deposit feeding	<i>Upogebia pusilla</i> (Crustacea: Decapoda)
	<i>Polykladichnus</i>	I- or U-shaped burrow with Y-shaped bifurcations	5–10 cm	Deposit feeding, Suspension feeding	<i>Nereis diversicolor</i> (Annelida: Polychaeta)
U-burrows	<i>Arenicolites</i> XL	U-burrow	20–40 cm	Deposit feeding	<i>Sipunculus nudus</i> (Sipuncula: Sipunculidae)
	<i>Arenicolites</i> L	U-burrow	20–40 cm	Deposit feeding	<i>Sipunculus nudus</i> (Sipuncula: Sipunculidae)
	<i>Arenicolites</i> S	U burrow	3–10 cm	Deposit feeding Suspension feeding	<i>Corophium volutator</i> (Crustacea: Amphipoda)
Chambered burrows	'Squat burrow'	Squat burrow with terminal disc-shaped chamber	5–15 cm	Mating	<i>Carcinus maenas</i> (Crustacea: Decapoda)
	<i>Macanopsis</i>	Clavate burrow	2–7 cm	Feeding, sheltering, reproducing	<i>Heterocerus flexuosus</i> (Insecta: Coleoptera)
Winding structures	<i>Helminthoidichnites</i>	Unbranched horizontal burrow	<1 mm	Undermat mining	Dipteran larvae (Insecta: Diptera)
Simple structures	<i>Skolithos</i> L	Vertical burrow with 8-shaped opening	>15 cm	Suspension feeding	<i>Solen marginatus</i> , <i>Ensis ensis</i> , <i>Ensis minor</i> (Mollusca: Bivalvia)
	<i>Skolithos</i> M	Vertical burrow with constructional lining	10–15 cm	Suspension feeding	<i>Megalomma</i> sp. (Annelida: Polychaeta)
	<i>Skolithos</i> S	Vertical burrow	3–7 cm	?Suspension feeding	Worm-like organisms
	<i>Skolithos</i> XS	Vertical unlined burrow	1–5 cm	Sheltering	<i>Talitrus saltator</i> (Crustacea: Amphipoda)
	<i>Monocraterion</i>	Vertical burrow with funnel-shaped opening	10 cm	?Suspension feeding	Worm-like organisms
Miscellaneous group	<i>Lockeia</i> S	Almond-shaped burrow	3–5 cm	Suspension feeding	<i>Mactra coralline</i> , <i>Venus</i> sp. (Bivalvia: Venroidea)
	<i>Lockeia</i> XS	Almond-shaped burrow	<3 cm	Suspension feeding	<i>Abra alba</i> , <i>Donax trunculus</i> (Bivalvia: Veneroidea)
	Mottling	Indistinct bioturbation	1–40 cm	Rooting Locomotion	<i>Zostera marina</i> , <i>Zostera noltii</i> , <i>Cymodocea nodosa</i> (Magnoliophyta: Najadales), <i>Nereis diversicolor</i> (Annelida: Polychaeta)

Table 3. Morphological, ethological and taxonomical features of the here studied ichnotaxa. Based on Baucon and Felletti (2013).

Node	Degree	Betweenness Centrality	Clustering Coefficient
Skolithos S	12	15.150	0.5
Arenicolites S	10	6.117	0.6
Lockeia XS	9	4.033	0.667
Arenicolites XL + L	8	3.317	0.643
Thalassinoides XL +			
Parmaichnus	8	1.833	0.75
Polykladichnus	7	0.75	0.857
Helminthoidichnites	6	0	1
Macanopsis	6	0	1
Monocraterion	6	1.2	0.733
Thalassinoides L	6	0.4	0.867
Skolithos L	5	0.2	0.9
Mottling	4	0	1
Skolithos M	3	0	1
Lockeia S	0	0	0
Skolithos XS	0	0	0
NETWORK AVERAGE (with isolated nodes)	6	2.2	0.701
NETWORK AVERAGE (without isolated nodes)	6.923	2.54	0.809

Table 4. Metrics of the ichnonet graph.

	Step	Software	Operation	Command
GEOSTATISTICAL ANALYSIS	1. Data preparation	Libre Office Calc	Open the quadrat sampling file and copy data	[File>Open] [Edit>Copy]
		PAST	Paste data into PAST	[Edit>Paste]
	2. Point map	PAST	Select three columns (X, Y and one ichnotaxon), then plot values	Shift-click on column label to select multiple columns, then [Plot>Bubble Plot]
	3. Variogram	PAST	Select three columns (X, Y and one ichnotaxon), then analyze them	Shift-click for multiple selection, then [Geomet>Gridding] and select [Kriging] and click [Semivariogram]
4. Interpolation	PAST	Fit the variogram model and interpolate	Modify the values of the variogram dialog, then choose [Go!]	
NETWORK ANALYSIS	1. Data preparation	Libre Office Calc	Open the quadrat sampling file and copy data	[File>Open] [Edit>Copy]
		PAST	Paste data into PAST	[Edit>Paste]
	2. Create the association matrix	PAST	Transpose the data, then calculate the association matrix for ichnotaxa	[Edit>Transpose] Shift-click for multiple selection, then [Statistics>Similarity and distance indices> Index=Jaccard]
	3. Export the association matrix	PAST	Copy the association matrix	Click on the rightmost icon of the dialog
		Libre Office Calc	Paste it into a Libre Office spreadsheet	[Edit>Paste]
	4. Data setup	Libre Office Calc	Use first row and first column to store node names. Save as a semicolon-delimited csv file	[File>Save as...], then check the [Edit Filter Settings] box. Choose the semicolon as field delimiter. Make sure that the csv file uses full stop as the decimal separator
	5. Open data	Gephi	Open the previously saved file with Gephi.	[File>Open] and select the Undirected option
	6. Ichnonet Graph	Gephi	Use the Circular Layout	[Overview>Layout>Circular Layout] If Circular Layout is not available, download it: [Tools>Plugins>Available Plugins: Circular Layout] [Preview>Presets>Default Curved], then click on Refresh
	7. Network analysis	Gephi	Network analysis is accessed from the ranking panel, after running the statistics dialogs	
	8. Infomap	Gephi	Save the network in pajek (net) format:	[File>Export>Graph File]
www.mapequation.org/		Load the network and run the Infomap algorithm	[Map Generator>Load Network>Open File (for undirected network)] [Calculate Clusters]	
9. NMDS	PAST	Perform non-metric multidimensional scaling	[Multivar>Non-Metric MDS: Jaccard]	
10. Cluster analysis	PAST	Perform cluster analysis	[Multivar>Cluster Analysis: Jaccard]	

Table 3. IchnoGIS analysis with free software: Libre Office (<http://www.libreoffice.org/>), PAST (<http://folk.uio.no/ohammer/past/>), Gephi (<https://gephi.org/>) and www.mapequation.org. Each step is the output for the successive one. This example assumes two spreadsheets with quadrat and trench sampling data; ichnotaxa and coordinates are stored in columns, sampling sites in rows.

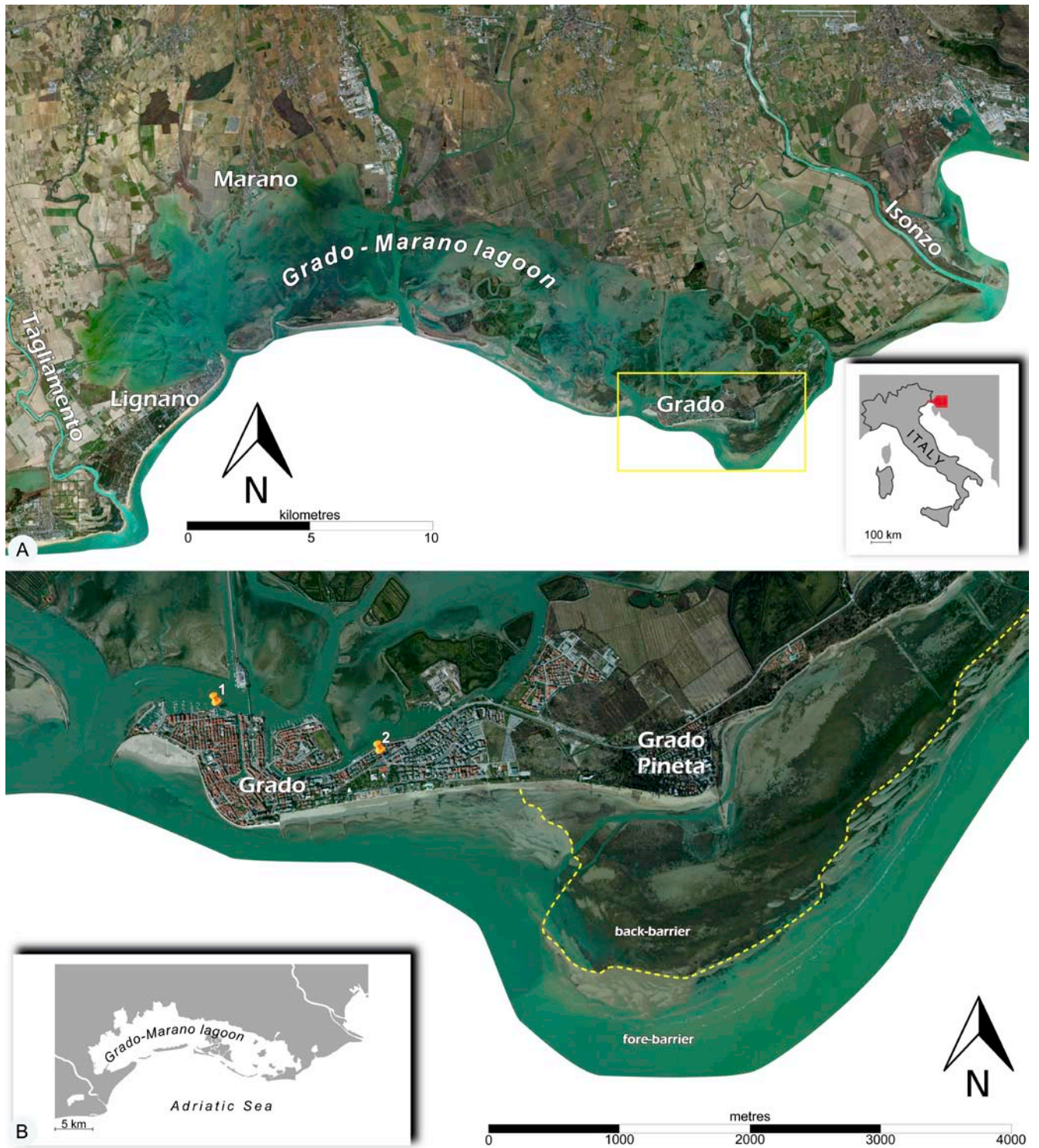


Fig. 1.

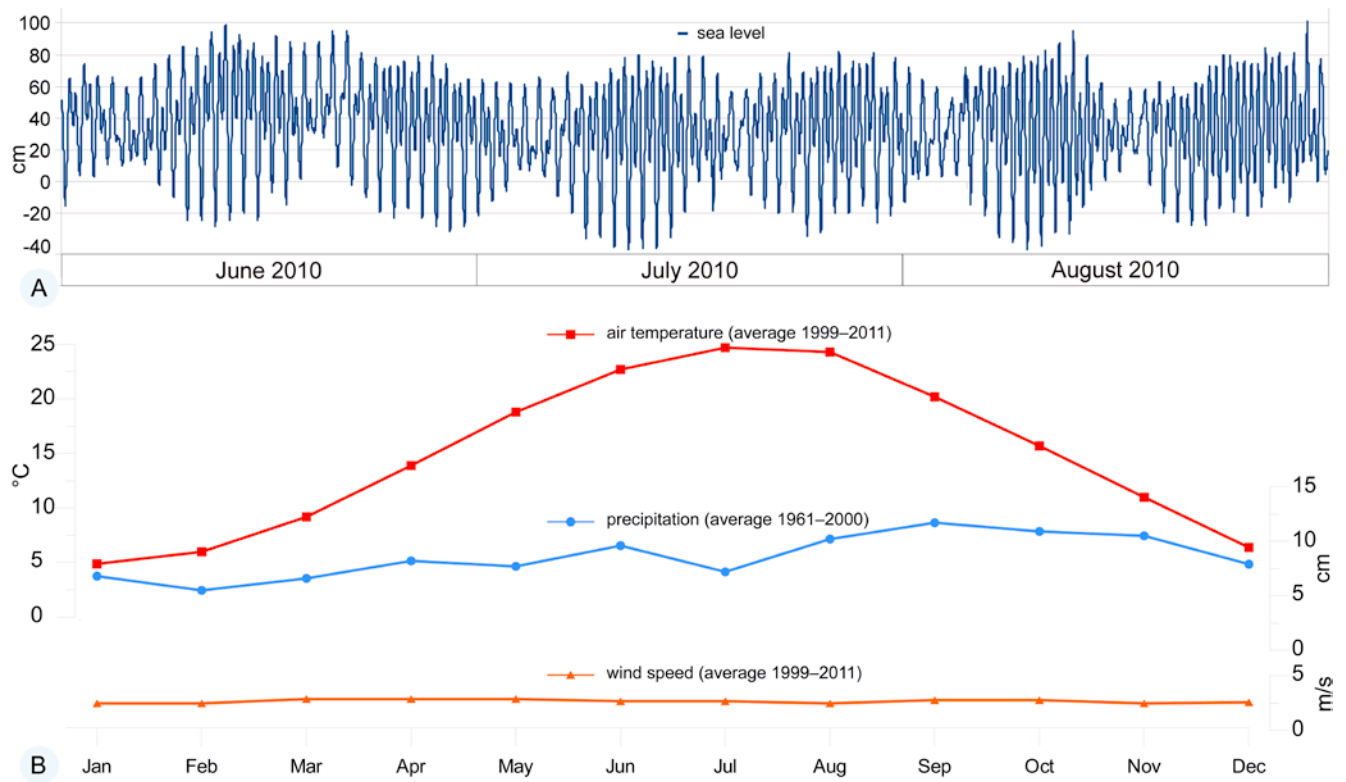


Fig. 2.

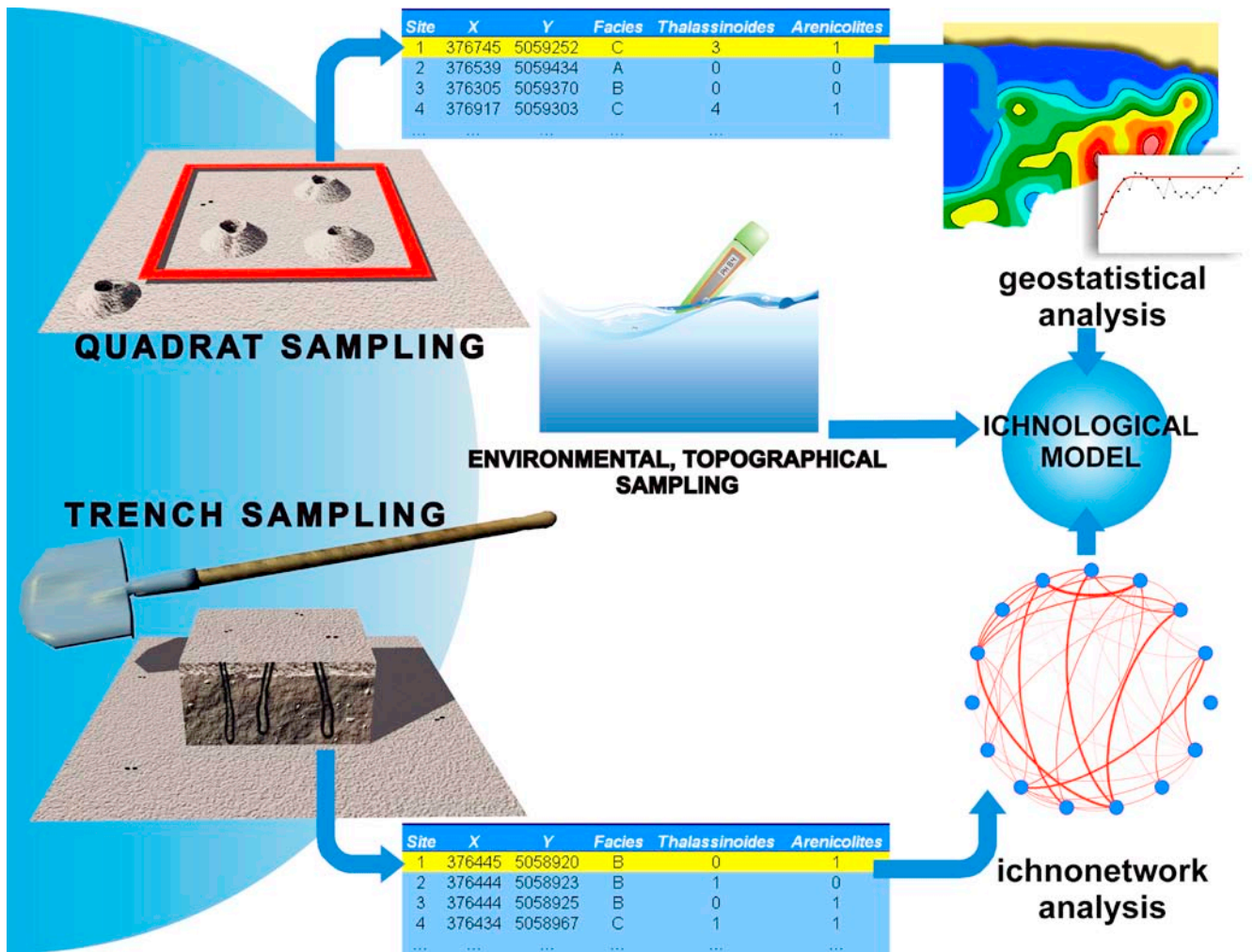


Fig. 3.

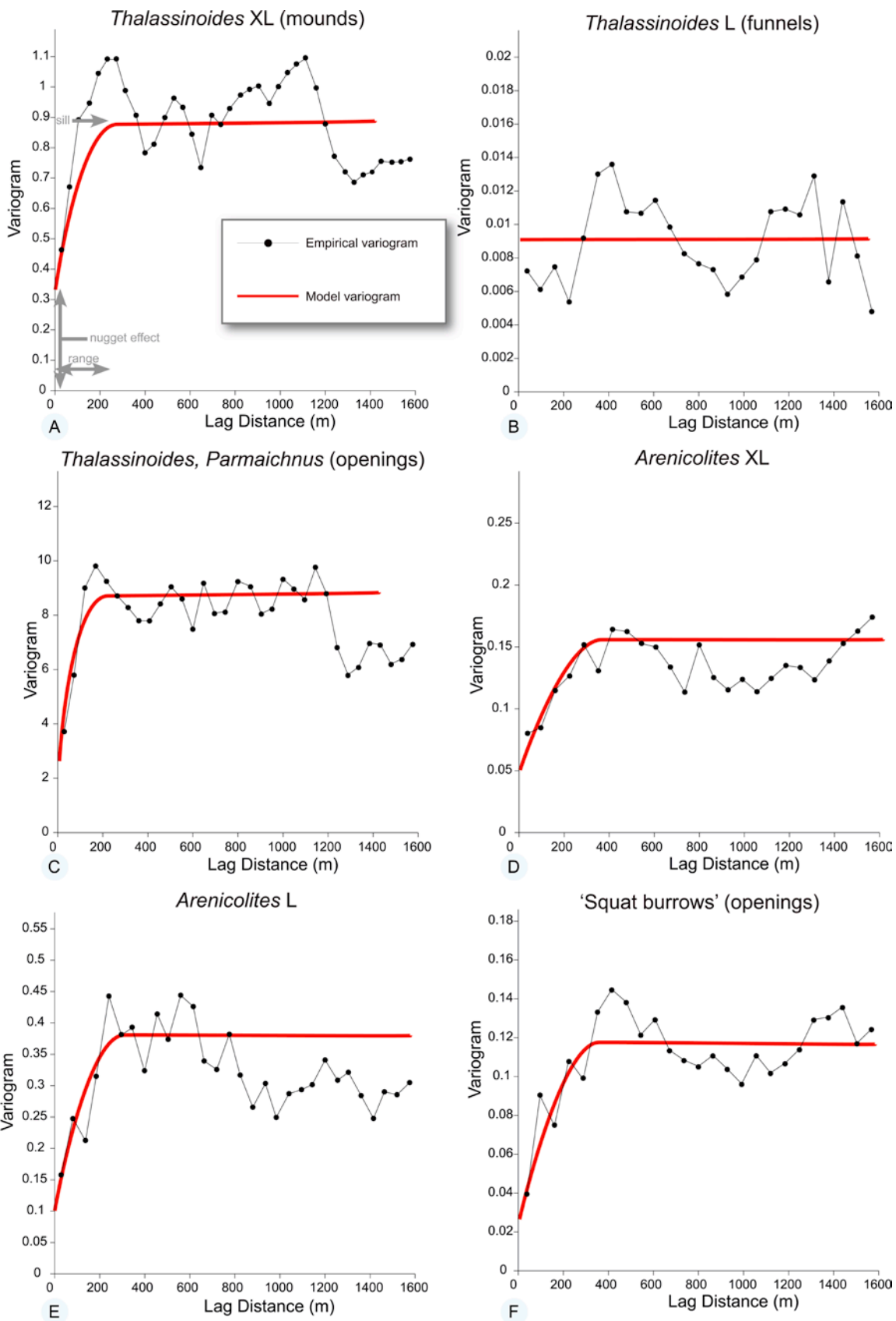


Fig. 4.

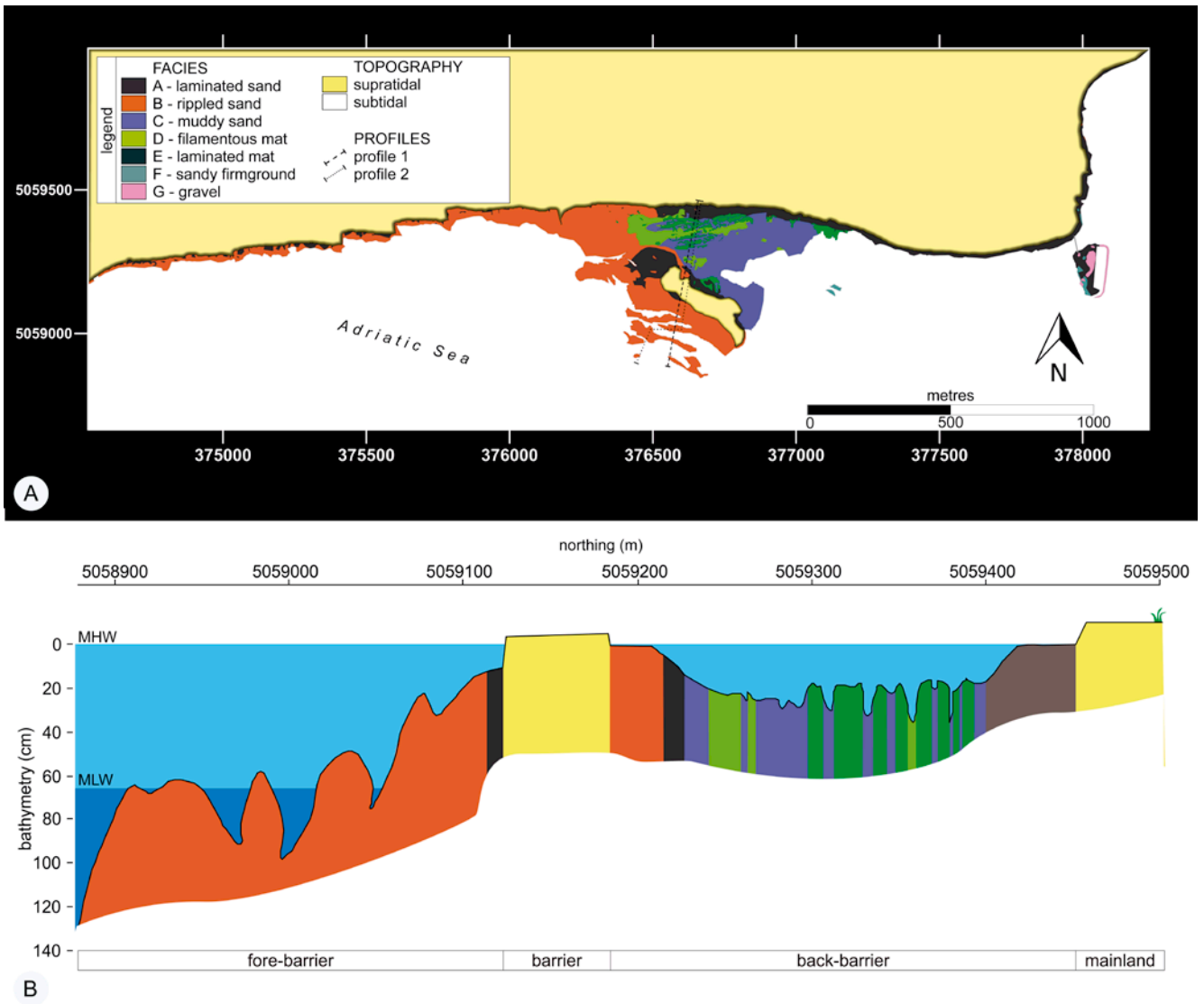


Fig. 5.



Fig. 6.

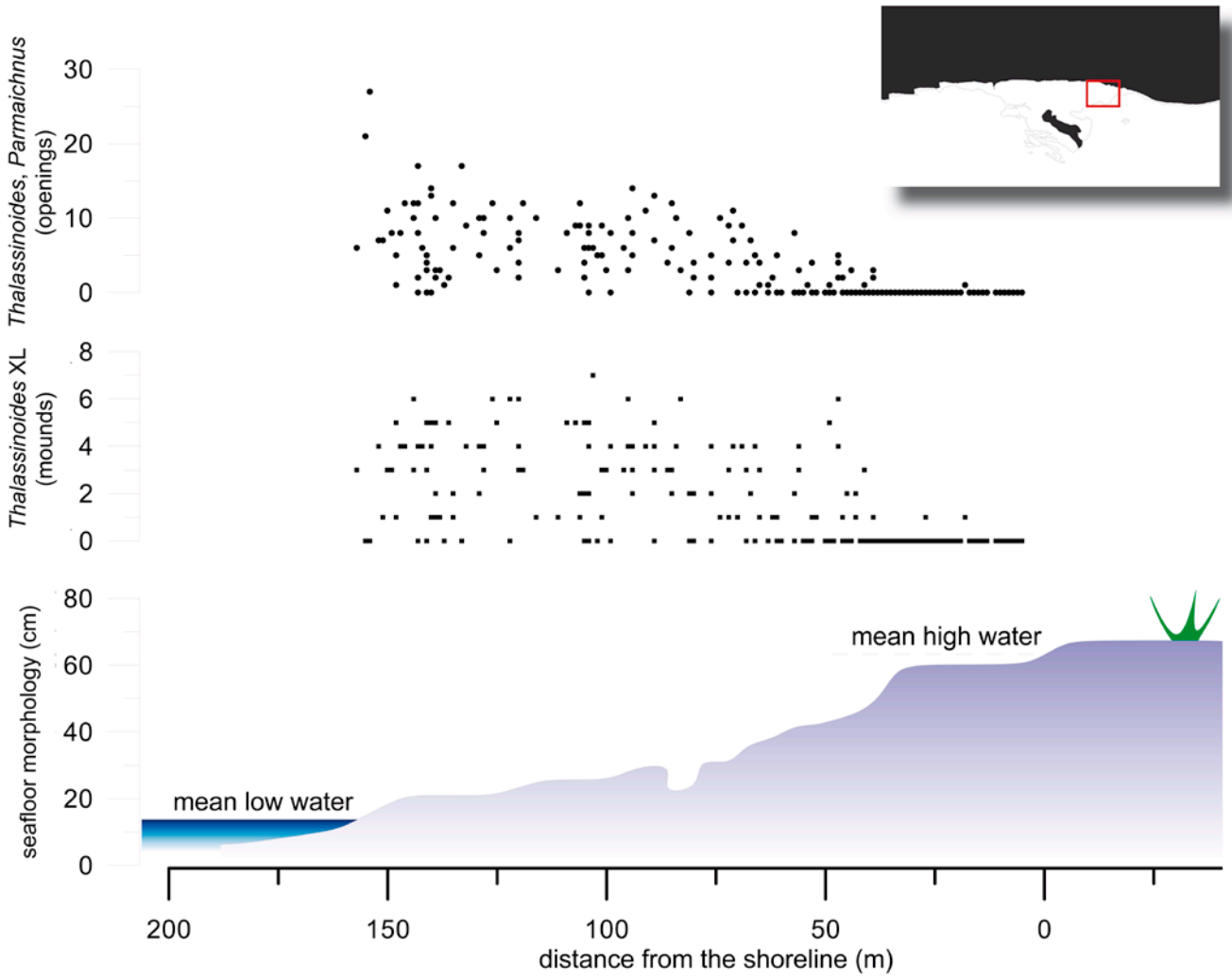


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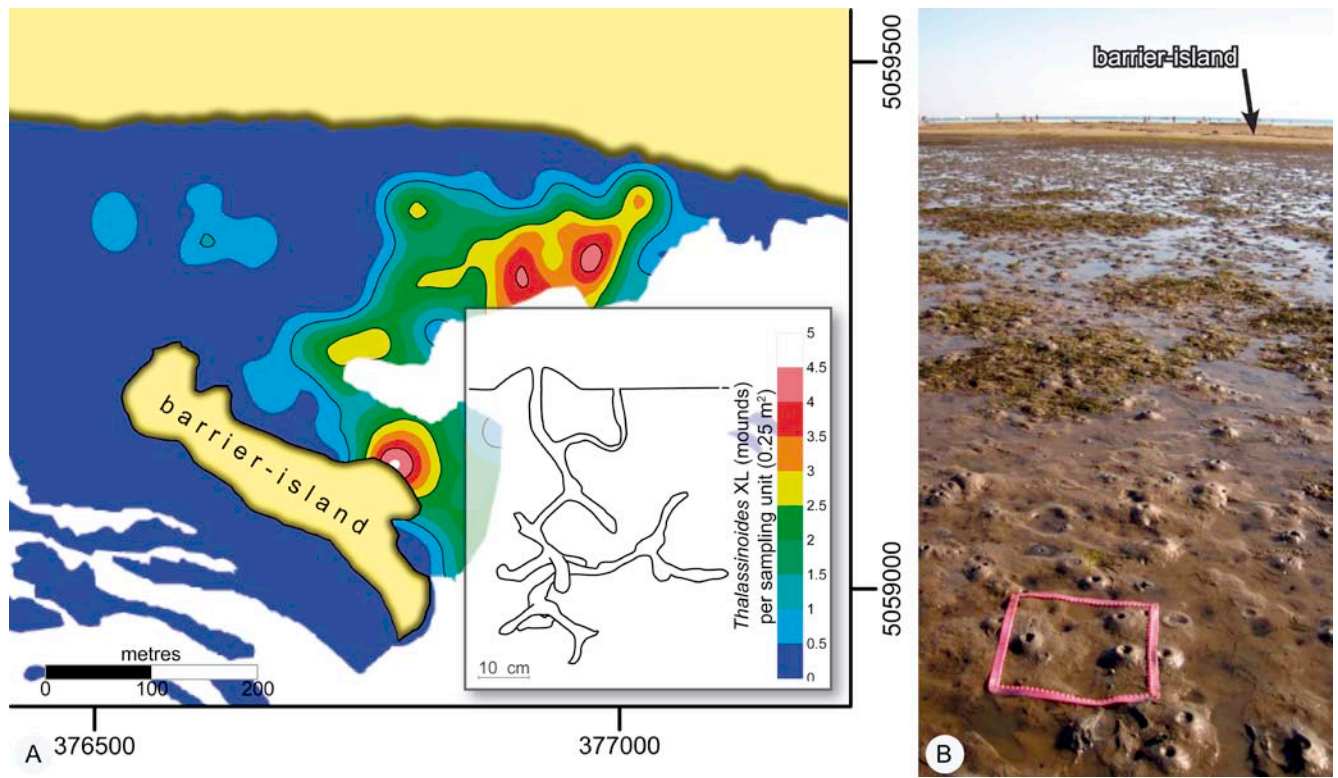


Fig. 8.

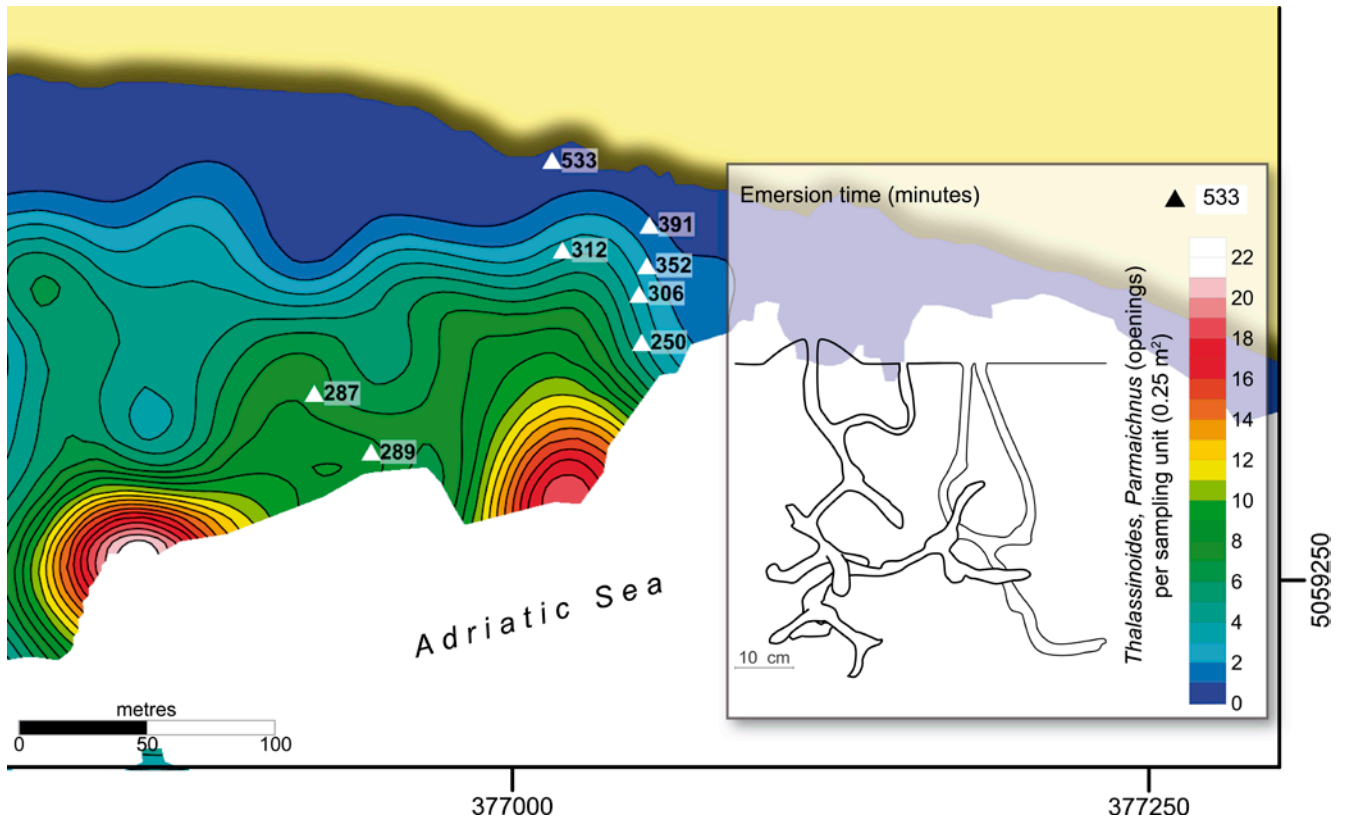


Fig. 9.

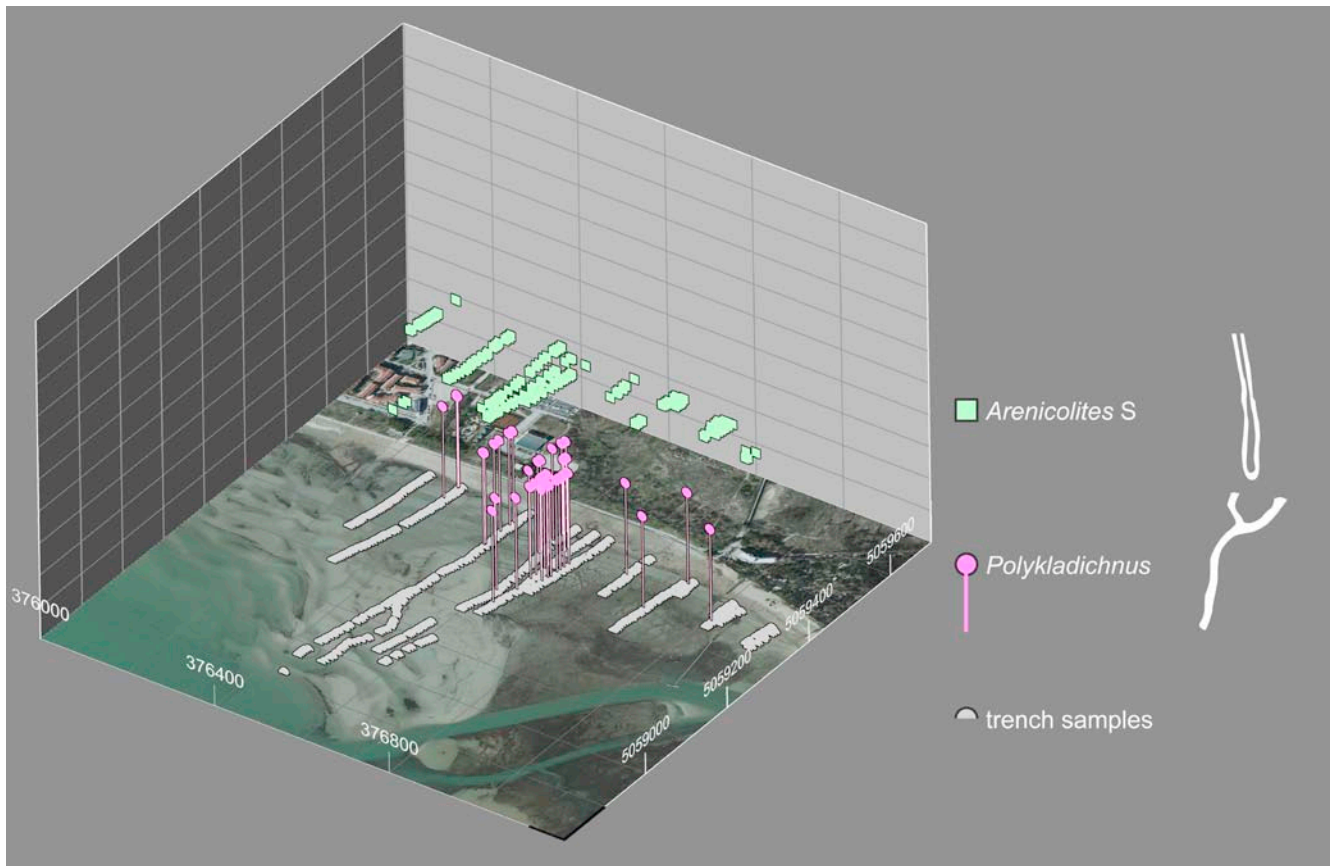


Fig. 10.

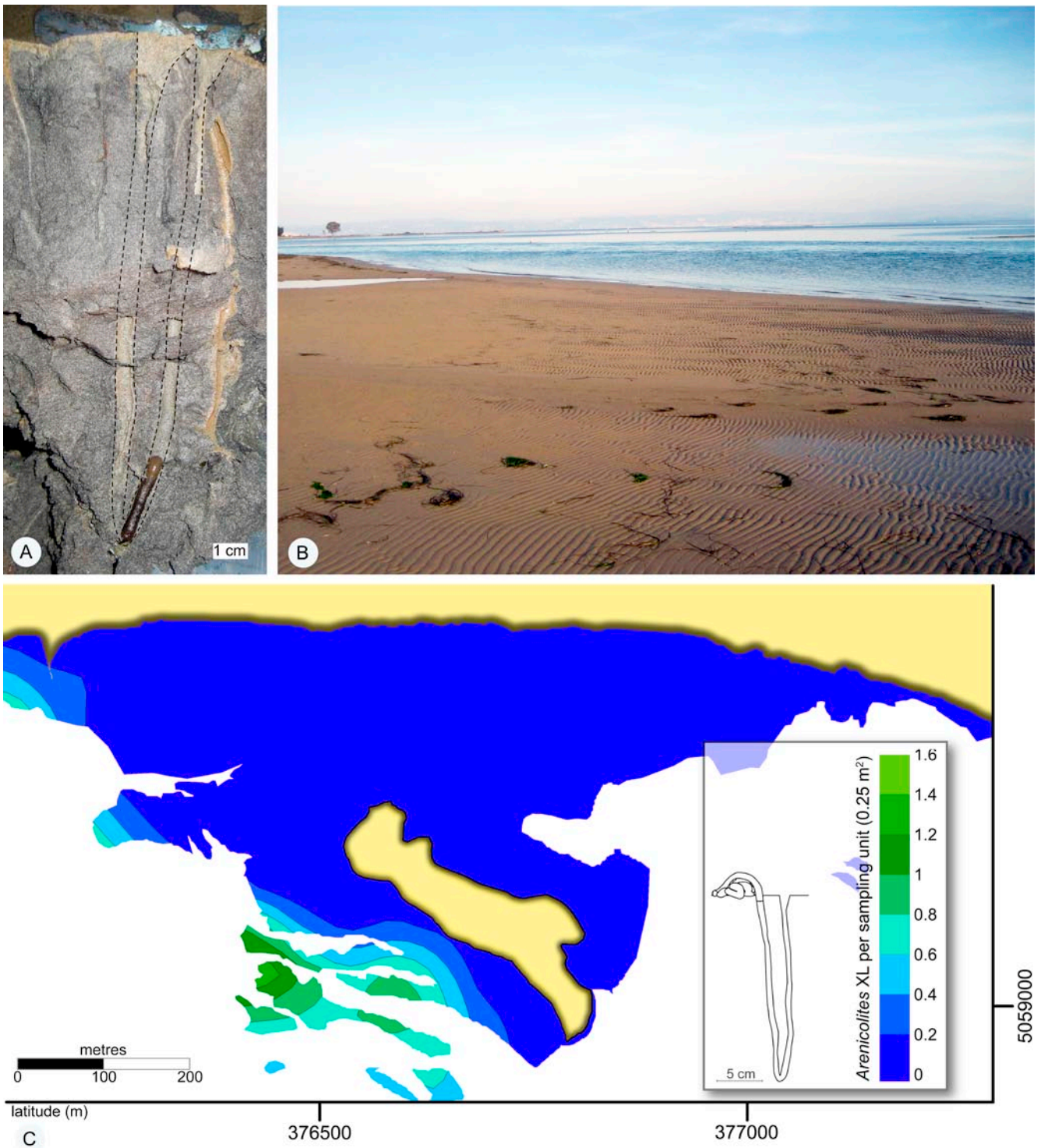


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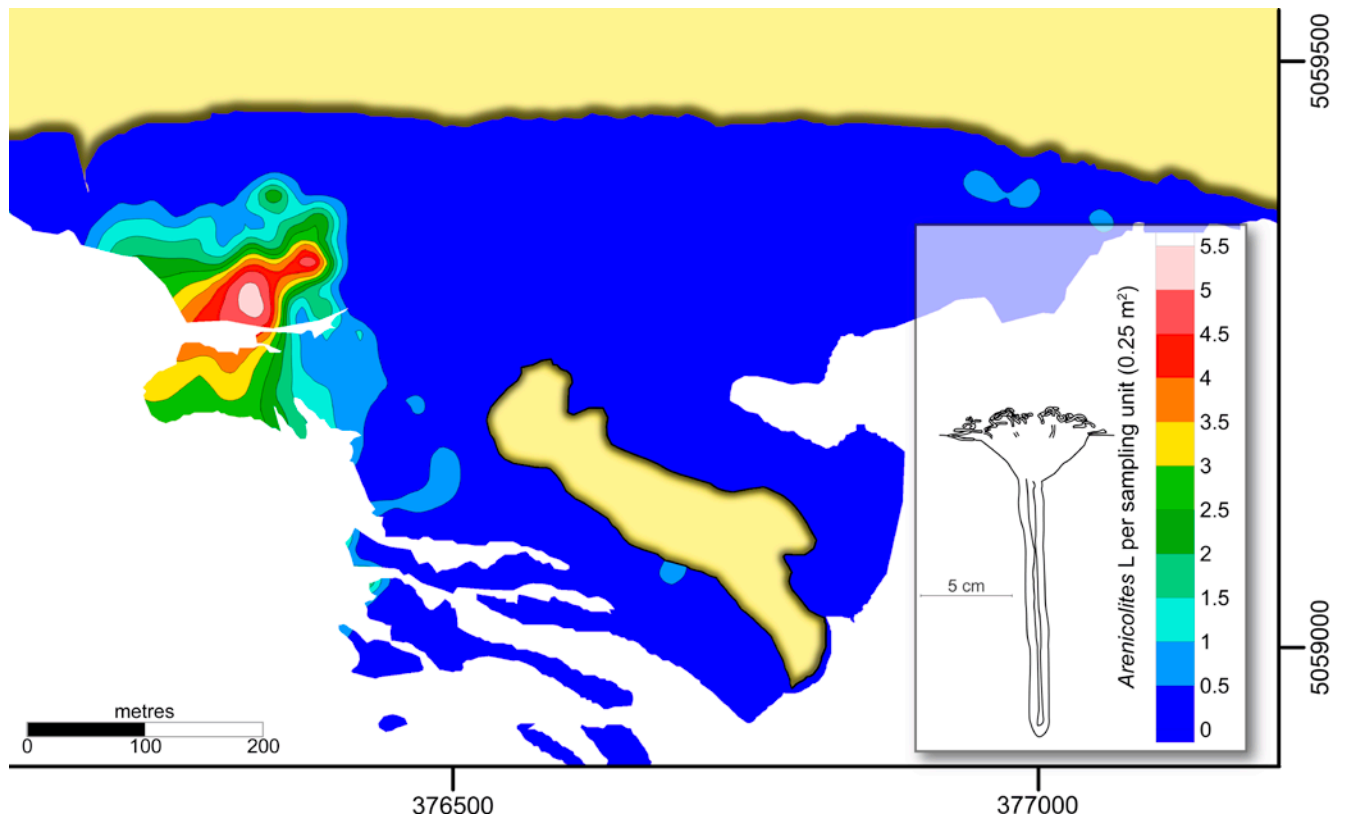


Fig. 12.

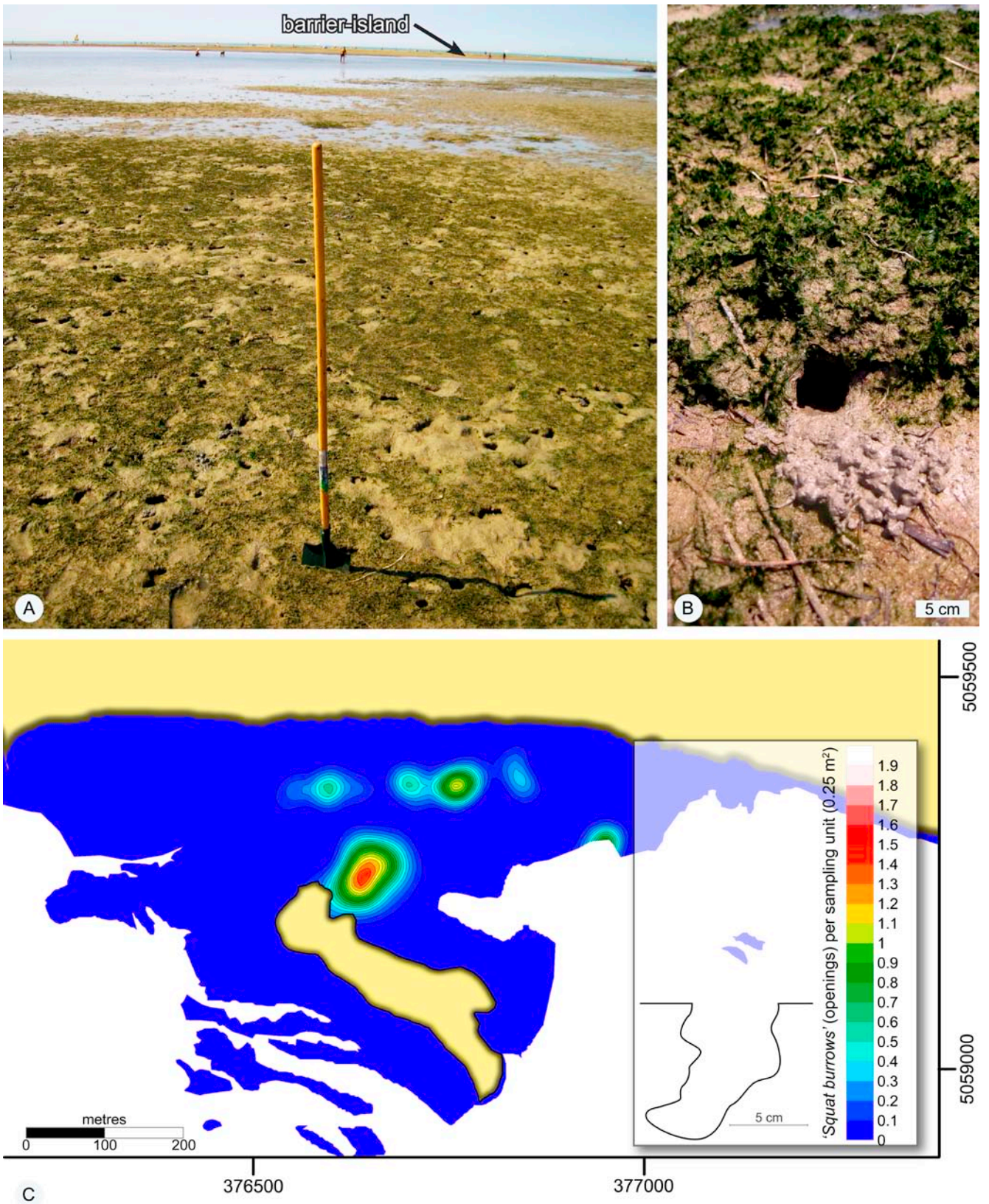


Fig. 13.

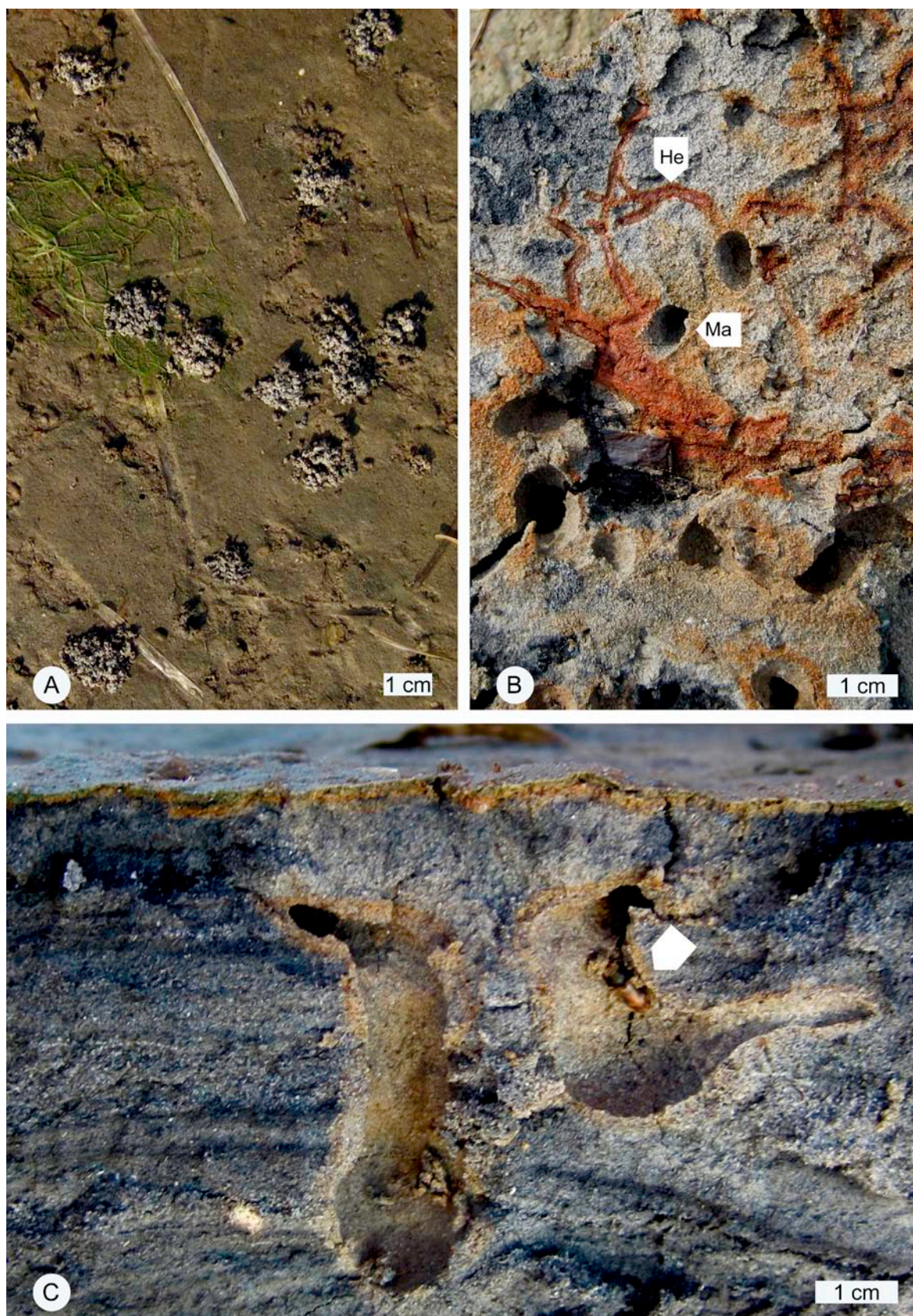


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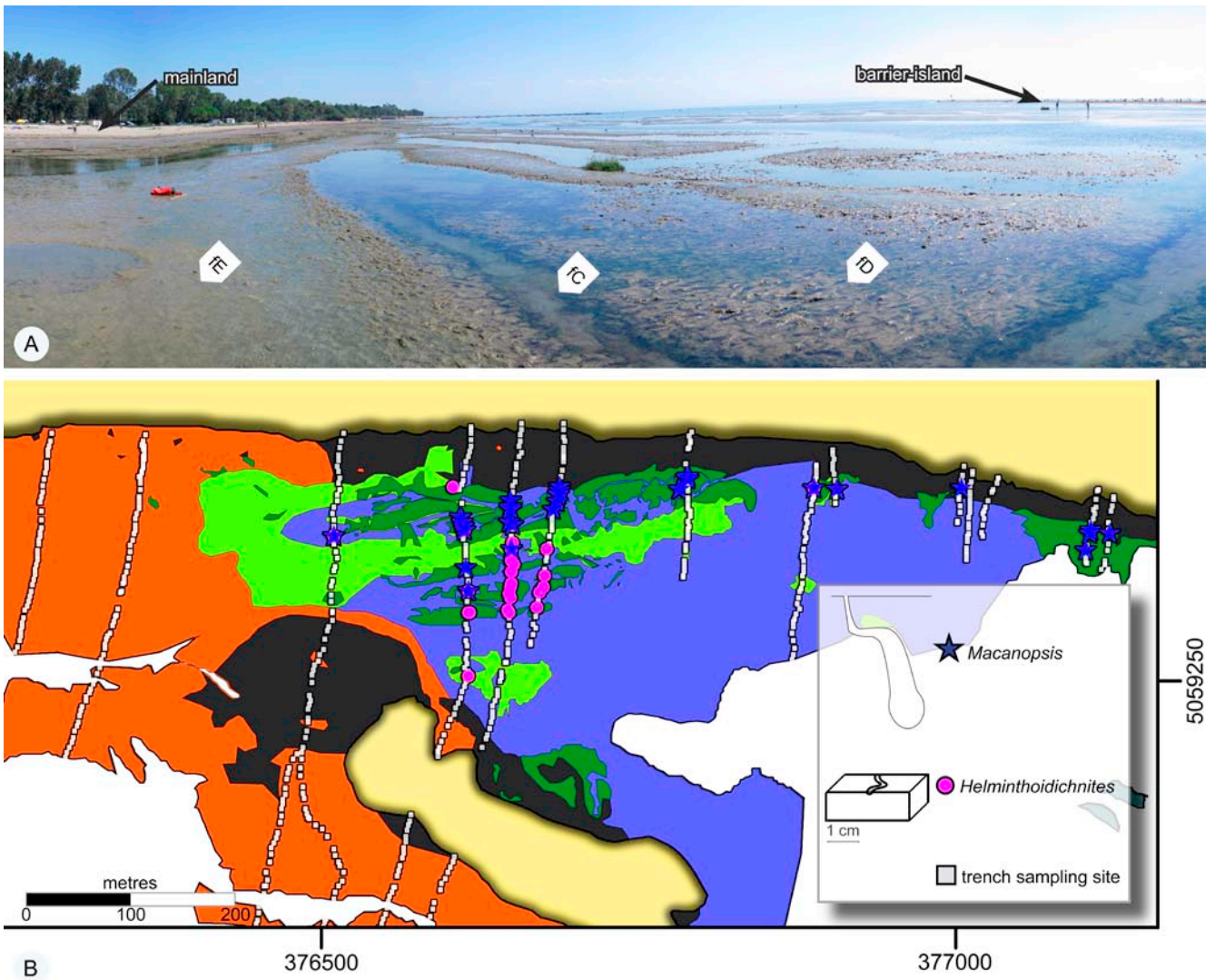


Fig. 15.

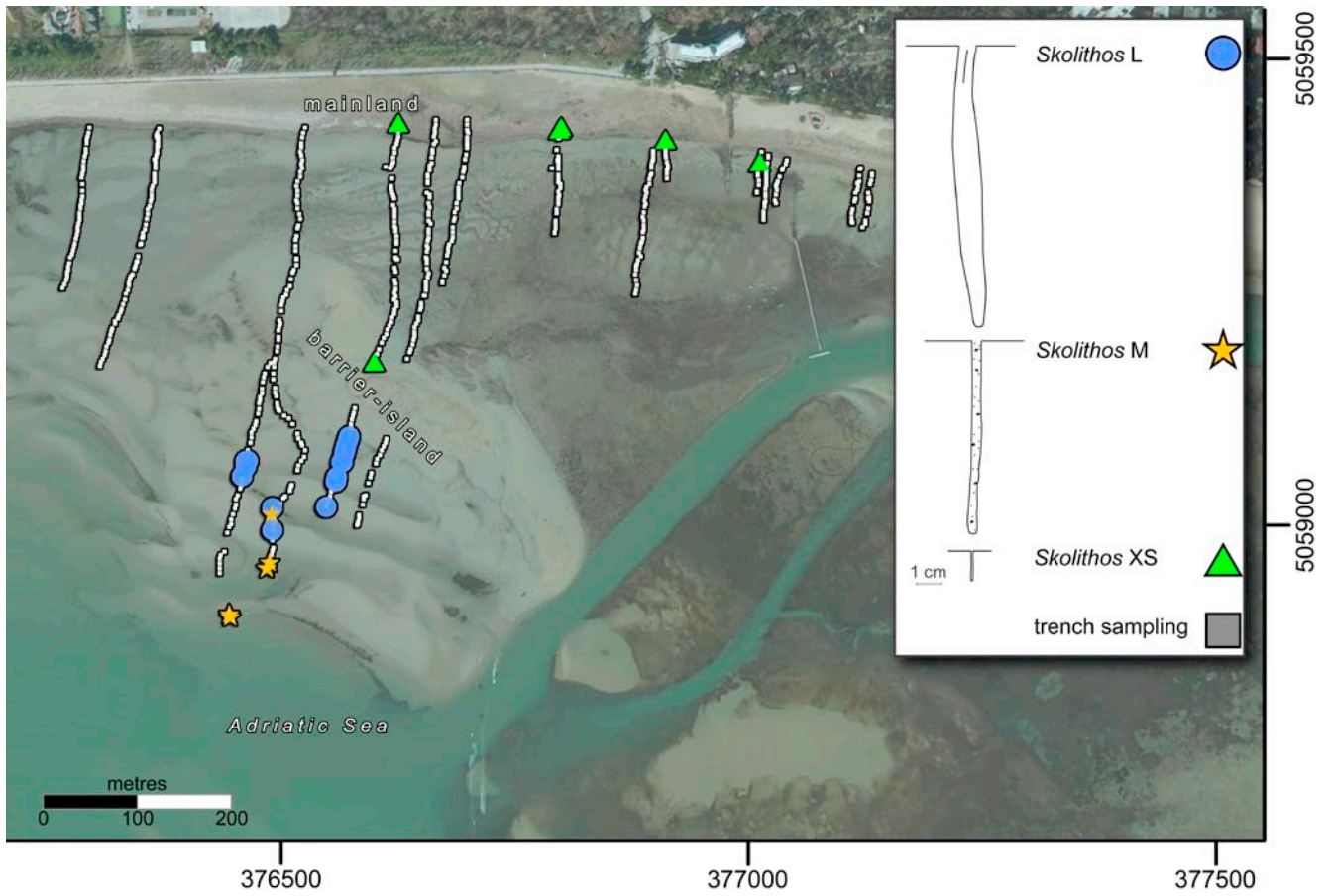


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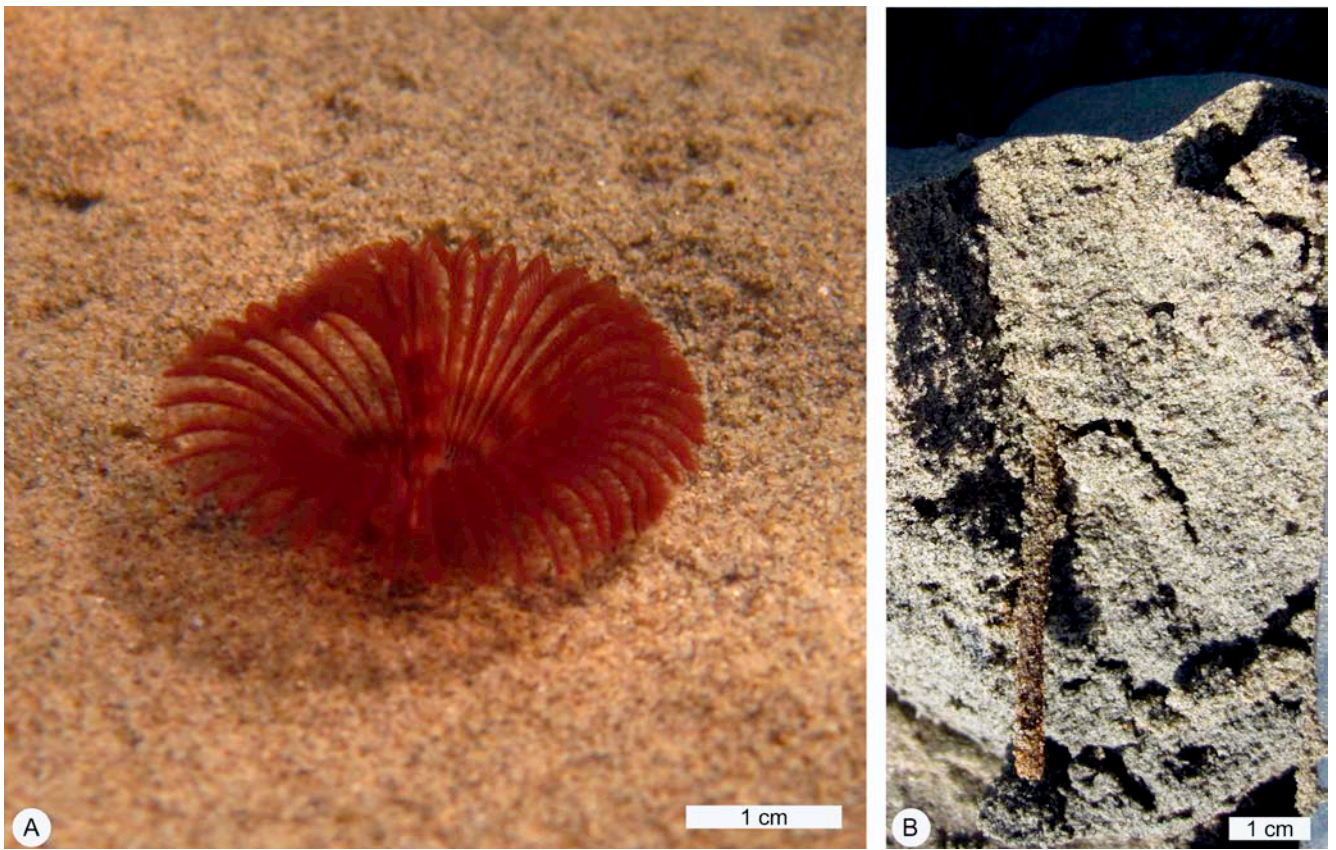


Fig. 17.

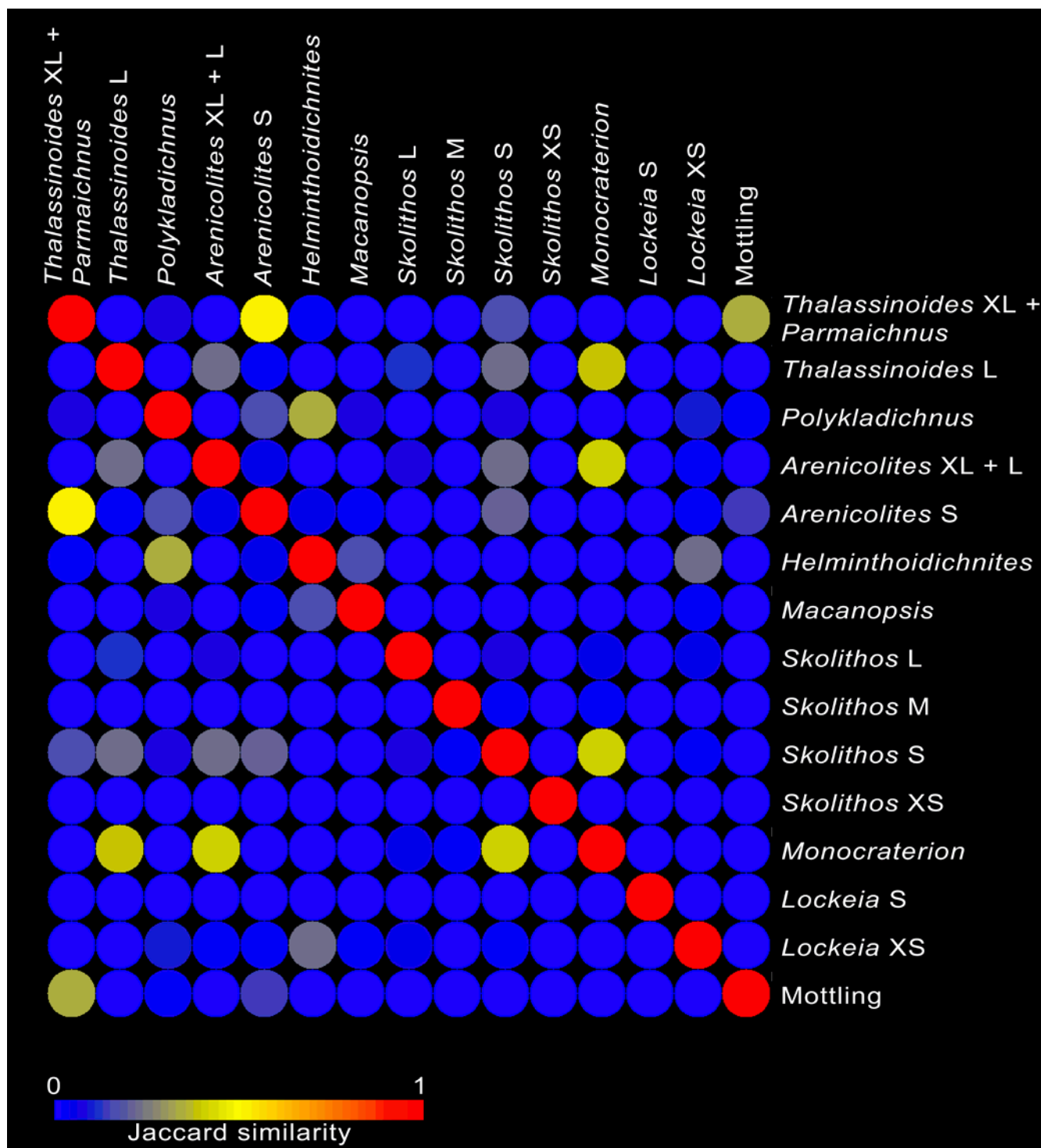


Fig. 18.

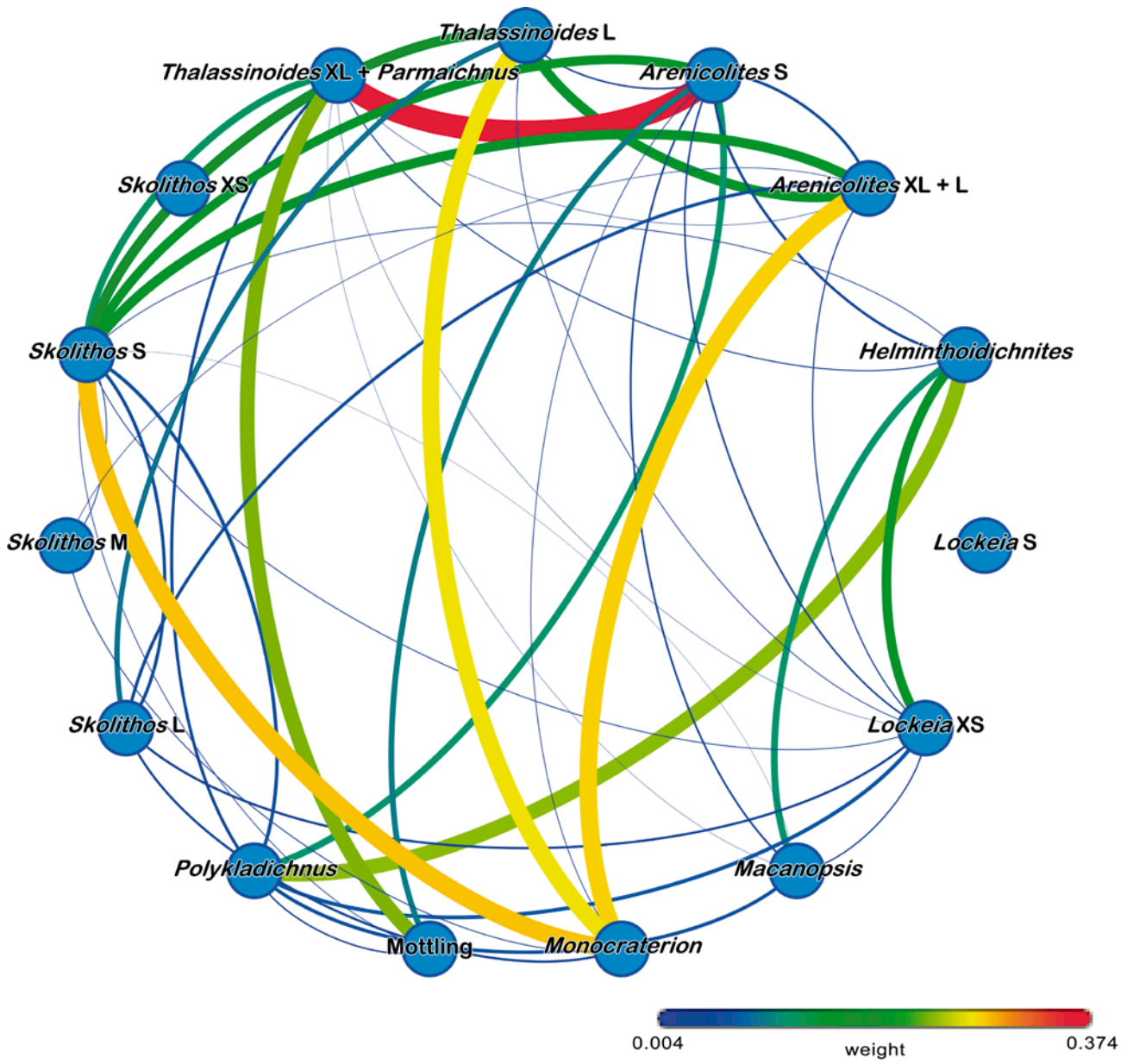


Fig. 19.

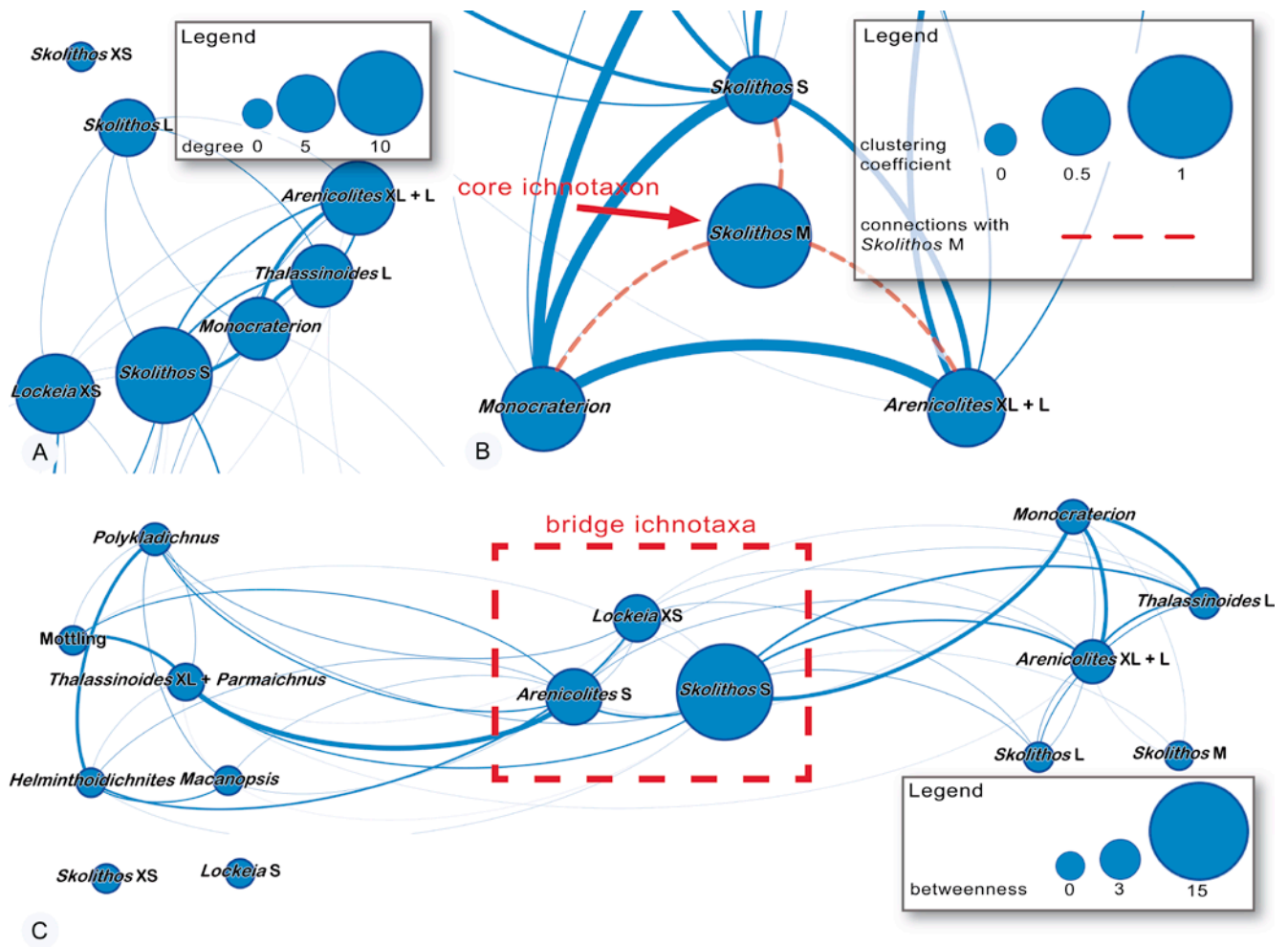


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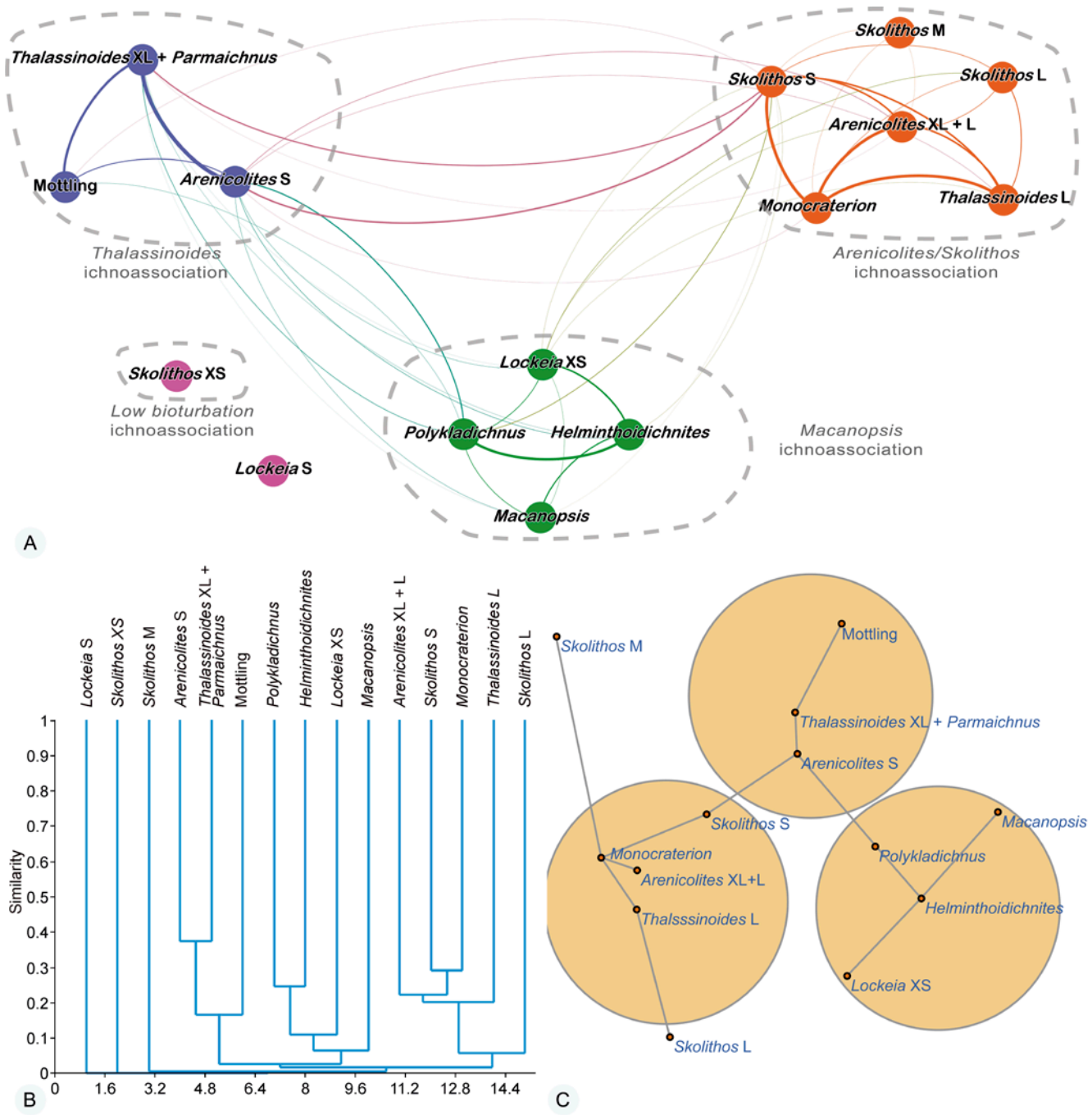


Fig. 21.

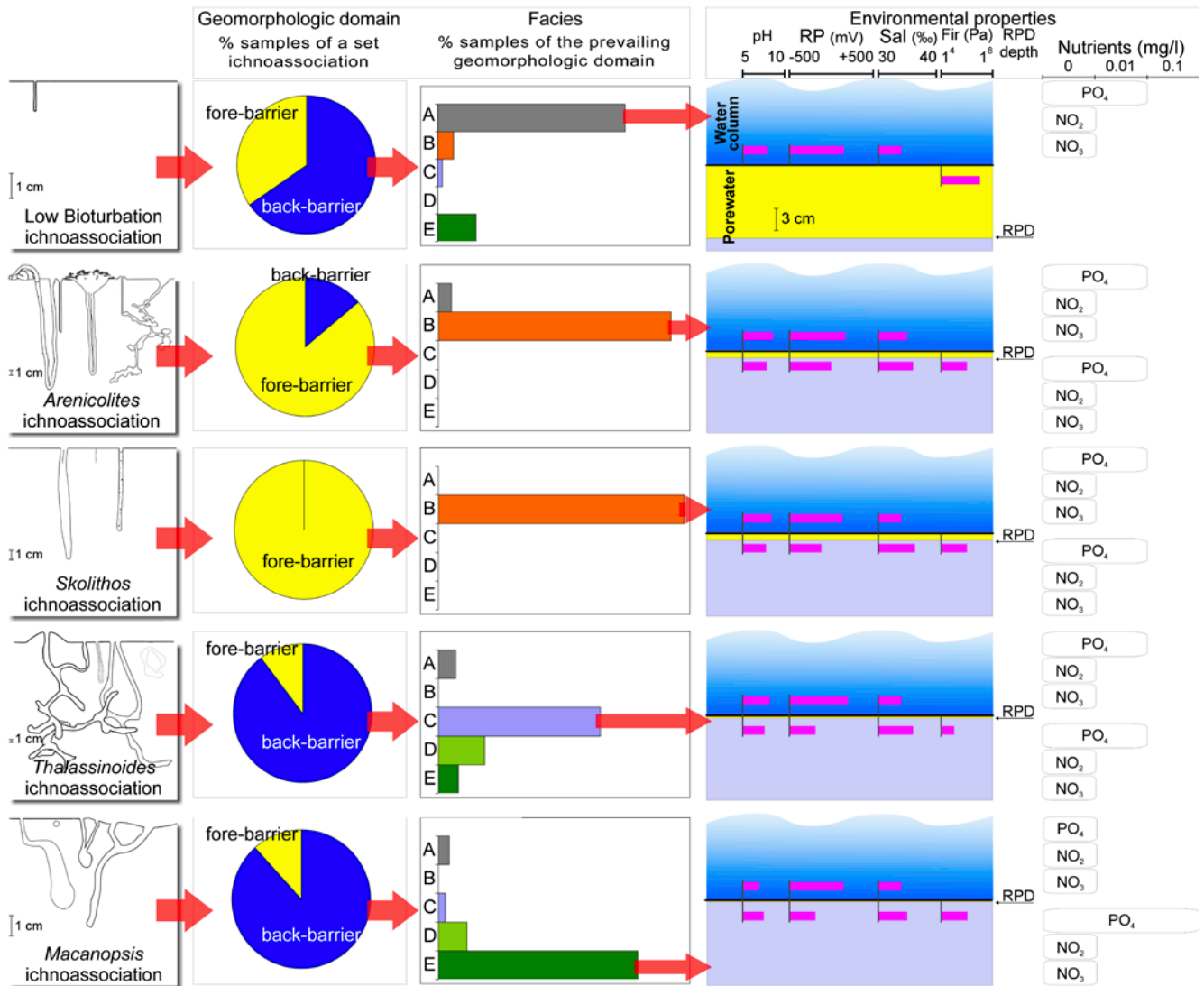


Fig. 22.

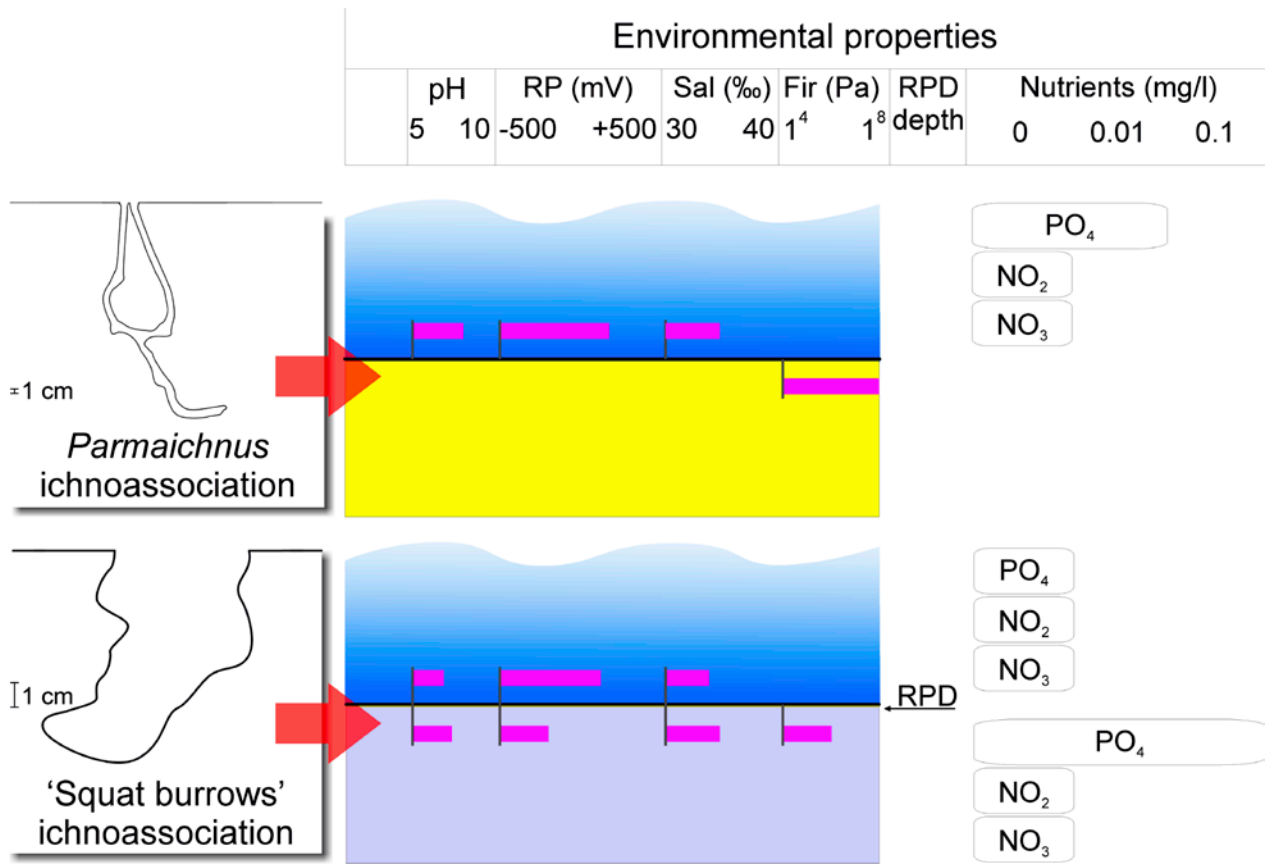


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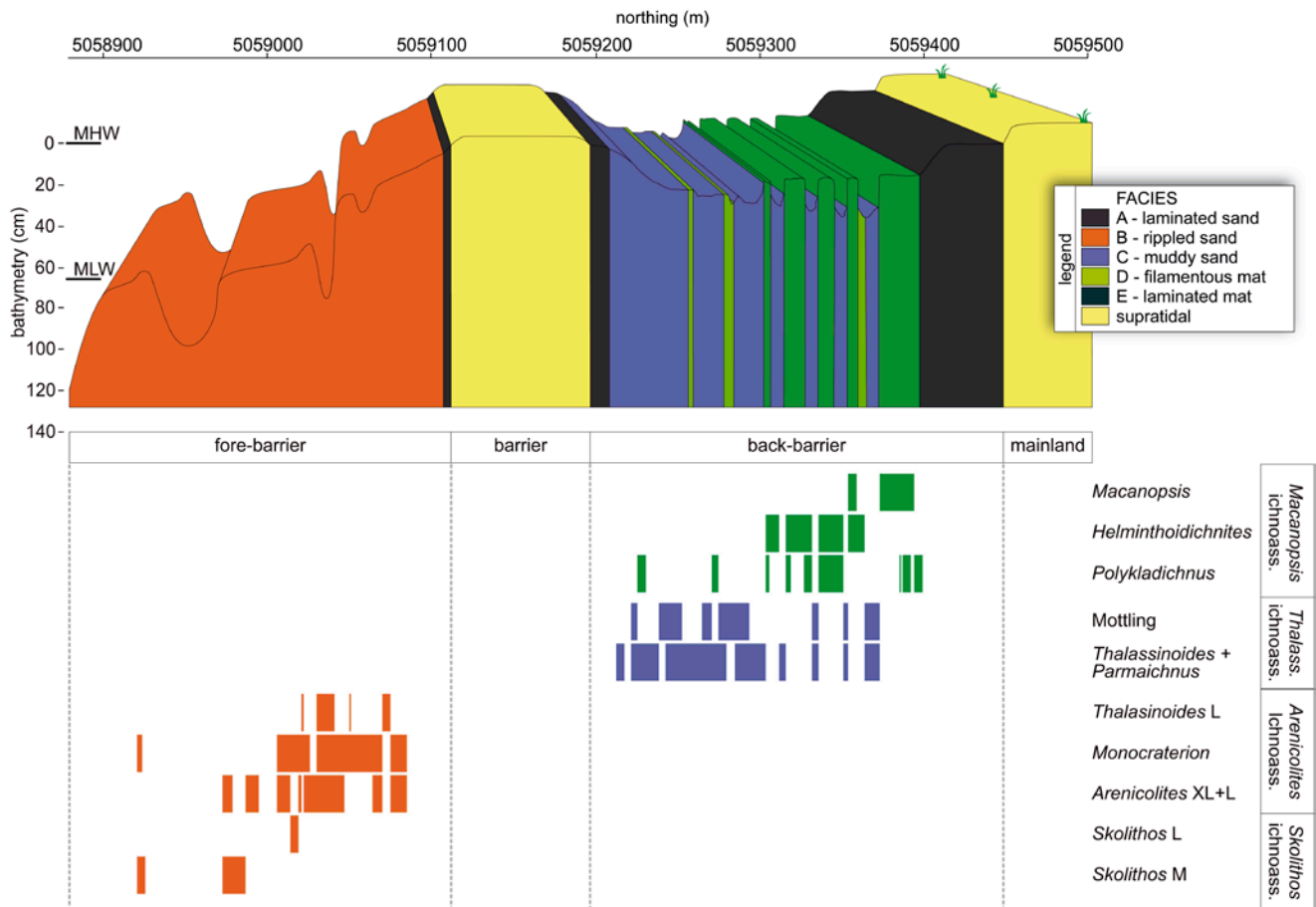


Fig. 24.

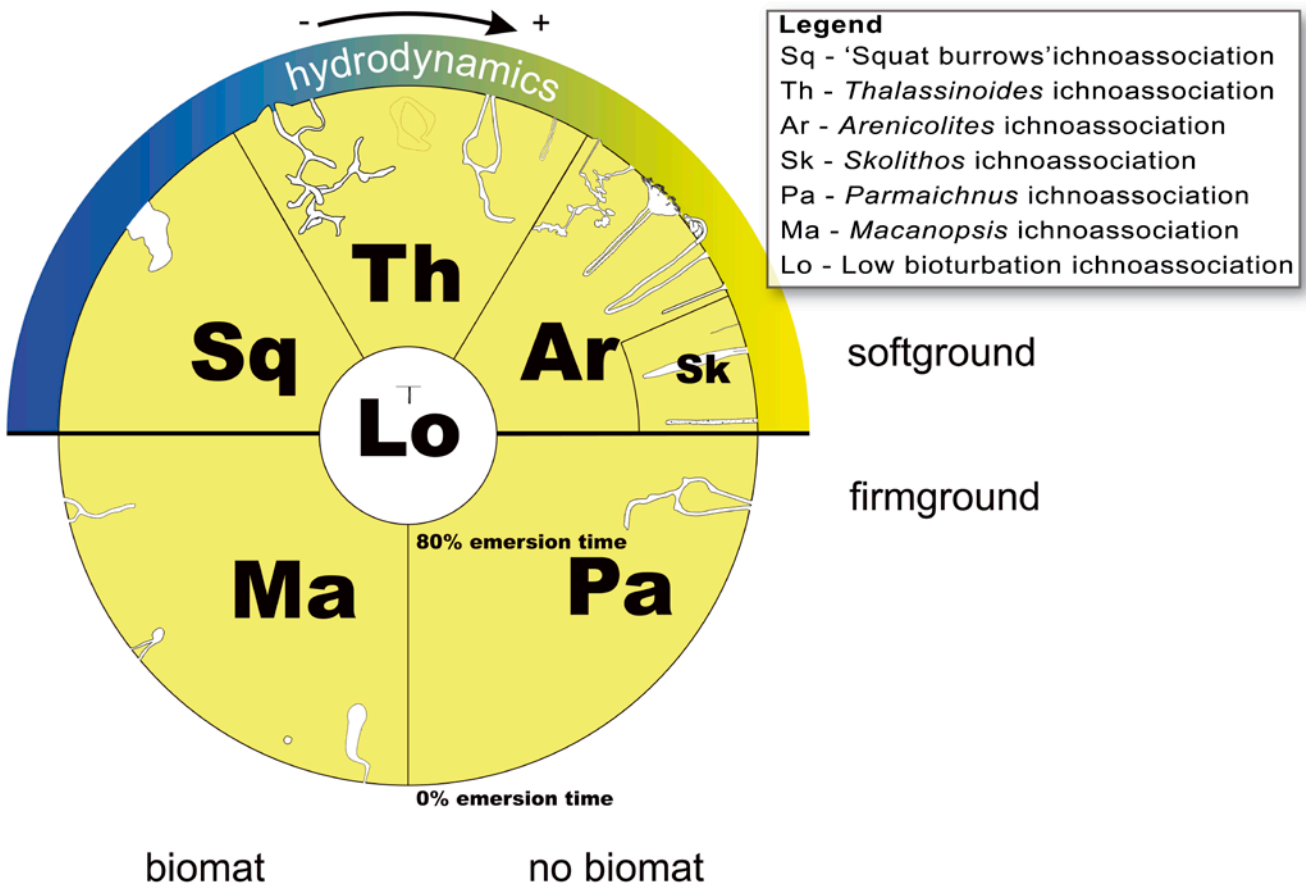


Fig. 25.

Chapter 3

3.3 Does the IchnoGIS method work? Prediction performance at the Mula di Muggia (Northern Adriatic, Italy).

Baucon, A., Felletti, F. 2014. Does the IchnoGIS method work? Prediction performance at the Mula di Muggia (Northern Adriatic, Italy). IAS Special Publications (accepted manuscript).

DOES THE ICHNOGIS METHOD WORK? A TEST OF PREDICTION PERFORMANCE AT THE MULA DI MUGGIA (NORTHERN ADRIATIC, ITALY)

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ABSTRACT

The purpose of the present study is to evaluate the performance of the IchnoGIS method, which is a high-resolution framework to capture, manage, analyse and display geographically referenced ichnological data. By surveying neoichnological, sedimentological and environmental variables, the IchnoGIS method allows users to identify the environmental factors controlling the distribution of modern ichnoassociations. If the IchnoGIS method holds what it promises, then it should be possible to predict environmental parameters directly from ichnoassociations. Based on this hypothesis, the prediction performance of an ichnological model derived from the IchnoGIS method (Grado Model) was tested against a real-world situation: the Banco della Mula di Muggia (Northern Adriatic, Italy). The study site is a shallow-water microtidal system consisting of a sheltered zone protected by elongated sand ridges (bars, barrier islands). The performance test proceeded by first assessing the potential distribution of environmental parameters on the basis of both the ichnoassociations and the Grado model. Thereafter, the performance of the model was evaluated successively from its success at predicting environmental parameters. The results of the performance test show that the model is able to predict modern environmental parameters from neoichnological data. It is suggested that the IchnoGIS method may have great potential for the interpretation of ancient sedimentary sequences.

Keywords Ichnology, Adriatic Sea, network analysis, geostatistics, barrier islands

INTRODUCTION

Biogenic sedimentary structures generated in tide-influenced environments commonly have a good preservation potential in the geological rock record (Gingras & MacEachern, 2012; Gingras *et al.*, 2012). As traces are manifestations of biologic behaviour and this behavior, in turn, is a function of the environment, they can be used to assess the environmental conditions concurrent with their formation (Seilacher, 2007). In modern tidal environments, traces and associated behaviour can be directly observed together with the local environmental variables which, as a consequence, provide a solid basis for palaeoenvironmental analysis.

In light of these assumptions, a new method for ichnological analysis (IchnoGIS) based on geostatistics and network analysis has recently been developed (Baucon & Felletti, 2012, 2013a, 2013b). Its application to modern intertidal flats revealed a predictive capacity which suggested that environmental variables could be derived from ichnological features. The

question therefore arose to what extent this observation could be generalized, i.e. whether the IchnoGIS method produced realistic results in all kinds of environmental settings. Thus, if a predicted scenario is consistent with observations, then the method can in principle be regarded to work. Based on this hypothesis, the purpose of the present study was to test the validity of the IchnoGIS method by evaluating its prediction performance in the shallow subtidal Mula di Muggia system (Adriatic Sea, Italy). A successful outcome of the test would have important implications not only for the analysis and understanding of modern tidal systems but potentially also for the reconstruction of palaeoenvironmental parameters from trace fossils.

GEOGRAPHICAL SETTING

The study area is located in the Northern Adriatic Sea (Italy), on the seaward margin of the Grado barrier island/lagoon system (Fig. 1). More precisely, the predictive model was derived from observations on the intertidal flats lining the coast between Grado and Grado Pineta (model area)

adjacent to a shallow subtidal zone surrounding the intertidal Mula di Muggia sandbank (test area). In correspondence, the model has been named ‘the Grado model’ (Baucon & Felletti, 2013b).

Both the test and the model area are part of the same marginal-marine depositional system, where intertidal and shallow subtidal flats are protected from the open sea by elongated sand ridges. With respect to the sea level, three types of ridges are distinguished: supratidal (barrier islands *sensu* Otvos, 2012), intertidal and subtidal (bars *sensu* Otvos, 2012) ridges. The largest sand bar in the study area is the Mula di Muggia sandbank, the shallowest parts of which are few centimeters below the high tide level; the barrier-island of the model area represents its western prolongation (Fig. 1). It is commonly assumed to represent the remnants of the former Isonzo river delta (Venturini, 2003, and references therein), having formed during the Middle Ages. Today, muddy sands and microbial mats prevail in its shelter, whereas rippled sands dominate the shallow waters seaward of the sandbank (Baucon & Felletti, 2013a, b). The two regions, i.e. the areas landward and seaward of the Mula di Muggia sandbank (Fig. 2A) are here referred to as the back-bar and the fore-bar respectively.

The study area experiences semidiurnal tides that are unusually high for the Mediterranean Sea, ranging from 22 cm (neap tidal range) to 105 cm (spring tidal range); mean tidal range is 65 cm (Dorigo, 1965; Sconfiatti *et al.*, 2003; Covelli *et al.*, 2008; Fontolan *et al.*, 2012; Fig. 3).

Concomitant with spring tides, seiches generated by the Scirocco wind and the passage of atmospheric low pressure systems are able to amplify tidal water levels up to 160 cm (‘acqua alta’; Fontolan *et al.*, 2007). The prevailing winds blow from ENE (Bora wind) and SE (Scirocco wind), the latter being less intense but with a longer fetch (Fontolan *et al.*, 2007; Pervesler & Hohenegger, 2006). Wave heights conform to the general conditions of the Northern Adriatic, fair-weather waves being smaller than 0.5 m (Fontolan *et al.*, 2007). Within the confines of the sheltered Adriatic Sea, these conditions conform with the definition of fetch-limited barrier island systems (Pilkey, Cooper & Lewis, 2009).

METHODOLOGY

Test of the Grado model

To test the reliability of the Grado model (Fig. 4), the actual distribution of environmental variables was compared to that predicted by the model itself. For this purpose, the test area was crossed in several directions by feet or by kayak, thus drawing sampling tracks along which the distribution of ichnoassociations and environmental indicators was mapped (Fig. 2B). Trackpoints were positioned by a GPS unit (Garmin GPSmap 62s; positioning error less than 10 m); each trackpoint refers to an observation area of approximately 5 m².

In most cases, environmental indicators and ichnoassociations were observable from subaerial position or by snorkeling at surface. In rarer cases, poor visibility of the seafloor required extensive underwater diving, during which the GPS unit had to be left on the kayak to prevent exposure to seawater. Consequently, sampling points to be inspected had to be positioned by the GPS unit and, successively, they were ichnologically and sedimentologically analyzed.

Overall, the sampling tracks consisted of 9794 points, which allowed to describe the observed and the predicted environmental scenarios:

1. Observed environmental scenario. In line with the Grado model, the mapped attributes were emersion time, hydrodynamics, sediment firmness and degree of microbial binding, as derived from field indicators ('observed environmental indicators' in Fig. 2C). More specifically, the environmental parameters were assigned scores based on direct and indirect field diagnostic indicators (Table 1). The test area was also analyzed from selected observation zones ('viewing areas' in Fig. 2B), offering optimal viewpoints on the surrounding intertidal and subtidal flats. Trackpoints, and viewing areas allowed to trace an environmental map synthesizing the observed environmental scenario. Satellite imagery was used to confirm and complement interpretation of field data.
2. Predicted environmental scenario. Each sampling point was classified ichnologically by identifying the dominant ichnoassociation in conformity with the classes previously distinguished by Baucon & Felletti (2013b). This information, together with viewing areas, allowed to develop an ichnoassociation map of the studied area. Satellite imagery was used to confirm and complement interpretation of field data. As the Grado model establishes a relationship between ichnoassociations and the environment, it can be applied to the observed

ichnoassociations in order to derive a predicted environmental scenario (Fig. 2C), represented as a map.

Finally, comparison of the predicted with the observed scenario allowed to measure the reliability of the Grado model (Fig. 2C).

Additional data

In addition to the test of the Grado model, ichnological data (bioturbation intensity, ichnofaunal composition, burrow morphology) were observed. A camera with built-in GPS was used to take georeferenced pictures, while bathymetry was measured by a meterstick in both the fore- (10 measurements) and the back-bar (10 measurements).

Development of the Grado model

This paper aims to test the Grado model, which was developed during previous research (Baucon & Felletti, 2013b) by applying the IchnoGIS method. The IchnoGIS approach integrates hardware, software, and data for capturing, managing, analyzing, and displaying geographically referenced ichnological data. IchnoGIS is based on four survey tasks relying on relatively low-cost tools (GPS unit, water quality instruments) and free/open-source software (Libre Office, PAST, Gephi):

1. Survey design. The first stage is the definition of the traces of interest and their correspondence with existing ichnotaxa.
2. Ichnological and sedimentological sampling. Two sampling approaches are followed to collect ichnological and sedimentological data, which are georeferenced by a GPS unit:
 - a) Quadrat sampling. At each sampling site, a quadrat of a set size is placed on the substrate; facies type and abundance of each ichnotaxon are recorded in conjunction to the spatial coordinates of the sampling site.
 - b) Trench sampling. Quadrat sampling is complemented by the study of vertical trenches, realized at regularly spaced sites. At each sampling site, facies type and presence/absence of each ichnotaxon are recorded in conjunction to the spatial coordinates of the sampling site.

3. Environmental and topographical sampling. Water properties (e.g. pH, Eh, nutrients, salinity) and sediment features (e.g. depth of the redox potential discontinuity, substrate firmness, emersion time) are recorded at representative sampling sites. Major topographic features (e.g. intertidal/subtidal limit, landform boundaries) are mapped by a GPS unit.
4. Data visualization and analysis. Finally, the relationship between traces and the environment is deduced from both the spatial distribution of ichnotaxa and their association patterns:
 - a) Spatial organization. Trench sampling data are displayed by point maps showing presence/absence of each ichnotaxon. A geostatistical approach based on kriging (Matheron, 1962) is adopted to interpolate the number of traces at unsampled positions, thus producing density maps of each ichnotaxon. Both point and density maps allow to compare spatial distribution of traces with environmental and topographical data, including satellite imagery.
 - b) Patterns of association. Ichnological data collected during trench sampling are described by a network graph (ichnonetwork), which maps ichnotaxa as nodes and their association relationships as links. Consequently, network theory (Brandes and Erlebach, 2005; Fortunato, 2010) can be used to explore the ichnological system on the basis of the association relationships between ichnotaxa. Ichnonetwork analysis allows to determine how individual ichnotaxa are embedded in the studied system and discern patterns of organization (ichnoassociations). Successively, regularities are searched in the environmental properties associated to each ichnoassociation in order to recognize the major structuring processes of ichnoassociation composition and distribution.

RESULTS

Ichnoassociations

In conformity with Baucon & Felletti (2013a, b), traces are abundant and morphologically diverse in the study area, tending to be organized in distinct groups (ichnoassociations). This section describes

the ichnoassociations characterizing the study area, based on the classes previously distinguished by Baucon & Felletti (2013b). More in particular, each ichnoassociation is addressed with respect to three major aspects:

1. **ichnological features:** major ichnological attributes include characteristic ichnotaxa, which have been used as key recognition criteria during sampling. The recognized ichnotaxa, to be considered incipient (see Bromley, 1996), are described in Table 2; the reader is addressed to Baucon & Felletti (2013a) for a more comprehensive treatment of individual traces. In addition, ichnofabric index (II; Droser & Bottjer, 1986) and bedding plane bioturbation index (BPBI; Miller & Smail, 1997) are used to describe typical bioturbation intensity as expressed in vertical profile and on the seafloor surface, respectively (Tab. 3). Ichnodiversity focuses on the number of ichnotaxa present at the observation scale (see Bromley, 1996).
2. **occurrence:** the presence of a given ichnoassociation with respect to the test and the model area (Fig. 1) is underlined.

environmental significance: this aspect concerns the environmental significance of a given ichnoassociation, as expressed by the Grado model (Fig. 4). In this regard, substrate firmness is described with the terms ‘softground’ (unconsolidated sediment) and firmground (partially consolidated sediment; see Bromley, 1996). Emersion time refers to the percentage of time during which a given area is above the water level. For instance, 100% emersion time indicates subaerial conditions for the entire tidal cycle. Finally, the Grado model provides hydrodynamic information in relative terms (‘high’ to ‘low’) as specific studies are lacking in the study area. Nevertheless, an approximate estimate of average current velocity near the sea bottom (Tab. 1) can be deduced by considering sedimentary features (Baucon & Felletti, 2013a, b in conjunction with Nichols, 2009 and Stow *et al.*, 2008) and general hydrographic features (Dorigo, 1965; Sconfiatti *et al.*, 2003; Covelli *et al.*, 2008; Fontolan *et al.*, 2012).

Low bioturbation ichnoassociation (Fig. 5A)

Ichnological features: This ichnoassociation is characterized by no bioturbation or low bioturbation intensity (II 1-2; BPBI 1-2; Fig. 5A), as evidenced by the frequent preservation of parallel lamination.

Occasionally, vertebrate trampling may produce higher bioturbation intensities. In this context, *Skolithos* XS marks the landward limit of a wide low-bioturbation belt, while tetrapod footprints are rarer.

Occurrence: This ichnoassociation is documented from the model area only.

Environmental significance: According to the Grado model, the low bioturbation ichnoassociation characterizes areas undergoing prolonged emersion (emersion time longer than 80% of tidal cycle duration).

***Thalassinoides* ichnoassociation (Fig. 5B)**

Ichnological features: High densities of decapod burrows (*Thalassinoides*, *Parmaichnus*) and intense root-related mottling are common (Fig. 5B, C). Small U-burrows (*Arenicolites* S) are locally abundant. Typical bioturbation intensity is moderate to high (II 3-5; BPBI 3-5). Based on field observations of the test area, two subunits are distinguished:

2.1) mottling-dominated subunit is characterized by intense sediment reworking, which is usually produced by roots and rhizomes of seagrasses (*Cymodocea*, *Zostera*, *Posidonia*). For mapping purposes, dominance of seagrass (percent cover > 50%) has been considered to be the major diagnostic criterion, together with the absence of sediment mounds. In fact, sediment mounds correspond to the ichnogenus *Thalassinoides* XL (Tab. 2), which is the characteristic ichnotaxon of the *Thalassinoides*-dominated subunit.

2.2) *Thalassinoides*-dominated subunit is characterized by the diagnostic presence of large sediment mounds, corresponding to the ichnotaxon *Thalassinoides* XL. Sediment mounds are commonly found within dense seagrass meadows, which are accompanied by extensive mottling, but occurrences in unvegetated substrates are also common. *Parmaichnus* and *Thalassinoides* L may be present as accessory components.

Occurrence: The *Thalassinoides* ichnoassociation is documented from both the model and the test area.

Environmental significance: According to the Grado model, the *Thalassinoides* ichnoassociation characterizes softgrounds with moderate hydrodynamics. Substrate may be colonized by biomats,

while emersion time is shorter than 80% of the tidal cycle duration.

***Arenicolites/Skolithos* ichnoassociation (Fig. 5C, 6)**

Ichnological features: Large U-burrows (*Arenicolites* XL, L), vertical burrows (*Skolithos* M, L, S, *Monocraterion*) and horizontal trails (*Nereites*, *Archaeonassa*) are the most distinctive ichnotaxa, while biodeformational structures, *Lockeia*, ‘diverging shafts’ and *Thalassinoides* may also be present. Bioturbation intensity is low (II 1-2; BPBI 2), although more intensely bioturbated patches may be present.

Based on field observations, two subunits are distinguished:

3.1) Low ichnodiversity subunit is characterized by large *Arenicolites* (types XL and L, Tab. 2), *Skolithos* M, L, S and *Nereites*. Ichnodiversity and bioturbation intensity are fluctuating in space, but generally very low (BPBI 2; II 1-2). In fact, traces of epibenthic activity (*Nereites*, *Archaeonassa*) are frequently the only distinct structures, being interposed with metrical patches of virtually unbioturbated sediment. Nevertheless, higher bioturbation intensities are also found especially at landward sites, with density of *Arenicolites* up to 20 individuals per m². *Thalassinoides* and ‘diverging burrows’ are also documented.

Baucon & Felletti (2013b) subdivided the *Arenicolites/Skolithos* ichnoassociation in two subclasses, which are respectively characterized by prevailing vertical burrows (*Skolithos* ichnoassociation) and the dominance of U-shaped burrows (*Arenicolites* ichnoassociation). The present subunit is more affine to the *Skolithos* ichnoassociation for presenting similar ichnotaxa (*Skolithos* M, L, S) and bioturbation intensities, although it covers a wide ichnological spectrum including elements of the *Arenicolites* ichnoassociation (i.e. *Arenicolites*) as well.

3.2) Moderate ichnodiversity subunit shares most of the ichnotaxa with the previously described one, but it differs for the higher ichnodiversity and bioturbation intensity (II 2; BPBI 2-5). In fact, the uppermost tier appears frequently reworked by the activity of epibenthic organisms, resulting in distinct trails (*Nereites*, *Archaeonassa*) being frequently superimposed to an indistinctly bioturbated background. Distinct burrows are sparsely distributed, with denser assemblages at the transition with the *Thalassinoides* ichnoassociation. *Skolithos* M is one of

the most typical components, although not being ubiquitous. ‘Diverging shafts’ are frequently documented, while large specimens produced by *Solecurtus* (opening width: 0.3-1.5 cm) seem to be diagnostic of this subichnoassociation. *Thalassinoides*, *Skolithos* L, *Lockeia* are also commonly found.

With regard to the subclasses distinguished by Baucon and Felletti (2013), this ichnoassociation is more affine to the *Arenicolites* ichnoassociation although it incorporates features of both *Thalassinoides* and *Skolithos* ichnoassociations (i.e. *Thalassinoides*, moderate to high bioturbation; *Skolithos*).

Occurrence: The *Arenicolites/Skolithos* ichnoassociation is recognized both in the model and the test areas.

Environmental significance: According to the Grado model, the *Arenicolites/Skolithos* ichnoassociation corresponds to softgrounds without biomat cover. Hydrodynamics is moderate-high, while emersion time is shorter than 80% of the tidal cycle duration. Given the ichnological affinities of the low and moderate ichnodiversity subunits, they are referred to low and moderate energy levels, respectively.

***Macanopsis* ichnoassociation (Fig. 7A)**

Ichnological features: Insect burrows (*Macanopsis*, *Helminthoidichnites*) are the most typical component of this ichnoassociation, which is often accompanied by *Polykladichnus*. Bioturbation intensity is low (II 2; BPBI 1-2).

Occurrence: This ichnoassociation occurs in the model area only.

Environmental significance: According to the Grado model, the *Macanopsis* ichnoassociation is restricted to biomat-dominated firmgrounds undergoing to emersion times shorter than the 80% of the tidal cycle duration. Although the Grado model focuses on intertidal settings (0%<emersion time<100%), Baucon & Felletti (2013 a, b) suggested that microbial mats are found only in intertidal settings of the study area.

‘Squat burrows’ (Fig. 7B)

Ichnological features: Crab mating burrows (‘squat burrows’) are the diagnostic element of

this ichnoassociation, which is related to filamentous mats. Small specimens of *Arenicolites* and *Polykladichnus* may be abundant locally. Bioturbation intensity is moderate to high (II 2-5; BPBI 2-5).

Occurrence: This ichnoassociation is found in the model area.

Environmental significance: According to the Grado model, this ichnoassociation characterizes biomat-dominated softgrounds, which are emerged for less of the 80% of the tidal cycle duration.

***Parmaichnus* ichnoassociation (Fig. 7C)**

Ichnological features: Monoichnospecific assemblages of *Parmaichnus* characterize this ichnoassociation. Bioturbation intensity is low to high (II 2-5; BPBI 2-4).

Occurrence: Both the model and the test area present this ichnoassociation.

Environmental significance: According to the Grado model, the *Parmaichnus* ichnoassociation is found in firmgrounds without microbial mats. Emersion time is shorter than the 80% of the entire tidal cycle.

The spatial organization of the aforementioned ichnoassociations is revealed by the ichnoassociation map (Fig. 8), in which the spatial distribution of the major ichnological features of the test area are represented. The map shows a marked dichotomy between *Thalassinoides* and *Arenicolites/Skolithos* ichnoassociations, the latter of which is distributed in the more distal fore-bar environment. Here, ichnodiversity and bioturbation intensity are lower, with U-burrows (*Arenicolites* L, XL), vertical traces (*Skolithos* M) and trails (*Nereites*, *Archaeonassa*) as the dominant biogenic structures. Isolated patches with the *Arenicolites/Skolithos* ichnoassociation are also found in the back-bar area but the ichnological features are different from the fore-bar manifestations (i.e. moderate ichnodiversity subunit of the *Arenicolites/Skolithos* ichnoassociation).

The map also shows a correlation between the occurrence of *Parmaichnus* and the position of a dredged channel, although observations were more difficult in this area because of the frequent presence of boats and poor visibility. It should also be noted that the *Macanopsis* and 'squat burrows' ichnoassociations are not represented in the test area, despite their widespread presence in the intertidal model area (Baucon & Felletti, 2013b).

Predicted vs observed scenario

The Grado model (Fig. 4) allows the derivation of the potential distribution of environmental variables from the previously discussed ichnoassociation map (Fig. 8). The resulting map (Fig. 9A) predicts a marked hydrodynamic contrast between the back-bar area and the fore-bar, both of which would be dominated by softgrounds without microbial binding. According to the prediction map, firmgrounds would be widespread in the dredged channel and adjacent areas.

The observed distribution of environmental parameters (Fig. 9B), as deduced from process-based indicators (Table 1), is consistent with the predicted distribution of environmental parameters. In fact, the back-bar/fore-bar dichotomy is evident and finds full correspondence with the predicted data. Both the predicted and the observed map shows areas of moderate hydrodynamics within the sheltered back-bar. These areas are identified by the moderate ichnodiversity subunit of the *Arenicolites/Skolithos* ichnoassociation, despite it does not fit exactly with the *Arenicolites* subclass distinguished by Baucon & Felletti (2013b),

Minor differences regard small patches, some of which are indicated by arrows in Fig. 9.

Major discrepancies regard the distribution of firmgrounds, which is deduced from the presence of the *Parmaichnus* ichnoassociation. In fact, although the *Parmaichnus* ichnoassociation is commonly related to firmgrounds (Fig. 7C), it is also documented from softgrounds. More specifically, softground occurrences of *Parmaichnus* are found in the artificial channel and its surroundings, where firmgrounds are also common but patchily distributed (Fig. 8).

DISCUSSION

The model and the test areas are located adjacent to each other, therefore they are exposed to similar environmental parameters despite of their slightly different bathymetric setting. Whereas this similarity prevents from assessing the global validity of the Grado model, it allows to better evaluate the prediction performance of the IchnoGIS method. In fact, similarity of environmental factors restricts the interpretation of results.

In terms of the overall pattern of ichnoassociation distribution, the predicted scenario is significantly consistent with the observed distribution of environmental parameters. Quantitatively, the predicted and observed map are overlapping for the 97.031%, implying that the Grado model describes consistently the trace-environment relationships of the studied site.

Although the aforementioned result is central for this research, the role played by control factors (hydrodynamics, biomat binding, emersion time, substrate firmness) is important as well. In fact, understanding how control factors are embedded in the studied system is crucial not only for evaluating coherence of the model, but also for better comprehending the ichnosite itself. More specifically, this issue is synthesized by two complementary questions: (a) how control factors influence other biologically-significant parameters? (b) how control factors are modulated by general physiographic features?

In this regard, hydrodynamics is strongly controlled by the Mula di Muggia sandbank, which represents one of the major geomorphological features of the studied site. In fact, it functions as a barrier against entering waves, the influence of which is less intense in the back-bar than in the fore-bar (Fig. 10). A similar environmental dichotomy is regarded widely as amongst the major features of barrier island systems, which are typically characterized by sediment barriers separating a shallow lagoon from the open sea (Otvos, 2012; see also Baucon & Felletti, 2013a). However, being periodically submersed, the Mula di Muggia sandbank does not fit with the strict definition of barrier island (Otvos, 2012), but it represents an intertidal bar. Rather, it may be in the early process of evolving into a barrier island system, as exemplified by the supratidal ridge which constitutes its western prolongation ('barrier island' in Fig. 1). It should also be noted that, in the context of the test of the Grado model, both the predicted and the observed scenarios denote a marked hydrodynamic contrast between the fore-bar and the back-bar regions.

Hydrodynamics controls sedimentation and, consequently, influences nutrient availability. In conformity with the 'food resource paradigm' (Pemberton *et al.*, 2001), sheltered, low-energy areas favor the deposition of particulate organic matter, which tend to remain suspended in more turbulent areas. For this reason, deposit-feeding strategies (e.g. *Thalassinoides*) dominate the back-bar, while suspension-feeding burrows (e.g. *Skolithos* M) are commonly found in the fore-bar and in the more

energetic sectors of the back-bar.

These interpretations are confirmed by georeferenced photographic documentation (Fig. 11), showing the marked ichnological and sedimentological dichotomy of the studied area.

In line with the intertidal model area, hydrodynamics exerts a significant control on interstitial oxygenation as well (Fig. 10). In fact, sediment permeability controls the depth of the redox potential discontinuity (RPD); that is, the horizon where oxidizing processes become replaced by reducing processes (Fenchel & Riedl, 1970). Since permeability increases with grain size, which is ultimately controlled by hydrodynamics, the RPD is located at greater depth in coarser sediments (Raffaelli & Hawkins, 1996). Consequently, the RPD is found at greater depth in the turbulent fore-bar and a shallower depth in the sheltered back-bar (Fig. 12).

The highest bioturbation intensities are found in the back-bar, in spite of the fact that the muddy sands display widespread dysoxic conditions. This is explained by the greater abundance of organic matter which has deposited in the back-bar, as a consequence of its quieter hydrodynamic regime (see Baucon & Felletti, 2013a). For this reason, lagoonal animals commonly develop adaptations for survival in low-oxygen and sulphide-rich environments (Fenchel & Riedl, 1970; Vismann, 1990, and references therein). Marine seagrass are favoured by low-energy conditions and, at the same time, they attenuate current speed and wave energy (Koch, 2001). Wave action, in turn, represents a source of mechanical stress in the fore-bar, which is well oxygenated but relatively nutrient-depleted (Fig. 12C). Georeferenced documentation shows clearly that tracemaking organisms are more abundant in the back-bar (Figs. 11, 13, 14), whereas the lower bioturbation intensity of the fore-bar is explained by inherently low density of tracemaking organisms.

This interpretation is in line with previous studies, as muddy sands and sandy muds are known to support higher population densities than either sandier or muddier environments because of inherently higher concentrations of organic matter in the sediment (Flemming & Delafontaine, 2000; Flemming, 2012).

These observations show that the fore-bar and the back-bar are characterized by a marked environmental and ichnological dichotomy (Fig. 9), which is also recognized for the back- and fore-barrier regions of the model area (Fig. 15; Baucon & Felletti, 2013 a, b). This aspect is particularly

manifest in the spatial distribution of *Arenicolites*, as revealed by the geostatistical module of the IchnoGIS method, which mapped the density of large-sized *Arenicolites* (types L and XL; Fig. 15A, B) from quadrat samples. The interpolation of such data resulted in a density map of large *Arenicolites* (Fig. 15A), showing its preferential distribution in the fore-barrier. Symmetrically, Baucon & Felletti (2013b) demonstrated that *Thalassinoides* is preferentially distributed in the back-barrier. The same trends are recognized in the test area, as shown by the contrasting ichnoassociations of the fore- and back-bar (Fig. 9). A similar scenario is portrayed by the ichnonetwork of the model area (Fig. 15B), representing ichnotaxa (nodes) and their association relationships (edges; Baucon & Felletti, 2013b). According to the ichnonetwork approach, a pair of traces is connected if they co-occur at least in one trench sample, whereas the strength of the connection (represented as edge thickness) depends on the number of samples in which two ichnotaxa co-occur (Fig. 15C). Consequently, the existence of different structural areas – manifested as sets of densely connected nodes - reveals inhomogeneities in the association patterns, suggesting a certain degree of organization of the ichnological system. In the specific case of the ichnonetwork of the model area, major inhomogeneities mirror the fact that the fore- and the back-barrier are characterized by specific ichnoassociations (Fig. 15C; Baucon & Felletti, 2013b).

The structuring role of hydrodynamics is demonstrated by georeferenced photographs and qualitative observations realized at the Mula di Muggia sandbank (Figs. 10-14). In fact, within fore-bar settings, water turbulence decreases with decreasing distance from the intertidal Mula di Muggia sandbank. This aspect is explained by the sheltering function of sand bars, as energy of entering waves is progressively dissipated over them. This energy gradient is accompanied by a bioturbation gradient: within the fore-bar, higher bioturbation indexes (BPBI 2; II 2) are found on the intertidal sandbank and its immediate surroundings, where ‘diverging shafts’, *Arenicolites* L, *Arenicolites* XL, *Skolithos* M, L, *Nereites* are sparsely distributed. In these settings, hydrodynamic energy may be used by deposit-feeding burrowers for ventilating their burrows, in order to exploit nutritious layers at greater depth (Fig. 14A, B). Bioturbation intensity and ichnodiversity rapidly decrease towards the open sea, where *Nereites* and biodeformational structures are largely prevailing over vertical burrows, reworking only the uppermost layers of the sediment (BPBI 1-2; II 1; Fig. 14C, D). Bioturbation intensity seems to

increase at higher depths (≈ 5 m), as wave influence on the seafloor is weaker.

Wave action is notably reduced within back-bar environments, which are sheltered from entering waves by subtidal and intertidal bars.

The aforementioned aspects support the validity of the Grado model, but they arise a problem of resolution. In fact, the Grado model predict the back-/fore-bar dichotomy, but the fore-bar gradient is not coherently depicted. In addition, the effect of wave turbulence and tidal currents on ichnofauna needs to be better investigated, whereas trails (i.e. *Nereites*, *Archaeonassa*) have to be implemented in the model, as their distribution appears to be environmentally controlled. Consequently, general validity of the Grado model is demonstrated, but further application of the IchnoGIS method in subtidal settings is needed to achieve greater accuracy and resolution.

Although the aforementioned hydrodynamic dichotomy is depicted conveniently by the predicted scenario, minor discrepancies exist with the observed conditions (e.g. Fig. 9, arrow). In fact, small differing patches are present, which can represent (a) stochastic fluctuations in ichnoassociation distribution (from which the predicted map is derived) or (b) areas in which physical indicators (Table 1) are less precise. However, neither case seriously challenges the general validity of the predicted map.

Alongside with hydrodynamics, substrate firmness is a major driver of ichnoassociation composition. In this regard, firm substrates are characteristically of interest to the *Parmaichnus* ichnoassociation, which is represented by nearly monoichnospecific assemblages of Y-shaped burrows (Fig. 7C). The absence of other ichnotaxa is explained by the mechanical requirements necessary to burrow into partially consolidated substrates; firm substrates are also difficult to exploit for deposit-feeders, for which reason firmgrounds are dominated by suspension-feeding strategies (i.e. *Parmaichnus* itself).

Nevertheless, a major discrepancy concerns the distribution of firm substrates, as derived from the *Parmaichnus* ichnoassociation. In fact, the affinity of the *Parmaichnus* ichnoassociation with softgrounds appears to question its utility as a firmground indicator. However, in the present case, *Parmaichnus*-bearing softgrounds are always close to firmgrounds (Figs 8 and 9B), supporting a proximity relationship with cohesive substrates and/or current-swept erosive settings. This assumption

is supported by numerous reports of *Parmaichnus* in fossil and modern firmgrounds (i.e. Asgaard *et al.*, 1997; Pervesler & Hohenegger, 2006).

Besides hydrodynamics and firmness, microbial binding and emersion time are the major control factors of ichnoassociation distribution (see Baucon & Felletti, 2013b). In the light of the bathymetric characteristics of the test area (Fig. 1), which is largely subtidal, the effect of emersion time is less evident than in the intertidal model area. Nevertheless, the widespread presence of large suspension-feeding structures (i.e. *Skolithos* M) reflects the short or zero emersion times characterizing the test area.

In fact, the feeding time of suspension feeders increases with the increasing submergence time because a water column is needed to support nutritious particle suspensions.

Despite their abundance in the intertidal model area, microbial mats do not occur in the test area. Biomat-related ichnoassociations are therefore absent, which is an aspect to be considered when extending the Grado model to the subtidal realm.

The studied site is characterized by a notable abundance and diversity of biogenic sedimentary structures, but to what degree will its ichnological heritage be preserved in the rock record? The answer is difficult due to the complexity of the ichnological system, concomitant with the diversity of the physical phenomena influencing the sedimentary dynamics at the Mula di Muggia. In this context, several tiering levels are present, with the deeper ones having a higher preservation potential (Bromley, 1996; Savrda, 2007). For this reason, large specimens of *Thalassinoides* and *Arenicolites* have good preservation potential. Furthermore, burrow overprinting may obliterate previously emplaced structures (Bromely, 1996; Savrda, 2007), therefore lower tiers of high-bioturbation ichnoassociations (i.e. *Thalassinoides* ichnoassociation) are likely to be completely reworked. This scenario is complicated by the interplay of sedimentary dynamics and high-energy events, as evidenced by previous research on modern and fossil systems (van Straaten, 1954; Reineck & Singh, 1980; Dott, 1983, 1988; van der Spek, 1996; Bromley, 1996; Chang *et al.*, 2006; Davis and Flemming, 1995; Flemming, 2012). In this regard, lined burrows such as large specimens of *Skolithos* (Fig. 6) may resist to the mechanical stress induced by storm events. In conclusion, the taphonomic future of the ichnological heritage of the Mula di Muggia is difficult to assess with confidence, although large

specimens of *Thalassinoides*, *Arenicolites* and *Skolithos* are likely to become fossilized.

CONCLUSIONS

This study has identified the spatial distribution of ichnoassociations as a function of environmental factors, thus confirming concordance with the Grado model. The prediction performance of the model is excellent, opening new avenues for its extension to the subtidal realm. The results confirm that hydrodynamics, sediment firmness, microbial binding and emersion time are the major control factors of the tidal ichnoassociations in the wider study area. Studies on biological zonation of other tidal systems (Dahl, 1952; Dittmann, 2000; Jaramillo *et al.*, 1993; Raffaelli & Hawkins, 1996; Salvat, 1964) support this idea and suggest a global adaptability of the model, although further studies are required to confirm corresponding trends at a global scale, in particular with regard to the *Parmaichnus* ichnoassociation.

The excellent results of the performance test confirm the reliability of the IchnoGIS method, which has been able to describe and analyse the studied ichnological system. Nevertheless, finer patterns of ichnological variation are found within the fore-bar, therefore further application of the IchnoGIS method is required to achieve optimal accuracy and resolution of prediction.

Finally, this study encourages future application of the IchnoGIS method on other tidal systems. It has demonstrated that knowledge of the mechanisms regulating the distribution of biogenic traces is important for understanding present and past environments.

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FIGURE CAPTIONS

Fig. 1. Schematic topography of the studied area.

Fig. 2. Geological and methodological setting. (A) View of the back-bar area as seen from the Mula di Muggia at low tide. (B) The data sources for testing the Grado model are sampling routes, along which environmental and ichnological parameters were noted, and control routes, along which robustness of data interpretation was checked. (C) Synthetic illustration of the testing method.

Fig. 3. Environmental setting. (A) Atmospheric conditions: average daily temperature at 180 cm (average 1999–2012); monthly precipitation (average 1961–2000); daily wind speed (average 1999–2012). Data from OSMER FVG, Grado station. (B) Sea-level for 2011 (interval: 10 minutes). Data from ISPRA, Grado station.

Fig. 4. Graphic depiction of the environmental significance of ichnoassociations in the Grado model in the form of specific positions in a circular diagram. More specifically, the upper hemisphere refers to softgrounds, the lower one to firmgrounds; the left hemisphere of the scheme is related to matgrounds. Decreasing emersion times are mapped with the distance from the centre of the scheme, while hydrodynamics is shown through a speedometer-like representation.

Fig. 5. Ichnoassociations of softgrounds without microbial binding. (A) Low bioturbation ichnoassociation. Quadrat side (0.5 m) for scale; top view. (B) The *Thalassinoides* ichnoassociation is characterized by intense bioturbation. Picture shows numerous openings and mounds produced by decapod crustaceans. (C) The pictured paired openings correspond to the U-shaped burrow *Arenicolites*. Note faecal casts. Top view.

Fig. 6. *Arenicolites/Skolithos* ichnoassociation. The suspension-feeding polychaete *Megalomma* extends its crown of tentacles from its vertical burrow, which corresponds to the ichnogenus *Skolithos*.

Other individuals are marked by arrows; 0.5 m water depth.

Fig. 7. Ichnoassociations of microbial mats and firmgrounds. (A) Laminated microbial mat with the *Macanopsis* ichnoassociation. Two specimens of *Macanopsis* are visible, one of which presents the trace maker (heterocerid beetle: He). Note the organic-rich horizon of the microbial mat (Or). Profile view. (B) Filamentous microbial mat with the ‘Squat burrows’ ichnoassociation. *Polykladichnus* (Po) and a ‘Squat burrow’ (Sq) are visible. Profile view; dashed line indicates the water/sediment interface. (C) Firmground with the *Parmaichnus* ichnoassociation. Numerous openings produced by upogebiid crustaceans are visible. Top view, ca. 1 m water depth.

Fig. 8. Ichnoassociation map of the test area.

Fig. 9. Environmental maps of the test area. (A) Predicted scenario. Arrows show selected differences with the observed scenario. (B) Observed scenario. Arrows show selected differences with the predicted scenario.

Fig. 10. Conceptual diagram of the major trace-environment relationships. Figured area corresponds to the eastern sector of the study site (see Fig. 1 for exact location).

The represented area is 815 m wide and 2255 m long; vertical scale is exaggerated (maximum depth: 2.5 m) while sedimentary structures (i.e. ripples) are not to scale. Figured sea level corresponds to mean low water level (MLWL), whereas mean high water level (MHWL) is indicated by a dashed line. For better showing bathymetry, water has not been represented in the narrow westernmost belt. Flow-chart shows how environmental features control trophic strategies and ichnoassociations. Position of georeferenced photos is indicated by placeholders (number refers to figure number). Icons presents ichnoassociations and their typical ichnotaxa: low-bioturbation ichnoassociation (*Skolithos* XS), *Parmaichnus* ichnoassociation (*Parmaichnus*), *Macanopsis* ichnoassociation (from left to right: *Helminthoidichnites*, *Macanopsis*, *Polykladichnus*), *Thalassinoides* ichnoassociation (A - *Thalassinoides*-dominated subunit, from left to right: *Thalassinoides*, *Parmaichnus* *Arenicolites*;

B - mottling-dominated subunit, mottling), *Arenicolites/Skolithos* ichnoassociation (C – moderate ichnodiversity subunit, from left to right: *Thalassinoides* L, *Arenicolites*, *Skolithos* M; D – low ichnodiversity subunit, from left to right: *Arenicolites* XL, *Nereites*, *Skolithos* M, *Arenicolites* L; E - low ichnodiversity subunit, *Nereites*). Burrow morphology based on field observations and literature (Dworschak, 1987, 2002; Atkinson and Froggia, 2000).

Fig. 11. Ichnological and sedimentological dichotomy between the fore-and the back-bar. Picture locations are given in Fig. 10; for difficult underwater conditions, scale bar dimensions are approximate. A – Dense seagrass meadows characterize the back-bar area. B – Rippled sand characterizes the fore-bar.

Fig. 12. Redox potential discontinuity (RPD). (A) Redox potential discontinuity (RPD, dashed line) in the rippled sands of the fore-bar. Profile view; note various but thin vertical burrows. (B) Redox potential discontinuity (RPD, dashed line) in the muddy sands of the back-bar area. Profile view; note a small U-shaped burrow (U: *Arenicolites*) and a decapod burrow (D: *Parmaichnus* or *Thalassinoides*). Profile view.

Fig. 13. Features of the *Arenicolites/Thalassinoides* ichnoassociation (moderate ichnodiversity subunit). For difficult underwater conditions, scale bar dimensions are approximate. A – Shallower tiers are reworked by epifauna, such as the figured gobiid fish (Fi) and hermit crab (Cr). Note the track (Tr) behind the hermit crab. B – Occasionally, vertical burrows with mounds (Mo) are associated to biodeformational structures produced by epifauna, such as the figured flatfish (*?Platichthys flesus*, Fl). Note also seagrass, which is responsible for root-related mottling. C – A sabellarid worm protrude from its burrow, corresponding to the ichnogenus *Skolithos* M (Sk). Note also the *Archaeonassa* trail (Ar). D – Hermit crab with its trail (*Nereites*, Ne) behind.

Fig. 14. Bioturbation gradient involving the *Arenicolites/Skolithos* ichnoassociation (low ichnodiversity subunit). For difficult underwater conditions, scale bar dimensions are approximate

in B, C, D. A – Fecal casts, revealing the presence of *Arenicolites* XL, are common on the Mula di Muggia sandbank. B – Fecal casts, here partially washed-out by waves, are found in the more proximal sectors of the fore-bar. C – *Nereites* (Ne), produced by hermit crabs, is a dominant ichnotaxon in distal fore-bar settings. D - Trails dominate over vertical burrows in the distal fore-bar.

Fig. 15. Data from the model area. (A) Density of *Arenicolites* (large forms: XL and L) in the intertidal model area. (B) A sipunculan worm inside its U-shaped burrow (*Arenicolites*). Profile view; sediment-water interface not pictured. (C) The fore-bar/back-bar dichotomy is mirrored in the Grado ichnonetwork, which displays a set of densely connected ichnotaxa (Ba, *Thalassinoides* ichnoassociation: *Arenicolites* S, mottling, *Thalassinoides* XL and *Parmaichnus*) corresponding to back-barrier conditions. In symmetric view it is possible to distinguish fore-barrier ichnotaxa (Fo, *Arenicolites*/*Skolithos* ichnoassociation: *Skolithos* S, M, L, *Monocraterion*, *Thalassinoides* L, *Arenicolites* XL, L). Edge thickness and colour measure the degree of association between nodes representing ichnotaxa. See text for more detailed discussion.

TABLE CAPTIONS

Table 1. Mapped attributes, their physical significance and the indicators used to recognize them.

Small ripples are characterized by a crest-to-crest distance ranging between 10 and 25 cm. Emersion time refers to the amount of time during which the sediment is above water level; expressed as percentage of a complete tidal cycle. Sediment texture is determined by visual comparison and manipulation.

Current velocity is intended as the average current velocity near the sea bottom, induced either by unidirectional or oscillatory flows.

Physical significance of attribute classes is deduced by field measurements (Baucon and Felletti, 2013a, b).

Table 2. Incipient ichnotaxa of the Grado ichnosite (based on Baucon & Felletti, 2013a). Different morphotypes are indicated by the suffixes XL (very large), L (large), M (medium), S (small), XS (very small).

Tab. 3. Descriptors of bioturbation intensity used in this study. Ichnofabric index (II) quantifies bioturbation as seen in section, while bedding plane bioturbation index (BPBI) refers to the seafloor surface as seen from top-view.

Attribute	Value class	Environmental indicators		Inferred physical significance
		Direct	Indirect	
HYDRO-DYNAMICS	High	<ul style="list-style-type: none"> ▪ Wave height > 15 cm ▪ Constant wave action ▪ Small breakers ▪ Capillary waves never dominant 	<ul style="list-style-type: none"> ▪ Sandy sediment (sand > 50%) ▪ Shell coquina (diameter > 1 cm) ▪ Small, straight to sinuous ripples ▪ Fore-bar position 	current velocity: 20-50 cm/s
	Moderate-low	<ul style="list-style-type: none"> ▪ Wave height < 15 cm 	<ul style="list-style-type: none"> ▪ Sandy sediment (sand > 50%) ▪ Back-bar position 	
	Low	<ul style="list-style-type: none"> ▪ Wave height < 15 cm ▪ Frequent calm conditions (glassy sea) 	<ul style="list-style-type: none"> ▪ Conspicuous muddy fraction 	current velocity < 20 cm/s
EMERSION TIME	Supratidal	<ul style="list-style-type: none"> ▪ Constant emersion 		Emersion time = 100%
	Intertidal	<ul style="list-style-type: none"> ▪ Emersion at low tide 		100% > Emersion time > 0%
	Subtidal	<ul style="list-style-type: none"> ▪ Submersion at high and low tide 		Emersion time = 0%
MICROBIAL BINDING	Biomat	<ul style="list-style-type: none"> ▪ Dominance of laminated or filamentous mats (coverage > 90%) 		
	No biomat	<ul style="list-style-type: none"> ▪ Absence of evident biomat features (coverage < 90%) 		
FIRMNESS	Firmground	<ul style="list-style-type: none"> ▪ Relative movement of sediment particles not possible 	<ul style="list-style-type: none"> ▪ Brinell test 	firmness $\geq 10^6$ Pa
	Softground	<ul style="list-style-type: none"> ▪ Relative movement of sediment particles possible 	<ul style="list-style-type: none"> ▪ Brinell test 	firmness < 10^6 Pa

Table 1. Mapped attributes, their physical significance and the indicators used to recognize them. Small ripples are characterized by a crest-to-crest distance ranging between 10 and 25 cm. Emersion time refers to the amount of time during which the sediment is above water level; expressed as percentage of a complete tidal cycle. Sediment texture is determined by visual comparison and manipulation.

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Physical significance of attribute classes is deduced by field measurements (Baucon and Felletti, 2013a, b).

	Incipient ichnotaxon	Amended description	Tiering depth	Dominant behaviour	Tracemaker
Branched structures	<i>Thalassinoides</i> XL	Burrow network with multiple openings, one of which corresponds to a sediment mound	40 cm	Deposit feeding	<i>Pestarella candida</i> (Crustacea: Decapoda)
	<i>Thalassinoides</i> L	Burrow network with chambers filled by seagrass	20–40 cm	Deposit feeding	<i>Pestarella tyrrhena</i> (Crustacea: Decapoda)
	<i>Parmaichnus</i>	Y shaped burrow with swellings	20–40 cm	Suspension feeding, ?deposit feeding	<i>Upogebia pusilla</i> (Crustacea: Decapoda)
	<i>Polykladichnus</i>	I- or U-shaped burrow with Y-shaped bifurcations	5–10 cm	Deposit feeding, Suspension feeding	<i>Nereis diversicolor</i> (Annelida: Polychaeta)
U-burrows	<i>Arenicolites</i> XL	U-burrow with single fecal cast	20–40 cm	Deposit feeding	<i>Sipunculus nudus</i> (Sipuncula: Sipunculidae)
	<i>Arenicolites</i> L	U-burrow with radial fecal casts	20–40 cm	Deposit feeding	<i>Sipunculus nudus</i> (Sipuncula: Sipunculidae)
	<i>Arenicolites</i> S	U-burrow	3–10 cm	Deposit feeding Suspension feeding	<i>Corophium volutator</i> (Crustacea: Amphipoda)
	'Squat burrow'	Squat burrow with terminal disc.—shaped chamber	5–15 cm	Mating	<i>Carcinus maenas</i> (Crustacea: Decapoda)
	<i>Macanopsis</i>	Clavate burrow	2–7 cm	Feeding, sheltering, reproducing	<i>Heterocerus flexuosus</i> (Insecta: Coleoptera)
Plug-shaped structures	<i>Bergaueria</i>	rounded plug-shaped depressions	3–10 cm	'omnivorous' suspension feeding	<i>Cereus</i> (Cnidaria: Sagartiidae), <i>Condylactis</i> and <i>Anemonia</i> (Cnidaria: Actiniidae).
Winding	<i>Helminthoidichnites</i>	Unbranched horizontal burrow	<1 mm	Undermat mining	Dipteran larvae (Insecta: Diptera)
Simple structures	<i>Skolithos</i> L	Vertical burrow with 8-shaped opening	>15 cm	Suspension feeding	<i>Solen marginatus</i> , <i>Ensis ensis</i> , <i>Ensis minor</i> (Mollusca: Bivalvia)
	<i>Skolithos</i> M	Vertical burrow with constructional lining	10–15 cm	Suspension feeding	<i>Megalomma</i> sp. (Annelida: Polychaeta)
	<i>Skolithos</i> S	Vertical burrow	3–7 cm	?Suspension feeding	Worm-like organisms
	<i>Skolithos</i> XS	Vertical unlined burrow	1–5 cm	Sheltering	<i>Talitrus saltator</i> (Crustacea: Amphipoda)
	<i>Monocraterion</i>	Vertical burrow with funnel-shaped opening	10 cm	?Suspension feeding	Worm-like organisms
Trackways and footprints	<i>Avipeda</i> -/ <i>Ardeipeda</i> -like	footprints with three digits directed forward	0.1–1 cm	Locomotion / Feeding	<i>Ardea cinerea</i> , <i>Egretta garzetta</i> (Aves: Ardeidae), <i>Laurus michahellis</i> (Aves: Laridae)
	<i>Canipeda</i>	tetradactyl footprints with heel pad	0.3–2 cm	Locomotion	<i>Canis lupus familiaris</i> (Mammalia: Canidae)
	Parallel furrows	sets of parallel, elongated furrows	0.2 cm	Locomotion	<i>Carcinus maenas</i> (Decapoda: Brachyura)
Trails	<i>Archaeonassa</i>	median furrow flanked by two lateral ridges	0.1 cm	Locomotion	<i>Bolinus brandaris</i> , <i>Hexaplex trunculus</i> (Gastropoda: Muricoidea), <i>Cerithium vulgatum</i> (Gastropoda: Cerithiidae), <i>Pirenella conica</i> (Gastropoda: Potamididae), <i>Sphaeronassa mutabilis</i> , <i>Nassarius nitidus</i> (Gastropoda: Nassariidae)
	<i>Nereites biserialis</i>	a furrow flanked on both sides by lobes	0.1 cm	Locomotion and feeding	hermit crabs, probably <i>Pagurus</i> (Decapoda: Paguridae)
	<i>Nereites uniserialis</i>	furrow flanked by a single row of lobes	0.1 cm	Locomotion and feeding	hermit crabs, probably <i>Pagurus</i> (Decapoda: Paguridae)
Miscellaneous group	'Diverging shafts'	V-shaped tunnels with circular cross-section	0.3–5 cm	Suspension feeding	<i>Abra alba</i> , <i>Donax trunculus</i> , <i>Solecurtus</i> sp., <i>Venus</i> sp. (Bivalvia: Veneroidea)
	<i>Lockeia</i> S	Almond-shaped burrow	3–5 cm	Suspension feeding	<i>Mactra corallina</i> , <i>Venus</i> sp. (Bivalvia: Venroidea)
	<i>Lockeia</i> XS	Almond-shaped burrow	<3 cm	Suspension feeding	<i>Abra alba</i> , <i>Donax trunculus</i> (Bivalvia: Veneroidea)
	Mottling	Indistinct bioturbation	1–40 cm	Rooting Locomotion	<i>Zostera marina</i> , <i>Zostera noltii</i> , <i>Cymodocea nodosa</i> , <i>Posidonia oceanica</i> (Magnoliophyta: Najadales), <i>Nereis diversicolor</i> (Annelida: Polychaeta)

Table 2. Incipient ichnotaxa of the Grado ichnosite; based on Baucon and Felletti (2013a). Different morphotypes are indicated by the suffixes XL (very large), L (large), M (medium), S (small), XS (very small).

Index	% bioturbation	Ichnofabric index (Droser and Bottjer, 1986)	Bedding plane bioturbation index (Miller and Smail, 1987)
1	0	No bioturbation recorded; all original sedimentary structures preserved	No bioturbation. If the surface is not flat and featureless, the only disruption is that caused by physical or chemical processes
2	0-10	Discrete, isolated trace fossils	Bioturbation may be represented by zones of generalized disruption or by discrete trace fossils. Most discrete structures are isolated, but some intersect.
3	10-40	Burrows are generally isolated, but locally overlap	Bioturbation represented by discrete traces, zones of generalized disruption, or by both.
4	40-60	Last vestiges of bedding discernible. Burrows overlap and are not always well defined	Bioturbation represented by discrete traces, zones of generalized disruption, or by both. Interpenetration of discrete structures is more common than in less bioturbated surfaces.
5	60-100%	Bedding completely disturbed, but burrows are still discrete in places and the fabric is not mixed	Surface has been disrupted by biological activity.

Tab. 3. Descriptors of bioturbation intensity used in this study. Ichnofabric index (II) quantifies bioturbation as seen in section, while bedding plane bioturbation index (BPBI) refers to the seafloor surface as seen from top-view.

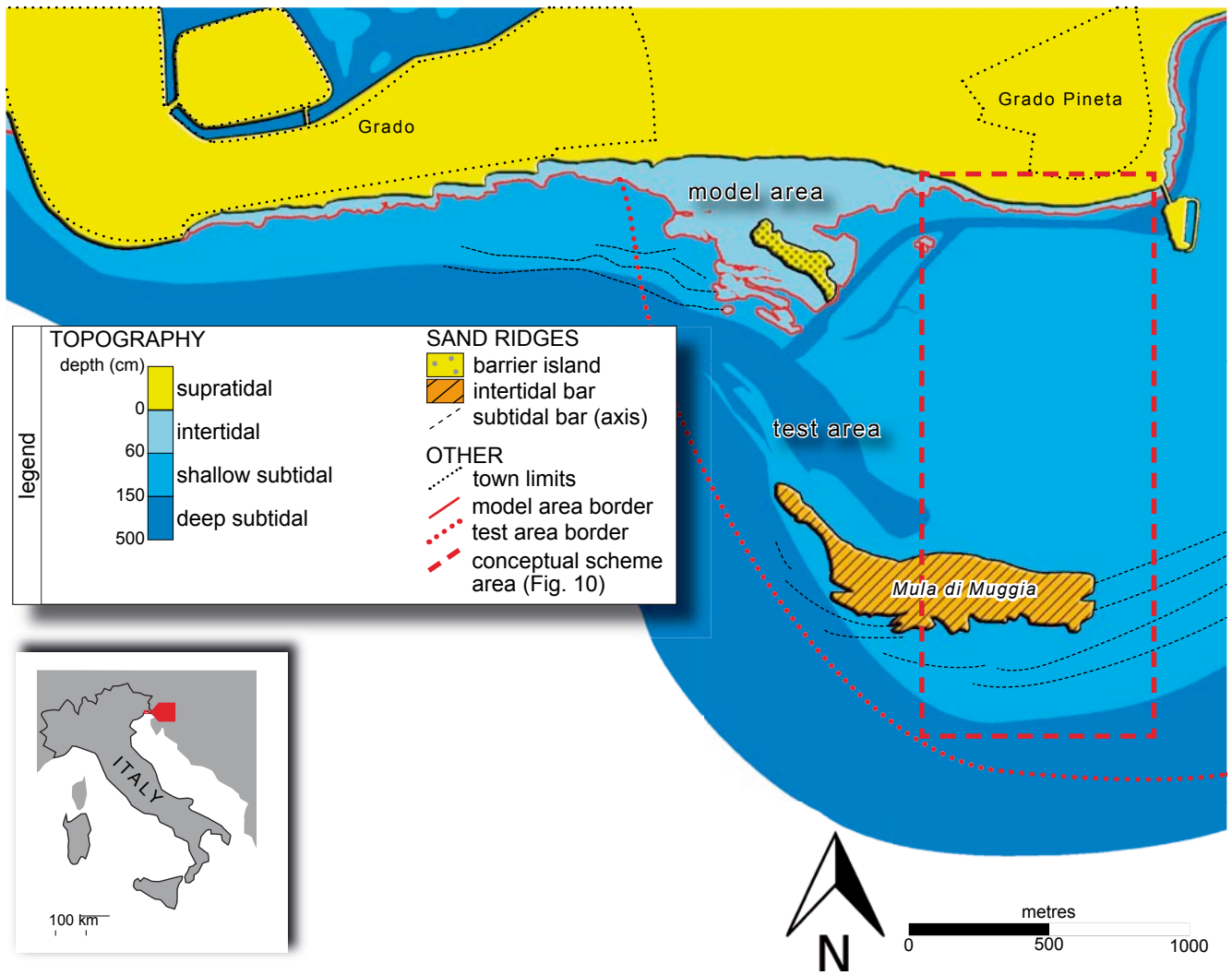


Fig. 1.

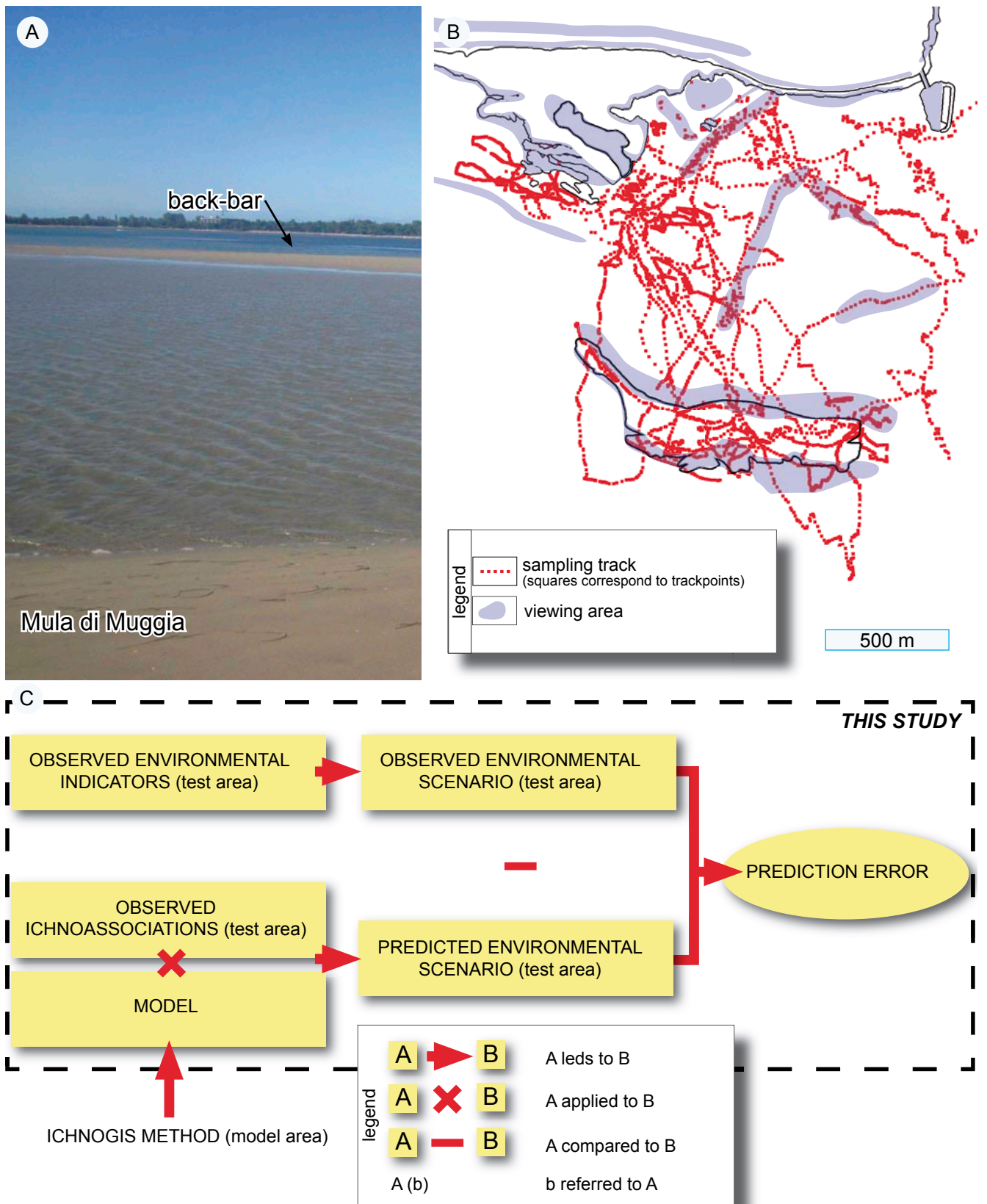


Fig. 2.

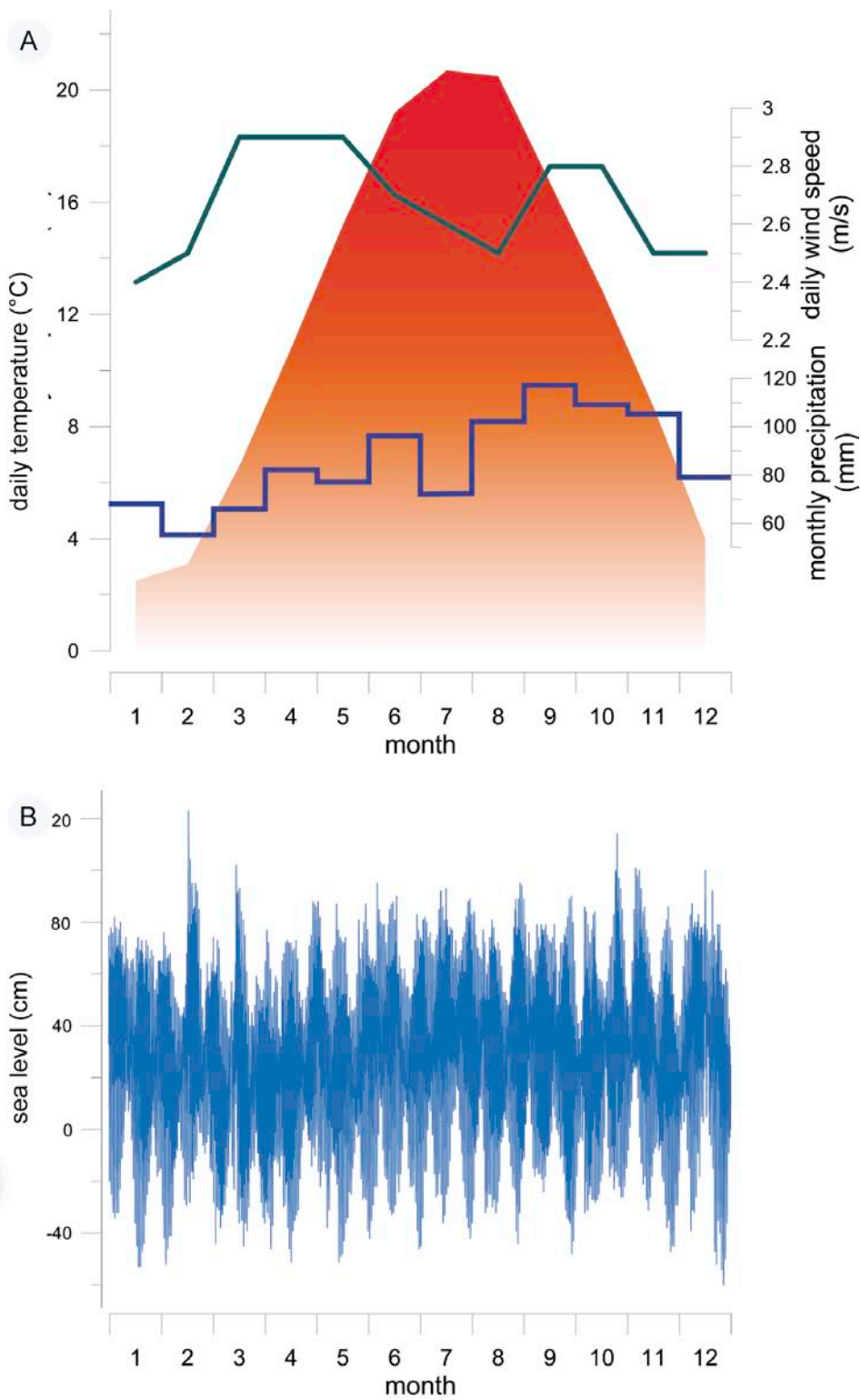


Fig. 3.

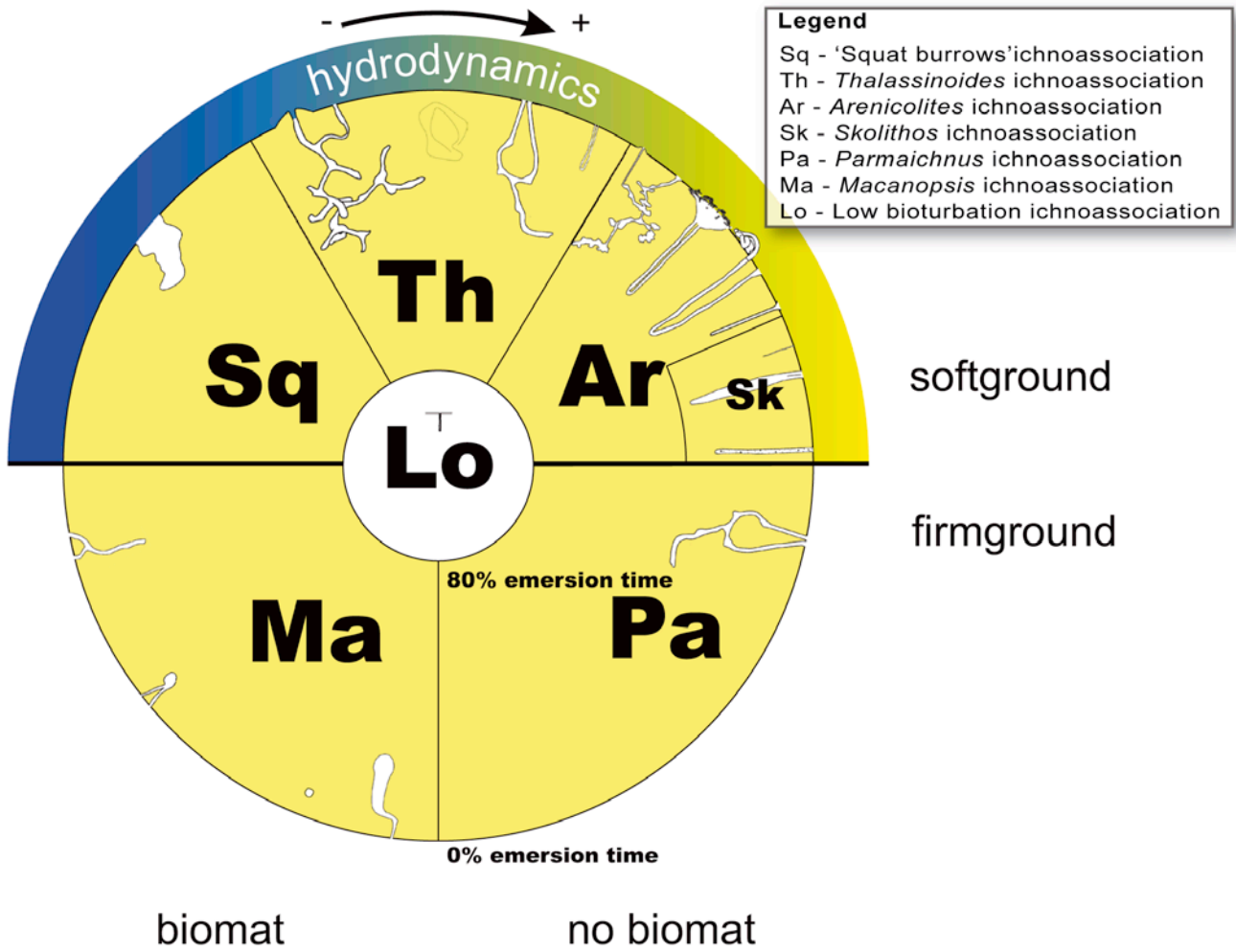


Fig. 4.

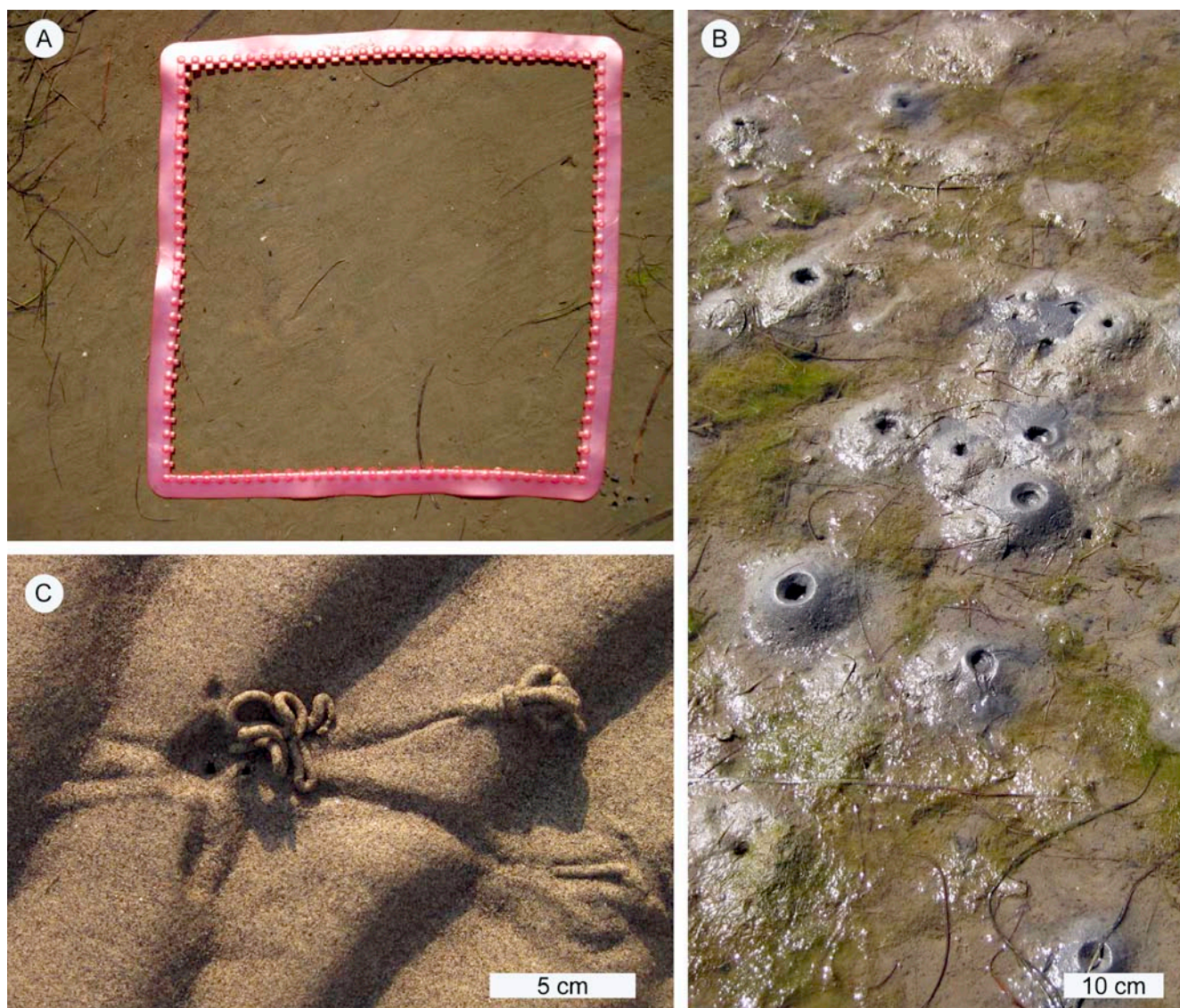


Fig. 5.



Fig. 6.

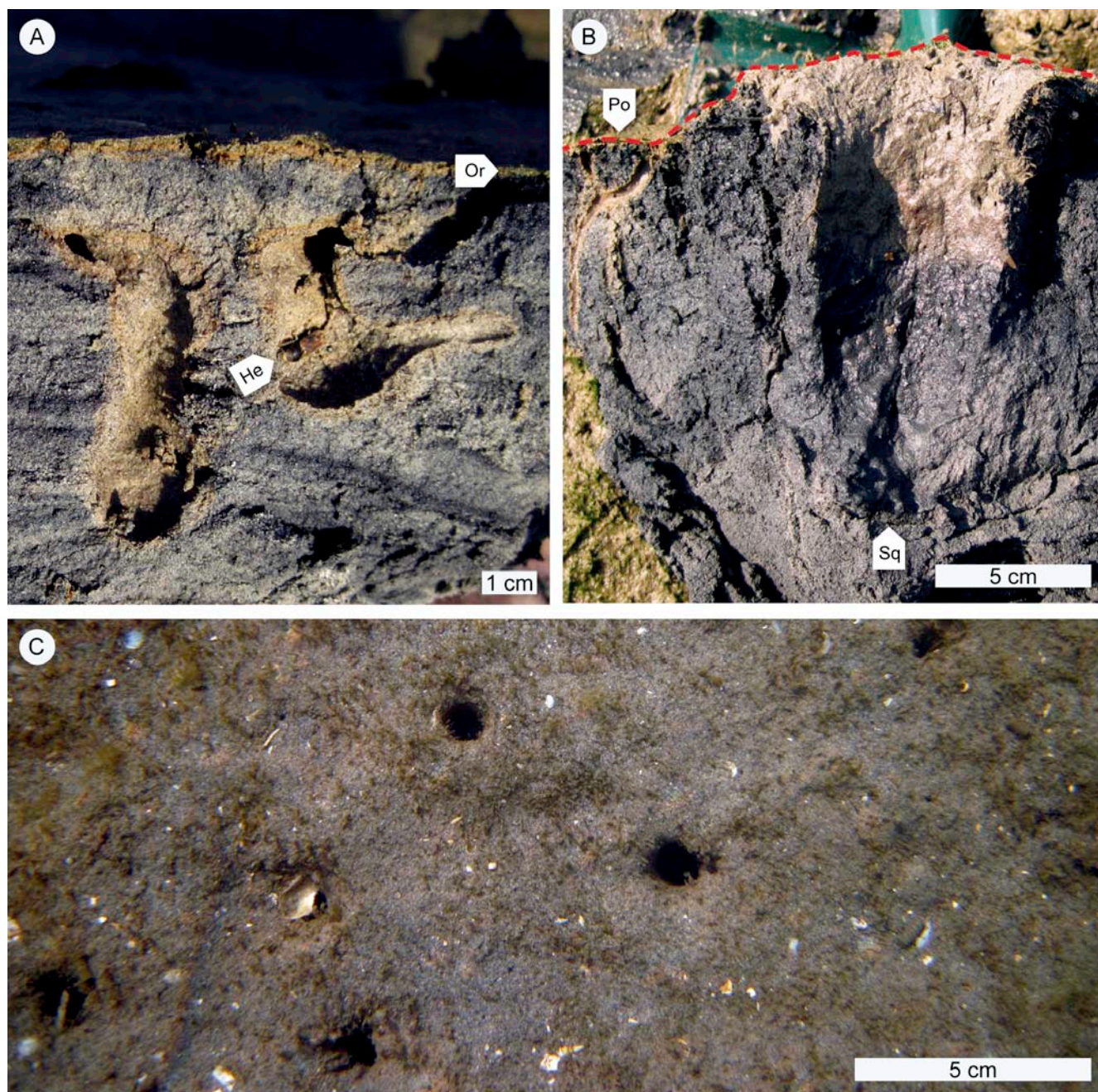


Fig. 7.

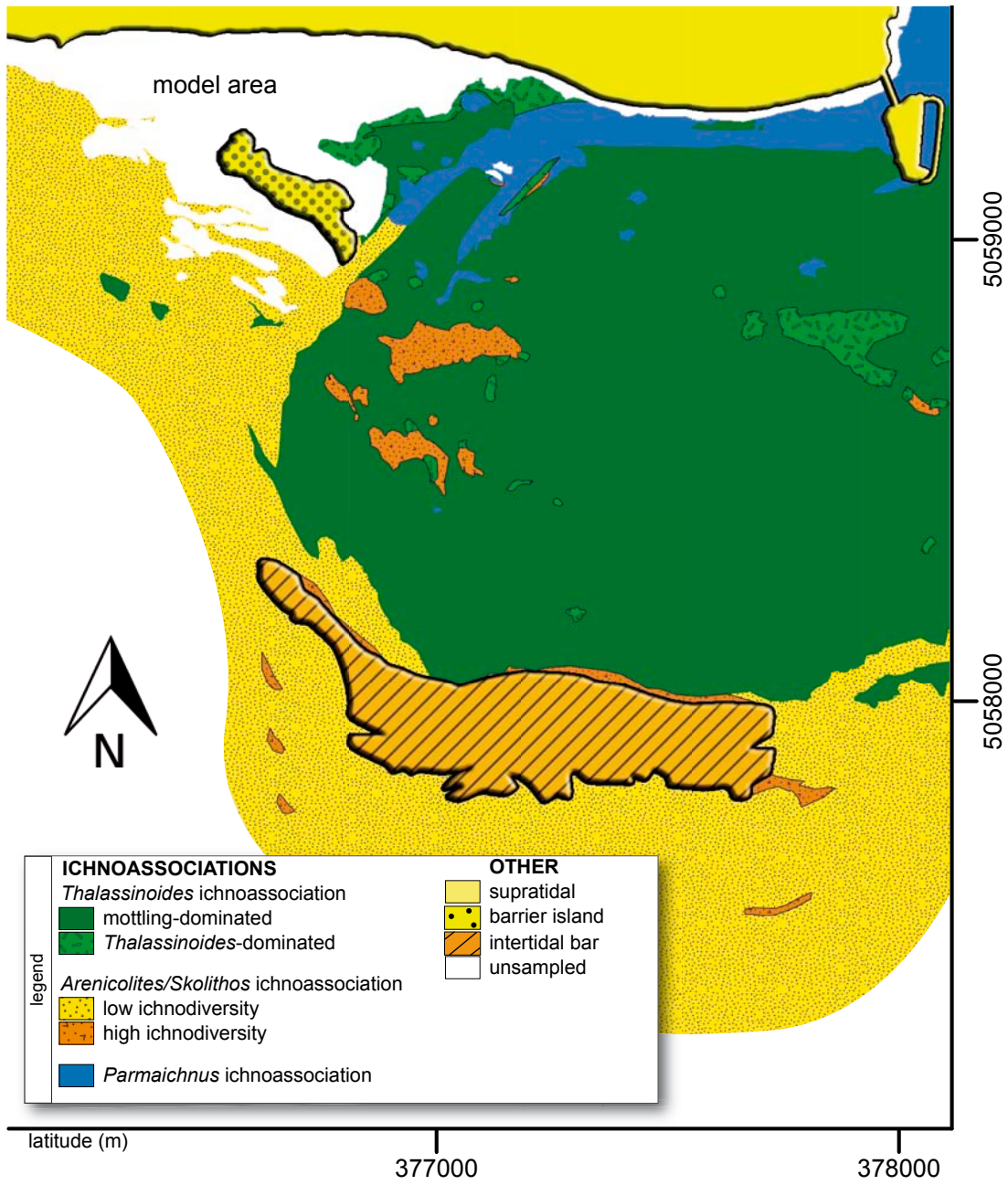


Fig.8.

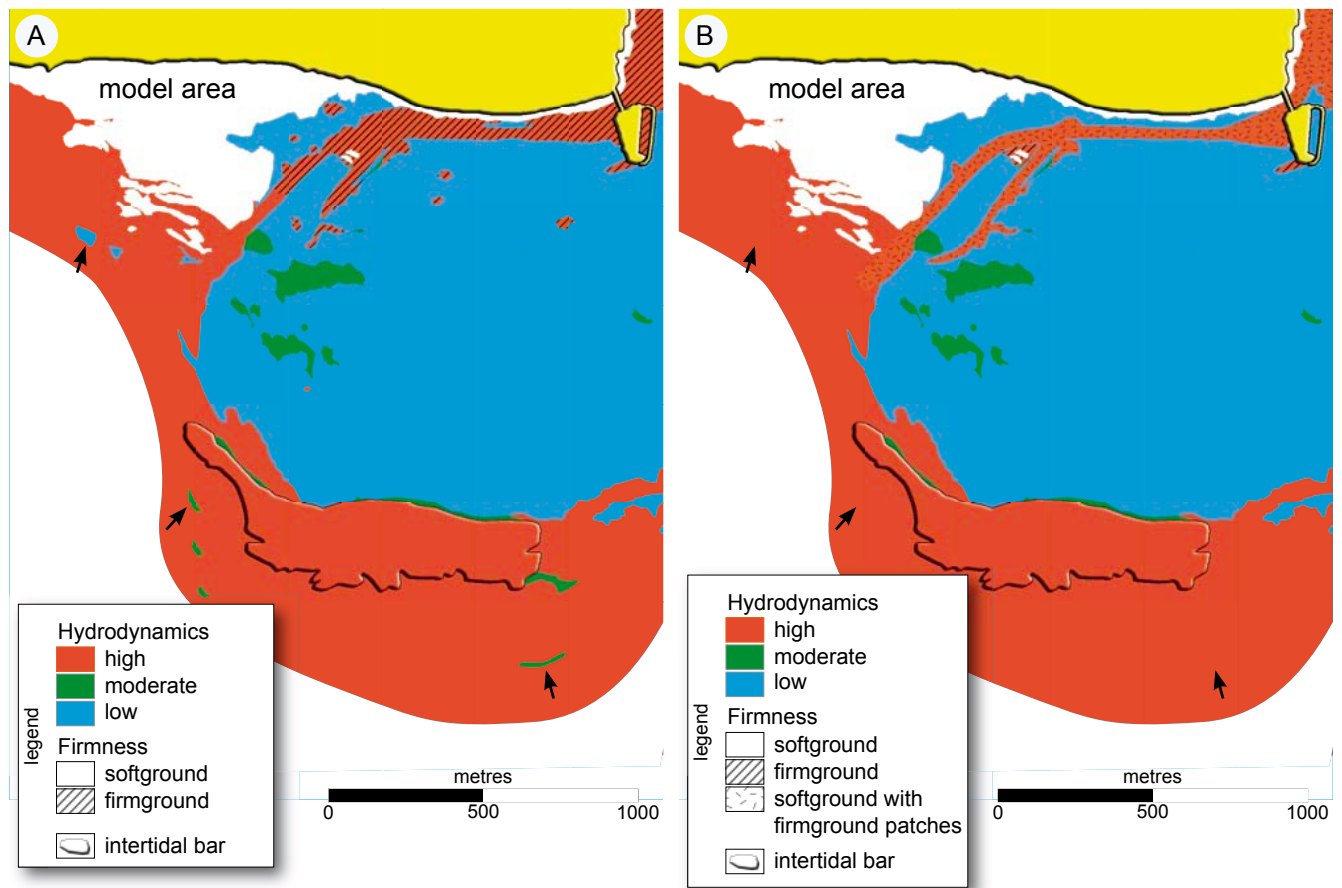


Fig. 9.

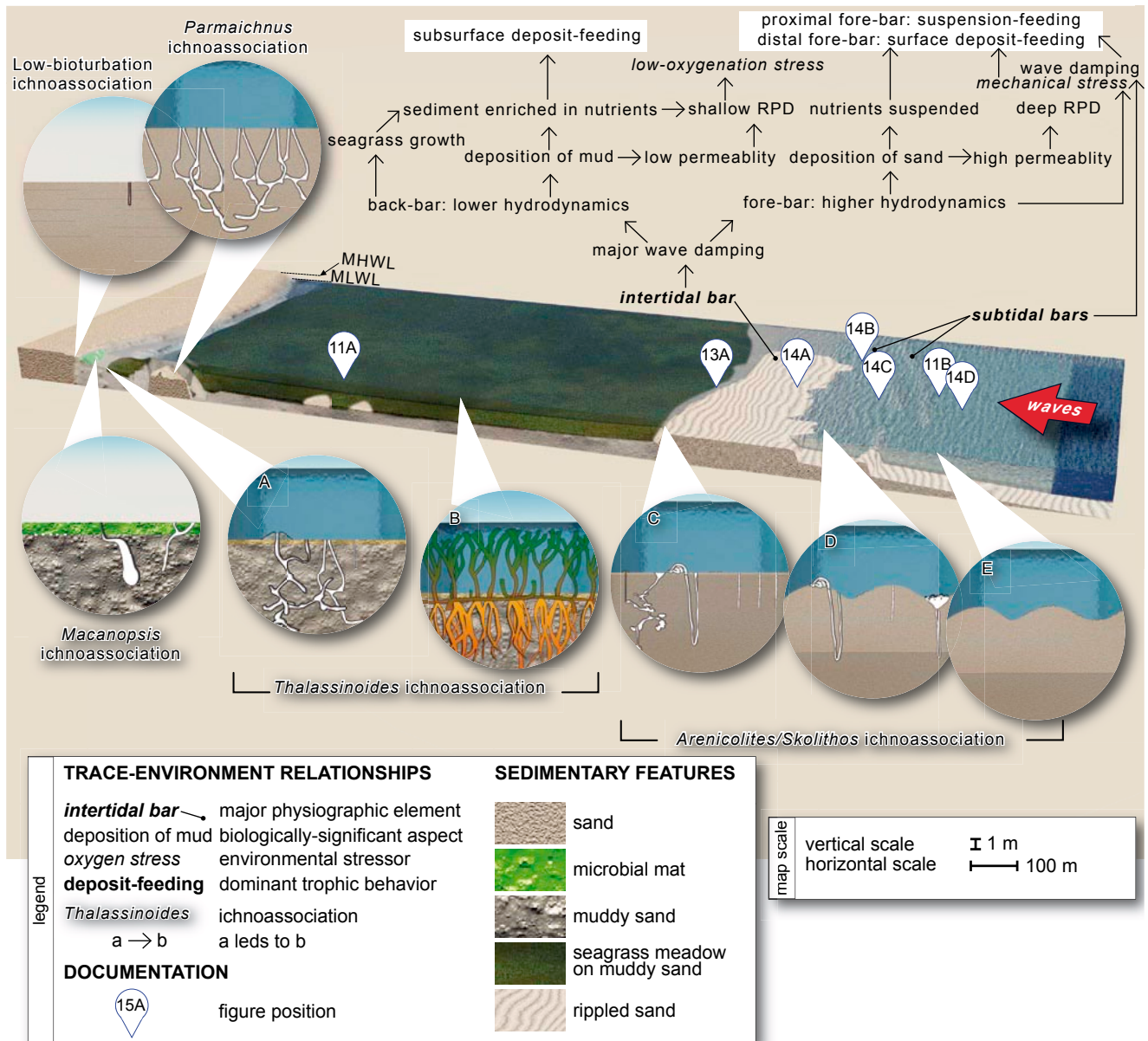


Fig. 10.

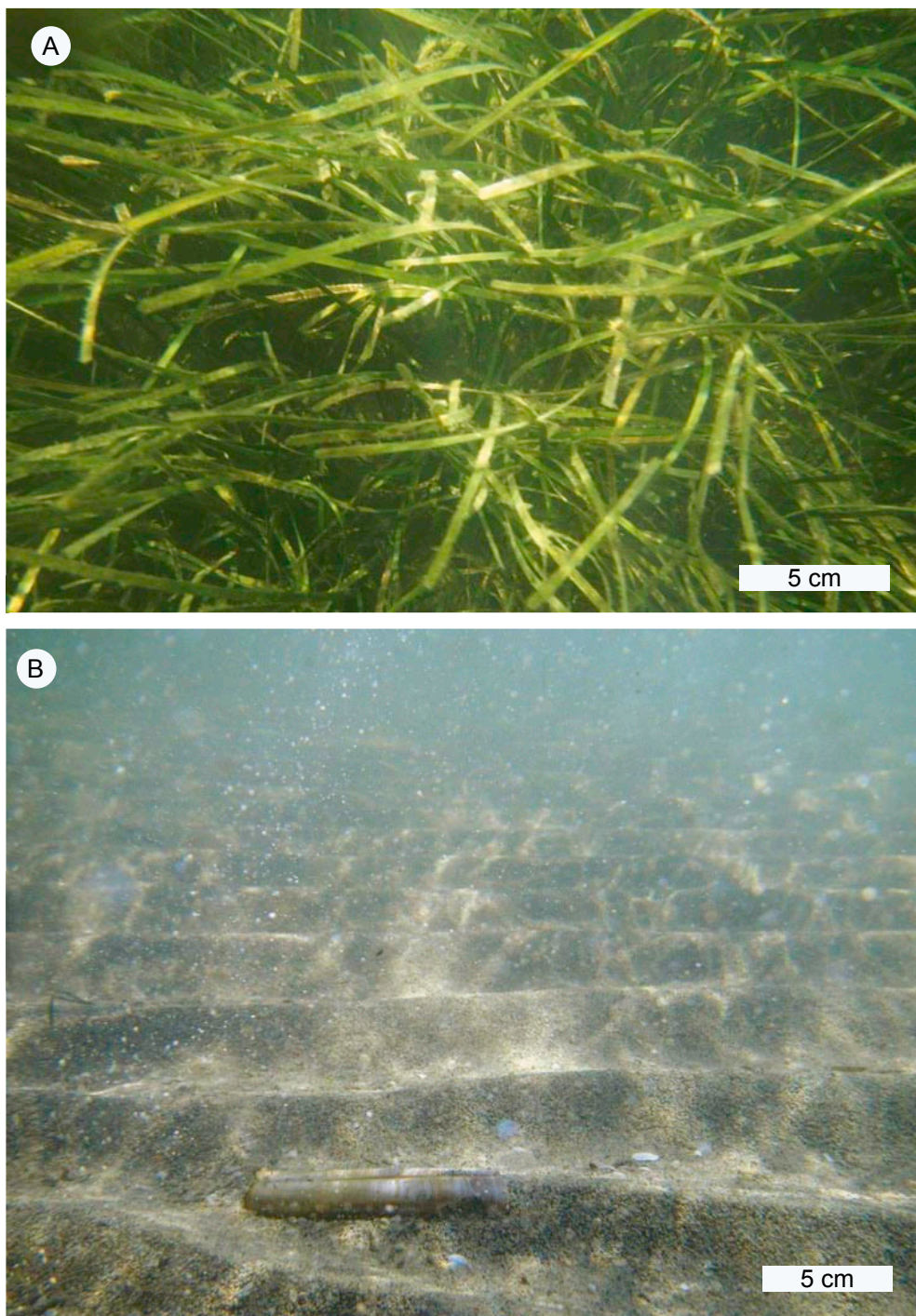


Fig. 11.

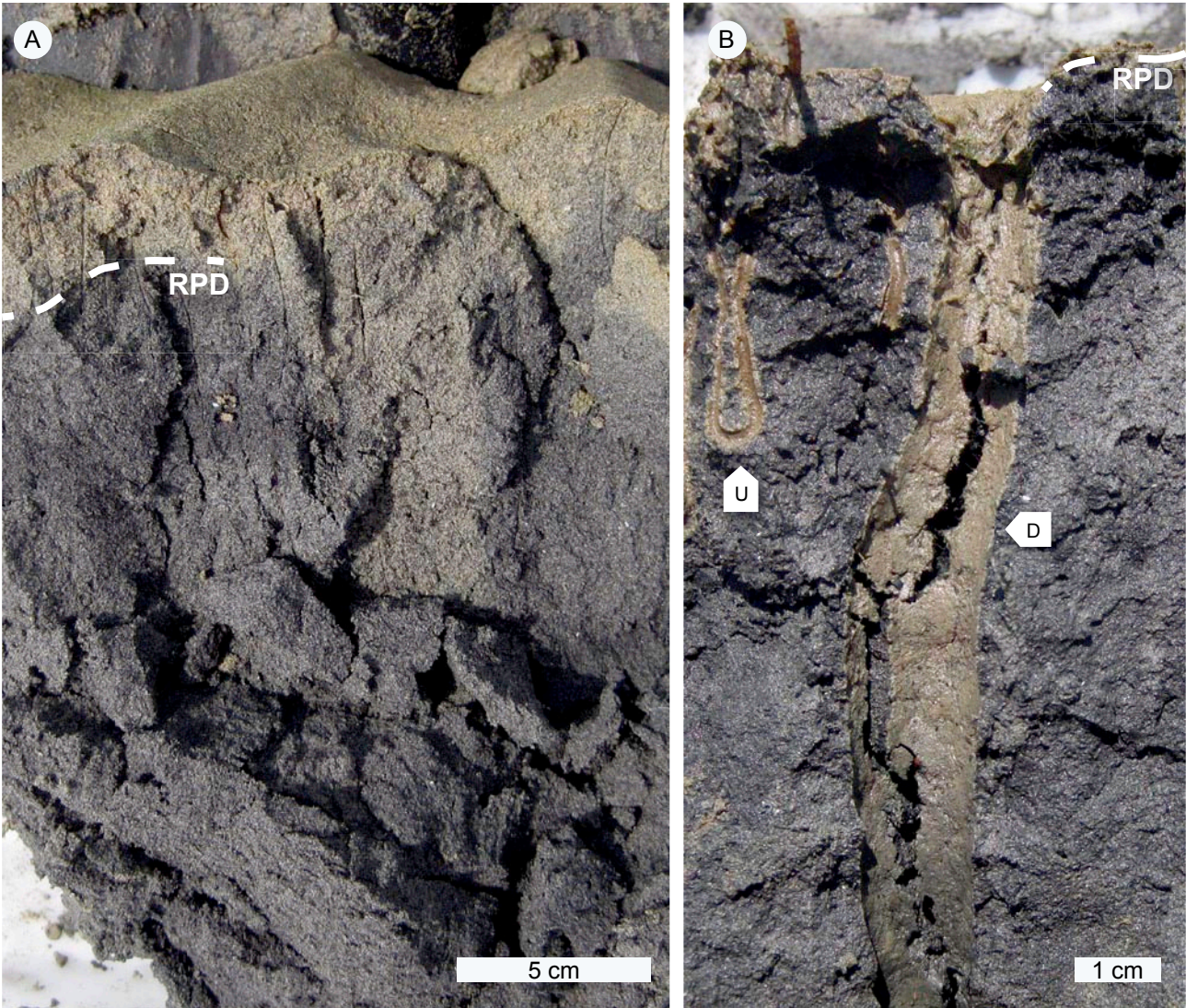


Fig. 12.

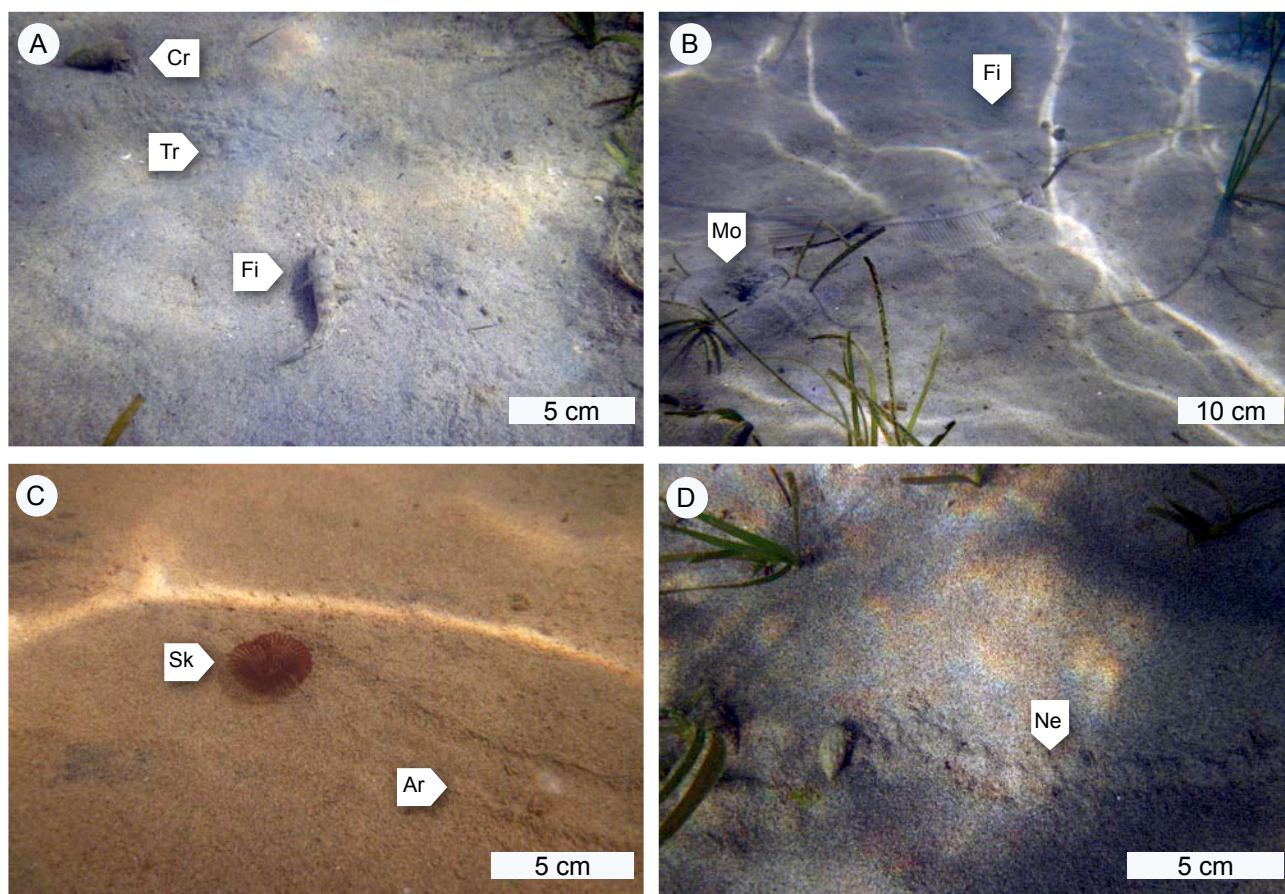


Fig. 13.

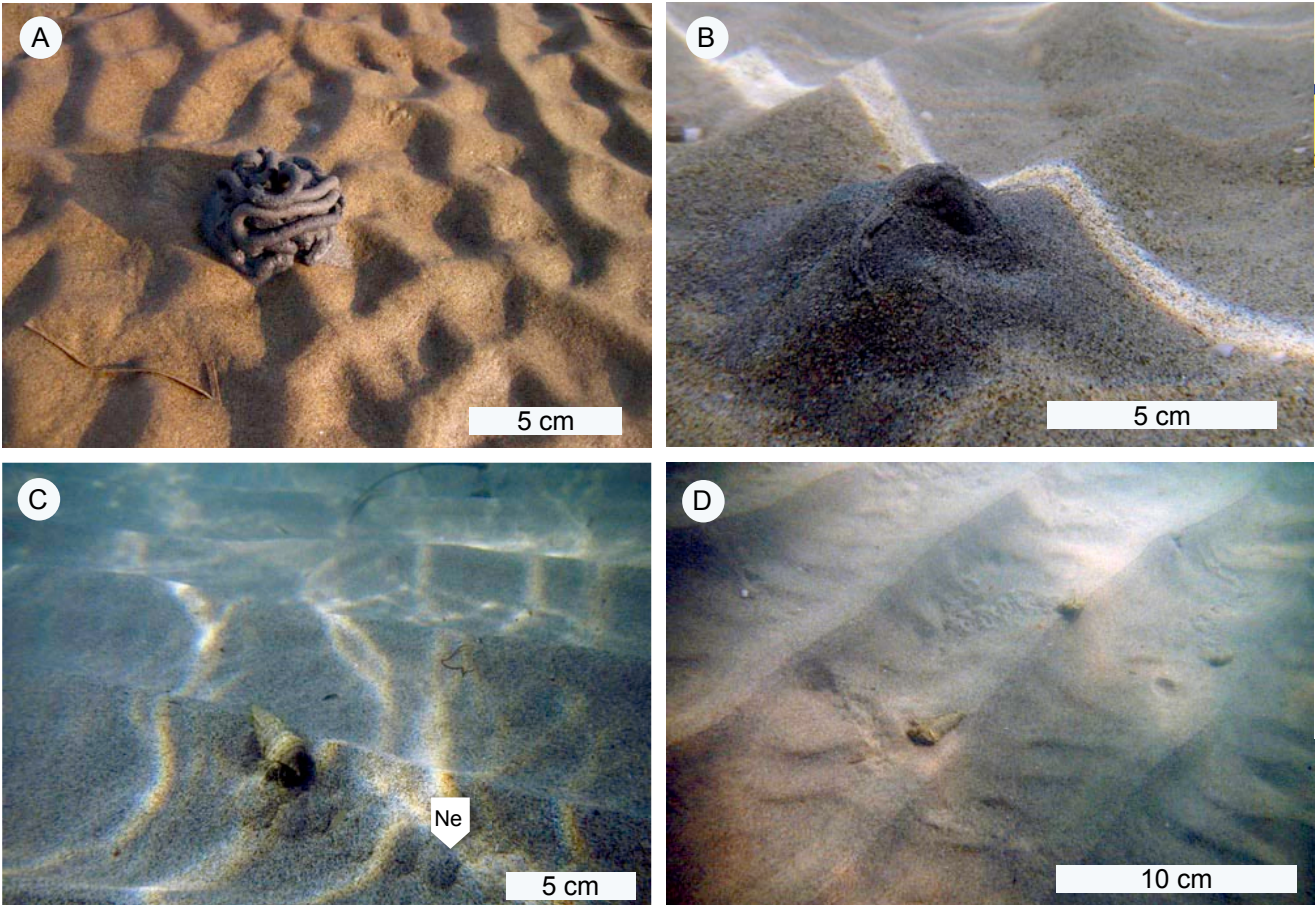


Fig. 14.

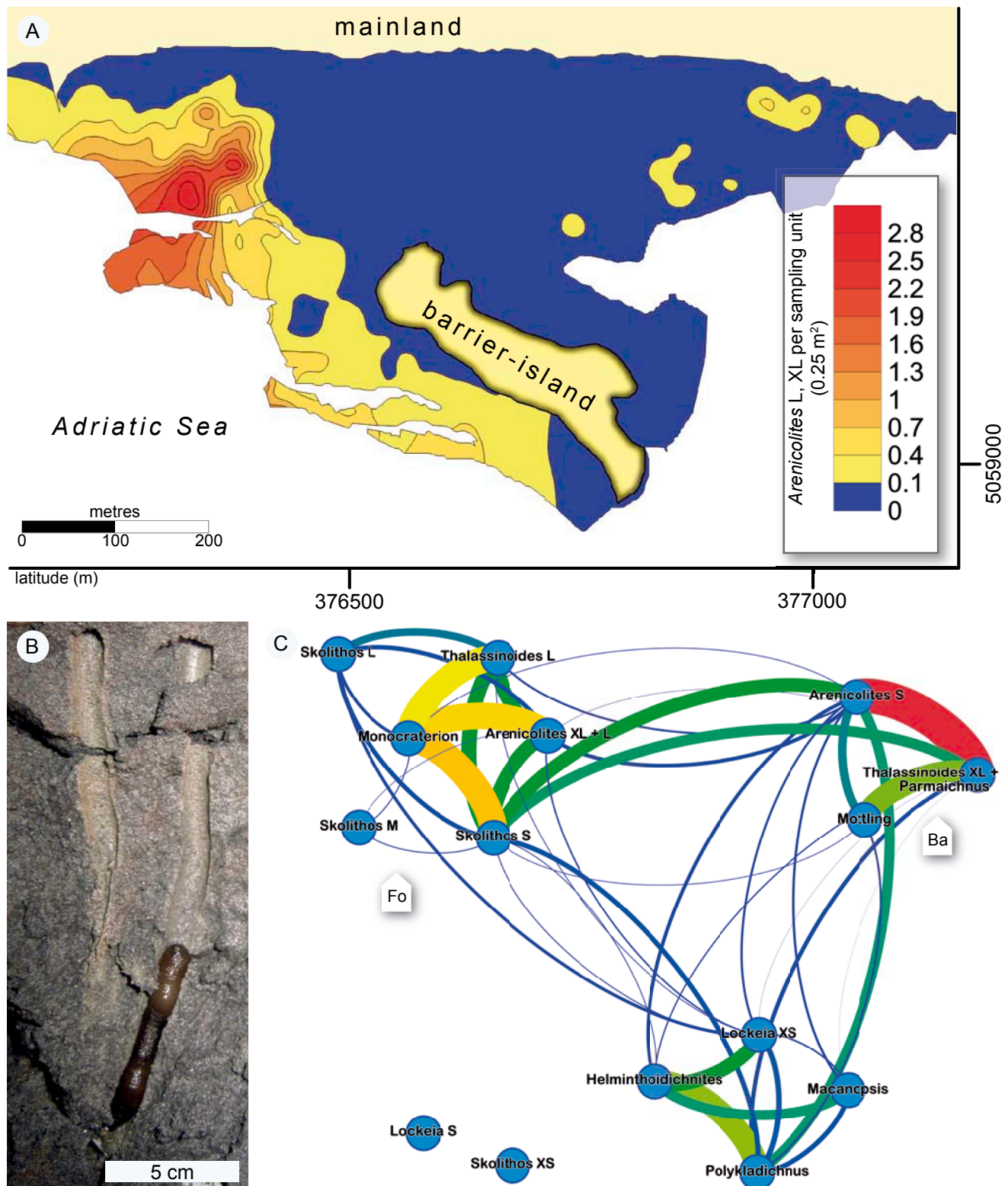


Fig. 15.