

SEA GRASS, MAERL, FORAMINIFERA AND MARINE CONSERVATION

MALCOLM B. HART

School of Geography, Earth & Environmental Sciences and Marine Institute, Plymouth University, Plymouth PL4 8AA, UK.

Sea grass meadows and areas of rhodophyte algae (maerl) are important biodiversity 'hot spots' around the south-western coastline of the British Isles, many of which are found in Special Areas of Conservation (SAC) or Marine Conservation Zones (MCZ). Both environments are host to a wide range of other taxa including foraminifera (marine protists), ostracods, sponges and bryozoans – all of which can be found in sediment samples collected in these shallow-water, marine environments. The foraminifera associated with sea grass meadows are quite distinctive and change composition with latitude (an indicator of sea temperature); the *Zostera* meadows of more northerly latitudes contain a quite different assemblage of benthic foraminifera compared to those in the *Posidonia* meadows of the Mediterranean Sea. Recently fossil sea grass meadows have been recorded in the chalks of the Maastricht area which are ~70 million years old. Here the *Posidonia*-like rhizomes and fronds are preserved both as impressions and, in some cases, in three dimensions. The latter provide an opportunity to study the internal structure in amazing detail, as well as investigate the associated Cretaceous epifauna. These are the earliest known sea grass fossils and provide a unique window into the evolution of this (palaeo)environment.

INTRODUCTION

Marine conservation in the UK is a relatively late addition to the processes that are already well established in land-based areas and has recently been described by Burek *et al.* (2013). On land, the National Parks and Access to the Countryside Act (1949 and subsequent revisions in 1968, 1973, 1981 and 2006) created the National Parks, Areas of Outstanding Natural Beauty (AONB) and Sites of Special Scientific Interest (SSSI). In the marine environment it was the Habitats Directive (Council Directive 92/43/EEC, 1992) that required EU member states to create a network of protected wildlife areas, known as Natura 2000 sites, across the European Union. Special Areas of Conservation (SAC) are for wildlife in general, while Special Protection Areas (SPA) are especially for birds. This was followed by the

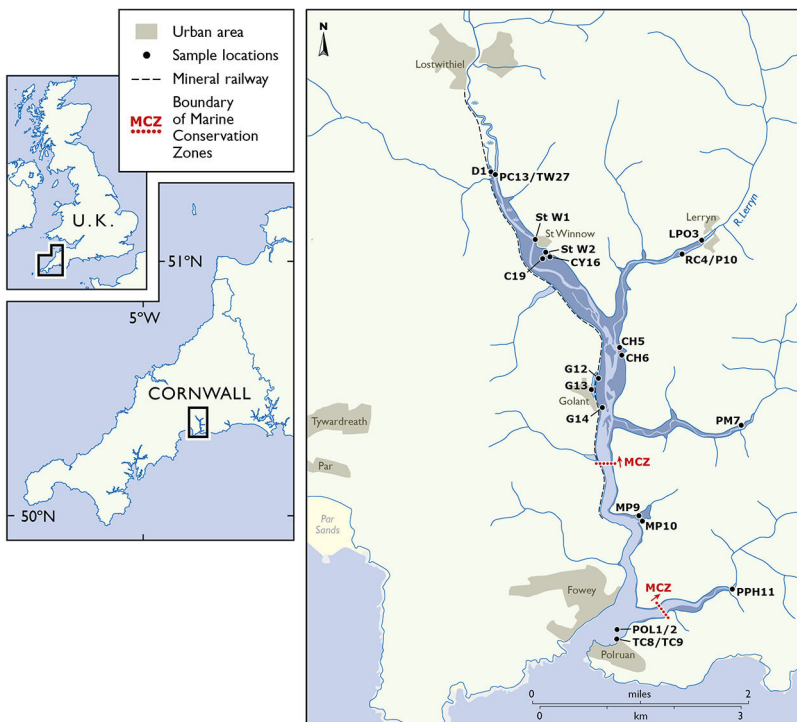


FIGURE 1. General map of the Fowey Estuary (Cornwall) showing the key features, boundaries of the 'Upper Fowey and Pont Pill Marine Conservation Zone' and the sample locations used in the research described by Hart *et al.* (2014a). Map adapted from Hart *et al.* (2014a).



FIGURE 2. Plymouth Sound and Estuaries Special Area of Conservation (SAC). Plymouth University image.

Marine and Coastal Access Act (2009) which provides the framework for the creation of Marine Conservation Zones (MCZ) in UK territorial waters. As indicated in Burek *et al.* (2013), there were four regional groups that considered the scientific case for areal designations and, for example, those in the south-west were documented in Leiberknecht *et al.* (2011) and uploaded on to the website managed by the Joint Nature Conservation Committee (JNCC) which led the project. Following some criticisms of the lack of a science base, there have been two rounds of designations, with more to follow. Many of the MCZ are in shallow-water environments, including – in the south-west – the Tor Bay MCZ, Upper Fowey and Pont Pill MCZ (Figure 1), Skerries Bank and Surrounds (MCZ) and the Whitsand and Looe Bay MCZ. The Plymouth Sound and Estuaries SAC (Figure 2) and the Fal and Helford SAC are also in shallow-water, estuarine environments, as is the important Slapton Ley SSSI (and National Nature Reserve). As all of these (and many other designated areas) are in shallow-water, near-shore, environments, it is important to recognise that, in the Recent ‘geological’ past, many of these were dry land. It is, therefore, important to consider their Pleistocene – Holocene history.

PLEISTOCENE – HOLOCENE CLIMATE AND SEA LEVEL CHANGES

While the mid-Late Cretaceous and Early Paleogene interval was characterised by ‘greenhouse’ conditions, with little evidence of land ice on the planet, the climate of the Earth deteriorated through the Oligocene leading, eventually, in the Pleistocene to the presence of both an Antarctic and an Arctic ice cover (Zachos *et al.*, 2001). During the Pleistocene the Arctic and Antarctic ice caps advanced and retreated a number of times, with the UK almost completely covered in ice on 4/5 occasions (Lee *et al.*, 2011; Gibbard and Clarke, 2011). The link between $p\text{CO}_2$ in the atmosphere and these climate cycles has been demonstrated by stable isotope analysis of marine, carbonate-rich, successions (e.g., Le Friant *et al.*, 2008, fig. 3), and analysis of gas bubbles in ice cores (e.g., Barnola *et al.*, 1987). These glacial advances in the UK extended south as far as the M4 corridor (approximately) and the North Devon coast, with sea ice extending as far south as the Isles of Scilly (Scourse, 1991; Hiemstra *et al.*, 2006). The presence of ice on Dartmoor has recently been confirmed, though it is still debated as to whether this ice was connected to the main body of ice, or simply a detached, static mass (Fretwell *et al.*, 2008; Evans *et al.*, 2012).

Sea level changes during glacial episodes were quite significant and, following the Last Glacial Maximum, sea level rose by ~130 m during the deglaciation phase (Lambeck and Chappell, 2001; Lambeck, 2004). This rise was relatively rapid and the changes recorded in areas such as South Devon and South Cornwall show a very rapid drowning in the 12,000–6,000 years B.P. interval followed by a reduced, but continuing, rise to the present day (Massey *et al.*, 2008). Calculations of the rate of sea level rise are complicated by isostatic readjustments, even in areas that were not themselves glaciated. There were a number of changes caused by this abrupt rise in sea level:

- Drowning of over-deepened valleys in south-west England, forming the well known *rias* of, for example, Plymouth Sound, Fal Estuary, Helford Estuary, River Fowey, Looe River, River Erme;
- Separation of the Channel Islands from France (Consolaro *et al.*, 2014);
- Migration of shingle bars on-shore at Loe Pool (Toy, 1934; Simola *et al.*, 1981; Coard *et al.*, 1983; May, 2003a) and, more significantly, Slapton Sands (Hails, 1975a, b; Morey, 1976, 1980, 1983; Van Vlymen, 1979; Kraft and Chrzastowski, 1985; Johnes and O’Sullivan, 1989; May, 2003b; Massey *et al.*, 2008). The on-shore migration of the shingle formed Slapton Ley, now an SSSI and National Nature Reserve. As sea level continues to rise, the shingle bar will move further on-shore, eventually fringing the hills on the inner side of the present water body; and
- Coastal landslides, such as those in the Axmouth to Lyme Regis Undercliffs National Nature Reserve, became much more active during periglacial conditions and, with lowered sea levels, extended out into Lyme Bay (Pitts, 1983). Now drowned, the toes of these landslides form the off-shore reefs that are an important marine habitat (Attrill *et al.*, 2011).

In south-west England the Fal and Helford SAC and the Plymouth Sound and Estuaries SAC were eroding river valleys during the Last Glacial Maximum (LGM), only being flooded when sea levels recovered during the latest Pleistocene and Holocene (Figure 2). The near and off-shore MCZs such as Tor Bay, Skerries Bank and Surrounds, Whitsand and Looe Bay, Upper Fowey and Pont Pill, Skomer, etc., were all inundated at this time and so have very limited marine histories (geologically speaking). With continual sea level rise, they are still evolving to adjust to the changing conditions and must not become regarded as static ecosystems.

UNDERSTANDING ECOLOGICAL CHANGE

Plymouth Sound and Estuaries SAC includes a range of environments (Figure 3), including muds, sand waves and coarse gravels (Fitzpatrick, 1990, 1991). There are limited sea grass meadows (in fine sands near Jennycliff) but no recorded beds of rhodophyte algae (maerl). Using marine geophysics, Eddies and Reynolds (1988) located the buried channel of the River Tamar and investigated the sedimentary infill by means of two marine boreholes (Figure 4). Lying

above the Devonian slates ('bedrock') is a succession of gravels, organic-rich muds, shell-rich sands and the present muddy sands of the modern estuary. Eddles and Hart (1989) and Castignetti (1993, 1997) were able to identify an estuarine assemblage of foraminifera (marine protists), passing upwards into more open marine conditions. A similar succession showing the transition from saltmarsh to estuarine and open marine foraminifera has been described in a core collected between France and Grouville Bay on the east coast of Jersey (Consolaro *et al.*, 2014).

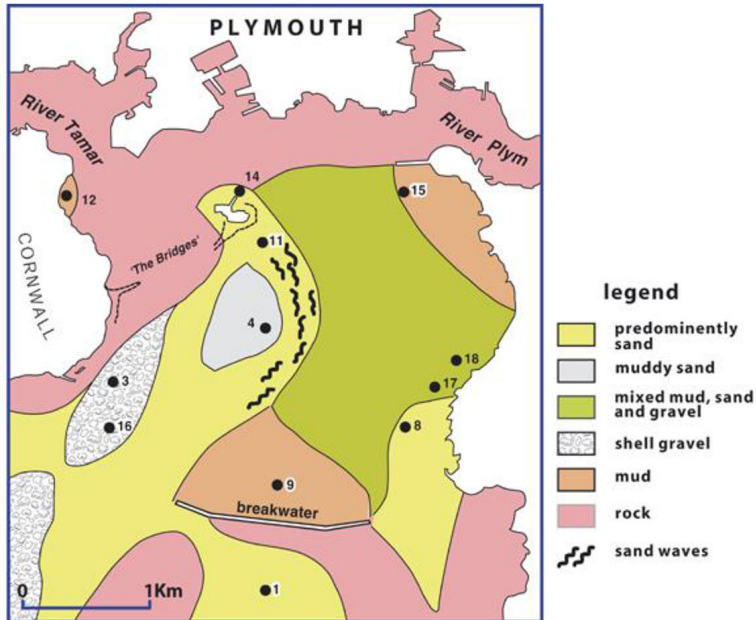


FIGURE 3. Sediment distribution map of Plymouth Sound based on underwater mapping by Fiona Fitzpatrick (1990, 1991).

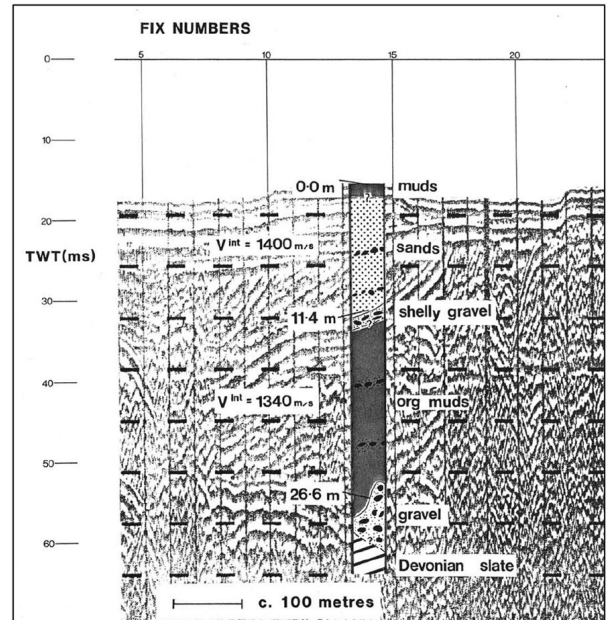


FIGURE 4. Marine geophysics profile and borehole interpretation of Plymouth Sound.

It is possible to determine the environments represented by such assemblages of foraminifera by using data from surface samples collected in estuaries such as the River Erme (Stubbles, 1999), Looe River, River Fowey (Stubbles, 1999; Hart *et al.*, 2014a) and the tributaries of the Fal Estuary (Hart *et al.*, 2015). The Fowey Estuary (Figure 5) is probably one of the simplest examples to understand as it follows a relatively straight, north to south, route with only a few short tributaries (Lerry, Penpol and Pont Pill: Figure 1). At the tidal limit, just south of Lostwithiel, there is a very limited saltmarsh and upper mudflat area as this area was, until recently, a landfill site. Samples collected (Hart *et al.*, 2014a, figs 1, 3) from here contain a very limited assemblage of foraminifera, including *Balticammina pseudomacrescens*, *Jadammina macrescens* and *Trochammina inflata*. This assemblage is typical of higher mudflat and saltmarsh environments, being composed of only agglutinated taxa (Hart *et al.*, 2014a, fig. 6). As indicated by Hart *et al.* (2014a, fig. 6) the foraminifera of the Fowey Estuary gradually change in both composition and species dominance down-estuary, eventually becoming fully marine in the sediments within the sea grass meadow in Polruan Pool.

In Plymouth Sound and in some of the boreholes between Jersey and France, this saltmarsh to estuarine to fully marine transition is seen progressively up-core. This is to be expected and follows Walther's Law (published in 1894). 'Walther's Law of Facies' implies that a vertical sequence of facies will be the product of a series of depositional environments which lie adjacent to each other (Figure 6). This pattern of sedimentation was first recognised by Johannes Walther (1860–1937), a German geologist and stratigrapher: see comments on his work by Middleton (1973) and Gischler (2011). Walther's Law uses the concept of 'facies' which implies that a sediment formed under specific depositional conditions represents a series of processes within an environment (and often containing a distinct set of faunal/floral characters). The upwards progression from saltmarsh to estuarine and, eventually, open marine conditions can be seen almost wherever boreholes provide information on the post-glacial rise in sea level. In the Rade de Brest (Gregoire *et al.*, 2016), the sediment succession also contains evidence of maerl in the immediate sub-Recent, even though maerl is not recorded at the present day. This is also known from some of the cores east of Jersey and elsewhere in northern France. The maerl occurrences may be indicative of a warming interval within the Holocene ~3000 years B.P.



FIGURE 5. Micropalaeontological sampling in the Fowey Estuary near St Winnow Church.

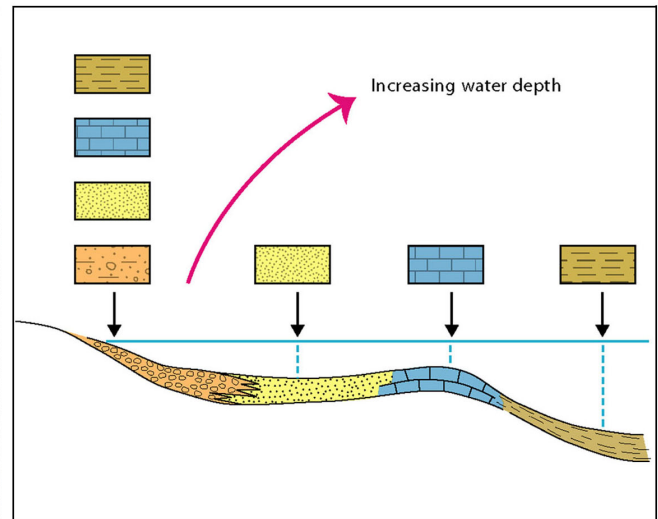


FIGURE 6. Explanation of Walther's law showing both the horizontal distribution of facies and their vertical sequence during the rising sea level (after Hart, 2009).

Maerl is the collective name for a number of red seaweeds (Rhodophyta) that secrete hard, calcareous skeletons (Corallinaceae): see Hall-Spencer (1994). Maerl forms twig-like, branching forms and, as the living alga, requires sunlight to grow, is found down to depths of 51 m in the NE Atlantic Ocean but are best developed in depths of <20 m (Peña *et al.*, 2014). Some Corallinaceae are known to encrust a variety of substrates but unattached forms can often form rhodoliths (nodular forms) in near-shore environments (Martin and Hall-Spencer, 2016). In tropical regions (e.g. Brazil) rhodoliths (Hart *et al.*, 2015, fig. 3A) can be 10 cm in diameter and have a characteristic internal structure (Pascelli *et al.*, 2013). Rhodophyte algae have a well-established geological record, including both the encrusting forms and the rhodoliths. Maerl requires water movement (tidal flow or wave action) to remove fine sediment that may restrict growth. Dead maerl slowly accumulates on the sea floor, often with a thin layer of purple/pink-coloured living maerl on the top. In English waters there are approximately 15 km² of maerl habitat, which represents just 0.03% of the near-shore marine environment (Hall-Spencer *et al.*, 2010). The maerl beds of the Fal Estuary are, therefore, a significant proportion of this total. They were until relatively recently, dredged for agricultural use. Following designation of the SAC there was growing pressure on the Falmouth Harbour Commissioners to terminate their exploitation. This was eventually done in 2005 (Hall-Spencer, 2005). Subsequently the Falmouth Harbour Commissioners have proposed dredging the access to the commercial port. As this would remove large areas of maerl, there have been a series of experiments at removing maerl and replacing it at the proposed new depths (Sheehan *et al.*, 2015). The maerl in the Fal Estuary is composed of two species: *Phymatolithon calcareum* (Pallas) and *Lithothamnion corallioides* (P. & H. Crouan) and has been described by Bosence (1976), Farnham and Bishop (1985), Irvine and Chamberlain (1994), Birkett *et al.* (1998) and Hall-Spencer *et al.* (2010). Beds of maerl are concentrated along the western coastline of Europe in the NE Atlantic Ocean (Peña *et al.*, 2014, fig. 1; Dutertre *et al.*, 2015), including south-west England, Brittany, Western Ireland, the Inner Hebrides and Iceland.

Maerl beds are particularly important near-shore habitats as they are recorded as supporting a high benthic diversity of marine invertebrates (Bosence, 1979). Areas of maerl are a 'Priority Habitat' within the UK Biodiversity Action Plan (see <http://jncc.defra.gov.uk/page-6023> and links to UK BAP priority species and habitats). Dead maerl accumulates very slowly, over thousands of years, and can also contain small patches of living maerl such as near the channel into Falmouth Docks (Sheehan *et al.*, 2015). Austin and Cage (2010) showed, in an investigation of only two samples, that a maerl bed offshore the Isle of Bute (Scotland) contained a high diversity of foraminifera and comparable diversities of foraminifera in maerl beds have also been reported by Boillot (1964), Blanc-Vernet (1969), Rosset-Moulinier (1972) and Freiwald and Henrich (1994) as well as in sub-Recent sediments in the south of France (Morhange *et al.*, 2003) and Brittany.

Samples of maerl from the Fal Estuary have been investigated for their associated foraminifera using material collected by Sheehan *et al.* (2015). The samples were preserved in buffered formalin before being stained with the protoplasmic stain, Rose Bengal, in an attempt to distinguish the 'living' (stained) assemblage and the 'dead' (unstained) components of the assemblage. The time of collection (September to October) meant that there were relatively few living (= stained) foraminifera recorded, and the dead component contained an admixture of both open marine forms and species normally associated with estuarine environments. There were also some species that often appear to

be associated with sea grass meadows (Hart *et al.*, 2016). The nature of this mixed assemblage requires further investigation, with samples being collected in May to August when the living assemblage should be more developed.

SEA GRASS MEADOWS

About fifty species of marine angiosperms, commonly known as sea grasses, live in today's inner continental shelves (den Hartog, 1977). Sea grass ecosystems are recognised to be amongst the richest and most productive coastal ecosystems where a sizeable part of the primary production is being carried out by a variety of epiphytic algae, which directly provide food to a range of meiofauna and microfauna (Sen Gupta, 2002).

The presence of sea grasses in sub-tidal and inter-tidal environments can have substantial effects on these habitats and, as a result, cause pronounced changes in the benthic communities. Such sea grass meadows are considered to be amongst the most productive of shallow water sedimentary environments. For instance, prior to the evolution of sea grass, there were none of the associated habitats and – by default – no sea grass-related foraminiferal assemblages (Murray, 2006). Sea grass meadows have also been reported to enrich the dissolved nutrient concentration of their surrounding marine environments by absorbing from the sediment ammonia and phosphate generated by bacterial activities and/or organic matter accumulation and releasing it to the environment (Lee and Anderson, 1991).

Under the European Water Framework Directive angiosperms (flowering plants), phytoplankton, macroalgae, benthic invertebrate fauna and fish are considered as important bio-indicators and helpful in defining the ecological status of coastal waters. They are referred to as *biological quality elements* (WFD, 2000). Sea grasses are the only truly marine flowering plants and can be used for monitoring purposes because they are highly sensitive to human disturbance (Foden and Brazier, 2007). Five sea grass species are found around the British Isles: two species of 'tassel weed' (*Ruppia maritima* and *R. cirrhosa*) and three species of 'eelgrass' (*Zostera* spp.).

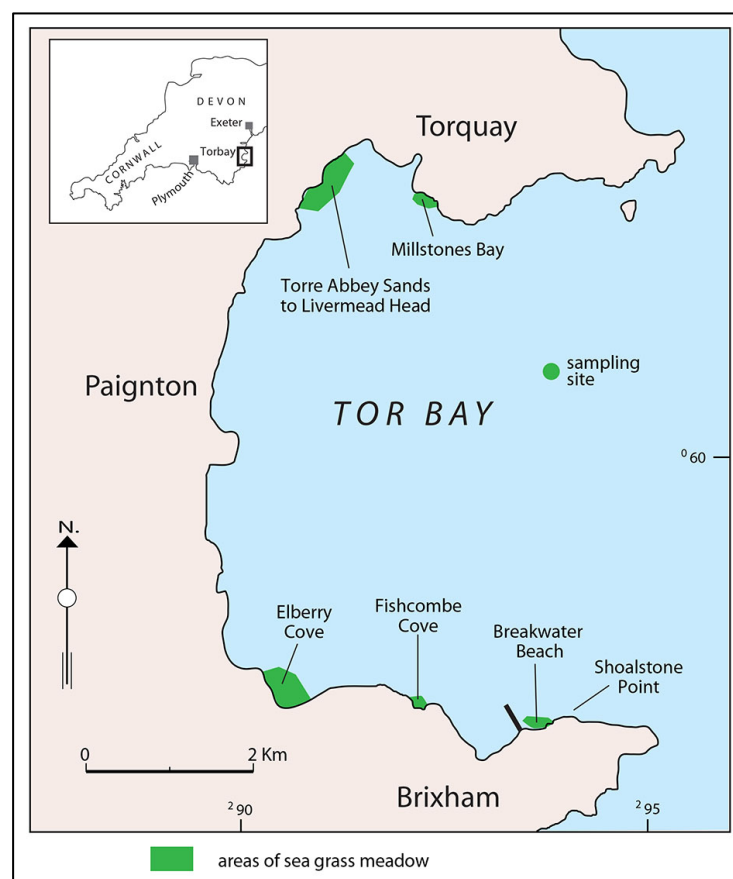


FIGURE 7. Sea grass meadows in Tor Bay investigated by Sadri *et al.* (2011). A sediment site in the centre of Tor Bay, well away from the sea grass meadows, was also selected for comparison purposes.

In the United Kingdom, *Zostera marina* is the dominant eelgrass species and, similar to those of the brackish waters along the Atlantic coast, displays an annual growth closely linked to water temperature with the optimum range being between 5 °C and 30 °C (UKSACS, 2010). Living *Zostera marina* leaves are the favourite substratum for many epiphytic algae, and there have been reports of other algae living between the sea grass shoots and within the

surface layers of the sediment below. Whelan and Cullinane (1985) have identified 60 algal species in a *Zostera marina* bed in Ventry Bay, Ireland. Dense meadows of *Zostera marina* leaves have been shown to slow down water flow and, thereby, increase rates of sedimentation. The rhizome and root networks of sea grass hold the substrate together, resulting in reduced erosion and stabilisation of the sediment. The penetration of *Zostera* roots into the sediment ventilates the upper layers, allowing for a deeper penetration of oxygen into the sediment layer and providing a more favourable habitat for burrowing animals (UKSACS, 2010). De Boer (2007) has highlighted the importance of light on sea grass growth and identified the process by which the reduction of turbidity results in a decrease of the sediment load and the resulting improved light conditions as the most significant positive feedback in sea grass systems.

Tor Bay is located on the south coast of Devon in south-west England (see Figure 7). Recent studies by the Torbay Coast and Countryside Trust's (TCCT) Torbay Seagrass Project (*personal communication*: Dominic Flint, Seagrass Project Officer, 2009) has shown that there are at least 80 ha of sea grass meadows in Tor Bay representing nearly 31% of total reported area of all sea grass species in Devon. Samples were collected at 3 geographical sites (Sadri *et al.*, 2011): two from within the sea grass meadows at Fishcombe Cove (050° 24.16' N, 003° 31.3' W) and Millstones Bay (050° 27.34' N, 003° 31.3' W) and one from the bare sediments in the middle of Tor Bay's coastal waters (050° 26.06' N, 003° 30' W). The sea grass meadows are within the normal salinity range (25-34 ‰), sub-tidal and appear to be mainly comprised of *Zostera marina*. The sea grass bed depth in Fishcombe Cove ranges from 1 to 3.5 metres and 0.1 to 4.3 metres in Millstones Bay. The sea grass patches in Fishcombe Cove are dense and of large to medium in size whereas, in Millstone Bay, they are sparse and range from medium to small. However, the area of the Millstones Bay meadow is almost 3 times larger than those at Fishcombe Cove with the former reported at 1.5 hectares and the latter 0.41 hectares. Figure 7 shows a map of the sea grass meadows with the green polygons representing the extent of the sea grasses, all of which now fall within the Tor Bay MCZ. The weather event statistics acquired by the Torbay Coast and Countryside Trust (TCCT) during the sea grass survey project in 2006 has shown that, as a result of their geographical locations, these sea grass meadows are subject to different levels of storm exposure with Fishcombe Cove being very sheltered and mainly subject to north-easterly winds while Millstones Bay is less sheltered with a medium risk from (often stronger) south and south-easterly winds.

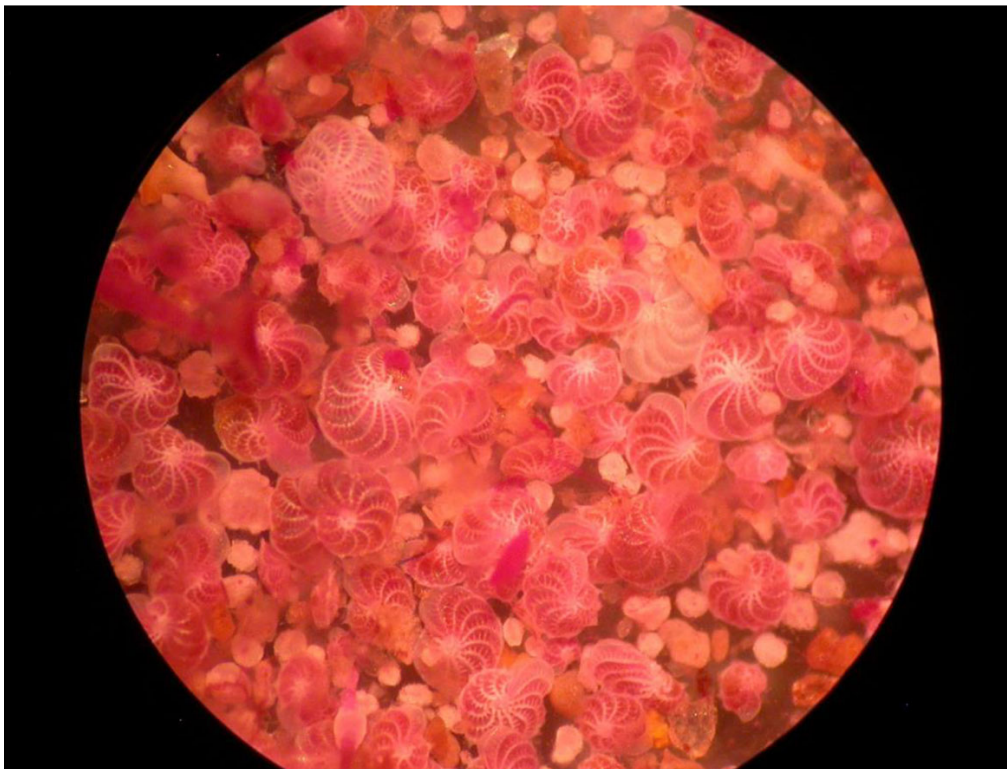


FIGURE 8. Stained (= presumed living at time of collection) *Elphidium crispum* (foraminifera) that were attached to the sea grass fronds at the time of summer sampling (June).

The foraminifera described by Sadri *et al.* (2011) included a range of taxa that are well-known along the south-west coast of the United Kingdom (Castignetti, 1997 and references therein). There were a few taxa with a plano-convex growth style that may indicate their presence on the fronds of the sea grass: including *Cibicides lobatulus* and *Planorbulina mediterraneensis*. In the summer months (June and August) large numbers of living (= stained by Rose

Bengal) *Elphidium crispum* were found on the fronds (Figure 8), although this bi-convex form does not appear to be adapted to an epiphytal mode of life. It is, however, well known to be geotropic and 'climbs' up any available surfaces (see Sadri *et al.*, 2011, p. 273, for a discussion of this life style).

It was a model based on published data and the results from Tor Bay and Ischia (Dias *et al.*, 2010) that has helped in the interpretation of the sea grass fossils that are known from the Maastricht Formation (Maastrichtian, Cretaceous). In the rocks of the Maastricht Chalk Formation in Limburg (Netherlands) the foraminifera that are present appear to represent a potential sea grass habitat (Renema and Hart, 2012). Debay, as early as 1848 and 1851, had described what he thought were sea grass rhizomes from the Maastrichtian chalks of the Netherlands and Germany, but as these are ~70 million years old his work was disregarded. More recently, Raymond van der Ham of the 'Naturalis Biodiversity Centre' in Leiden has described more potential sea grass fossils from the chalk quarries of the Maastricht area (van der Ham *et al.*, 2007), although some palaeobotanists have suggested that these are not true sea grasses, but probably plants washed in from the surrounding land areas. More recently, John Jagt (Maastricht Museum), Sijr Renkens and the author have collected large amounts of foliage, roots and rhizomes from one part of the succession, all of which is now in the Natuurhistorisch Museum (Maastricht). In October 2015, during another visit, a complete sea grass meadow with thousands of specimens has been collected and is now being described (Figure 9). This occurrence, coupled with the microfauna and macrofauna that one would associate with a shallow-water sea grass community, firmly identifies this as one of the earliest sea grass assemblages yet described (Hart *et al.*, 2016).



FIGURE 9. Sea grass fossils from the Maastricht Chalk Formation of the ENCI quarry near Maastricht. Image kindly provided by Dr J.W.M. Jagt (Natuurhistorisch Museum, Maastricht).

POLLUTION INDICATORS

When the Fal and Helford SAC was designated in April 2000, Restronguet Creek, unlike the other tributaries in the estuary, was excluded from the designated area (Figure 10). This was the result of Restronguet Creek being in 'recovery' from the Wheal Jane pollution incident in January 1992. After a period of prolonged rainfall, 50,000 m³ of acidic mine water and sludge escaped from the moth-balled mine on the 16th January 1992. At the Devoran monitoring station, where the River Carnon enters Restronguet Creek, a pH of 3.2 was recorded (Olugbode *et al.*, 2005, fig. 3), though mitigation work and a new treatment process has restored the water quality. The foraminifera disappeared from much of Restronguet Creek from between two and three years and, while assemblages have now recovered (Stubbles, 1993, 1999; Stubbles *et al.*, 1996; Olugbode *et al.*, 2005), many individuals with test deformities are still being recorded. Pirrie *et al.* (2003) have mapped the metal content of the sediments (Cu, Zn, Sn, Fe, etc.) throughout the Fal

Estuary and have shown that the impact is generally restricted to Restronguet Creek and the adjacent, western side of Carrick Roads. The other tributaries (Truro River, Tresillian River, Fal River, Percuil River and the creek near St Just-in-Roseland) show none of this pollution and foraminifera were recorded throughout the post-incident period up to, and including, the present day (Hart *et al.*, 2015). Deformed foraminifera are also recorded in the Fowey Estuary (Stubbles, 1999; Hart *et al.*, 2014a), to a lesser extent, although there has been no recorded pollution incident. The geochemistry of the estuarine sediments clearly shows the impact of historical mining in the catchment as well as background ‘pollution’ from the mineralized country rocks.

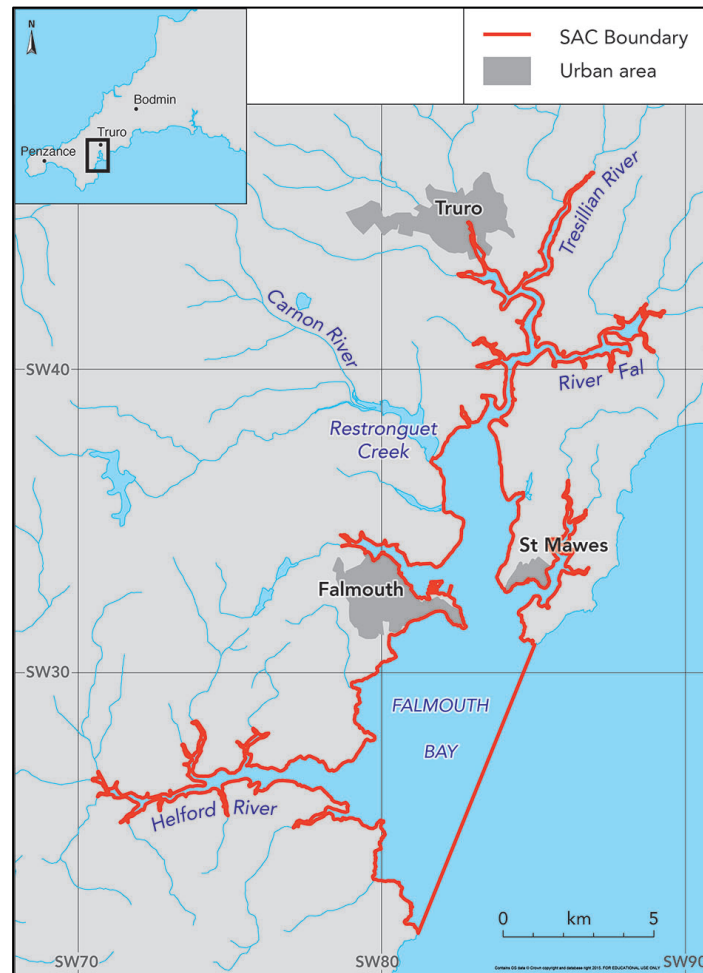


FIGURE 10. Outline map of the Fal and Helford Special Area of Conservation (SAC) showing the ‘excluded area’ of Restronguet Creek and the Carnon River which was the location of the Wheal Jane (1992) mine pollution incident. After Hart *et al.* (2015).

While the abruptly lowered pH in Restronguet Creek clearly arrested the calcification of the foraminiferal tests of species such as *Elphidium williamsoni*, *Haynesina germanica* and *Ammonia* sp. cf. *A. aberdoveyensis*, once the pH recovered, these species were able to re-colonize the area, presumably by migration from areas outside Restronguet Creek. It is known that benthic foraminifera, in order to calcify new chambers, raise their internal pH to ~9.0 (de Nooijer *et al.*, 2009a, b), and that the lowered pH temporarily present in Restronguet Creek was clearly a barrier to their normal life cycle. This response to the change in pH leads into modern issues of climate change and the process of ocean acidification.

OCEAN ACIDIFICATION – THE OTHER CO₂ PROBLEM

The modern phenomenon of ocean acidification may have severe consequences for marine ecosystems and it has been described in the media as the ‘other CO₂ problem’. Since the industrial revolution, the oceans have absorbed ~30% of the carbon dioxide produced by the increased human population, the expansion of animal farming and – especially – the burning of fossil fuels (Houghton *et al.*, 1997, 2001; Sabine *et al.*, 2004; Houghton, 2009; IGBP, IOC, SCOR, 2013). This increasing atmospheric *p*CO₂ today at 407.70 ppm, as well as driving some changes in climate, has

caused a series of other chemical changes, including the lowering of marine pH, in a process known as ocean acidification (Caldeira and Wickett, 2003, 2005). Since pre-industrial times, the ocean surface pH has fallen by approximately 0.1 units to a current day global average of 8.1, which is equivalent to a 30% increase in the concentration of hydrogen ions (Guinotte and Fabry, 2008; Raven *et al.*, 2005). The current rate, and magnitude, of the pH changes are thought to be greater than any postulated from the past 300 million years of geological history and the ocean surface pH may fall by a further 0.3 – 0.4 units by the end of the century (Caldeira and Wickett, 2003) using current IPCC scenarios. This change in oceanic pH will have significant consequences for marine organisms, particularly those with calcareous shells (Orr *et al.*, 2005; Raven *et al.*, 2005; Kroeker *et al.*, 2010; Rodolfo-Metalpa *et al.*, 2011; Wall-Palmer *et al.*, 2012, 2013). Benthic foraminifera are an important group to examine as they occur worldwide, are environmentally sensitive, have short life-histories and provide an excellent fossil record. Much of the research conducted on foraminifera in relation to ocean acidification has involved short-term laboratory experiments (Spero *et al.*, 1997; Bijma *et al.*, 1999, 2002; Khanna *et al.*, 2013), deep sea CO₂ storage scenarios with very high levels of CO₂ (Bernhard *et al.*, 2009a, b) or micropalaeontological investigations (Barker and Elderfield, 2002; Zeebe and Westbroek, 2003; Gonzalez-Mora *et al.*, 2008; Moy *et al.*, 2009; Nguyen *et al.*, 2009; Dias *et al.*, 2010; Pettit *et al.*, 2013, 2015) of living assemblages.

Natural CO₂ vents can be used to study the effects of ocean acidification *in situ* (Dias *et al.*, 2010; Pettit *et al.*, 2013). Such CO₂ vents create localised areas of lowered pH where carbon dioxide gas bubbles up through the sea floor (Boatta *et al.*, 2013). Some of these vents release gas (and water) at ambient seawater temperatures while others inject super-heated water from volcanic sources. The vents tend to be present on time scales of hundreds to thousands of years, so the communities present in the area are likely to be adapted to the low pH conditions. The study of such natural sites avoids some of the problems of short-term, rapid perturbation, experiments where the culture conditions may create their own impacts (e.g. higher incidence of test deformity).

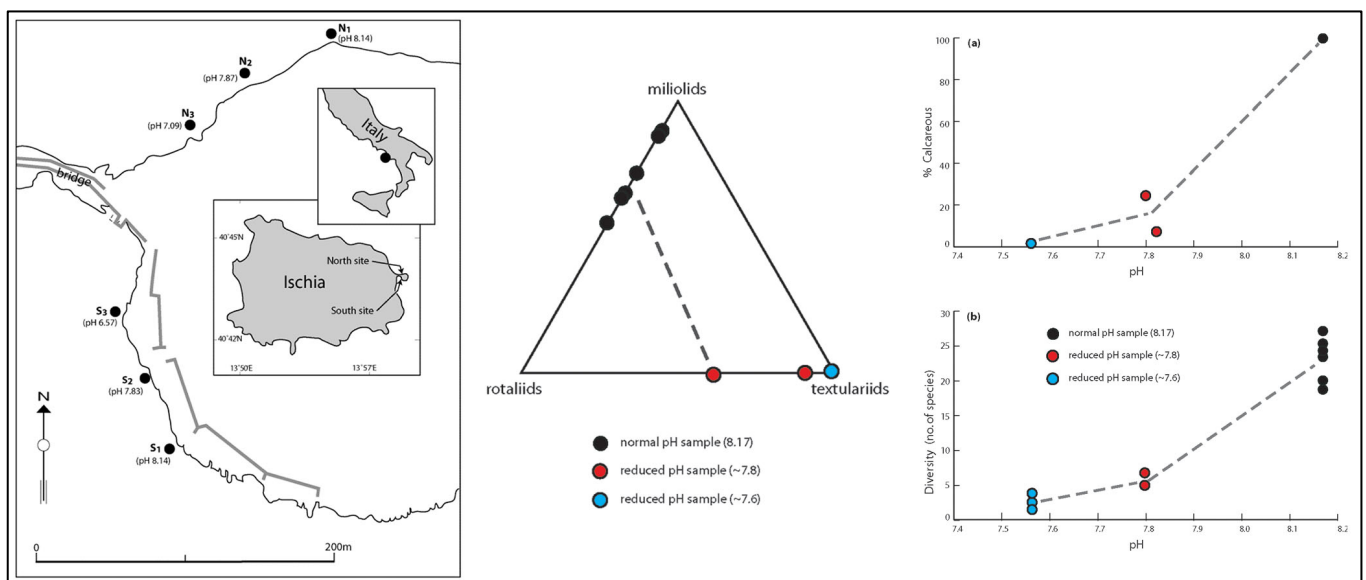


FIGURE 11. Map of Ischia showing sampling locations and the recorded changes in the assemblage of benthic foraminifera caused by the reduction in pH across the site. After Hart *et al.* (2014b).

In 2010, Dias and colleagues examined the benthic foraminifera around natural CO₂ vents adjacent to the island of Ischia, Italy (Figure 11). They found that there was a reduction in the species diversity of calcifying benthic foraminifera near the vents (Dias *et al.*, 2010). The reduction in species diversity and abundance near the CO₂ vents mirrored those found for larger benthic calcifying organisms (Hall-Spencer *et al.*, 2008). Along a gradient from 'normal' pH (~8.17) to acidified areas (pH ~7.6), species diversity fell from 24 to just 4 species of benthic foraminifera (Figure 11). The assemblage also changed from one dominated by calcareous species to one dominated by agglutinated forms. This is significant as many agglutinated taxa form their tests of sediment particles held together by organic 'fibres' rather than secreting their chambers of calcium carbonate derived from sea water. Off-shore the volcanic island of Vulcano (Boatta *et al.*, 2013) a pattern of foraminifera distribution comparable to that recorded near Ischia has recently been described (Pettit *et al.*, 2015). At CO₂ vents off-shore in Papua New Guinea, sediment at high *p*CO₂ sites (up to 953 ppm) was found to be almost free of calcareous biota (including benthic foraminifera) and sites with lower *p*CO₂ (up to 494 ppm) contained many pitted or eroded tests of foraminifera (Fabricius *et al.*, 2011).

The Gulf of California is a narrow marginal sea, with variable circulation patterns (Halfar *et al.*, 2004). There are, as a result, large seasonal variations in temperature (8.25 – 32.28 °C) and salinity (35 – 41 ‰). The Wagner Basin, in the northern part of the Gulf of California has large areas in which the pH is naturally lower as a result of gas seepage across the basin. In 2007 and 2010, marine surveys located over 300 large, diffuse sea floor gas vents that are causing dramatic changes to the sea water chemistry (Canet *et al.*, 2010). The vent gases are probably composed of methane and carbon dioxide (Canet *et al.*, 2010). Sediment samples from the Wagner Basin have also been used to examine the potential biological impacts of the local variations in pH (Pettit *et al.*, 2013). At all the sample locations the benthic foraminifera are abundant, diverse and well-preserved (Pettit *et al.*, 2013, Figs 4, 5), with dissolution features only being seen as the result of post-mortem exposure to waters with a reduced pH. The presence of living, calcareous, benthic foraminifera at pH values between 7.88–7.55 are balanced by the high carbonate saturation of the water, and this has implications for the fossil record during the Mesozoic where similar levels are predicted (Ridgwell, 2005; Hönisch *et al.*, 2012; Hart *et al.*, 2014b).

SUMMARY

Many of the shallow-water Marine Conservation Zones and Special Areas of Conservation in south-west England were created by marine inundation following the Last Glacial Maximum when sea levels rose by ~130 m. This was, however, the latest in a series of sea level cycles during the Pleistocene. The nature of such environments must, therefore, be regarded as both transitory and still in the process of adjustment. What is 'conserved' today is, therefore, not the end of their evolution.

In many near-shore, marine environments there are important ecosystems characterized by salt-marsh, mud-flats, estuarine sands and silts and important areas of sea grass meadow and beds of maerl. Within all these habitats are important assemblages of foraminifera that are more often studied by geologists, rather than marine biologists. While their life histories are complex, they are remarkable organisms with well-known environmental tolerances and which can provide a wealth of information on the health of an environment. As foraminifera have a long, well-known, fossil record they are ideal for palaeoecological interpretations, and the documentation of Pleistocene–Holocene sea level changes. The modern assemblages of foraminifera that are associated with sea grass meadows have been invaluable in the identification of fossil sea grass communities ~70 million years old.

Foraminifera can also be used to investigate historical changes in ocean acidification and the possible impact of this phenomenon on extinction events (e.g., Cretaceous/Paleogene boundary).

ACKNOWLEDGEMENTS

Permission to collect research materials, assistance with sampling, and general discussion of the issues have been provided by English Nature, Natural England, Torbay Coast and Countryside Trust, Fowey Harbour Commissioners, Plymouth Marine Laboratory and a wide range of colleagues (all of whom have contributed ideas, knowledge, expertise and encouragement). Dr J. Jagt, Sijr Renkens (both Natural History Museum, Maastricht) and Dr R. van der Ham (Naturalis, Leiden) have provided valuable support in the investigation of the fossil sea grass of the Maastricht area boundary. Tim Absalom and James Quinn (Geo-Cartographic Unit, Plymouth University) are thanked for their assistance with some of the figures.

REFERENCES

- Attrill, M.J., Austen, M.C., Bayley, D.T.I., Carr, H.L., Downey, K., Fowell, S.C., Gall, S.C., Hattam, C., Holland, L., Jackson, E.L., Langmead, O., Mangi, S., Marshall, C., Munro, C., Rees, S., Rodwell, L., Sheehan, E.V., Stevens, J., Stevens, T.F., and Strong, S. (2011). *Lyme Bay – a case study: measuring recovery of benthic species; assessing potential "spillover" effects and socio-economic changes, 2 years after closure. Response of the benthos to the zoned exclusion of bottom towed fishing gear and the associated socio-economic effects in Lyme Bay*. Final Report 1. June 2011. Report to the Department of Environment, Food and Rural Affairs from the University of Plymouth-led consortium. University of Plymouth Enterprise Ltd, 108pp.
- Austin, W.E.N. and Cage, A.G. (2010). High benthic foraminiferal species counts in a Clyde Sea maerl bed, western Scotland. In: Howe, J.A., Austin, W.E.N., Forwick, M. and Paetzel, M. (eds), *Fjord Systems and Archives*, Geological Society, London, Special Publications, **344**, 83–88.
- Barker, S. and Elderfield, H. (2002). Foraminiferal calcification response to glacial-interglacial changes in atmospheric CO₂. *Science*, **297**, 833–836.
- Barnola, J.-M., Raynaud, D., Korotkevich, Y.S. and Lorius, C. (1987). Vostock ice core provides 160,000-year record of atmospheric CO₂. *Nature*, **329**, 408–414.
- Bernhard, J.M., Barry, J., Buck, K. and Starczak, V. (2009a). Impact of intentionally injected carbon dioxide hydrate on deep sea benthic foraminiferal survival. *Global Change Biology*, **15**, 2078–2088.
- Bernhard, J.M., Mollo-Christensen, E., Eisenkolb, N. and Starczak, V.R. (2009b). Tolerance of allogromid Foraminifera to severely elevated carbon dioxide concentrations: implications to future ecosystem functioning and palaeoceanographic interpretations. *Global and Planetary Change*, **65**, 107–114.

- Bijma, J., Spero, H. and Lea, D. (1999). Reassessing foraminiferal stable isotope geochemistry: Impact of the oceanic carbon system (experimental results). In: Fischer, G. and Wefer, G. (eds), *Use of proxies in paleoceanography: examples from the South Atlantic*, Springer-Verlag, Berlin, 489–512.
- Bijma, J., Hönisch, B. and Zeebe, R. (2002). Impact of the ocean carbonate chemistry on living foraminiferal shell weight: comment on “Carbonate ion concentration in glacial-age deepwaters of the Caribbean Sea” by W.S. Broecker and E. Clark. *Geochemistry, Geophysics, Geosystems*, **3**, 1064.
- Birkett, D.A., Maggs, C.A. and Dring, M.J. (1998). *Maërl (volume V). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs*. Scottish Association for Marine Science (UK Marine SACs Project), 116pp.
- Blanc-Vernet, L. (1969). Contribution à l'étude des foraminifères de Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume*, **64**, 48, 1–279.
- Boatta, F., D'Alessandro, W., Gagliano, A., Liotta, M., Milazzo, M., Rodolfo-Metalpa, R., Hall-Spencer, J.M. and Parello, F. (2013). Geochemical survey of Levante Bay, Vulcano Island (Italy), a natural laboratory for the study of ocean acidification. *Marine Pollution Bulletin*, **73**, 485–494.
- Boillot, G. (1964). Géologie de la Manche occidentale. *Annals de l'Institut Océanographique*, **42**, 1–219.
- Bosence, D.W.J. (1976). *Ecological and sedimentological studies on some carbonate sediment producing organisms*. Unpublished PhD Thesis, University of Reading.
- Bosence, D.W.J. (1979). Live and dead faunas from coralline algal gravels, Co. Galway. *Palaeontology*, **22**, 449–478.
- Burek, C.V., Ellis, N.V., Evans, D.H., Hart, M.B. and Larwood, J.G. (2013). Marine conservation in the United Kingdom. *Proceedings of the Geologists' Association, London*, **124**(4), 581–592.
- Caldera, K. and Wickett, M.E. (2003). Anthropogenic carbon and ocean pH. *Nature*, **425**, 365.
- Caldera, K. and Wickett, M.E. (2005). Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *Journal of Geophysical Research*, **110**, C09S04, doi: 10.1029/2004JC002671, 2005.
- Canet, C., Prol-Ledesma, R.M., Dando, P.R., Vázquez-Figueroa, V., Shumilin, E., Birosta, E., Sánchez, A., Robinson, C.J., Camprubí, A. and Tauler, E. (2010). Discovery of massive seafloor gas seepage along the Wagner Fault, northeastern Gulf of California. *Sedimentary Geology*, **228**, 292–303.
- Castignetti, P. (1993). Foraminiferal analysis of boreholes from Plymouth Sound. *Proceedings of the Ussher Society*, **8**, 189–92.
- Castignetti, P. (1997). *Population dynamics and facies association of Recent foraminifera from a near-shore marginal marine environment: Plymouth Sound*. Unpublished PhD Thesis, University of Plymouth (2 volumes).
- Coard, M.A., Cousen, S.M., Cuttler, A.H., Dean, H.J., Dearing, J.A., Eglinton, T.I., Graves, A.M., Lacey, K.P., O'Sullivan, P.E., Pickering, D.A., Rhead, M.M., Rodwell, J.K. and Simola, H. (1983). Paleolimnological studies of annually-laminated sediments in Loe Pool, Cornwall, UK. *Hydrobiologia* **103**(1), 185–191.
- Consolaro, C., Hart, M., Chambers, P., Evans, G., Nichols, R., Smart, C. and Whittaker, J. (2014). The Holocene separation of Jersey from France: the microfossil evidence. *Geophysical Research Abstracts*, EGU General Assembly, EGU2014.16.4149C.
- De Boer, W.F. (2007). Seagrass-sediment interaction, positive feedbacks and critical thresholds for occurrence. *Hydrobiologia*, **591**(1), 5–24.
- Debay, M.H. (1848). Übersicht der urweltlichen Pflanzen des Kreidegebirges überhaupt und der Aachener Kreideschichten insbesondere. *Verh. Naturhist. Ver. Preuss. Rheinlande Westfalens*, **5**, 113–125.
- Debay, M.H. (1851). Beitrag zur fossilen Fauna der holländischen Kreide (Vaels bei Aachen, Kunraed, Maastricht). *Verh. Naturhist. Ver. Preuss. Rheinlande Westfalens*, **8**, 568–569.
- Den Hartog, C. (1977). Structure, function and classification in seagrass communities. In: McRoy, C.P. and Helfferich, C. (eds), *Seagrass Ecosystems, A Scientific Perspective*. Marcel Dekker, New York, 89–121.
- Dias, B.B., Hart, M.B., Smart, C.W. and Hall-Spencer, J.M. (2010). Modern seawater acidification: the response of foraminifera to high-CO₂ conditions in the Mediterranean Sea. *Journal of the Geological Society, London*, **167**(5), 843–846.
- Dutertre, M., Grall, J., Ehrhold, A. and Hamon, D. (2015). Environmental factors affecting maerl bed structure in Brittany. *European Eddies*, R.D. and Reynolds, J.M. (1988). Seismic characteristics of buried rock valleys in Plymouth Sound and the River Tamar. *Proceedings of the Ussher Society*, **7**, 36–40.
- Eddies, R.D. and Reynolds, J.M. (1988). Seismic characteristics of buried rock-valleys in Plymouth Sound and the River Tamar. *Proceedings of the Ussher Society*, **7**, 36–40.
- Eddles, A.P. and Hart, M.B. (1989). Late Quaternary Foraminifera from Plymouth Sound; preliminary investigation. *Proceedings of the Ussher Society*, **7**, 168–171.
- Evans, D.J.A., Harrison, S., Vieli, A. and Anderson, E. (2012). The glaciation of Dartmoor: the southernmost independent Pleistocene ice cap in the British Isles. *Quaternary Science Reviews*, **45**, 31–53.
- Fabricius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M.S. and Lough, J.M. (2011). Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change*, **1**, 165–169.
- Farnham, W.F. and Bishop, G.M. (1985). *Survey of the Fal Estuary, Cornwall*. 18th Symposium of the Underwater Association for Scientific Research, 53–63.
- Fitzpatrick, F. (1990). Remotely sensed sedimentology of Plymouth Sound. *Proceedings of the Ussher Society*, **7**, 289–294.
- Fitzpatrick, F. (1991). *Studies of sediments in a tidal environment*. Unpublished PhD Thesis, Polytechnic South West (now Plymouth University), 340pp.
- Foden, J. and Brazier, D.P. (2007). Angiosperms (seagrass) within the EU water framework directive: A UK perspective. *Marine Pollution Bulletin*, **55**(1–6), 181–195.
- Freiwald, A. and Henrich, R. (1994). Reefal coralline algal build-ups within the Arctic Circle: morphology and sedimentary dynamics under extreme environmental seasonality. *Sedimentology*, **41**, 963–984.

- Fretwell, P., Smith, D.E. and Harrison, S. (2008). The Last Glacial Maximum British-Irish ice sheet: a reconstruction using digital terrain mapping. *Journal of Quaternary Science*, **23**(3), 241–248.
- Gibbard, P.L. and Clarke, C.D. (2011). Pleistocene glaciations limits in Great Britain. In: Ehlers, J., Gibbard, P.L. and Hughes, P.D. (eds), *Quaternary Glaciation – extent and chronology: A closer look*, Developments in Quaternary Science 15, Elsevier, The Netherlands, 75–94.
- Gischler, E. (2011). Johannes Walther (1860-1937): More than the law of facies correlation. *Geological Society of America, GSA Today*, **August 2011**, 12–13.
- Gonzalez-Mora, B., Sierro, F. and Flores, J. (2008). Controls of shell calcification in planktonic foraminifers. *Quaternary Science Reviews*, **27**, 956–961.
- Gregoire, G., Le Roy, P., Erhold, A., Jouet, G. and Garlan, T. (2016). Recording of the Holocene sediment infilling of a confined tide-dominated estuary: the bay of Brest. *Geophysical Research Abstracts*, **18**, EGU2016 – 13702, 2016.
- Guinotte, J.M. and Fabry, V.J. (2008). Ocean acidification and its potential effects on marine ecosystems. *New York Academy of Sciences*, **1134**, 320–342.
- Hails, J.R. (1975a). Some aspects of the Quaternary history of Start Bay, Devon. *Field Studies* **4**, 207-222.
- Hails, J.R. (1975b). Submarine geology, sediment distribution and Quaternary history of Start Bay, Devon. *Journal of the Geological Society, London* **131**, 1-101.
- Halfar, J., Godinez-Orta, L., Mutti, M., Valdez-Holguín, J.E. and Borges, J.M. (2004). Nutrient and temperature controls on modern carbonate production: an example from the Gulf of California, Mexico. *Geology*, **32**, 213–216.
- Hall-Spencer, J.M. (1994). *Biological studies of nongeniculate Corallinaceae*. Unpublished PhD Thesis, University of London, 269pp.
- Hall-Spencer, J. (2005). Ban on maerl extraction, in News. *Marine Pollution Bulletin*, **50**, 121.
- Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M., Rowley, S.J., Tedesco, D. and Buia, M.-C. (2008). Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature*, **454**, 96–99.
- Hall-Spencer, J.M., Kelley, J. and Maggs, C.A. (2010). Background document for maerl beds. London: OSPAR Commission: 2010. Publication 491/2010, 36pp.
- Hart, M.B. (2009). *Dorset and East Devon: Landscape and Geology*, Crowood Press, Marlborough, 240pp.
- Hart, M.B., Stubbles, S.J., Smart, C.W., Fisher, J.K., Hoddinott, C., Marshall-Penn, I. and Yeo, A. (2014a). Foraminifera from the Fowey Estuary, Cornwall. *Geoscience in South-West England*, **13**, 304–315.
- Hart, M.B., Leighton, A.D., Smart, C.W., Pettit, L.R., Medina-Sánchez, I.N., Harries, P.J., Cárdenas, A.L., Hall-Spencer, J.M. and Proledesma, R.M. (2014b). Ocean acidification in modern seas and its recognition in the geological record: the Cretaceous/Paleogene boundary in Texas and Alabama. *Gulf Coast Association of Geological Societies, Transactions*, **64**, 193–213.
- Hart, M.B., Cartwright, K., Fisk, B., Smart, C.W., Consolaro, C. and Hall-Spencer, J.M. (2015). Foraminifera of the Fal Estuary (Cornwall), including taxa associated with maerl beds. *Geoscience in South-West England*, **13**, 483–490.
- Hart, M.B., FitzPatrick, M.E.J. & Smart, C.W. (2016). The Cretaceous/Paleogene boundary: Foraminifera, sea grasses, sea level change and sequence stratigraphy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **441**, 420–429.
- Hiemstra, J.F., Evan, D.J.A., Scourse, J.D., McCarroll, D., Furze, M.F.A. and Rhodes, E. (2006). New evidence for a grounded Irish Sea glaciations of the Isles of Scilly, UK. *Quaternary Science Reviews*, **25**(3), 299–309.
- Hönisch, B., Ridgwell, A., Schmidt, D.N., Thomas, E., Gibbs, S.J., Sluijs, A., Zeebe, R., Martindale, R.C., Greene, S.E., Kiessling, W., Ries, J., Zachos, J.C., Royer, D.L., Barker, S., Marchitto Jr, T.M., Moyer, R., Pelejero, C., Ziveri, P., Foster, G.L., and Williams, B. (2012). The geological record of ocean acidification. *Science*, **335**, 1058–1063.
- Houghton, J. (2009). *Global warming: the complete briefing* (4th Edition). Cambridge University Press, Cambridge.
- Houghton, J.T., Meira Filho, L.G., Griggs, D.J. and Maskell, K. (eds) (1997). *Stabilization of atmospheric greenhouse gases: physical, biological and socio-economic implications*. IPCC Technical Paper III, p. 1–52, IPCC Secretariat.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguier, M., van der Linden, P.J., Dai, X., Maskell, K. and Johnson, C.A. (2001). *Climate Change 2001: the scientific basis*. Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, 83pp.
- IGBP, IOC, SCOR (2013). Ocean Acidification Summary for Policymakers – Third Symposium on the Ocean in a High-CO₂ World. International Geosphere-Biosphere Programme, Stockholm, Sweden.
- Irvine, L.M. and Chamberlain, Y.M. (1994). *Seaweeds of the British Isles: Volume 1, Rhodophyta, Part 2B, Corallinales, Hildenbrandiales*. British Phycological Society and The Natural History Museum, London, HMSO, 276pp.
- Johnes, P.J. and O'Sullivan, P.E. (1989). The natural history of Slapton Ley Nature Reserve XVIII. Nitrogen and phosphorus losses from the catchment – an export coefficient approach. *Field Studies* **7**, 285-309.
- Khanna, N., Godbold, J.A., Austin, W.E.N. and Patterson, D.M. (2013). The impact of ocean acidification on the functional morphology of foraminifera. *PLOS ONE*, **8**, issue 12, e83118.
- Kraft, J.C. and Chrastowski, M.J. (1985). Coastal stratigraphic sequences. In: Davis, R.A. Jr (ed.), *Coastal Sedimentary Environments*, Springer, New York, 625–663.
- Kroeker, K.J., Kordas, R.I., Crim, R.N. and Singh, G.G. (2010). Meta-analysis reveals negative, yet variable affects of ocean acidification on marine organisms. *Ecology Letters*, **13**, 1419–1434.
- Lambeck, K. (2004). Sea level change through the last glacial cycle: geophysical, glaciological and palaeogeographic consequences. *Comptes Rendus Geoscience*, **336**, 677–686.
- Lambeck, K. and Chappell, J. (2001). Sea level change through the last glacial cycle. *Science*, **292**(5517), 679–686.
- Lee, J.J. and Anderson, O.R. (eds) (1991). *Biology of Foraminifera*. Academic Press, London, 368pp.
- Lee, J.R., Rose, J., Hamblin, R.J.O., Moorlock, B.S.P., Riding, J.B., Phillips, E., Barendregt, R.W. and Candy, I. (2011). The glacial history of the British isles during the Early and Middle Pleistocene: implications for the long-term development of the British ice sheet. In: Ehlers, J., Gibbard, P.L. and Hughes, P.D. (eds), *Quaternary Glaciation – extent and chronology: A closer look*, Developments in Quaternary Science 15, Elsevier, The Netherlands, 59–74.

- Le Friant, A., Lock, E.J., Hart, M.B., Boudon, G., Sparks, R.S.J., Leng, M.J., Smart, C.W., Komorowski, J.C., Deplus, C. and Fisher, J.K. (2008). Late Pleistocene tephrochronology of marine sediments adjacent to Montserrat, Lesser Antilles volcanic arc. *Journal of the Geological Society, London*, **165**, 279–289.
- Lieberknecht, L.M., Hooper, T.E.J., Mullier, T.M., Murphy, A., Neilly, M., Carr, H., Haines, R., Lewin, S. and Hughes, E. (2011). *Finding Sanctuary final report and recommendations*. A report submitted by the Finding Sanctuary stakeholder project to Defra, the Joint Nature Conservation Committee, and Natural England. Available at www.finding-sanctuary.org and The UK National Archives http://tna.europarchive.org/*/<http://www.finding-sanctuary.org/>
- Middleton, G.V. (1973). Johannes Walther's Law of Correlation of facies. *Geological Society of America, Bulletin*, **84**, 979–988.
- Martin, S. and Hall-Spencer, J.M. (2016, in press). Effects of ocean warming and acidification on rhodolith/maerl beds. In: Riosmena-Rodriguez, R., Nelson, W. and Aquirre, J. (eds), *Rhodolith/maerl beds: A Global Perspective*, Springer, Coastal Research Library.
- Massey, A.C., Gehrels, W.R., Charman, D.J., Milne, G.A., Peltier, W.R., Lambeck, K. and Selby, K.A. (2008). Relative sea-level change and postglacial isostatic adjustment along the coast of south Devon, United Kingdom. *Journal of Quaternary Science*, **23**(5), 415–433.
- May, V.J. (2003a). Loe Bar, Cornwall. In: May, V.J. and Hansom, J.D. (eds), *Coastal Geomorphology of Great Britain*, Geological Conservation Review Series, No. 28, Joint Nature Conservation Committee, Peterborough, 241–244.
- May, V.J. (2003b). Slapton Sands and Hallsands, Devon. In: May, V.J. and Hansom, J.D. (eds), *Coastal Geomorphology of Great Britain*, Geological Conservation Review Series, No. 28, Joint Nature Conservation Committee, Peterborough, 244–251.
- Morey, C.R. (1976). The natural history of Slapton Ley Nature Reserve IX. The morphology and history of the lake basins. *Field Studies* **4**, 353–368.
- Morey, C.R. (1980). *The origin and development of a coastal lagoon system, Start Bay, south Devon*. Unpublished PhD Thesis, Council for National Academic Awards (CNAAs).
- Morey, C.R. (1983). The evolution of a barrier-lagoon system – a case study for Start Bay. *Proceedings of the Ussher Society* **5**, 454–459.
- Morhange, C., Blanc, F., Schmitt-Mercury, S., Bourcier, M., Carbonel, P., Oberlin, C., Prone, A., Vivent, D. and Hesnard, A. (2003). Stratigraphy of late-Holocene deposits of the ancient harbour of Marseilles, southern France. *The Holocene*, **13**, 593–604.
- Moy, A.D., Howard, W.R., Bray, S.G. and Trull, T.W. (2009). Reduced calcification in modern Southern Ocean planktonic foraminifera. *Nature Geosciences*, **2**, 276–280.
- Murray, J.W. (2006). *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press, Cambridge, UK, 426 pp.
- Nguyen, T.M.P., Petrizzo, M.-R. and Speijer, R.P. (2009). Experimental dissolution of a fossil foraminiferal assemblage (Paleocene-Eocene Thermal Maximum, Dababiya, Egypt): Implications for paleoenvironmental reconstructions. *Marine Micropaleontology*, **73**, 241–258.
- Nooijer, L.J. de, Toyofuku, T. and Kitazato, H. (2009a). Foraminifera promote calcification by elevating their intracellular pH. *Proceedings of the National Academy of Science, USA*, **106**, 15374–15378.
- Nooijer, L.J. de, Langer, G., Nehrke, G. and Bijma, J. (2009b). Physiological controls on seawater uptake and calcification in the benthic foraminifer *Ammonia tepida*. *Biogeosciences*, **6**, 2669–2675.
- Olugbode, O.L., Hart, M.B. and Stubbles, S.J. (2005). Foraminifera from Restronguet Creek: monitoring recovery from the Wheal Jane pollution incident. *Geoscience in south-west England*, **11**, 82–92.
- Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesiken, A., Gruber, N., Ishida, A., Joos, F., Key, R.M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R.G., Plattner, G.-K., Rodgers, K.B., Sabine, C.L., Sarmiento, J.L., Schlitzer, R., Slater, R.D., Totterdell, I.J., Weirig, M.-F., Yamanaker, Y. and Yool, A. (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, **437**, 681–686.
- Pascelli, C., Ri, P., Riosmena-Rodríguez, R., Scherner, F., Nunes, M., Hall-Spencer, J.M., Cabral De Oliveira, E. and Horta, P. (2013). Seasonal and depth-driven changes in rhodolith bed structure and associated macroalgae off Arvoredo Island (southeastern Brazil). *Aquatic Botany*, **111**, 62–65.
- Peña, V., Bárbara, I., Grall, J., Maggs, C.A. and Hall-Spencer, J.M. (2014). The diversity of seaweeds on maerl in the NE Atlantic. *Marine Biodiversity*, doi: 10.1007/s12526-014-0214-7.
- Pettit, L.R., Hart, M.B., Medina-Sánchez, A.N., Smart, C.W., Rodolfo-Metalpa, R., Hall-Spencer, J.M. and Prol-Ledesma, R.M. (2013). Benthic foraminifera show some resilience to ocean acidification in the northern Gulf of California, Mexico. *Marine Pollution Bulletin*, **73**, 452–462.
- Pettit, L.R., Smart, C.W., Hart, M.B., Milazzo, M. and Hall-Spencer, J.M. (2015). Seaweed does not mitigate impact of ocean acidification on calcified foraminifera along a shallow water CO₂ gradient. *Ecology and Evolution*, **5**(9), 1784–1793.
- Pirrie, D., Power, M.R., Rollinson, G., Camm, G.S., Hughes, S.H., Butcher, A.R. and Hughes, P. (2003). The spatial distribution of arsenic, copper, tin and zinc within the surface sediments of the Fal Estuary, Cornwall, UK. *Sedimentology*, **50**, 579–595.
- Pitts, J. (1983). The temporal and spatial development of landslides in the Axmouth-Lyme Regis Undercliffs National Nature Reserve, Devon. *Earth Surface Processes and Landforms*, **8**(6), 589–603.
- Raven, J., Caldeira, K., Elderfield, H., Hoegh-Guldberg, O., Liss, P., Riebesell, U., Shepherd, J., Turley, C. and Watson, A. (2005). *Ocean acidification due to increasing atmospheric carbon dioxide*. The Royal Society, London, 60pp.
- Renema, W. and Hart, M. (2012). Larger benthic foraminifera of the type Maastrichtian. In: Jagt, J.W.M., Donovan, S.K. and Jagt-Zazykova, E.A. (eds), *Fossils of the Type Maastrichtian (Part 1)*, *Scripta Geologica*, Special Publication, **8**, 33–43.
- Ridgwell, A. (2005). A mid Mesozoic revolution in the regulation of ocean chemistry. *Marine Geology*, **217**, 339–357.
- Rodolfo-Metalpa, R., Houlbrèque, F., Tambutté, E., Boisson, F., Baggini, C., Patti, F., Jeffree, R., Fine, M., Foggo, A. and Gattuso, J. (2011). Coral and mollusc resistance to ocean acidification adversely affected by warming. *Nature Climate Change*, **1**, 308–312.
- Rosset-Moulinier, M. (1972). Etude des foraminifères des côtes nord et ouest de Bretagne. *Travaux du Laboratoire de Géologie, Ecole Normale Supérieure, Paris*, **6**, 1–225.
- Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Wanninkhof, R., Wong, C.S., Wallace, D.W.R., Tilbrook, B., Millero, F.J., Peng, T.-H., Kozyr, A., Ono, T. and Rios, A.F. (2004). The oceanic sink for anthropogenic CO₂. *Science*, **305**, 367–371.

- Sadri, S., Hart, M.B. and Smart, C.W. (2011). Foraminifera from the sea grass communities of the proposed Marine Conservation Zone in Tor Bay. *Geoscience in South-West England*, **12**, 269–277.
- Scourse, J.D. (1991). Late Pleistocene stratigraphy and palaeobotany of the Isles of Scilly. *Philosophical Transactions of the Royal Society*, **B**, doi. 10.1098/rstb.1991.0125.
- Sen Gupta, B. (2002). *Modern Foraminifera*. Kluwer Academic Publishers, Massachusetts, USA, 371pp.
- Sheehan, E.V., Bridger, D., Cousens, S.L. and Attrill, M.J. (2015). Testing the resilience of dead maerl infaunal assemblages to the experimental removal and re-lay of habitat. *Marine Ecology Progress Series*, **535**, 117–128.
- Simola, H.L.K., Coard, M.A. and O’Sullivan, P.E. (1981). Annual laminations in the sediments of Loe Pool, Cornwall. *Nature* **290**, 238–241.
- Spero, H., Bijma, J., Lea, D. and Bemis, B. (1997). Effect of seawater carbonate concentration on foraminiferal carbon and oxygen isotopes. *Nature*, **390**, 497–500.
- Stubbles, S.J. (1993). Recent benthic foraminifera as indicators of pollution in Restronguet Creek, Cornwall. *Proceedings of the Ussher Society*, **8**, 200–204.
- Stubbles, S.J. (1999). *Response of Recent benthic foraminifera to metal pollution in South West England estuaries: a study of impact and change*. Unpublished PhD Thesis, University of Plymouth.
- Stubbles, S.J., Green, J.C., Hart, M.B. and Williams, C.L. (1996). Response of foraminifera to the presence of heavy metal contamination and acidic mine drainage. In: *Minerals, Metals and the Environment II, Prague*. Institute of Mining and Mineralogy, London, Special Publication, 217–235.
- Toy, H.S. (1934). The Loe Bar near Helston, Cornwall. *Geographical Journal* **83**, 40–48.
- UKSACS, UK Marine Special Areas of Conservation, 2010. Habitat Requirements of Eelgrass (*Zostera marina*). Available from http://www.ukmarinesac.org.uk/communities/habitats-review/hr22_1.htm [accessed July 2010].
- van der Ham, R.W.J.M., Konijnenburg-van Cittert, J.H.A. and Indeherberge, L. (2007). Seagrass foliage from the Maastrichtian type area (Maastrichtian, Danian, NE Belgium, SE Netherlands). *Revue of Palaeobotany and Palynology*, **144**, 301–321.
- van Vlymen, C.D. (1979). The natural history of Slapton Ley Nature Reserve XIII. The water balance of Slapton Ley. *Field Studies* **5**, 59–84.
- Wall-Palmer, D., Hart, M.B., Smart, C.W., Sparks, R.S.J., Le Friant, A., Boudon, G., Deplus, C. and Komorowski, J.C. (2012). Pteropods from the Caribbean Sea: variations in calcification as an indicator of past ocean carbonate saturation. *Biogeosciences*, **9**, 309–315.
- Wall-Palmer, D., Smart, C.W. and Hart, M.B. (2013). In-life pteropod shell dissolution as an indicator of past ocean carbonate saturation. *Quaternary Science Reviews*, **81**, 29–34.
- WFD 2000. Water Framework Directive 2000/60/EC. European Communities Official Journal L327 22.12.2000, p. 73. http://ec.europa.eu/environment/water/water-framework/index_en.html
- Whelan, P.M. and Cullinane, J.P. (1985). The algal flora of a subtidal *Zostera* bed in Ventry Bay, South-west Ireland. *Aquatic Botany*, **23**, 41–51.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. and Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, **292**, 686–693.
- Zeebe, R.E. and Westbroek, P. (2003). A simple model for the CaCO₃ saturation state of the ocean: The “Strangelove”, the “Neritan”, and the “Cretan” Ocean. *Geochemistry, Geophysics, Geosystems*, **4**, 1104, doi:10.1029/2003GC000538.

TAXONOMIC NOTES ON THE FORAMINIFERA MENTIONED IN THE TEXT (ALPHABETICAL ORDER)

- Ammonia* sp. cf. *A. aberdoveyensis* Haynes, 1973, pp. 184–186, pl. 18, fig. 15, text-fig. 38, nos 1–7.
- Balticammina pseudomacrescens* Brönnimann, Lutze and Whittaker, 1989, p. 169, pls 1–3.
- Cibicides lobatulus* (Walker and Jacob): *Nautilus lobatulus* Walker and Jacob, 1798, p. 642, pl. 14, fig. 36.
- Elphidium crispum* (Linné): *Nautilus crispus* Linné, 1758, Vol. 1, p. 709.
- Elphidium williamsoni* Haynes, 1973, p. 207, pl. 24, fig. 7, pl. 25, figs 6–9, pl. 27, figs 1–3.
- Haynesina germanica* (Ehrenberg): *Nonionina germanica* Ehrenberg, 1840, p. 23; figure in Ehrenberg, 1841, pl. 2, fig. 1a–b.
- Jadammina macrescens* (Brady): *Trochammina inflata* (Montagu) var. *macrescens* Brady, 1870, pp. 290–291, pl. 11, figs 5a–c.
- Planorbulina mediterranensis* d’Orbigny, 1826, p. 280, no. 2.
- Trochammina inflata* (Montagu): *Nautilus inflatus* Montagu, 1808, p. 81, pl. 18, fig. 3