



Role of low intensity environmental disturbance in structuring the earliest (Ediacaran) macrobenthic tiered communities



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ARTICLE INFO

Article history:

Received 29 May 2014

Received in revised form 3 March 2015

Accepted 20 March 2015

Available online 28 March 2015

Keywords:

Charnia masoni

Indeterminate growth

Avalon Assemblage

Recovery community

Bimodal population

Cohorts

Sub-lethal disturbance

ABSTRACT

Rangeomorphs were important components of Ediacaran macrobenthic ecosystems, yet their biology and ecology remain poorly constrained. They formed high-density, tiered communities that were subjected to intermittent burial events, the largest of which killed entire communities. Abundant thin event beds in the Ediacaran succession of Charnwood Forest indicate the additional, frequent impact of minor obrution events. The type surface of *Charnia masoni* is immediately underlain by one such lamina (a tuff) and preserves a distinctly bimodal population. It is dominated by *Charnia* fronds that are of smaller or comparable length to the holotype (19.4 cm), but also includes notably larger specimens (>45 cm) that would traditionally have been assigned to *Charnia grandis*. Multiple morphological- and morphometric parameters (length, width, spacing of primary branches) demonstrate that these are indistinguishable from the holotype of *C. masoni*, affirming the synonymy of the two taxa. Nevertheless, these outsized individuals are distinguished by their proportionally fewer primary branches per unit length. Taphonomic evidence indicates that they were survivors of an incumbent population, the rest of which was culled by a minor ashfall. We suggest that this temporary reduction in competition from neighbours allowed the survivors to grow larger and thereby gain access to a greater proportion of the water column. As the community recovered, their large size would have continued to provide them with an advantage, divorcing them from the density-dependent competition seen in the new understory. The interlude between cohorts implies that new recruits were substrate-sensitive, presumably awaiting re-establishment of the biomat. Sub-lethal disturbance events thus played a significant role in structuring Ediacaran communities, and help explain the observed bed-by-bed variability. Taken as a whole, the growth trajectory of *C. masoni* resembles that of extant organisms with indeterminate growth programmes and no genetically-controlled upper size limit.

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1. Introduction

The Ediacaran (635–542 Ma) was a seminal period in the development of macrobenthic marine communities. It records a major expansion in morphological complexity (Shen et al., 2008; Xiao and Laflamme, 2009; Yuan et al., 2011) and the first appearance of many of the most successful ecological innovations of the succeeding Phanerozoic. These include planktonic dispersal and settlement (Droser and Gehling, 2008), epibenthic tiering (Clapham and Narbonne, 2002), biomineralization (e.g. Hofmann and Mountjoy, 2001), mobility (Liu et al., 2010) and grazing (Fedonkin et al., 2007; Gehling et al., 2014). Nevertheless, the limited influence of bioturbation (Jensen et al., 2005; Seilacher et al., 2005) and predation (e.g. see Hua et al., 2003), and the purported significance of osmotrophic feeding

strategies (Laflamme et al., 2009; Sperling et al., 2011), led Ediacaran ecosystems to function in a fundamentally different way to those in the Phanerozoic (see Bottjer et al., 2000; Erwin et al., 2011; Laflamme et al., 2013; Buatois et al., 2014; Mángano and Buatois, 2014).

Amongst the earliest complex communities are those assigned to the so-called Avalon Assemblage (see Waggoner, 2003; Narbonne, 2005). These immediately post-date the Gaskiers Glaciation (582.4 ± 0.5 Ma, Bowring in Schmitz, 2012) and occupied deepwater niches on the peri-Gondwanan Avalonian island arc system (Narbonne and Gehling, 2003; Wood et al., 2003; Ichaso et al., 2007; Li et al., 2008). They are best known from the Avalon and Bonavista peninsulas of Newfoundland (Clapham et al., 2003; Hofmann et al., 2008) and from broadly coeval volcanoclastic successions in Charnwood Forest in the UK (Wilby et al., 2011; Noble et al., 2015). The Assemblage is dominated by rangeomorphs, a high-order clade of uncertain biological affinity that is characterised by a pseudo-fractal branching architecture (Narbonne, 2004; Brasier et al., 2012). Variations in the detail of this architecture are thought to be of phylogenetic significance (Brasier et al., 2012).

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Co-occurring fronds assigned to the genus *Charniodiscus* (Ford, 1963) are considered to be members of the equally enigmatic high-order clade Arboreomorpha (Xiao and Laflamme, 2009; Erwin et al., 2011) or Frondomorpha (Grazhdankin et al., 2008), whose detailed architecture has yet to be fully resolved. Individual communities are typically high-diversity and high-density, and are preserved in situ beneath event beds (Narbonne, 2005). This has led to their interpretation as snapshots of communities cast in death as they were in life (Seilacher, 1992; Clapham et al., 2003), enabling inferences about tiering (Clapham and Narbonne, 2002; Ghisalberti et al., 2014), community successions (Clapham et al., 2003; Liu et al., 2012) and mode of reproduction (Darroch et al., 2013) to be made. Whilst there is no doubt that the organisms in the Avalon Assemblage were preserved in situ, as evidenced by the strong current alignment of fronds (Wilby et al., 2011), it has been argued that the preserved communities are somewhat time-averaged (Liu et al., 2011). Central to this argument is the interpretation of enigmatic forms referred to as ‘ivesheadiomorphs’, which Liu et al. (2011) consider to be the remnants of organisms already dead and decomposing at the time of inundation. The nature of ivesheadiomorphs is disputed (Laflamme et al., 2011; Wilby et al., 2011) and significant time averaging of the preserved fronds in the manner envisaged by Liu et al. (2011) has been refuted based on taphonomic considerations (e.g. see Darroch et al., 2013). If correct, however, the communities embody a greater degree of complexity than is generally accounted for, and palaeoecological studies should reflect these nuances.

Modern deepwater benthic marine communities are shaped by a variety of physical, temporal and biological parameters (see Gage and Tyler, 1991; Etter and Grassle, 1992; Gooday, 2003; Carney, 2005; Rex et al., 2006; Jennings et al., 2013). Arguably, many of these (e.g. substrate variability, ecological interactions, nutrient supply) would have been subdued or irrelevant in the Ediacaran because of the ubiquity of surficial mats (e.g. Gehling, 1999 and refs. therein; Seilacher, 1999), the limited presence of infaunal and predatory guilds (Hua et al., 2003; Jensen et al., 2005; Seilacher et al., 2005; Mángano and Buatois, 2014) and the presumed dominance of osmotrophic feeding strategies (Laflamme et al., 2009; Sperling et al., 2011). The latter would have rendered the Avalon communities less susceptible to spatial and temporal variations in nutrient supply because dissolved organic carbon is much more evenly mixed in oceans (see Hansell and Carlson, 2001; Hopkinson and Vallino, 2005) than the sinking particulate organic matter that governs extant communities (e.g. Billett et al., 1983; Ruhl, 2007).

By contrast, physical environmental disturbance is likely to have been an enduring factor in structuring deepwater communities (e.g. Grassle and Saunders, 1973). According to ecological theory, disturbance creates temporal and spatial heterogeneities (Sousa, 1984) that are important in maintaining diversity (Connell, 1978), and the trajectory followed during recovery is determined by the magnitude and frequency of the disturbance event(s). Where the spatial extent of disturbance is large relative to the recruitment ability of the community, recovery may be slow; where the intervals between disturbance events are short, the community may be held at an early succession stage and exhibit a high degree of variance with time; and where disturbance is intense, the reinstated community may differ from the original one (Turner et al., 1993; O’Neill, 1999).

High intensity (i.e. lethal) disturbance events fundamentally controlled Avalon Assemblage communities (Clapham et al., 2003). Here, we test the hypothesis that lower intensity (i.e. locally sub-lethal) disturbance also played an important role in structuring them. To do this, we compare the population structure of *Charnia masoni* (Ford, 1958) on its type bedding-plane surface in Charnwood Forest (UK) to that of coeval rangeomorphs in demonstrably mature communities in Newfoundland (Clapham et al., 2003). We predict that minor disturbance events will induce short-term departures from the classic right-skewed, unimodal, log-normal population structures seen in the Newfoundland assemblages (Darroch et al., 2013), and that these will

be preserved if there is insufficient time for the community to recover prior to its final burial. We first establish the relationship between two putative species of *Charnia* (*C. masoni* and the larger, co-occurring form, *Charnia grandis*) on the bedding-plane using allometry; we then analyse the population’s structure by comparing its size–frequency distribution to theoretical probability distributions; and finally, we resolve different phases in the growth of key specimens and relate these to an obrution event. These data are used in combination to elucidate the dynamics of recovery and to infer diverse aspects of rangeomorph palaeoecology. This work contributes to understanding the development of deepwater macrobenthic ecosystems (see Rowe, 1983) and to the relative significance of environmental stability (‘Stability–Time Hypothesis’ of Sanders, 1968) versus environmental disturbance (e.g. Grassle, 1989) in driving their diversity.

2. Geological setting

The late Neoproterozoic rocks of Charnwood Forest occupy the core of a faulted anticline, defined on the west by a major reverse fault, and on the south and east by Cambrian-aged strata (Fig. 1). The succession has a total exposed thickness of ca. 3.2 km and collectively comprises the Charnian Supergroup. It is dominated by well-stratified volcanoclastic sediments that were deposited in a deepwater setting, but it includes contemporaneous calc-alkaline volcanic centres in the north-west (Carney, 1999). Thick slumped units and laterally extensive pyroclastic deposits form important marker horizons and the framework for lithostratigraphic subdivision (Fig. 2). The base of the exposed succession is constrained to between ca. 611 Ma and $>569.1 \pm 0.9$ Ma, and its top is dated at ca. 557 Ma (Noble et al., 2015). It therefore overlaps much of the broadly comparable successions in Newfoundland that host the classic Avalon Assemblage (see Narbonne, 2005; Hofmann et al., 2008; Liu et al., 2012).

More than a dozen horizons are known to preserve fossils in Charnwood Forest (see Fig. 2). These encompass virtually the entire Charnian Supergroup, but most of the currently recorded examples lie towards the top of the succession, within the upper part of the Beacon Hill Formation and the overlying Bradgate Formation. Both of these units are dominated by centimetre- to decimetre-scale tabular beds of siltstone and mudstone, with subordinate fine- to medium-grained sandstone and thin (typically <1 cm), siliceous, pale-weathering beds. The latter are most abundant in the Beacon Hill Formation and are interpreted as primary water-lain ash-fall tuffs (cf. Carney, 1999). The tabular beds have sharp bounding surfaces and are internally planar-laminated or (weakly) normally-graded; tractional structures are scant and, where present, typically consist of indistinct, millimetre-scale, starved-ripple cross-lamination. Erosional bases have not been observed, except for minor scours. The combined evidence suggests that the Beacon Hill and Bradgate formations were principally deposited by dilute, high-frequency, gravity-flow events, interspersed with vertically-settled ashes. Some of the bedding-planes have a wrinkled and/or pustular texture which, in petrographic sections, comprises a distinctive surficial layer of ‘wispy’ or ‘crinkly’ laminae and enrolled particles (Fig. 3 (1)). These features compare closely with microbial mat fabrics (Schieber, 1999) and so-called microbially induced sedimentary structures (MISS, e.g. Noffke et al., 2001, 2002), and confirm that biomats colonised the substrates between depositional events.

Macrofossils in the Beacon Hill and Bradgate formations are preserved as high resolution, low-relief (typically a few millimetres), external impressions on the top surfaces of bedding-planes (i.e. in negative epirelief); the nature of any corresponding counterparts on the lower surfaces of the overlying beds is unknown. Discoidal fossils dominate, especially the holdfast *Aspidella* (see Gehling et al., 2000), but several surfaces additionally host high-diversity and high-density assemblages of closely-aligned fronds (Wilby et al., 2011). Adjacent fossils rarely overlap and conspecific fronds within any one assemblage exhibit minimal taphonomic variation, strongly suggesting that they

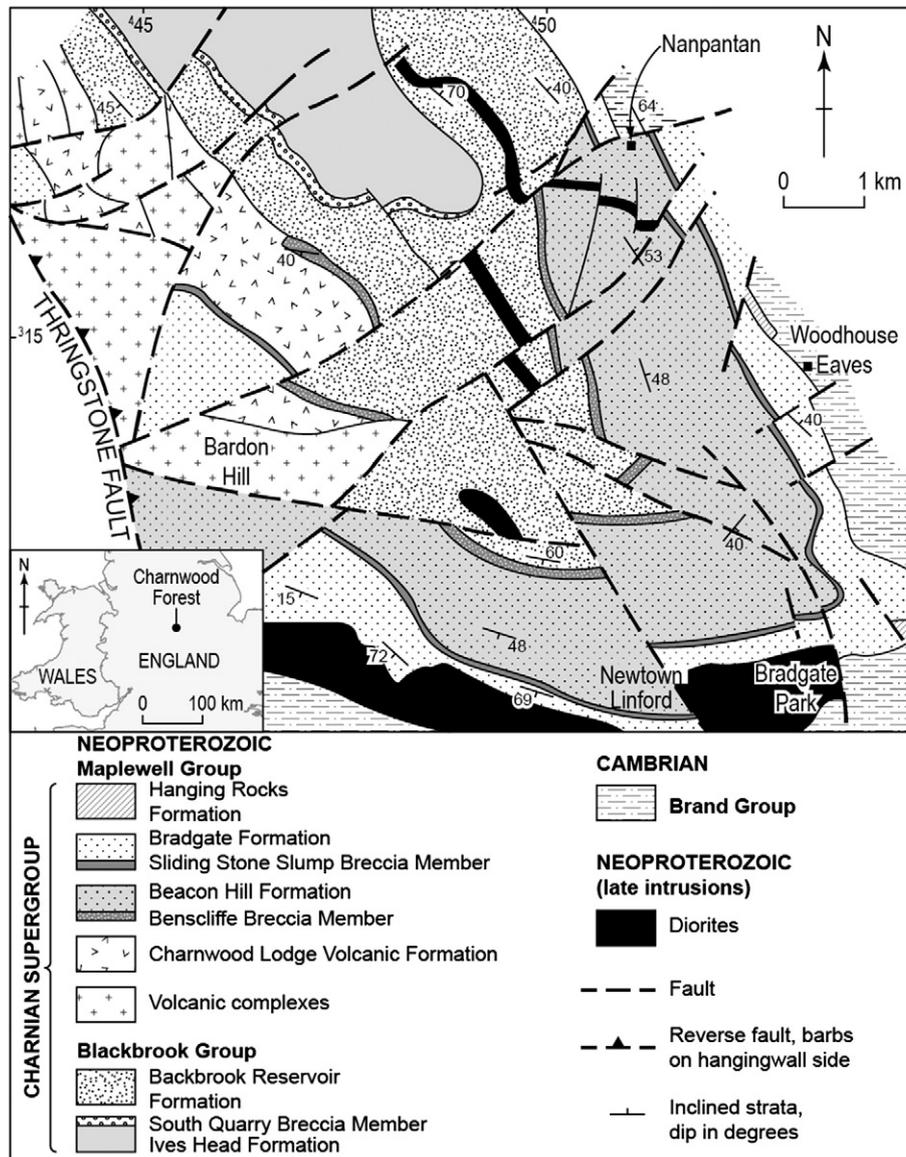


Fig. 1. Location (inset) and simplified geological map of Charnwood Forest, U.K. Eastings and Northings are British National Grid.

were felled *en mass* and preserved in situ (i.e. still anchored) by the overlying event bed. The degree of time averaging remains contentious (see above), but it is possible that at least some of the co-occurring *Aspidella* specimens record the former positions of earlier inhabitants (see below), rather than contemporary individuals whose fronds failed to be preserved. The impact of any time averaging on the present study is negated by considering only well-preserved, mutually-aligned fronds.

Separate bedding planes preserve markedly different assemblages, implying considerable variation in community composition at the time of obrution. Bed B (see Wilby et al., 2011), towards the top of the Bradgate Formation (Fig. 2), is especially fossiliferous. It hosts 795 specimens on a 100.5 m² exposure; a 14.8 m² contiguous surface at the southern end of the outcrop was originally considered part of the same depositional surface (see Wilby et al., 2011) but is now known to be a down-faulted section of the next highest bedding-plane. In addition to being the type surface for *C. masoni* and *Charniodiscus concentricus* (Ford, 1958, 1963), Bed B (*sensu stricto*) includes at least 7 other frondose taxa, both rangeomorphs and arboreomorphs. Particularly large fronds are a notable feature of the preserved assemblage, with 4 taxa – *Charnia* (see below), *Primocandelabrum* sp., so-called ‘dumbbells’, and a form provisionally assigned to *Charniodiscus* – having individuals whose fronds are >35 cm long.

Internally, Bed B (35.5 cm thick) is an amalgam of 3 separate turbidites. The top one, on which the fossils are preserved, is 8.8 cm thick and sharply overlies a 1.3 cm thick hemipelagite (Fig. 3 (3)). Its base is defined by a thin (0.3 cm), pink, very fine-grained sandstone which grades rapidly upwards into a green, increasingly fine-grained siltstone. Indistinct low-angle cross-lamination (Bouma C) is present just beneath its top, and it is capped by a thin (1.25 mm) planar siltstone lamina (Bouma D/E). The turbidite itself is sharply overlain by a variegated, coarser-grained, fining-upward siltstone (2 mm thick), which itself is succeeded by a 0.4 mm thick red-brown, sharp-based, silt-grade crystal tuff (Fig. 3 (2)). These last two units record separate small-scale sedimentation events, one epiclastic and the other primary volcanic. Overlying them is a biomat (Fig. 3 (1)) which defines the top of Bed B and which preserves the frond impressions. It has a distinctive red-brown colour and evidently forms a continuous cover to the bed. Significantly, profiles through certain specimens of *Aspidella* indicate that at least some of the holdfasts relate to fronds that were anchored to the variegated siltstone, rather than the overlying crystal tuff and biomat which formed the substrate for the fronds preserved on Bed B. Such specimens of *Aspidella* are infilled with the crystal tuff (Fig. 3 (4)), and indicate the existence of a prior, now largely concealed, fossil horizon less than a millimetre beneath the top of Bed B. This is

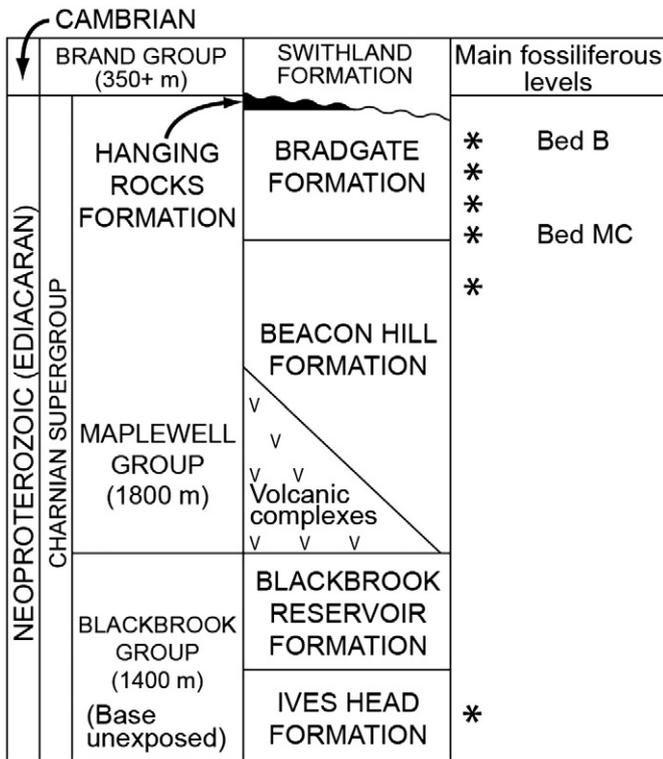


Fig. 2. Simplified lithostratigraphy for the late Neoproterozoic and basal Cambrian succession of Charnwood Forest, U.K., with the most fossiliferous intervals highlighted. Bed B and Bed MC are those of Wilby et al. (2011).

consistent with the presence of other specimens of *Aspidella* on Bed B which have been overgrown by the holdfasts of particularly large fronds preserved on the surface (Fig. 4).

3. *Charnia* from Charnwood Forest

Two morphs of *Charnia* have been recorded from Charnwood Forest – *C. masoni* (Ford, 1958) and *C. grandis* (Boynton and Ford, 1995). The holotype of *C. masoni*, collected from Bed B, is characterised by an ovate frond that tapers abruptly at its distal end and comprises two rows of primary branches (Fig. 5 (1)). These project distally at an acute angle and are arranged alternately along the frond’s midline, forming a distinctive zigzag suture. The primary branches within each row are broadly parallel to one-another, have a sigmoidal outline and are imbricated: those in the left-hand row overlap the proximal margin of their distal neighbour, whilst those in the right-hand row overlap in the opposite sense (see Laflamme et al., 2007, Fig. 2b). Each primary branch is regularly subdivided along its length into a series of up to 25 sub-parallel secondary branches with a broadly rectangular outline. These are oriented slightly obliquely to their parent primary branch and become progressively shorter towards and away from the axis, where they have a more triangular outline. Because of their marked regularity, they define a sweeping arc when traced across adjacent primary branches from one side of the frond to the other. The secondary branches are themselves subdivided by an array of regularly spaced, obliquely oriented tertiary branches, and thence a series of finer fourth-order branches (Fig. 5 (3)). Brasier et al. (2012) interpret the overall architecture of *C. masoni* as being one in which the single growth axis is concealed, and the first to third order rangeomorph units are furled and undisplayed.

Contrary to conventional belief, the holotype of *C. masoni* is very nearly complete and tapers proximally towards a comparatively small globular structure (see Fig. 5 (1)), interpreted here as the top of its holdfast. The intervening area (not usually figured) contains traces of

indistinct secondary branches (Fig. 5 (6)), suggesting that the first primary branches extend all the way down to where the frond would have intersected the sediment surface in life (i.e. to the top of the holdfast).

C. grandis is a poorly defined taxon that has been used to describe particularly large fronds that otherwise resemble *C. masoni* in overall morphology. Such fronds are typically poorly preserved: no previously reported example is complete, and most have ill-defined lateral margins. A single, incomplete, 57 cm long specimen (GSM105925) has previously been reported from Charnwood Forest (Boynton and Ford, 1995; see Fig. 5 (8)) from approximately 300–400 m stratigraphically below the *C. masoni* type surface, and others are known from coeval strata in Newfoundland: one (retrodeformed length 66.5 cm, width 21.1 cm, 21 primary branches) is documented on the Bonavista Peninsula (Hofmann et al., 2008, Fig. 14). In addition, incomplete examples of *Glaessnerina grandis*, a junior synonym of *C. grandis* (Germs, 1973; Runnegar and Fedonkin, 1992; Hofmann et al., 2008), form a minor contingent in the younger Ediacara Member of Australia (Glaessner and Wade, 1966).

The nature of the relationship between *C. grandis* and *C. masoni* is disputed. Most workers have treated them as discrete species (e.g. Hofmann et al. (2008)) and Laflamme et al. (2007) proposed that the former might be differentiated based on thresholds in size (length >50 cm) and number of primary branches (>20). However, this concept of *C. grandis* does not allow for the inclusion of juveniles, and has limited meaning when comparing specimens from different strain regimes. In contrast, Antcliffe and Brasier (2008) emphasised the gross morphological similarity between the two forms and regarded *C. grandis* as merely a large growth variant of *C. masoni*; Brasier et al. (2012) subsequently reinforced this interpretation by synonymising the two taxa. They proposed an ontogenetic model in which new primary branches were inserted at the apex of the frond and progressively inflated proximally. In support, they cited the smaller number of primary branches in the holotype of *C. masoni* (17) relative to the large frond (GSM105925) that Boynton and Ford (1995) described from Charnwood Forest (>20). However, the latter specimen is not well preserved (see Fig. 5 (8)), rendering it ill-suited to comparison. It: 1) lacks its distal end; 2) is notably more asymmetric; 3) lacks a ‘zigzag’ midline; 4) has more widely diverging primary branches (particularly the left-hand row), none of which are sigmoidal; 5) is composed of primary branches that imbricate in the opposite sense; 6) doesn’t display an arcuate sweep of secondary branches across its midline, or secondary branches with a clearly triangular outline; and 7) lacks convincing evidence of fourth order branching. Whilst each of these differences might easily have a taphonomic explanation, detailed analysis of better preserved material is required to definitively resolve the taxon’s status.

4. Material and methods

C. masoni is particularly well suited to population- and ontogenetic studies. It is readily identifiable, has a well-defined and well-ordered branching pattern (providing ample biometric parameters for analysis), retains its growth history within its anatomy (Antcliffe and Brasier, 2007; Brasier and Antcliffe, 2009), and is relatively common, even dominating some assemblages (e.g. see Clapham et al., 2003; Laflamme et al., 2007). It also has considerable potential to act as a ‘standard’ by which the structure of different communities may be compared. It has a long range (>20 Myrs), a wide palaeoenvironmental tolerance (see Grazhdankin, 2004) and a cosmopolitan distribution: outside of Charnwood Forest it is reported from the White Sea (Fedonkin, 1985, 1992; Grazhdankin, 2004), Siberia (Fedonkin, 1985; Grazhdankin et al., 2008), South Australia (Nedin and Jenkins, 1998) and Newfoundland (Laflamme et al., 2007). Nevertheless, there is scant published biometric data available for the taxon. Laflamme et al. (2007, Table 1) provide measurements for a small number of specimens from the Sword Point-, Long Beach- and Lower Mistaken Point surfaces (10, 3 and 1 specimens,

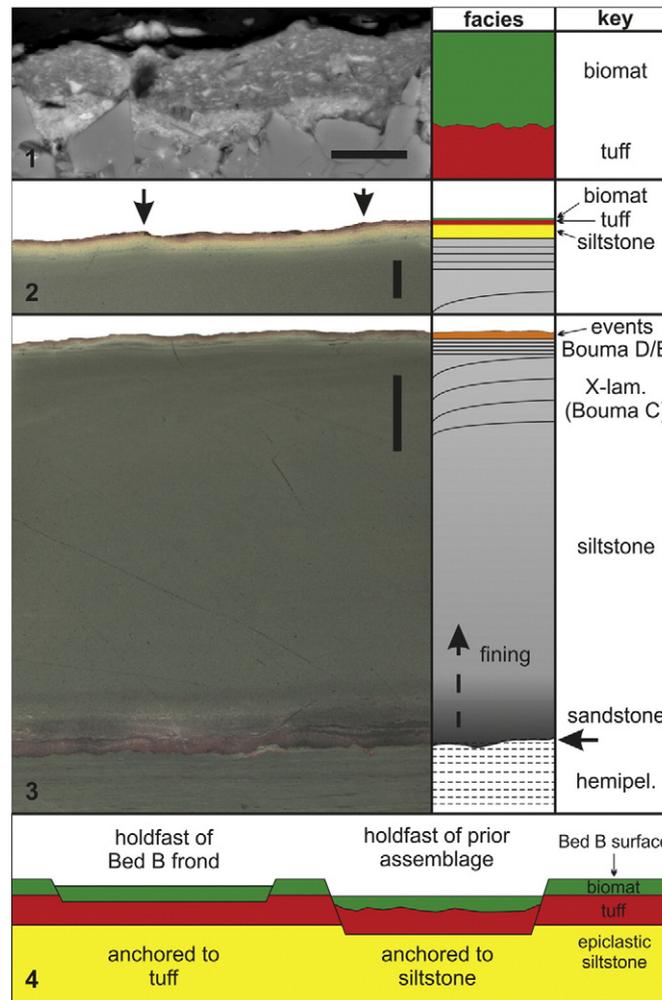


Fig. 3. Bed B sedimentology and preservation of *Aspidella*. (1) Back-scattered Scanning Electron Microscope image of the biomat draping Bed B. Note the abundance of apparently plastically deformed ('wispy') particles, as well as floating grains. (2) Close-up of the event beds that cap Bed B: a sharp-based variegated epiclastic siltstone and overlying red-brown, fine-grained tuff. The section intersects a small *Aspidella* disc (margins shown by arrows) which only mildly perturbs the epiclastic siltstone, but substantially disrupts the tuff; this suggests that the holdfast belonged to an earlier assemblage that was buried by the tuff prior to the main Bed B assemblage becoming established. (3) The base of Bed B (arrowed) is defined by a very fine-grained pink sandstone which sharply overlies laminated hemipelagites and grades rapidly upwards into a thick green siltstone. This is weakly cross-laminated (Bouma C) near its top and is overlain by a thin planar siltstone (Bouma D/E) that defines the top of the turbidite. Lying sharply on top are subsequent event beds, which are shown separated in (2). (4) Schematic cross-section of the top of Bed B illustrating the taphonomy of *Aspidella* holdfasts. The right-hand holdfast is anchored to the epiclastic siltstone horizon and forms part of an earlier assemblage that was smothered by the tuff; this tuff has collapsed into the space formed by the decaying holdfast. In contrast, the left-hand holdfast is anchored to the tuff and forms part of the subsequent assemblage that is preserved as fronds on the surface of Bed B. This holdfast does not substantially disrupt the tuff, but will itself contain a collapse-fill of sediment (not shown) derived from the unit that buried the Bed B surface. Scale bars: (1), 10 μm ; (2), 0.4 cm; (3), 1.6 cm.

respectively) in Newfoundland, and Clapham and Narbonne (2002, Fig. 2) show the taxon's size distribution on the Lower Mistaken Point- and Mistaken Point D and E surfaces as a function of cumulative percentage species composition.

C. masoni is abundantly preserved on its type bedding-plane surface in Charnwood Forest (Bed B), where it is the most common frondose organism (Fig. 5). Eighty specimens are present, with a preserved density of 0.8/m². Thirty two (ca. 40%) specimens on Bed B are complete; the remainder lack clear evidence of the proximal and/or the distal part(s) of their frond. Most of the fronds are straight and have ovate outlines with comparatively low length to width ratios (mean = 3.48, σ = 1.37), which Laflamme et al. (2007) take to be indicative of fronds with more completely preserved lateral margins.

Included in our study is the holotype of *C. masoni* (GSM106160, Fig. 5 (1)) and two considerably larger, co-occurring *Charnia* specimens. The latter are intermediate in length between the *C. masoni* holotype (19.4 cm long) and the large (57 cm long), but incomplete frond (GSM105925, Fig. 5 (8)) that Boynton and Ford (1995) assigned to *C. grandis* (see discussion above). Specimen GSM105873 (Fig. 5 (2)) is

46.9 cm long, complete, and bears 21 primary branches. Specimen GSM105915 (Fig. 5 (9), 5 (10)) has a visible length of 52.5 cm, but its distal end is concealed beneath a 2.8 cm wide patch of sediment. Based on comparison with GSM105873, which is of similar size, this obscured section is inferred to have had at least 4 primary branches, meaning GSM105915 conservatively bore 18 primary branches and was originally ca. 55 cm long. Both specimens are closely aligned to the other fronds on Bed B. We also examined fragments of 2 particularly large *Charnia* fronds (GSM106000 and GSM106001) on the immediately underlying bedding-plane surface (Bed A of Wilby et al., 2011). These are too incomplete to confidently determine their original size (see Fig. 5 (7)) but, based on the surface area of their largest secondary branches (1.68 cm² and 3 cm², respectively), at least one of them was likely of comparable size to the Boynton and Ford (1995) frond (3.85 cm²).

We assessed 3 different biometrics (Fig. 6 (1)) in all of the complete specimens on Bed B. These are: 1) the length of the frond (L), as measured from the base of the first primary branch (coincident with the most proximal secondary branch) to the distal tip; 2) the maximum

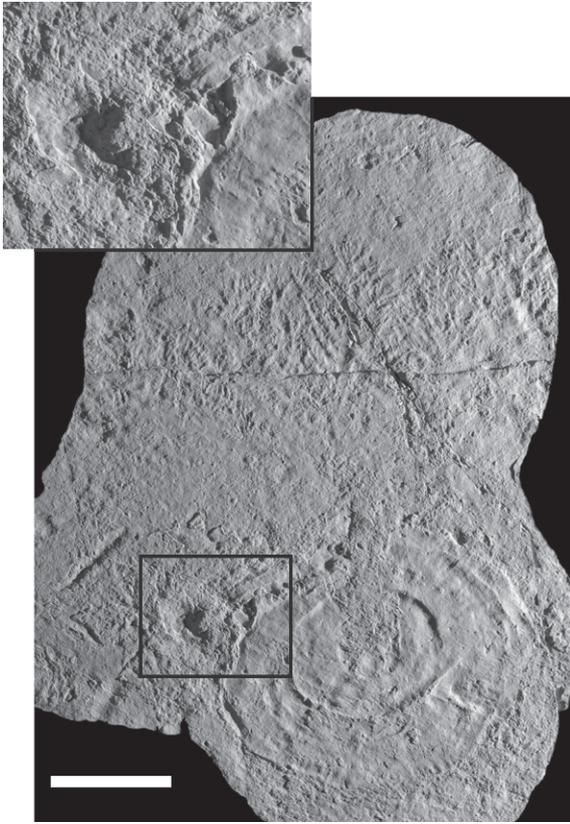


Fig. 4. 'Outsized' specimen of *Primocandelabrum* sp. (GSM105871) whose holdfast overlies an adjacent *Aspidella* (see inset). A thin layer of sediment intervenes between the two discs, and the peripheral margin of the *Primocandelabrum* holdfast has collapsed into the space formed by the *Aspidella*. Both fronds are interpreted as having been compatriots prior to a minor sediment influx which killed the smaller one and allowed the *Primocandelabrum* specimen to overgrow its former position. Scale bar: 15.5 cm.

width of the frond (W); and 3) the number of primary branches in the left- and right-hand side rows (P). For key specimens, we additionally measured: 4) the angle at which each successive primary branch projects from the central axis of the frond (θ); and 5) the maximum apparent spacing of each successive primary branch, as measured orthogonally from its margins (B). None of the measurements are corrected for strain (i.e. retrodeformed) because deformation has affected all length and width measurements equally: the fronds are consistently aligned relative to P_{\max} and there is little variation in the orientation or magnitude of deformation on the bedding surface. For example, the long axes of the *Aspidella* discs ($n = 27$) are consistently oriented ($\sigma = 11.2^\circ$) and exhibit little variation in ellipticity ($\sigma = 2.6\%$).

Measurements of all fronds were taken directly from high quality silicon rubber moulds and sets of scaled, high resolution photos taken using multiple lighting directions. All of the moulds (each with a separate 'GSM' number) are held at the headquarters of the British Geological Survey in Keyworth, UK. Reference was also made to published line drawings (Antcliffe and Brasier, 2008, Text-Figs. 2 and 3) of the *C. masoni* holotype and of the frond assigned by Boynton and Ford (1995) to *C. grandis*.

5. Results

5.1. Relationship of *C. grandis* to *C. masoni*

The especially large *Charnia* specimens (GSM105873 and GSM105915) on Bed B, which would traditionally have been assigned to *C. grandis* (pers. com. Boynton, 2010), provide a unique opportunity to test the relationship between *C. masoni* and *C. grandis*. GSM105873

(Fig. 5 (2)) closely conforms to the morphology of the *C. masoni* holotype, except that it possesses a greater number of primary branches (see below). Its most proximal primary branches have a distinctly curvilinear outline, comparable to those in the holotype, suggesting that the specimen is essentially complete. Approximately midway along its length there is a disrupted area in which the 8th and 9th primary branches are dislocated, with the more proximal branches displaced in unison towards the midline (i.e. they have a more acute angle of repose), thereby overlapping their more distal neighbours. This aside, the branching architecture is indistinguishable from the holotype over the four orders that are visible (compare Fig. 5 (3) and (4)).

GSM105915 (Fig. 5 (9), (10)) is less well preserved and is morphologically intermediate between the *C. masoni* holotype and the frond (GSM105925) assigned to *C. grandis* by Boynton and Ford (1995). Its distal tip is concealed beneath sediment, it does not preserve evidence of fourth order branching, it does not exhibit an arcuate sweep of secondary branches across its midline, and its primary branches have only a vaguely sigmoidal outline. Crucially, however, its overall form is the same as the *C. masoni* holotype (Fig. 6 (3), (4)), it possess a comparable bulbous holdfast, a poorly defined 'zigzag' suture (Fig. 5(10)), and a comparable first to third order branching pattern.

Multiple biometrics (Fig. 6 (1)) further support assignment of both of these large specimens to *C. masoni*. The length (L) to width (W) ratio of GSM105873 (3.94) is identical (within error) to that of the holotype (3.96) and honours the strong linear relationship ($R^2 = 0.96$) exhibited by all other smaller *C. masoni* specimens on Bed B (Fig. 6 (2)). Differences in the width of successive primary branches (B) in GSM105873 and GSM105915 (Fig. 6 (3)) similarly correlate closely with that in the holotype ($R^2 = 0.88$ and 0.9 , respectively). Interestingly, however, the corresponding correlation in branching angle (θ) is poor ($R^2 = 0.02$ and 0.44), except for the eight most proximal primary branches ($R^2 = 0.87$ and 0.73), although the overall trends are similar (Fig. 6 (4)). These last two facts imply that the primary branches in *C. masoni* had some freedom to rotate in the axial plane and that they moved in unison, maintaining their mutual separation, much like the barbs of a vaned feather. This adequately accounts for the greater (and variable) branching angle seen in the Boynton and Ford (1995) frond (GSM105925) and suggests that θ has negligible taxonomic relevance (contra Laflamme et al., 2007). Similarly, the sense of imbrication in the primary branches is inconsequential, and likely a taphonomic phenomenon (cf. Brasier et al., 2013). The primary branches of all of the specimens on Bed B, including GSM105873 and GSM105915, are imbricated in the same direction as the holotype (from the same surface). In contrast, the two large fragmentary fronds (GSM106000 and GSM106001) from the immediately underlying bed (Bed A of Wilby et al., 2011) are oriented in the opposite direction and their primary branches overlap one another in the opposite sense; nevertheless they maintain the characteristic, highly ordered, *C. masoni* branching pattern (see Fig. 5 (7)).

5.2. Population structure

Size–frequency distributions are used widely to investigate the structure of populations within modern and fossil communities (see references in Darroch et al., 2013). They can provide valuable insights into recruitment, mortality, dimorphism and reproductive strategy, as well the spatial and temporal dynamics of ecosystems. Darroch et al. (2013) provide size–frequency (length) histograms for three rangeomorph taxa (*Beothukis*, *Fractofusus*, *Pectinifrons*) and one non-rangeomorph taxon (*Thectardis*) from five separate bedding-planes in the Avalon Assemblage of Newfoundland. In each case, the rangeomorph populations have a right-skewed, unimodal, log-normal distribution with large variance; in contrast, the *Thectardis* population has relatively neutral skew, is less peaked and is normally distributed.

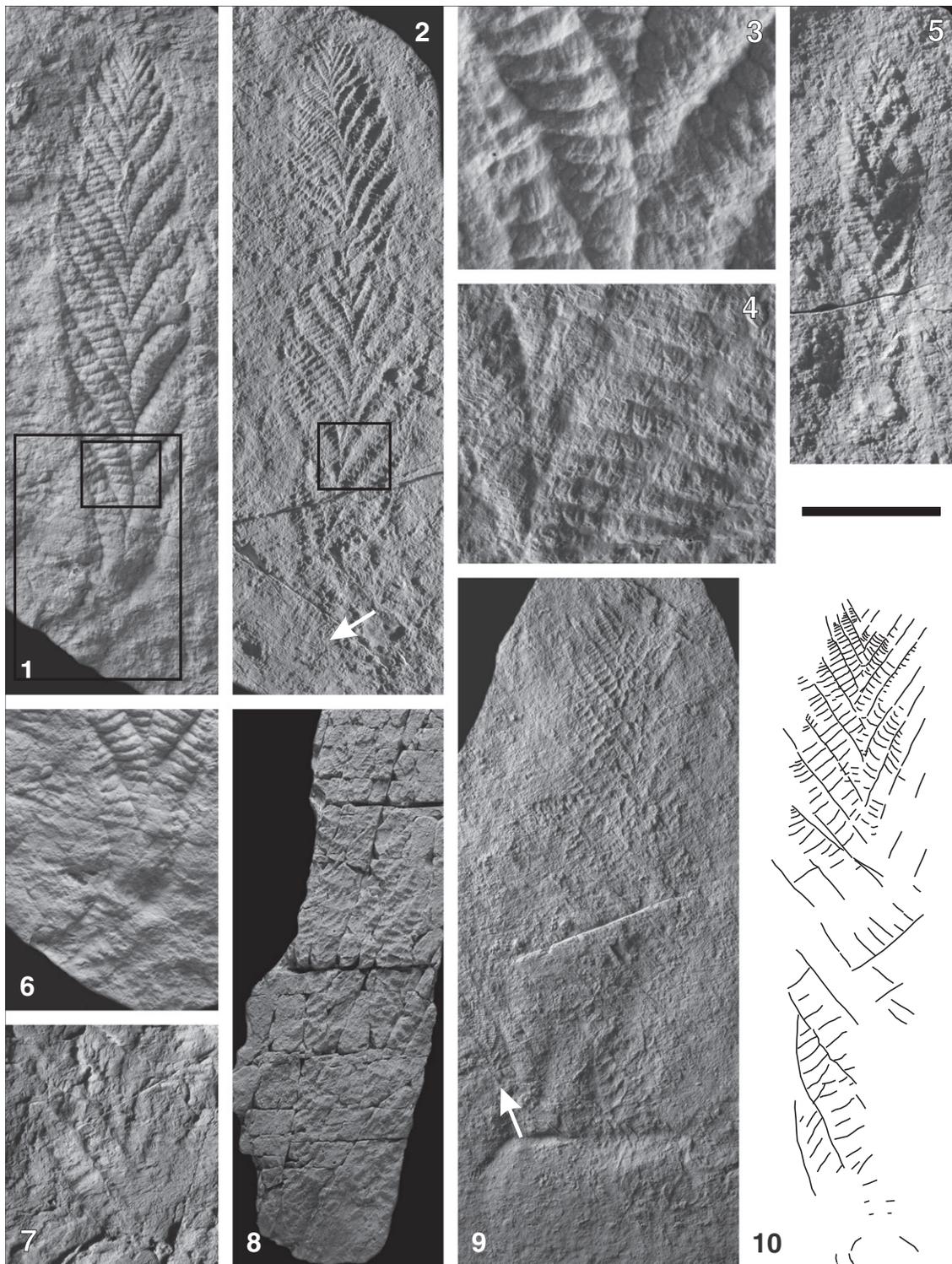


Fig. 5. *Charnia masoni* from Charnwood Forest. (1) Holotype (GSM106160) with preserved holdfast; boxes are enlarged areas shown in (3) and (6). (2) Complete 'outsized' specimen (GSM105873) with an indistinct holdfast (arrowed) and a region of disrupted branches mid-way along its length; box is enlarged area shown in (4). (3) Detail of the first to the fourth order branching in proximal region of the holotype. (4) Detail of the first to the fourth order branching in the proximal region of GSM105873; compare with (3). Image inverted. (5) presumed juvenile with distinct holdfast (GSM105979). (6) Detail of the holotype showing where the first primary branches join the holdfast. (7) Partial very large frond (GSM106001). (8) Incomplete frond (GSM105925) with notably less ordered form, previously assigned to *C. grandis* by Boynton and Ford (1995). (9) Poorly preserved 'outsized' frond (GSM105915) missing its distal tip; note similarly aligned smaller *C. masoni* specimen (arrowed). (10) Simplified camera lucida interpretation of (9). All specimens are from the type surface (Bed B) except (7) and (8), which are from the immediately underlying bed and Bed MC of Wilby et al. (2011), respectively. Silicon rubber moulds (1, 3–4, 6–7) and plaster casts (2, 5, 8–9) of in situ specimens, except GSM106160 which is held in New Walk Museum, Leicester, U.K. Scale bar: (1), 5 cm; (2), 11 cm; (3), 2.8 cm; (4), 5.6 cm; (5), 3.8 cm; (6), 3.4 cm; (7), 10 cm; (8), 14.6 cm; (9–10), 12.2 cm.

The *C. masoni* population on Bed B in Charnwood Forest exhibits a markedly different size (length) distribution (Fig. 6 (5)). It is right-skewed and bimodal, with a dominant peak at 7 cm and a smaller

peak centred at ca. 49 cm, this latter comprised of the two largest specimens. We tested the validity of the bimodal distribution by comparing the fit of the empirical data to five continuous distributions

(normal, Box–Cox transformation to normal, logarithmic, gamma and stretched exponential), both when the two largest specimens were excluded ($n = 32$, Fig. 6 (7)) and included ($n = 34$, Fig. 6 (8)). The five distributions differ in their versatility at handling outliers in data by adjusting scale (mean) and shape (skewness) parameters. For instance, the normal assumes equal likelihood of “dwarfs” and “giants”, whereas the gamma and stretched exponential are well-suited to representing long-tailed distributions. Goodness of fit for each distribution was assessed using the Kolmogorov–Smirnov (KS) D statistic and Shapiro–Wilk W test for normality (Table 1). The probability (Pr) of a specimen equalling or exceeding the two largest ones ($L = 46$ cm and $L = 52$ cm) was estimated in each case. Note: Welch’s t -test provides a means of determining whether two sets of data form non-overlapping populations, but is inappropriate in the present case because of its assumption of normality and the small population of outliers ($n = 2$). Where the two largest specimens are excluded ($n = 32$) from our analysis, the critical values for D and W at $p = 0.05$ are 0.211 and 0.93, respectively. Thus, the only distribution that does not provide a statistically significant fit to the empirical data is the stretched exponential. The log-normal distribution provides the best overall fit, and under these conditions the chances of the two outliers forming part of the same population are negligible ($\leq 0.00037\%$). Where the two largest specimens are included ($n = 34$) in our analysis, the critical values of D and W at $p = 0.05$ are 0.205 and 0.933, respectively. Now, only the log-normal and Box–Cox distributions provide significant fit to the empirical data and, although the likelihood of exceedance increases, the chance of a specimen with a length ≥ 46 cm remains exceedingly small (0.22–2.4%). Consequently, we conclude that the two largest specimens are not drawn ($p < 0.05$) from the same population as the rest of the specimens. A bimodal distribution is further supported by the absence of intermediate-sized individuals amongst the population ($n = 48$) of imperfectly preserved *C. masoni* fronds on Bed B.

5.3. Ontogeny

Ontogenetic analyses can highlight key stages in an organism’s life history, such as benthic settlement and adulthood, as well as changes in community structure and environmental disturbance. Brasier et al. (2012) offered a unified conceptual model for the growth of rangeomorphs which also has considerable potential for testing postulated affinities (e.g. Antcliffe and Brasier, 2008). Nevertheless, treatments of growth and development are currently available for only a few taxa (e.g. see Antcliffe and Brasier, 2007; Gehling and Narbonne, 2007; Bamforth et al., 2008), and these report differences in the dominance of inflation- versus insertion- programmes (see also Flude and Narbonne, 2008; Narbonne et al., 2009). The importance of deterministic versus non-deterministic growth also remains an intriguing question, especially given the pseudofractal architecture of the clade (Narbonne, 2004) and the size that some of its members may attain (e.g. see Narbonne and Gehling, 2003; Bamforth and Narbonne, 2009; Wilby et al., 2011); it has implications for how efficiently they may have been able to function as osmotrophs (Laflamme et al., 2009; Sperling et al., 2011).

Although potentially subject to environmental influence (see below), size metrics are a well established proxy for age. *C. masoni* grew by sequentially inserting new primary branches at its distal tip and progressively inflating them (Antcliffe and Brasier, 2007, 2008). However, further details of its ontogeny are unknown. The main population on Bed B (i.e. excluding the two largest specimens, see above) shows a strong linear relationship between frond length and width ($R^2 = 0.75$, see also Fig. 6 (2)), as well as frond length and number of primary branches ($R^2 = 0.77$, Fig. 6(6)). This is consistent with the isometric- (e.g. see Gehling and Narbonne, 2007) or mildly allometric scaling (Darroch et al., 2013) seen in other rangeomorphs. Interestingly, the L:P trendline for *C. masoni* intercepts the y-axis (P) at ca. 4, which

compares closely with the smallest number of primary branches ($P = 5$) recorded in any known *C. masoni* specimen (see Liu et al., 2012). We speculate that this may be of fundamental developmental or ecological significance, recording either the number of primary branches in a propagule or the point at which the fronds adopted their adult life habit. Certainly, the complete absence of very small ($L < 4$ cm) specimens on Bed B is otherwise at odds with the widespread preservation of sub-millimetric morphological details in the fossils.

Tellingly, the two largest fronds (GSM105873, GSM105915) on Bed B retain a very different record of growth to their conspecifics (see Fig. 6 (6)), further distinguishing them from the main population. For their respective lengths, they possess substantially fewer primary branches than the other fronds and diverge markedly from the projected (isometric) slope.

6. Discussion

We consider 3 possible explanations for the coexistence of the two distinct populations of *C. masoni* on Bed B:

- i. *Allometric growth.* At face value the data imply that *C. masoni* had a two-phase growth programme, with an initial insertion dominated phase of isometric growth replaced by an inflation dominated phase of allometric growth. The transition occurred at some point after the acquisition of the 19th primary branch. Analogous growth occurs in certain modern organisms, such as the passive feeding anemone *Anthopleura xanthogrammica*. It adds new feeding ‘modules’ (tentacles) in a defined arrangement during near-isometric growth, rapidly reaching a maximum number, after which it merely expands with age (Sebens, 1982). However, negative allometric scaling with respect to number of primary branches has not been reported in any other rangeomorph; its purported presence in *Fractofusus* (see Laflamme et al., 2009, Fig. 3b) is a consequence of 2 separate species having been conflated. Indeed, modelling of osmotrophic efficiency suggests that a reduction in the P:L ratio would be detrimental (Laflamme et al., 2009) unless, perhaps, it was accompanied by a reduction in metabolic demand and/or additional branch subdivision. The latter remains a theoretical possibility, given the apparent modular architecture of rangeomorphs (cf. Narbonne, 2004).
- ii. *Dimorphism.* Sexual dimorphism occurs in a wide range of modern and ancient organisms, and may be dramatic (e.g. Callomon, 1963). Circumstantial evidence suggests that rangeomorphs reproduced sexually (see discussion in Darroch et al., 2013), but morphological evidence is lacking. Neither of the two populations of *C. masoni* bears any novel morphological structure, recognisably reproductive or otherwise. Furthermore, a sexual explanation for the size differences would necessarily imply that the number of reproductively mature adults (i.e. $P > 19$) was extremely low, both locally and globally; this is at odds with the abundance and cosmopolitan distribution of the taxon. Consequently, a sexual dimorphic explanation is not considered further.
- iii. *Non-overlapping cohorts.* Bimodal size distributions can be generated in a number of different ways, each of which induces a distinctive signal (see Huston and DeAngelis, 1987; Barry and Tegner, 1990). They may be a consequence of: 1) the coincidence of sequential cohorts, 2) genetic variation within a single cohort, 3) random environmental factors, such as substrate suitability, 4) ecological effects, such as shading, and 5) differential mortality within a population, either as a result of varying vitality or of a random environmental event. In all cases, the bimodal signal may be enhanced if the size difference leads to a competitive advantage (Harper, 1967, 1977), or it may be dampened if growth slows sufficiently with age for the two groups to merge (Power, 1978; DeAngelis and Mattice, 1979; Barry and Tegner, 1990). The *C. masoni* demographic on Bed B is best described as two, non-overlapping cohorts, representing

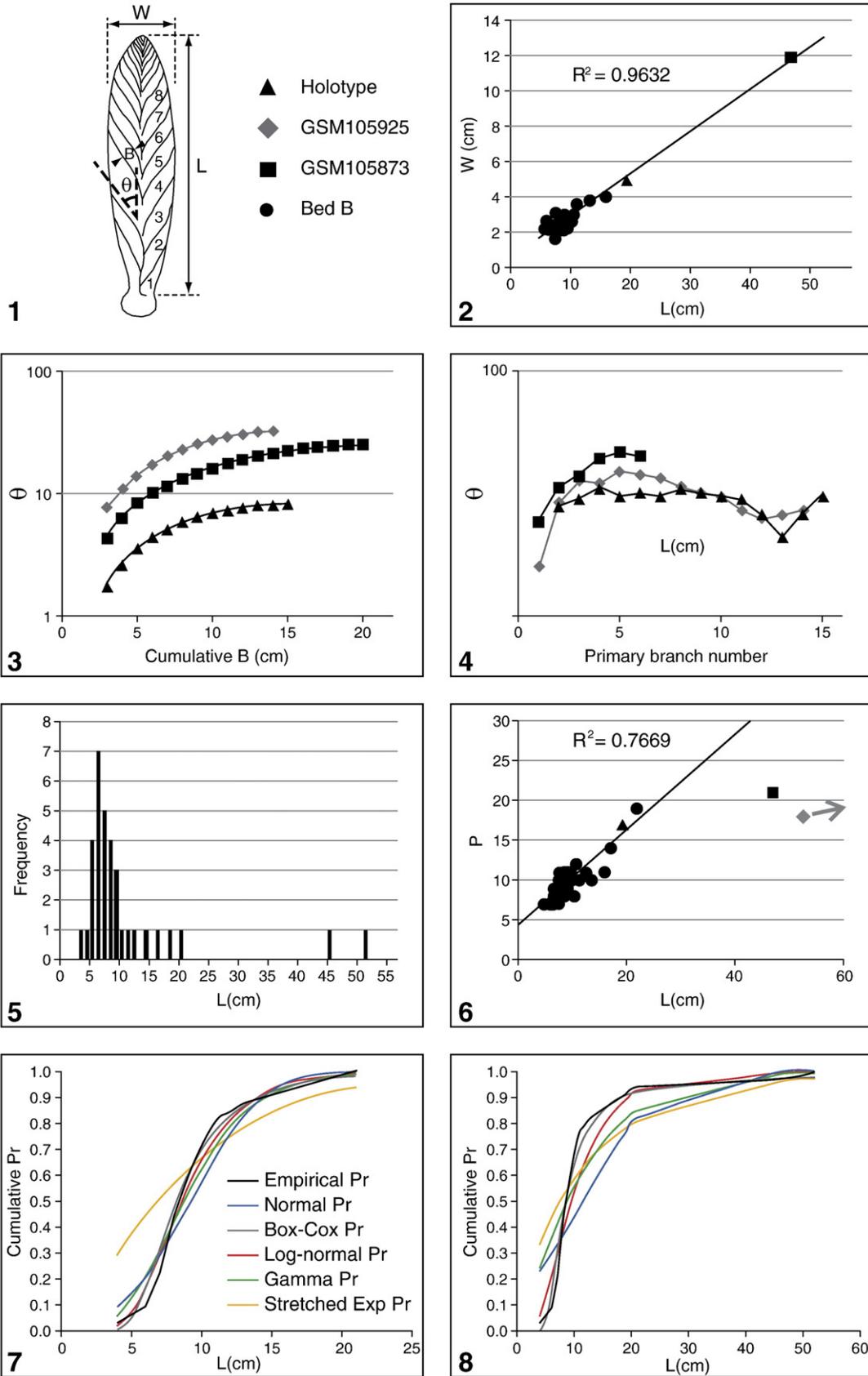


Table 1

Kolmogorov–Smirnov (D) statistics with likelihood of exceedance estimated when the two largest specimens are excluded ($n = 32$) or included ($n = 34$), respectively. Likelihoods shown in bold are estimated from distributions that are significant approximations of the data (i.e. $D \leq D_{crit}$, $p = 0.05$). Some illustrative examples of where these distributions have been encountered in natural populations are given in the last column.

Distribution	Excluding the two largest specimens ($n = 32$)			Including the two largest specimens ($n = 34$)			Notes	Example applications
	KS D	Pr{ $L \geq 46$ }	Pr{ $L \geq 52$ }	KS D	Pr{ $L \geq 46$ }	Pr{ $L \geq 52$ }		
Normal	0.143	1.7E–20	3.9E–27	0.288	1.4E–4	1.7E–5	The Gaussian distribution assumes symmetry about the mean.	Shell size distribution for Early Jurassic ammonites (Dommergues et al., 2002).
Box–Cox ^{ab}	0.091	4.1E–2	2.9E–2	0.096	2.4E–2	2.1E–2	A transformation that preserves the rank order of data whilst improving approximation of skewed data to a normal distribution.	Parameter identification of the Richards population growth model (Loibel et al., 2006)
Log-normal	0.074	3.7E–6	7.6E–7	0.162	2.2E–3	1.0E–3	A widely used transformation for age-size distributions.	Rates of origination and extinction in the marine fossil record (Alroy, 2008).
Gamma	0.119	9.2E–8	4.5E–9	0.272	1.2E–2	6.1E–3	A versatile two-parameter distribution typically used for fitting skewed data, including the special case of the exponential distribution.	Rates of morphological evolution amongst fossil invertebrates (Wagner, 2012).
Stretched exponential (Weibull)	0.345	4.9E–4	1.4E–4	0.346	3.9E–2	2.7E–2	Typically used in situations where 'heavy' tail behaviour is evident, obtained by inserting a fractional power law into the exponential function.	Distribution of biological extinction events over the last 600 million years (Laherrere and Sornette, 1998).

^a For $n = 32$, $W \geq W_{crit}$ (0.930, $p = 0.05$) so the null hypothesis that samples are drawn from a Gaussian distribution is not rejected (for $\Lambda = -0.6$).

^b For $n = 34$, $W \geq W_{crit}$ (0.933, $p = 0.05$) (for $\Lambda = -1$).

separate recruitment events. It's impossible to definitively exclude cyclical- (e.g. seasonal) or episodic reproduction as the driver for the bimodal population of *C. masoni* on Bed B, but there is no reason to presume that this taxon diverged from the continuous (i.e. aseasonal) reproductive strategy inferred for other rangeomorphs (and non-rangeomorphs) in the Avalon Assemblage (Darroch et al., 2013). With this in mind, the most parsimonious explanation for the observed demographic is that recruitment was interrupted. Taphonomic evidence implicates a minor depositional event; we infer that this culled part of an incumbent population and created opportunities for renewed recruitment, thereby superimposing a new cohort of *C. masoni* on a denuded earlier one (Fig. 7). Indeed, remarkably similar distributions are reported in extant communities recovering after a period of high mortality caused by disturbance (e.g. Stohlgren, 1992).

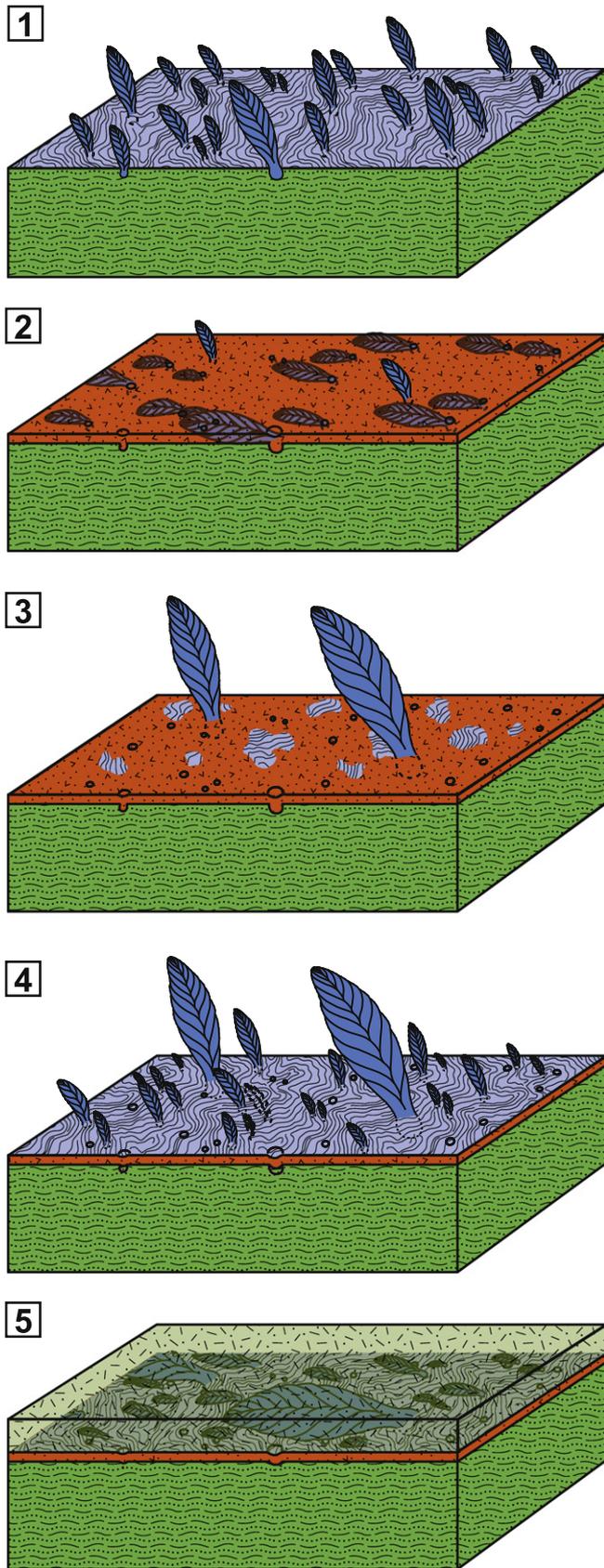
Catastrophic depositional events played a fundamental role in structuring Avalon Assemblage communities (Clapham et al., 2003), and intervening minor inundations are known to have impacted them too (e.g. see Menon et al., 2013). Survival of minor, gentle sedimentation events has also been demonstrated in Ediacara communities from Australia (Mapstone and McIlroy, 2006). Small-scale event-beds are abundant in the Beacon Hill and Bradgate formations and form the substrate to Bed B (see Fig. 3(2)). The uppermost one (an ashfall) is extremely thin and demonstrably (see above) smothered a resident population of fronds (Fig. 7 (1), (2)), some of which appear to have survived to form part of the Bed B (recovery) biota (Fig. 7 (3), (4)). Amongst these, we suggest, were GSM105873 and GSM105915.

The response of extant organisms to burial, including by deepwater turbidites and ashfalls (e.g. see Thistle et al., 1985; Glover et al., 2001; Lamshead et al., 2001; Hess et al., 2005; Kuhnt et al., 2005; Wařkowska, 2011), relates to their functional morphology as well

as to the thickness, frequency and nature of the blanketing material (e.g. see Bluhm et al., 1995; Glover and Smith, 2003; Larsson and Purser, 2011; Gates and Jones, 2012). Direct functional analogues to rangeomorphs are missing (see Laflamme et al., 2009) and their resilience and response to periodic influxes of sediment is unknown. However, their long-term dominance of the Charnwood and Newfoundland successions (see Noble et al., 2015), where such events were frequent, suggests that they were well equipped to cope. Indeed, at least certain components of the Avalon Assemblage responded to aggrading sediment by progressively 'jacking' themselves upwards (Menon et al., 2013); epibenthic suspension feeders in modern deep-water settings adopt a variety of other solutions to tolerate the stress (e.g. see Larsson and Purser, 2011).

Rangeomorphs formed dense, vertically tiered communities in response to competition (Clapham and Narbonne, 2002; Laflamme et al., 2012). Hydrodynamic water flow within such communities may be greatly affected by neighbours (e.g. see Eckman et al., 1981; Carey, 1983; Johnson, 1990; Ghisalberti et al., 2014) and, at least in suspension feeders, can result in resource depletion (e.g. see Glynn, 1973; Merz, 1984) and/or feeding interference (e.g. see Okamura, 1984), leading to smaller maximum sizes than would otherwise be achieved (Sebens, 1983; Johnson, 1990). Taken as a whole, the growth trajectory of *C. masoni* on Bed B (see Fig. 5(6)) most closely resembles that of organisms whose linear growth has been forced to an asymptotic state by limited resources and has subsequently been freed from the constraint (see Sebens, 1982, 1987). Such plasticity, where there is considerable capacity to respond to improved environmental conditions, such as reduced competition, is typical of organisms with indeterminate growth programmes and no genetically controlled upper size limit (e.g. Sebens, 1982). It is entirely consistent with the presence of even larger *C. masoni* specimens (GSM106000, GSM106001) on the bed immediately below Bed B, and with 'giant' fronds elsewhere (Fedonkin, 2003; Narbonne and Gehling, 2003). Recovery in deepwater communi-

Fig. 6. Morphometrics and ontogeny of *C. masoni* on Bed B. (1) Biometrics used in analyses. (2) Length to width ratio (L:W) of all complete specimens, indicating isometric growth. (3) Logged cumulative spacing of consecutive primary branches (B) in the holotype and the two largest specimens, illustrating comparable anatomical proportions (ontogenetic trajectories). (4) Logged variations in consecutive primary branch orientations (θ) in the holotype and the two largest specimens, showing broad similarities. (5) Size–frequency distribution of all complete specimens ($n = 34$), highlighting the presence of two coincident non-overlapping populations (cohorts). (6) Distribution of length (L) versus number of primary branches (P); all specimens up to approximately the size of the holotype are described by a linear relationship ($R^2 = 0.7669$), but beyond that they possess substantially fewer primary branches for their length. Where the trendline intercepts the y-axis ($P \approx 4$) may be of ontogenetic or palaeoecological significance. Note that the position of GSM105925 is conservative and that it more likely plots further to the right. (7) Cumulative empirical and theoretical probability distributions for specimens where $L \leq 21$ cm; only the stretched exponential distribution doesn't provide a statistically significant fit to the empirical distribution. (8) Cumulative empirical and theoretical probability distributions for all specimens, illustrating that only the log-normal and Box–Cox distributions now provide significant fits to the empirical distribution.



ties after even minor disturbance is sluggish (see Grassle and Morse-Porteous, 1987; Smith and Hessler, 1987) and so survivors may experience lengthy periods of minimal competition. Consequently, indeterminate growth would have been highly advantageous to survivors on Bed B because it would have enabled them to grow higher above the substrate where flow-rates are typically greater, and would have freed them from the density-dependent competition experienced by new recruits in the understory. Greater size may also have rendered survivors less vulnerable to subsequent smothering events, enabling them to persist in the community.

Assuming continuous propagation (Darroch et al., 2013), an obvious consequence of the above is that the substrate needed to mature prior to successful new recruitment; there is a gap between cohorts on Bed B which doesn't exist in apparently undisturbed populations. The preserved community therefore highlights four significant aspects of rangeomorph palaeoecology. Firstly, that new recruits were substrate sensitive. Many benthic organisms are sensitive to alteration of their substrate (e.g. see Lamshead et al., 2001; Smit et al., 2008), and even thin burial may affect interstitial microbial populations (e.g. see Gates and Jones, 2012) which have been shown to strongly influence recruitment (e.g. Kirchner et al., 1982; Dahms et al., 2004). Secondly, that rangeomorphs were not directly sustained by surficial microbial mats. Smothering of the original mat would have left the surviving fronds with an interlude (of unknown duration) during which a new mat had yet to become established. Thirdly, that the bedding-plane assemblages include a degree of time-averaging. This is in a different sense to that envisaged by Liu et al. (2011), because it relates to refuges that survived to become part of a recovery community, rather than deceased individuals that are conflated with the living community. In this regard, 'outsized' fronds provide a conspicuous proxy for sub-lethal disturbance; their comparative frequency in the Maplewell Group suggests that disturbance was an important force in structuring the communities. And, fourthly, that recovery was fostered by the presence of survivors. It's noteworthy that the 'outsized' fronds on Bed B (*C. masoni*, *Primocandelabrum* sp., 'dumbbells', *Charniodiscus* sp.) belong to the very same taxa that numerically dominate the rest of the community (see Wilby et al., 2011, Fig. 4). This relationship is not seen on every surface that supports such fronds, but it may nevertheless provide valuable insights into the reproductive and dispersal strategies of rangeomorphs. It echoes the situation in modern deepwater settings whereby the composition of the reinstated community most strongly relates to that of any survivors and to the immediately surrounding area (cf. Smith and Hessler, 1987). More speculatively, surviving rangeomorphs may also have facilitated recovery by baffling benthic currents on the otherwise uniform substrate (cf. Eckman, 1983, 1990; Gallagher et al., 1983), thereby promoting the settlement of their presumed planktonic larvae (see Darroch et al., 2013).

Survivors undoubtedly had a profound effect on both the rate and trajectory of community recovery, and their presence or absence was likely controlled by variations in the number, frequency and severity of disturbance events. This may account for at least some of the bed-to-bed variability in community composition observed within the

Fig. 7. Proposed sequence of events leading to the community observed on Bed B; only the constituent *C. masoni* population is shown. (1) Pre-existing (prior) population anchored to an epiclastic siltstone lamina (green) and surficial biomat (pale blue). (2) Smothering of the population by an ash (orange), killing all but a few residents; note that the holdfasts of the killed individuals collapse during decay and become filled with the settled ash. (3) The survivors of the smothering event prosper; their indeterminate growth programme enables them to respond to the reduced competition for resources by growing higher into the water column than would otherwise have been possible. (4) Re-establishment of a surficial biomat allows a new cohort to populate the surface, perhaps facilitated by the presence of the survivors. The new cohort forms a high-density understory to the survivors, and develops the 'classic' right-skewed, unimodal population structure. (5) Burial and in situ preservation of the entire community beneath a major event bed (pale green), thereby capturing the bimodal population structure of Bed B.

Avalon Assemblage that has previously been ascribed entirely to ecological succession (Clapham et al., 2003). Disturbance may also have influenced community diversity, since a dynamic equilibrium exists between population reduction through disturbance and competitive displacement (Huston, 1979). With increasing understanding of sedimentological and taphonomic processes, such ecological nuances will surely become more apparent.

7. Conclusions

High-frequency, small-scale sedimentation events are important in deep-water environments, and played a significant role in structuring the Avalon Assemblage communities. They selectively culled residents, creating intervals of reduced competition for the survivors, whose persistence influenced the development of the subsequent recovery community. These individuals are represented in bedding-plane assemblages by conspicuously outsized fronds, and impart a bimodal structure to the preserved populations. In a continuous reproduction model, the absence of intermediate-sized fronds implies that recruitment was interrupted, perhaps signalling substrate sensitivity. The presence of this dynamic may not be discernible in communities if the separation of cohorts is less pronounced. The response of *C. masoni* to disturbance reveals that it (and probably other rangeomorphs too) had an indeterminate growth programme. This plasticity enabled the organism to exploit improved conditions by growing higher into the water column, consequently freeing it from the density-dependent constraints experienced by new recruits in the understory. Thus, the overall community ecology of rangeomorphs is more complicated than previously appreciated.

Acknowledgements

PRW and CGK were supported by NERC grant NE/I005927/1. We thank our colleagues Mark Dean, Sue Martin, Louise Neep, Scott Renshaw and Paul Shepherd for assistance with moulding and casting; Paul Witney and Simon Harris for photography; and Henry Holbrook for drafting Figs. 1 and 2. We gratefully acknowledge the help in facilitating site access given by Natural England, the Mistaken Point Ecological Reserve (Parks and Natural Areas Division, Government of Newfoundland and Labrador) and landowners in Charnwood Forest. We enjoyed useful discussions with Alex Liu and Helen Boynton, and Mark Woods, Guy Harrington, Lidya Tarhan and two anonymous referees are thanked for their constructive comments on the manuscript.

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