Identification of Phymatolithon lamii (Me. Lemoine) Y.M. Chamberlain 1991 following bleaching in the upper intertidal zone of the Minas Basin, Nova Scotia, Canada

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ABSTRACT

Objective: To identify an unusual encrusting calcareous organism found growing on upper intertidal rocks along the coast of the Minas Basin, Nova Scotia, Canada, which was thought to potentially represent a new, perhaps invasive species to the area.

Methods: Observations were made of the organism growing in situ and of intact and dissected specimens under microscopes in the laboratory. Taxonomic keys were used to determine probable identity of the organism as a tunicate, sponge, bryozoan, marine lichen, or coralline red alga. These keys were then further used to identify samples to species.

Results: The organism was determined to be Phymatolithon lamii (Me. Lemoine) Y.M. Chamberlain 1991, an encrusting coralline red alga native to the study region. This species normally occurs in the subtidal zone, so its occurrence in the high intertidal zone was unusual and resulted in the alga becoming bleached and taking on an unusual appearance.

Conclusions: The sample did not represent a new or invasive species to the study area. However, occurrence of this species on the high intertidal zone was novel and may have resulted from unusual climatic and/or oceanographic conditions in the study area in 2015 that allowed this alga to settle and grow in the intertidal zone for a time before death and bleaching occurred. Events such as this resulting from climate change may negatively impact recruitment to populations of coastal marine species and should be investigated further.

1. Introduction

Human activities and climatic shifts have resulted in marked changes to coastal marine habitats and biological communities in recent years[1,2]. Coastal habitats support species of considerable socio-economic importance, including molluscs, crustaceans, and finfishes on which major fisheries depend, micro- and macroalgae from which important products for use in production of food and medicine are extracted, and “charismatic” organisms (marine mammals, corals, etc.) that support local tourism industries. Changes to the biotic and/or abiotic conditions in which these important organisms live can have strong, often negative impacts on their health, abundance, and productivity, which in turn impacts coastal communities that depend on the industries they support[1-3].

Introductions of non-native species to a coastal habitat can have particularly important harmful impacts on native marine biota if non-native organisms establish persistent, invasive populations[4,5]. Many invaders are able to outcompete native species for food, space, and other resources[4], which impacts species directly, and also indirectly affects other species that interact with directly-impacted ones such as predators, prey, competitors, commensals, symbionts, etc.[5]; this can have far-reaching and cascading effects on all species in the system[4,5]. Recently, a number of networks and organizations, for example Canadian Aquatic Invasive Species Network (http://www.caisn.ca/), have been established to facilitate monitoring marine habitats for introductions of new, non-native species, in the hope that early detection will allow invasions to be prevented, or at least anticipated and potential effects mitigated[6]. First records of species in new locations are also frequently published[7], which assist in such monitoring efforts and allow global trends in species introductions to be tracked within the scientific literature[4,7].

The Bay of Fundy is an inlet of the North Atlantic Ocean which runs from the Gulf of Maine into and between the provinces of Nova Scotia (NS) and New Brunswick, Canada (Figure 1). This embayment is known globally for its extreme tidal ranges, especially in the Minas Basin, NS (up to 16.8 m; see http://www.town.parrsboro.ns.ca/worlds-highest-tides.html), which attract a large number of tourists to the region. It also hosts several important fisheries, the largest of which is that for the American lobster (Homarus americanus) but others include soft shell clam (Mya arenaria), herring (Clupea harengus), various flatfishes (family Pleuronectidae), and also historically Atlantic cod (Gadus morhua) and spiny dogfish (Squalus acanthias)[8]. Other important marine coastal industries in the region include harvest of seaweeds, mainly dulse (Palmaria palmata), Irish moss (Chondrus crispus) and knotted wrack (Ascophyllum nodosum), aquaculture of...
Atlantic salmon (*Salmo salar*) and blue mussels (*Mytilus*) spp. and whale-watching[8]. Disruption of local marine ecosystems by biological invasions thus has potential to strongly impact human communities within this region.

Several well-known marine invasive species are already present in the Bay of Fundy system, including the European green shore crab (*Carcinus maenas*), vasic tunicate (*Ciona intestinalis*), "oyster thief" (*Codium fragile*, a green seaweed), golden star tunicate (*Botryllus schlosseri*), violet tunicate (*Botryllides violaceus*), and pancake batter tunicate (*Didemnum vexillum*).[7,9] These have had apparent negative impacts on shellfish clams fisheries, survival of juvenile lobsters, abundance and distribution of native crab species, and survival, reproduction, and settlement of native seaweeds, such as *kelps*.[5,9,10] Other non-native species are found in regions outside of the Bay, and could potentially be introduced there; these include the lacy crust or coffin-box bryozoan (*Membranipora membranacea*), compound sea squirt (*Diplosoma listerianum*), clubbed tunicate (*Styela clava*), A sian shore crab (*Hemigrapsus sanguineus*), and Chinese mitten crab (*Eriocheir sinensis*), among others[9]. With the exception of the green crab (present through the Bay since the 1990s[5]) and the pancake batter tunicate (reported in Parrsboro, NS, in 2013[7]), most of the aforementioned invaders have not yet been reported in the Minas Basin, upper Bay of Fundy, but the potential for further introductions and resultant impacts in this embayment exists[9].

In this study, I report on an encrusting organism found in the intertidal zone of Parrsboro, Minas Basin, Bay of Fundy, NS, Canada (Figure 1), which was observed in the summer of 2015 to be covering several rocky reefs. This organism presented in a way that was new to the author which it was found that was not covered by *Ascophyllum nodosum* canopy (Figure 2A), the foliose (leaf-like) appearance of the edges of 10 m above chart datum (mean low water; http://www.waterlevels.gc.ca/eng/station?sid=260) on the upper intertidal zone located off of Clarke Head, Old Farm Road, Parrsboro, NS (latitude 45.38151° N, longitude 64.242025° W; Figure 1). Samples were located at a point on the intertidal zone exposed on average ~2 h after flood tide, and thus exposed for ~9 h per tidal cycle. This point was located along the intertidal transition between a steeply-sloped gravel beach and a sand flat. Patches of the organism were present on three large rocky reefs (projecting up to ~6–9 m above the seabed) in the same general area, as well as on several smaller rocks around each reef that may have broken off of them prior to observations. Reefs consisted primarily of limestone.

Initial observations, photographs, and sample collections were made on 15 June 2015 (late spring), and then again on 2–3 August 2015 (mid-summer). Notes were made on the appearance *in situ*, and then samples were taken for more detailed observations by breaking small encrusted sections off of the main reefs and storing in chilled seawater for 24 h, followed by preservation in 95% ethanol.

2.2. Approaches used for identification

Samples were examined under a dissecting microscope with a built-in ocular micrometer under 1- and 4× magnification. Visible details of the samples were noted and measured. Digital photographs and measurements were taken through the microscope’s eyepiece, and then uploaded to ResearchGate (https://www.researchgate.net/) through its “Questions” feature, whereat the research community was solicited for advice regarding the possible identity of the samples. Five researchers responded with helpful suggestions, which were used to guide subsequent identification attempts.

The sample was thought to potentially represent one of five different classes of marine organisms: a colonial tunicate (*K ingdom Animalia, Phylum Chordata, Subphylum Urochordata (Tunicata), Class Ascidiacea, potentially one of the invasive species described in the Introduction*), an encrusting calcareous bryozoan (*Kingdom Animalia, Phylum Bryozoa, Class Stenolaemata, Order Cyclostomatida or Class Gymnolaemata, Order Cheilostomatata*), an encrusting calcareous sponge (*Kingdom Animalia, Phylum Porifera, Class Calcarea*), a marine lichen (*Kingdom Fungi, Phylum Ascomycota, Class Eurotiomycetes, Order Verrucariales, Family Xanthopyreniaceae*), *Verrucaria* spp. or *Order Pyrenulales, Family Xanthopyreniaceae, Pyrenocolla* spp.), or a non-geniculate (encrusting) coralline (calcareous) red alga (*Kingdom Plantae, Phylum Rhodophyta, Class Corallinophycidae*).

Eventually (see Results), further examination of the samples led to the conclusion that they represented a coralline red alga. Samples were then treated with acetic acid to soften calcified skeletons and allow receptacles to be dissected and examined[14]. Receptacles were examined under high magnification under a dissecting microscope (16× and 32× magnification) and a compound light microscope (up to 100× magnification). The published key of *Villalard-Bohnack*[14] was consulted to identify samples to genus and species.

3. Results

3.1. In situ description

When examined *in situ*, the most distinctive and noticeable features of the calcareous organism were its appearance as a white crust (Figure 2), the fact that it covered most of the surface of the rocky reefs on which it was found that was not covered by *Ascophyllum nodosum* canopy (Figure 2A), the foliose (leaf-like) appearance of the edges of

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**Figure 1. Region of this study.** The inset shows the Atlantic coast of North America, with the areas in the main map enclosed by the black outline. The red star on the main map is the location of Clarke Head, at which the calcareous organism was observed and sampled in this study.

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**Figure 2.** Photographs illustrating the new white crust (*Ascophyllum nodosum*), as well as on several smaller rocks around each reef that may have broken off of them prior to observations. Reefs consisted primarily of limestone.

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**Figure 3.** Example of the new white crust (*Ascophyllum nodosum*), as well as on several smaller rocks around each reef that may have broken off of them prior to observations. Reefs consisted primarily of limestone.
patches where exposed (Figure 2B), and its distinctive milky-white colour (Figure 2, especially Figure 2C). Less than 50% of reef surfaces (closer to 30%–40%) were covered by the calcareous organism (Figure 2A), while the remainder was mostly Ascosiphonum, or bare or barnacle-covered rock (Figure 2). Sections of rock beneath Ascosiphonum canopy appeared to be free of this white crust, as well as of other candidate encrusting taxa (e.g., pigmented coralline red algae) (not shown). This white crust and Ascosiphonum did not co-occur on the same sections of reef, such that either the crust prevented settlement/growth of the seaweed, or vice-versa, or the crust was only able to settle in patches free of the seaweed. The foliose appearance of patch edges of the crust suggested the growth form of a foliose lichen, or perhaps certain types of Bryozoa (Figure 2B); when examined closely with the naked eye, several dark flecks were observed on the surface of the crust (Figure 2C), which further suggested lichen affinity because these resembled the apothecia of lichens\[12,13\]. These dark flecks were found to co-occur in situ on the same reef surfaces with many mature and juvenile acorn barnacles (Semibalanus balanoides), sometimes in very dense clusters, but when viewed with the naked eye the crust did not appear to overtop or be overtopped by barnacles (Figure 2C).

3.2. Detailed observations of samples under microscope

When viewed under a dissecting microscope, it was apparent that the dark flecks observed earlier in situ (Figure 2C) were actually small, circular depressions or pits in the surface of the white crust organism, measuring ~ 0.1 mm or less each in diameter (Figure 3). Pits alternated without any particular pattern with smooth calcareous surfaces (Figure 3A), and some sections of the sample lacked pits entirely (not shown), though others contained dense aggregations (Figure 3A, B). Under the microscope, it was clear that in many cases this white crust did actually overtop and encrust dead barnacles, including very small newly-settled juvenile barnacle spat (Figure 3A). However, the overall pattern of the pits did not match in size, shape, or distribution what would have resulted purely from encrusted barnacle spat, so it is likely these pits did represent an actual feature of the encrusting organism (Figure 3B). There were few clear demarcations among individual “units” (e.g., zooids if bryozoan, carapace if barnacle, etc.\[11\]), and where some separation did appear to occur it was highly irregular, with some apparent overlap (Figure 3B).

3.3. Results of identification

The samples bore superficial resemblance to various colonial tunicates, particularly two of the invasive species present in the region: Didemnum vexillum and Diplomema listerianum\[7,9,11\]. This crust organism was also very similar in appearance to two genera of marine intertidal lichens: Verrucaria spp.\[12,15,16\] (especially Verrucaria calciseda\[12\]) and similar species in the genus with white-gray, rather than black-gray thallus colouration and black apothecia\[15,16\]) and Pyrenocollema spp. (e.g., Pyrenocollema halodytes, which is known to encrust intertidal surfaces\[15\]). Interestingly, these two genera of marine lichens have not been recorded in Eastern North America\[12,13\], so their presence here would signal a first record. However, both colonial tunicates\[11\] and marine lichens\[15\] are non-calcifying, and the samples were confirmed to be calcareous by treatment and subsequent reaction to acetic acid in the laboratory. Therefore, the sample was determined to not belong to either of these groups.

Detailed examination under microscope also confirmed that this sample was not a sponge, as proper pores and spicules were not present\[11\]. Samples did bear some resemblance to calcareous bryozoans of the Class Chelostomata, but not Cyclostomata, when examined under a microscope (Figure 3A). The most similar chelostome bryozoan species to the sample were those with small orifices, including perhaps Cryptosula pallasiana, Hippoporina contracta, and Microporella ciliata\[11\]. However, the structure and arrangement of the sample crust did not conform to the structure of any known bryozoan; pits were too rounded and irregular to be bryozoan orifices (Figure 3), patches lacking pits would not make sense for a bryozoan, and there were no clear demarcations between individual zooids or smaller pores aside from the orifice that should be present in Bryoza (Figure 3A). Therefore, this organism was not a bryozoan.
in the subtidal zone (at or below mean low water) of the same embayment were later also examined, and found to be very similar to the samples (results not shown). The identity of this white crust organism as a bleached red coralline alga was finally confirmed when two small patches, which were still alive and pigmented at the time of collection, were found along the periphery of some of the sampled material (Figure 4A, B). These patches had the purple-red pigment usually seen in native species of coralline algae, and had contrasting morphologies: one was rough, and bore conceptacles (Figure 4B) corresponding to the dark flecks observed in situ (Figure 2C) and pits observed in other samples (Figure 3A, B), while the other was smooth, and had some striations similar to those normally seen along the periphery of red algal crusts (Figure 4B) [14].

3.4. Determination of identity

A local key to red algae [14] was next used to determine the identity of the sampled organism to species-level. The algal thallus was calcareous, in the form of a crust (rather than upright or jointed), thick (0.2–2 mm thick) and difficult to remove from the substrate, and had lighter-coloured edges and concentric rings (rather than a smooth surface), which eliminated several local taxa (various non-calcareous forms, Corallina officinalis, Lithothamnion glaciale, Clathromorphium circumscriptum, and Leptophyllum spp., respectively) and narrowed the sample’s identity down to the genus Phymatolithon [14,17]. Conceptacle roofs were sunken (roof lower than margin) rather than rounded (roof higher than margin), which eliminated Phymatolithon lenormandii [14]. The darker (purplish-pink vs. pink to reddish) colour of pigmented patches and fine, lightly-coloured rather than white ridges and edges (Figure 4) strongly suggested that the samples were not Phymatolithon laevigatum, and were instead the similar and closely related P. lamii [14]. Subsequent examination of conceptacles following dissolution of the calcium carbonate skeleton of the alga and sectioning confirmed that the conceptacles were multiporate and had a roof lower than the margin [17], and that the diameter of conceptacles was relatively small (< 0.1 mm vs. > 0.2 mm; see Figure 2B; results of dissections not sure due to low quality of images), which strongly supported the conclusion that this species was P. lamii [14].

The identity of this calcareous organism, found on the intertidal zone, was thus confirmed to be P. lamii [18]. The full up-to-date (from [19]) taxonomic information for this species is outlined in Table 1. This species has a very wide distribution that includes Europe from Norway to France and Spain, Iceland, the British Isles, and Eastern North America from Newfoundland, Canada to Cape Cod, MA, USA [18,19]; it is thus native to the study region.

| Level | Name | Authority |
|-------|------|-----------|
| Domain | Eukarya | Chatton |
| Kingdom | Plantae | Haekel |
| Subkingdom | Biliphyta | Cavalier-Smith |
| Phylum | Rhodophyta | Wettstein |
| Subphylum | Eurhodophyta | Saunders and Hommersand [20] |
| Class | Florideophyceae | Cronquist [21] |
| Subclass | Corallinophycidae | Le Gall and Saunders [22] |
| Order | Hapalidiales (or Corallinales) | Nelson et al. [23] |
| Family | Hapalidiaceae | Silva and Johansen [24] |
| Subfamily | Melobesioidae | Gray [25] |
| Genus | Phymatolithon | Bizzarro [26] |
| Species | P. lamii | Foslie [27] |

Records from Environment Canada [28] for the study region were consulted to determine possible reasons for the presence and bleaching of P. lamii on the upper intertidal zone observed in this study. These indicated that the winter of 2014–2015 was unusually harsh throughout Atlantic Canada, including in Parrsboro, NS, with very low temperatures (Figure 5[28]) and high storm incidence compared to preceding years [28]. The spring of 2015 then remained relatively cool for longer and at lower temperatures than in preceding years at this site (Figure 5[28]). The harsh winter and cool spring may have initially facilitated settlement and growth by the alga. However, as the summer of 2015 continued this site began to warm more rapidly, and to reach higher temperatures, than in prior years (Figure 5 [28]), which would have induced sudden and extreme stress on P. lamii, likely leading to death and bleaching.

![Figure 4. Two different pigmented patches (A and B) of encrusting organism, signalling its identity as a coralline (calcareous), encrusting non-geniculate red alga (Phylum Rhodophyta, Class Florideophyceae, Subclass Corallinophycidae), viewed under dissecting microscope at 4 × magnification. A: Possible conceptacles and/or overtopped barnacles; B: Edge of a pigmented algal patch, later identified as Phymatolithon lamii (P. lamii). All photographs are taken by the author. Scale bars as labelled in the figure (A and B = 0.2 mm).](image)

![Figure 5. Mean daily air temperatures (averaged per day, and then per month) at Parrsboro, NS, Canada for each month in 2010–2015; data from Environment Canada [28]. Note the especially cold winter of 2014–2015, cool spring of 2015, and warm summer of 2015, to which organisms on the intertidal zone would be exposed at low tide.](image)
4. Discussion

The present study was initialized to determine whether the unusual calcareous encrusting organism observed in the intertidal zone in summer 2015 could represent a newly introduced, potentially invasive species in the study region of Parrsboro, Minas Basin, NS, Canada. This was investigated in an effort to contribute to monitoring for and control of species introductions[4-7,9,10] and reduce or prevent harm of such introductions on local industries and marine ecosystems[2,4,10]. New records of invasive species in the area have been published very recently, including as recently as 2013 for Didemnum vexillum[7], so there is much concern that further introductions could occur and have impacts on marine ecosystem and community health in the region[9]. It was confirmed that the organism in question was not a new species to the study area, but rather a native alga that had settled and grown in an unusual location. This was a reassuring finding, as it meant that yet another invasive species had not reached the area. Findings do point to some potential issues in species identification and monitoring for introductions that have not been discussed much, but should be kept in mind to save researchers time and effort. Additionally and importantly, observations suggest that other changes may be ongoing in this area, which could have important impacts of their own, and thus should be investigated further.

The encrusting red algal species P. lamii normally occurs only in the subtidal zone, at depths down to 15 m below chart datum or more[4,18], so bleached specimens are not often reported, and when these are observed they mainly occur on loose pebbles and stones that get displaced from the subtidal zone into higher elevations by tides and currents[14]. The congenic species Phymatolithon laevigatum, in contrast, occurs within the intertidal and subtidal zones[14], and as a result of this, bleached specimens of this species are often reported[14], but not with the particular and unusual morphology (Figures 2 and 3) observed for bleached P. lamii in the present study. This species resembled a number of different taxa when bleached, including some (e.g., marine lichens[15,16]) that would be new to the region[12,13], which necessitated the present study. This study appears to be the first record to the author’s knowledge of P. lamii occurring in the upper intertidal zone of Atlantic Canada. The mass occurrence of such a large aggregation of this species in an abnormally shallow intertidal location points to a series of unusual events, likely related to changed local weather and climate patterns, as well as oceanographic circulation.

The fact that canopy of Ascophyllum and other fucoid seaweeds did not occur in these rocky reefs in the same patches as P. lamii suggests that settlement and growth of the red alga was facilitated by a loss of Ascophyllum, likely by ice scouring. In the shallower upper reaches of the Bay of Fundy, including the Minas Basin, extensive ice flows usually form in the winter, which are moved back and forth across large segments of the seabed, especially the intertidal zone, during regular daily tidal cycles[29]. Ice scouring has been confirmed to play important roles in normal ecological succession within coastal marine systems by removing old, large individuals and/or competitive dominant sessile species and allowing settlement and growth of new recruits of smaller, perhaps less competitive individuals and species[30]. Ice scouring likely removed large sections of the Ascophyllum canopy in the location of the present study, which allowed for settlement of new organisms. Indeed, high densities of barnacle spat were also observed along with P. lamii on these reefs, signalling a major recruitment pulse to newly-exposed areas. The colder and stormier conditions in the winter of 2015 relative to other years (Figure 5[28]) likely led to more ice scouring, and thus more exposed surfaces on upper intertidal rocky reefs on which settlement could occur. Recruitment of barnacles and P. lamii may have prevented settlement of new seaweed plants, but this is uncertain; small fucoids were present on some of the samples observed (e.g., see Figures 3A and 4A), suggesting that these seaweeds were beginning to recruit in the opened patches. Therefore, it appears that overwintering losses of Ascophyllum canopy facilitated settlement of P. lamii in emptied patches of rock, but settlement of P. lamii did not prevent subsequent resettlement of these reefs by Ascophyllum.

Importantly, once settled and growing on these high intertidal rocky reefs, P. lamii would be exposed to conditions far more extreme than those it should normally encounter in its subtidal habitat[14,18], and thus likely beyond its physiological tolerance ranges; this mechanism is likely involved in preventing visible growth of this species in the intertidal zone, by killing off new recruits before they reach visible sizes, which defines the abiotic upper limits to the species’ distribution on the shore[31]. The relatively cool spring of 2015 at this site (Figure 5[28]) may have allowed P. lamii recruits to survive for longer and grow more extensive thalli in the upper intertidal zone than would normally be possible. Rapid warming and extremely high temperature during the summer of 2015 at this site (Figure 5[28]) would then have induced sudden and extreme stress on the normally-subtidal alga. As a result, the alga began to die, and as living tissues died and pigments deteriorated only the white colour of the calcareous thallus was left behind. This resulted in relatively large and prominent bleached patches being left on the rock, providing clearer evidence of the alga’s presence than would normally be possible.

Recent weather patterns, possibly related to large-scale climatic changes, thus appear to have created circumstances that temporarily allowed this species to grow outside of its usual range on the coast. Oceanographic processes, especially currents and circulation patterns, likely also played a large role in the intertidal occurrence of this species observed in this study. Specifically, it is possible that circulation within this embayment differed in 2015 from its historical pattern, facilitating a large recruitment pulse of barnacles and algal settlers shoreward to the upper intertidal zone; the data are not currently on-hand to quantify whether this may have been the case, but some recent observations from the study area suggest that such changes are occurring. Ocean circulation can vary considerably in the same region across different years and is expected to be strongly impacted by climate changes[11]. Interestingly, since 2013 observed densities of settling lobsters have been down throughout much of the Atlantic coast[32]. Strengthened and more offshore-directed currents and elevated temperatures of coastal nursery grounds bordering on stress thresholds of lobsters throughout the region have been implicated as possible causes of this decrease[32]. Concurrently, densities of invasive green crabs (Carcinus maenas), soft-shelled clams (Mya arenaria), and ragworms (e.g., Alitta virens) have been very low on the intertidal zone around Parrsboro, NS since 2013, especially in 2015 (unpublished observations), which may signal systemic problems affecting multiple taxa throughout the region. One possibility is that current patterns have shifted in such a way that larvae, spores, and other dispersive propagules are being advected to and settling in locations not suitable for the longer-term survival of individuals[11]; this could include deep, offshore areas, as suggested for lobster[31], or areas too high up on the shore for other taxa[14], such as P. lamii algae observed in this study. This possibility should be given further attention, as it has important implications to the health of coastal populations of affected species and their ecosystems[1-5,32], as well as the human communities and industries that many of these support.

To the untrained eye, or even to an individual with some
experience of local marine biota, the bleached algae patches observed in the present study could be (and indeed were) initially concluded to represent new, introduced species. This can lead to considerable effort and time being spent in sample collection and taxonomic identification of samples that might be better spent on other monitoring efforts and research on invasive species. It is the author’s hope that the present report of bleached *P. lamii* and its resemblance to other potential introduced species will facilitate more cautious observations of these taxa in the future and increase efficacy of coastal monitoring programs. Importantly, occurrence of a subtidal red alga (*P. lamii*) in a new habitat was observed and reported for the first time, which led to consideration of some potentially important recent changes to the coastal system investigated. Future research should attempt to follow up on the changes suggested by these observations, with particular attention to the impacts of changes to oceanic circulation and air and water temperatures in the Minas Basin.

**Conflict of interest statement**

I declare that I have no conflict of interest.

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