

Shady business: the darkening of estuaries constrains benthic ecosystem function

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ABSTRACT: Coastal intertidal soft-sediment habitats provide ecosystem services to millions of people worldwide, yet are under intense pressure from land-use change and sea-level rise (SLR). Both pressures interact to reduce light reaching the seafloor, thereby disrupting benthic primary producers and the ecosystem functions and services they provide. This study considers the implications of altered light climate on microphytobenthic (MPB) production in shallow estuaries. Continuous measurements of seafloor photosynthetically active radiation (PAR) were made over 9 mo on intertidal sandflats in 14 New Zealand estuaries spanning a turbidity gradient. A literature summary of benthic photosynthesis–irradiance curves was used to predict PAR limitation at sampling sites. Estimates of the proportion of time MPB would be light limited during emersion ranged from a median of 32–64 % compared to a median of 55–100 % during immersion. For estuaries close to 100 % PAR limitation during immersion, emerged intertidal areas represent a refuge for MPB production which is vulnerable to SLR. Based on hypsometric curves (a representation of estuary bathymetry), the intertidal area of our study estuaries is predicted to decrease by 27–94 % in response to SLR of 1.4 m. The combination of high PAR limitation during immersion and large losses of intertidal area will increase vulnerability to the loss of MPB production and the associated ecosystem services, which will push these ecosystems towards tipping points. The research highlights how the interplay between local and global scale stressors may ultimately trigger ecological collapse under future global change.

KEY WORDS: Light limitation · Photosynthesis–irradiance curves · Intertidal · Benthic · Sea-level rise · Hypsometry · Microphytobenthos · Estuary

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1. INTRODUCTION

Soft-sediment intertidal habitats are among the most extensive coastal ecosystems, supporting millions of people worldwide through the ecosystem services they provide (e.g. food production, storm protection and shoreline stabilisation) (MEA 2005, Field et al. 2014). Many of these services are underpinned by light, which sustains ecosystem functionality by fuelling benthic primary production and associated modification of biogeochemical processes

that are critical for the structure of the ecosystem's interaction network (Thrush et al. 2012, Pivato et al. 2019). However, as coastal ecosystems are situated at the transition between land and sea, they are affected by a multitude of pressures, such as coastal development, sea-level rise (SLR) and increases in nutrient and sediment supply from terrestrial run-off (MEA 2005, Arkema et al. 2013, Passeri et al. 2015). These pressures act in concert to modify the seafloor light climate by changing water column optical properties and/or depth, which, through changes in ben-

thic primary production, can have detrimental implications for coastal ecosystems and the vital ecosystem services they provide.

Benthic primary production is moderated by a number of factors, including temperature, nutrient availability, sediment resuspension and grazing pressure (Cebrián 2004, Howarth & Marino 2006, Kwon et al. 2018). However, without sufficient light (specifically photosynthetically active radiation [PAR]), photosynthesis is not possible and its availability can limit coastal primary production by vascular plants (e.g. seagrass), macroalgae, and microalgae (phytoplankton and microphytobenthos). Microphytobenthos (MPB) refers to the photosynthetic eukaryotic algae and cyanobacteria (MacIntyre et al. 1996) found in soft-sediment habitats from the intertidal zone to depths of ~200 m (Cahoon 1999). In coastal areas, MPB production is a significant contributor to total marine carbon fixation (Borum & Sand-Jensen 1996) and thus fuels nearshore food webs (Christiansen et al. 2017, Jones et al. 2017). In addition to the central role MPB play in carbon flow, they also contribute to a multitude of other ecological functions, which, through complex ecosystem interactions, can regulate ecosystem service delivery (Hope et al. 2020). This includes vital services such as the transformation and recycling of nutrients, sediment stabilisation, climate regulation, support of benthic biodiversity, improvement of water quality and numerous cultural services (e.g. Sundbäck et al. 2006, Kowalski et al. 2009, Joensuu et al. 2018, Hope et al. 2020). Therefore, any process that results in a decline in MPB production will not only alter food web dynamics but, through changes in the other functions they provide, will have cascading effects on coastal ecosystems.

Atmospheric conditions, tides and water column properties combine to make light highly variable within estuaries (Kirk 1994, Gattuso et al. 2006), but up to 80% of this variability can be driven by water column turbidity alone (Anthony et al. 2004). Water column turbidity is in part a consequence of eutrophication, where an oversupply of nutrients can result in increases of phytoplankton. In addition, the intensification of terrestrial soil erosion can act to elevate concentrations of suspended inorganic material (sediment) (Rabalais et al. 2005). Both eutrophication and suspended sediment concentrations are significant global stressors, which are continuing to increase worldwide (Airoldi 2003, Thrush et al. 2004, Rabalais et al. 2009), resulting in less sunlight reaching MPB on the seafloor. When light is persistently limiting to MPB, benthic primary productivity can be lost,

shifting a system to one dominated by pelagic primary production (Cooper & Brush 1993). Most obviously, this reduction or loss in MPB primary production diminishes the availability of labile organic material to benthic food webs, but it also changes nutrient transformation and recycling pathways (Sundbäck et al. 2000, Pratt et al. 2014). These changes have been documented across the globe and can have detrimental impacts to these multifaceted ecosystems (e.g. by accelerating eutrophication and promoting hypoxia).

In shallow estuaries, extensive intertidal areas provide some resilience to highly turbid coastal waters through the maintenance of MPB production, as the water shallows and drains off the intertidal flats (Drylie et al. 2018). The restriction of primary production to periods of emersion has been reported from turbid estuaries globally (Guarini et al. 2002, Migné et al. 2004, Yamochi et al. 2017, Drylie et al. 2018). To better understand the potential compensatory dynamics involving water depth, availability of PAR and potential MPB production, we need to know how intertidal light climate varies spatially and temporally, and how this variability influences the amount of time MPB are light limited. In estuaries with extensive intertidal and shallow sublittoral flats, this will indicate an estuary's vulnerability to increased turbidity or loss of intertidal area and susceptibility to tipping points associated with a loss of MPB productivity (Thrush et al. 2012, 2014).

Conducting research across natural turbidity gradients is a useful method to explore the sensitivity of an estuary to the loss of MPB production, and this kind of research is critical for improving the understanding of how these ecosystems will respond to future changes under both local (e.g. turbidity) and global stressors (e.g. climate). New Zealand's estuaries offer an ideal natural laboratory, with clear gradients in water column turbidity owing to the relatively recent arrival of humans that has created spatial variability in anthropogenic pressures across the country (McWethy et al. 2010). In this study, the light climate reaching MPB was measured at 22 intertidal sites situated within 14 estuaries across New Zealand. Our study was conducted over a 9 mo period, with the estuaries chosen to encompass a gradient of anthropogenic disturbance. This unique data set was combined with a global literature summary of MPB photosynthesis–irradiance (P–I) curves to estimate how often MPB production within these intertidal areas was potentially light limited and therefore the relative dependence of each estuary on periods of emersion. By coupling these measurements with estimates

of future sea-level rise scenarios, we were able to determine the sensitivity of each estuary to the loss of intertidal area predicted by the end of the century.

2. MATERIALS AND METHODS

2.1. Study sites

Fourteen estuaries throughout New Zealand were chosen to encompass a range of anthropogenic influence and water column turbidity (Fig. 1). The estuaries were predominantly shallow, barrier-enclosed coastal lagoons with extensive intertidal areas, characteristic of many New Zealand estuaries (Hume et al. 2007) and up to 22% of the global coastline (Dame 2008, Dürr et al. 2011). Catchment, estuarine and tidal properties are described in Table 1, and the GPS coordinates of the sensor deployment locations are given in Table S1 in the Supplement at www.int-res.com/articles/suppl/m647p033_supp.pdf. Within each estuary, 1–3 study sites (22 in total) were chosen in the mid-intertidal. All had predominantly sandy sediments and semi-diurnal tides (Table 1).

At each site, PAR levels were measured 10 cm above the seabed by deploying Odyssey PAR loggers (Dataflow Systems). Measurements were recorded every 10 min for 201–260 d between March and November 2017. Each sensor was checked monthly for fouling and cleaned, although data screening and monthly checks revealed no obvious fouling or sediment deposition throughout the deployment period.

2.2. PAR calculations

Each Odyssey sensor was calibrated prior to deployment with a LI-COR PAR sensor, with the calibration regression used to convert all count measurements to PAR in $\mu\text{mol m}^{-2} \text{s}^{-1}$. Data were then partitioned into either immersed or emerged periods, defined by the time of high or low tide ± 2 h. This ensured a distinct separation of tidal state at all sites and therefore a 4 h period, wherein the sensor was either completely covered by the

water column, including the time of maximum water depth (immersed), or was uncovered when the tide receded (emerged). Night-time periods were excluded by removing times where PAR measured $0 \mu\text{mol m}^{-2} \text{s}^{-1}$.

2.3. Calculation of MPB light saturation

Changes in light climate become ecologically important to marine sediments when phototrophic organisms become light limited. Light saturation is highly variable in both time and space, which limits the ability to extrapolate single, one-off estimations (Cahoon 2006, Kwon et al. 2018). To overcome this issue and determine potential periods of light limitation for MPB (the main primary producers on intertidal flats) across a large spatial gradient, we used estimates of light saturation levels obtained from an extensive literature search that incorporated a variety of different contexts. Estimates of light saturation were obtained from studies of P–I curves for benthic

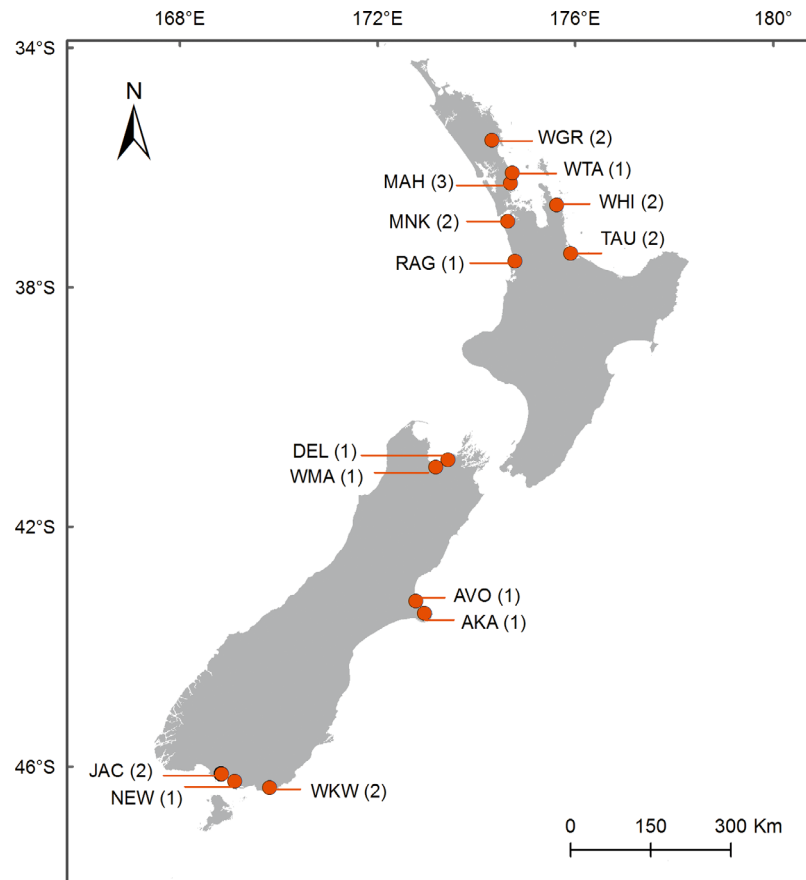


Fig. 1. Location of estuaries where light sensors were deployed. The number of sites within each estuary is shown in parentheses. Site abbreviations are defined in Table 1. For site-specific GPS locations, see Table S1

Table 1. Estuarine characteristics and site sediment properties ordered by latitude from north to south. Estuary Environment Classification (EEC) from Hume et al. (2007). Hydrological, C: river flow dominated; E: dominated by ocean forcing with high flushing and wind-wave sediment resuspension, extensive intertidal area; F: complex shoreline with numerous arms off basin, dominated by ocean forcing and high flushing, extensive intertidal area. Geological, AI: alluvium; HS: hard sedimentary; M: miscellaneous; SS: soft sedimentary; VS: volcanic strong; VW: volcanic weak; Land cover, N: natural; P: pastoral; U: urban. DW: dry weight. All sediment data are estuary/site mean \pm SD (n = 6–18). For site-specific GPS locations, see Table S1 in the Supplement

Estuary	Code	Total area (km ²) ^a	Intertidal area (%) ^a	Mean tidal range (m) ^a	Mean estuary depth (m) ^a	Land catchment area (km ²) ^a	EEC Hydrological	EEC Geological	EEC Land cover	Grain size median (μ m) ^b	Mud content (% <63 μ m) ^b	Sediment organic content (%) ^b	Sediment chl a (DW μ g g ⁻¹) ^b
Whangārei Harbour	WGR	104	58	1.72	4.42	297	F	HS	P	169 \pm 56	3.6 \pm 2.6	1.5 \pm 0.2	8.4 \pm 2.1
Whangateau Harbour	WTA	7.5	85	2.79	1.56	42	F	SS	P	255 \pm 8	3.4 \pm 0.9	1.4 \pm 0.1	7.7 \pm 0.9
Mahurangi Harbour	MAH	25	51	2.11	2.74	122	F	SS	P	263 \pm 40	3.6 \pm 1.7	2.3 \pm 0.3	5.4 \pm 2.3
Whitianga Harbour	WHI	16	72	1.91	0.84	450	F	VS	P	177 \pm 27	17.3 \pm 7.5	4.3 \pm 0.8	11.0 \pm 6.0
Manukau Harbour	MNK	366	62	2.20	6.06	1023	F	VW	P	200 \pm 6	5.3 \pm 4.7	1.6 \pm 0.5	11.6 \pm 4.5
Tauranga Harbour	TAU	200	77	1.50	2.12	1300	F	VW	P	179 \pm 23	9.3 \pm 5.4	2.0 \pm 0.6	12.5 \pm 2.8
Raglan Harbour	RAG	33	69	2.28	2.24	523	F	VW	P	130 \pm 4	16.5 \pm 2.1	3.8 \pm 0.2	17.1 \pm 4.6
Delaware estuary	DEL	3.1	93	2.69	2.02	93	E	HS	P	103 \pm 9	16.1 \pm 4.7	2.7 \pm 0.3	4.2 \pm 0.5
Waimea Inlet	WMA	29	59	1.51	3.40	933	F	SS	P	151 \pm 2	0.4 \pm 0.7	1.3 \pm 0.0	2.7 \pm 0.5
Avon-Heathcote	AVO	7.5	67	1.68	1.87	211	F	M	P	190 \pm 9	1.0 \pm 1.5	1.3 \pm 0.2	5.6 \pm 2.4
Akaroa Harbour	AKA	43	3	1.62	10.60	127	F	M	P	84 \pm 1	23.2 \pm 1.4	1.4 \pm 0.1	4.5 \pm 0.2
Jacobs River estuary	JAC	6.7	66	1.86	2.19	1570	F	AI	P	196 \pm 61	3.8 \pm 1.7	1.5 \pm 0.2	4.1 \pm 1.3
New River estuary	NEW	0.2	42	2.03	4.56	3948	C	SS	N	171 \pm 3	0.0 \pm 0.0	0.7 \pm 0.0	1.5 \pm 0.4
Waikawa Harbour	WKW	6.4	82	1.73	1.53	241	E	SS	P	201 \pm 24	6.6 \pm 6.1	1.5 \pm 0.4	8.4 \pm 2.6

^aData from EEC database

^bUnpublished data measured at the end of the photosynthetically active radiation sensor deployment

MPB, with a focus on natural, intact communities that integrated effects of environmental and behavioural responses, such as MPB vertical migration (Consalvey et al. 2004, Jesus et al. 2006). Therefore, studies conducted on suspended, cultured or sieved communities were omitted from this analysis (a summary of suspended MPB P–I curves can be found in Cahoon 2006). In addition, studies using pulse-amplitude modulated (PAM) fluorometry were also excluded because they are conducted at the surface sediment and are not readily comparable with primary production estimates via gas fluxes (O₂, CO₂) which dominate the literature (Consalvey et al. 2005).

Studies were divided into either subtidal or intertidal habitats. The majority of studies reporting P–I curves came from intertidal habitats (14 of 18) and most of these were conducted on emerged sediment only (11 of 14, a reflection of the high turbidity in many northern hemisphere estuaries), with only 3 including immersion periods (see Table S2 for details). Therefore, it was not possible to distinguish between immersed and emerged periods in estimates of light saturation point. Maximum gross community production rates were also obtained from the published P–I curves and where necessary for consistency were converted from mg O₂ m⁻² h⁻¹ to mg C m⁻² h⁻¹ using a conversion factor of 1.2 (Mills & Wilkinson 1986).

The median global light saturation value of all intertidal P–I curves (42 in total) was used to estimate light saturation in this study and thus we defined light limitation as the amount of time during the day when PAR was below 258 μ mol m⁻² s⁻¹. A daily proportion of light limitation was then calculated for immersed and emerged periods separately. To determine the robustness of these results to variations in choice of light saturation, we also calculated daily light limitation at saturation values of 170 and 424 μ mol m⁻² s⁻¹, which correspond to the 25th and 75th percentile, respectively, of the literature light saturation values. An overall estimate (over the entire 9 mo period) summarising the proportion of time benthic primary production was not light limited (i.e. saturated) within each site over the 2 daily tidal phases was then calculated using the proportion of time

during which PAR was greater than $258 \mu\text{mol m}^{-2} \text{s}^{-1}$. After testing for normality, a linear regression was used to test the relationship between the calculated daily proportions and latitude using the R stats package (v 3.6.2) in R Studio.

3. RESULTS

3.1. Spatial and temporal variability in light climate

Across all 22 sites, intertidal light climate was highly variable over the 9 mo period such that the interquartile range during emerged and immersed periods of the tide varied from 239–1060 and 71–554 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Fig. 2). Additionally, high spatial variability occurred within estuaries; for example, within WHI (see Table 1 and Fig. 1 for all site codes and locations, respectively), the interquartile range during immersion was $258 \mu\text{mol m}^{-2} \text{s}^{-1}$ at WHI-2 compared to $419 \mu\text{mol m}^{-2} \text{s}^{-1}$ at WHI-1 and, during emersion, it was 798 and $1019 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively.

Immersion tidal periods resulted in a reduction of seafloor light levels compared to emerged periods at each site (the difference in emerged and immersed median PAR for each site ranged from 118–526 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The degree of water column influence on light climate is illustrated in Fig. 3 using a calculated ratio of median immersed to emerged PAR (hereafter the immersed:emerged ratio). Values close to 0 indicate that light was heavily influenced by tidal state (i.e. water column properties) (e.g. 0.12 at site MNK-1), whilst other sites showed little variation between immersion and emersion (e.g. 0.84 at AVO). Within an estuary, there was both dissimilarity (e.g. WHI-1 and WHI-2: 0.44 and 0.32, respectively) and similarity (e.g. 0.59 and 0.60 for TAU-2 and TAU-1, and 0.19 and 0.22 for MNK-1 and MNK-2) in the immersed:emerged ratio between sites.

3.2. Impacts on benthic primary production

Literature-derived intertidal MPB light saturation values were predictably variable, with an interquartile range of $254 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a median of $258 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table S2). Using this median value of light saturation, the proportion of each day spent below $258 \mu\text{mol m}^{-2} \text{s}^{-1}$ was calculated for both immersed and emerged tidal periods (Fig. 4). The

proportion of each day spent light limited during emersion varied from a median of 32 % (WGR-2, WHI-1 and WTA) to 64 % (WKW-2) and was correlated to latitude ($R^2 = 0.65$, $p < 0.001$) such that lower latitudes received more light. The only exception was MAH-2 in the north of New Zealand, which was characterised by low light availability (88 % median light limitation) and was excluded from the above calculation. Here, steep, high cliffs to the north and east shadowed the small intertidal bay, reducing the quantity of light reaching the sediment surface. During immersion, however, the correlation of light limitation to latitude disappeared ($R^2 = 0.04$, $p = 0.39$) and sites varied from 55 % (AVO) to 100 % light limitation (MAH-2, MNK-1, MNK-2, NEW and JAC-2).

These estimates of light limitation predictably change depending on the value of light saturation used, as demonstrated using the 25th, 50th (median) and 75th percentile of literature values (Fig. 5). A lower light saturation value inevitably results in a reduced proportion of each day estimated to be light limited, and vice versa. For example, the median proportion of time that AVO was estimated to be light limited during immersion using the 25th, 50th and 75th percentile of light saturation was 39, 55 and 75 %, respectively. However, the changes in light limitation estimates are less pronounced for highly turbid estuaries (e.g. MNK, MAH-2). Despite the changes in absolute proportion of time spent light limited, overall patterns are conserved such that the relative differences between estuaries remain constant regardless of choice of light limitation value. For example, the difference between light limitation estimates for AVO and WMA are 1, 5 and 5 % when using the 25th, 50th and 75th percentile, respectively (Fig. 5).

When light reaching the sediment surface during tidal inundation is reduced, the dependence on periods of exposure will become increasingly more important for maintaining benthic primary production. Therefore, we estimated the proportion of time over the entire 9 mo where light was saturating to benthic primary production (using an estimated median light saturation literature value of $258 \mu\text{mol m}^{-2} \text{s}^{-1}$) during both immersion and emersion (Fig. 6). During immersion, the total proportion of time that light was saturated to MPB production ranged from 0–26 %, with two-thirds of the estuaries below 20 % saturation. Excluding MAH-2 because of topographic shading, during emersion, the amount of time light was saturating to MPB production increased to 23–33 %, resulting in cumulative proportions (emersion + immersion) of 34 % (MNK-1) to 57 % (WTA) light saturation.

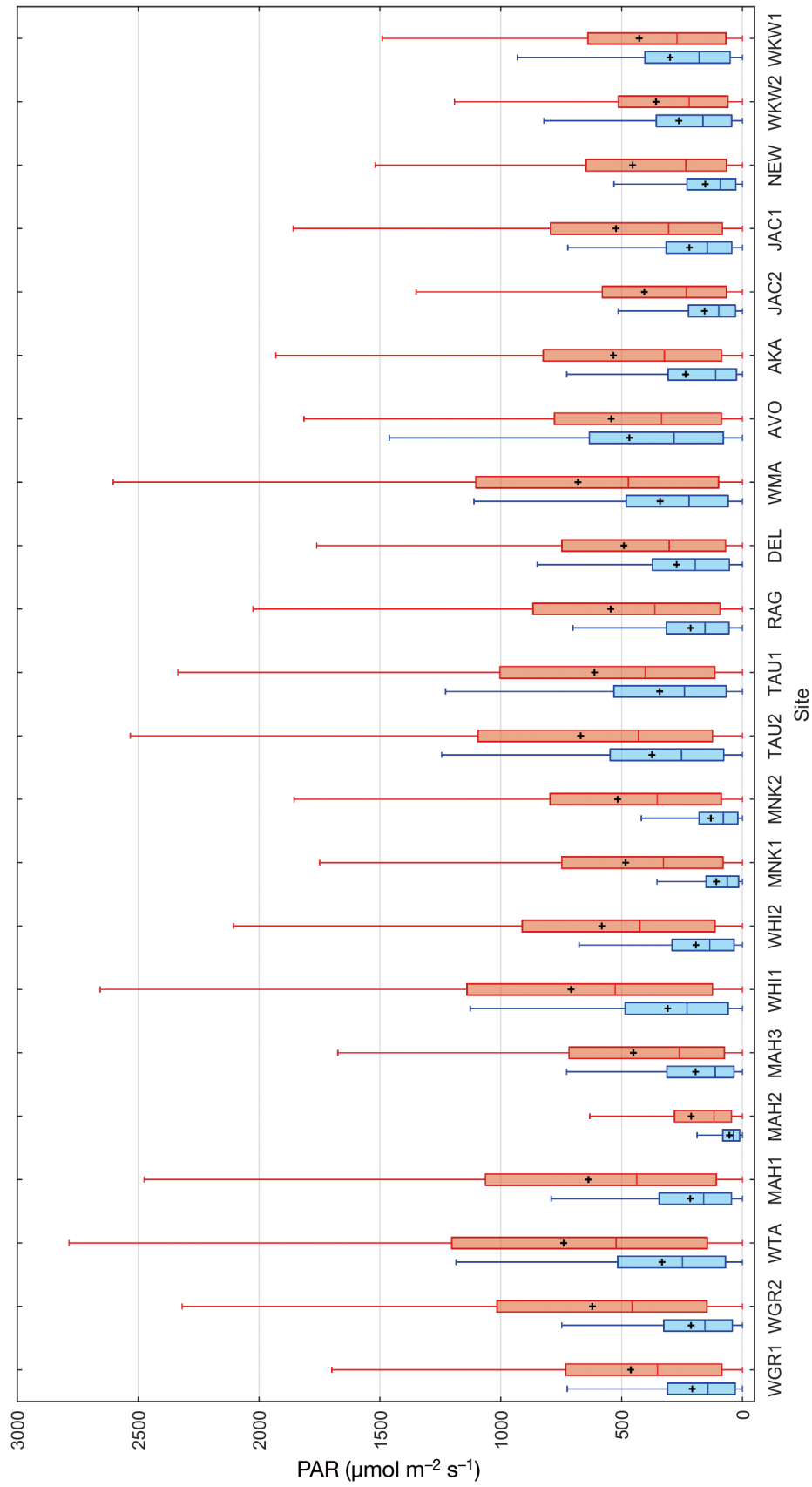


Fig. 2. Variability in daytime photosynthetically active radiation (PAR) during immersion (blue) and emersion (red) between March and November 2017, with sites ordered by latitude from north to south. Data are comprised of 10 min measurements over a 9 mo period. Boxes represent the 25th and 75th percentiles, and whiskers are the 5th and 95th percentiles. A solid line and black cross within each box denote median and mean, respectively. Site abbreviations are defined in Table 1

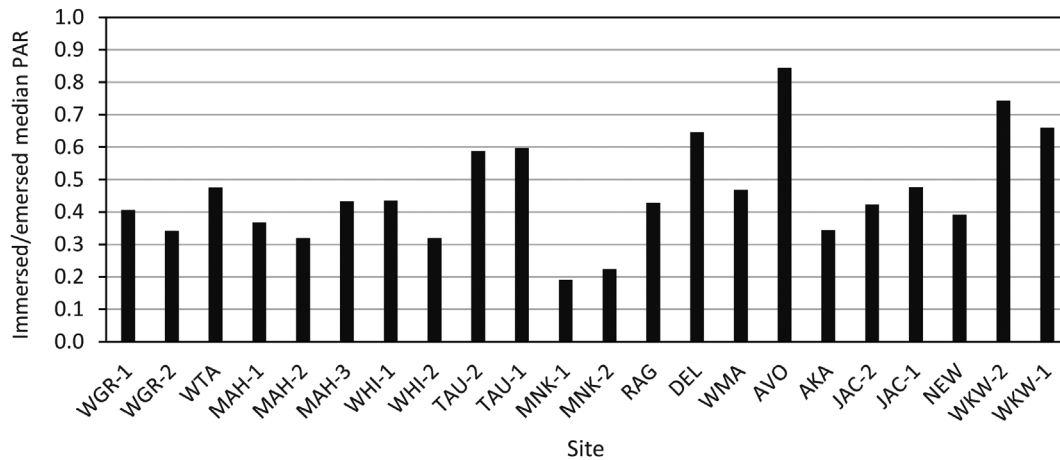


Fig. 3. Ratio of immersed to emerged median photosynthetically active radiation (PAR) between sites, ordered by latitude from north to south. A value close to 0 represents a greater dissimilarity between immersed and emerged PAR (i.e. greater influence of water column properties). Site abbreviations are defined in Table 1

4. DISCUSSION

The large variability in light climate measured over an extensive spatial and temporal sampling domain can be attributed to numerous factors, most of which differ depending on tidal state (Fig. 2). During periods of emersion, latitudinal and geographic characteristics (e.g. shading from topography) influence light availability. Previous studies have additionally reported significant effects of atmospheric conditions (Kirk 1994, Anthony et al. 2004); however, further analysis of light limitation over 4 h of midday tidal emergence found 0% light limitation for the 9 mo period at all but 1 site (which was limited 10% of the time due to topographic shading). This suggests that the atmospheric effects on MPB production are unlikely to be a contributing source of light limitation because of the high measured irradiance relative to MPB saturation values even on cloudy, low sun-angle days (e.g. in winter).

Assuming the differences in atmospheric conditions between high and low tide are likely to be negligible over large temporal scales, and considering the correlation of light to latitude diminished during immersion, the observed reduction in light availability from emerged to immersed periods is an indicator of the role played by water column optical properties at each site (Fig. 2). These properties are likely to be governed by the suspended organic and inorganic material because of the relatively shallow nature of these intertidal zones (site mean tidal range from 1.50–2.79 m) (Kirk 1994, Cussioli et al. 2019). Water column turbidity across the 22 sites was variable, including sites that remained relatively clear during immersion (immersed:emerged ratio close to 1, Fig. 3)

while others were highly turbid (immersed:emerged ratio close to 0). In addition, the high temporal variability observed within some sites (e.g. TAU) may be attributed to variability in meteorological events (e.g. storms) that can increase fine sediment inputs from the land and/or resuspend sediments off the seabed. The resulting gradient in water column turbidity provides an opportunity to estimate the proportion of time MPB production is light limited across large spatial and temporal scales.

Despite the significance of light availability within coastal ecosystems (Ackleson 2003), our literature search shows the limited knowledge of the functional relationship between light and *in situ* MPB production (only 18 studies identified). Based on a median light saturation value of $258 \mu\text{mol m}^{-2} \text{s}^{-1}$, MPB production was light limited between 55 and 100% of the day during tidal immersion (Fig. 4). These estimates will shift depending on the light saturation value used and the inclusion of different data periods (e.g. the omission of a summer period in our data, which would introduce differences in day length, sun angle and cloud cover). However, using the 25th or 75th percentile of the literature values (instead of the median) results in light limitation shifting to 39–100% and 75–100% of the time, respectively (Fig. 5), with little effect on overall patterns between estuaries. The maintenance of high light limitation under various saturation value scenarios and in all 14 estuaries that span a latitudinal gradient (and therefore a gradient in daylength and sun angle) demonstrates the substantial impact of light limitation irrespective of the exact value used, and the environmental or temporal context. Therefore, although choosing one light saturation value from the literature is an imperfect

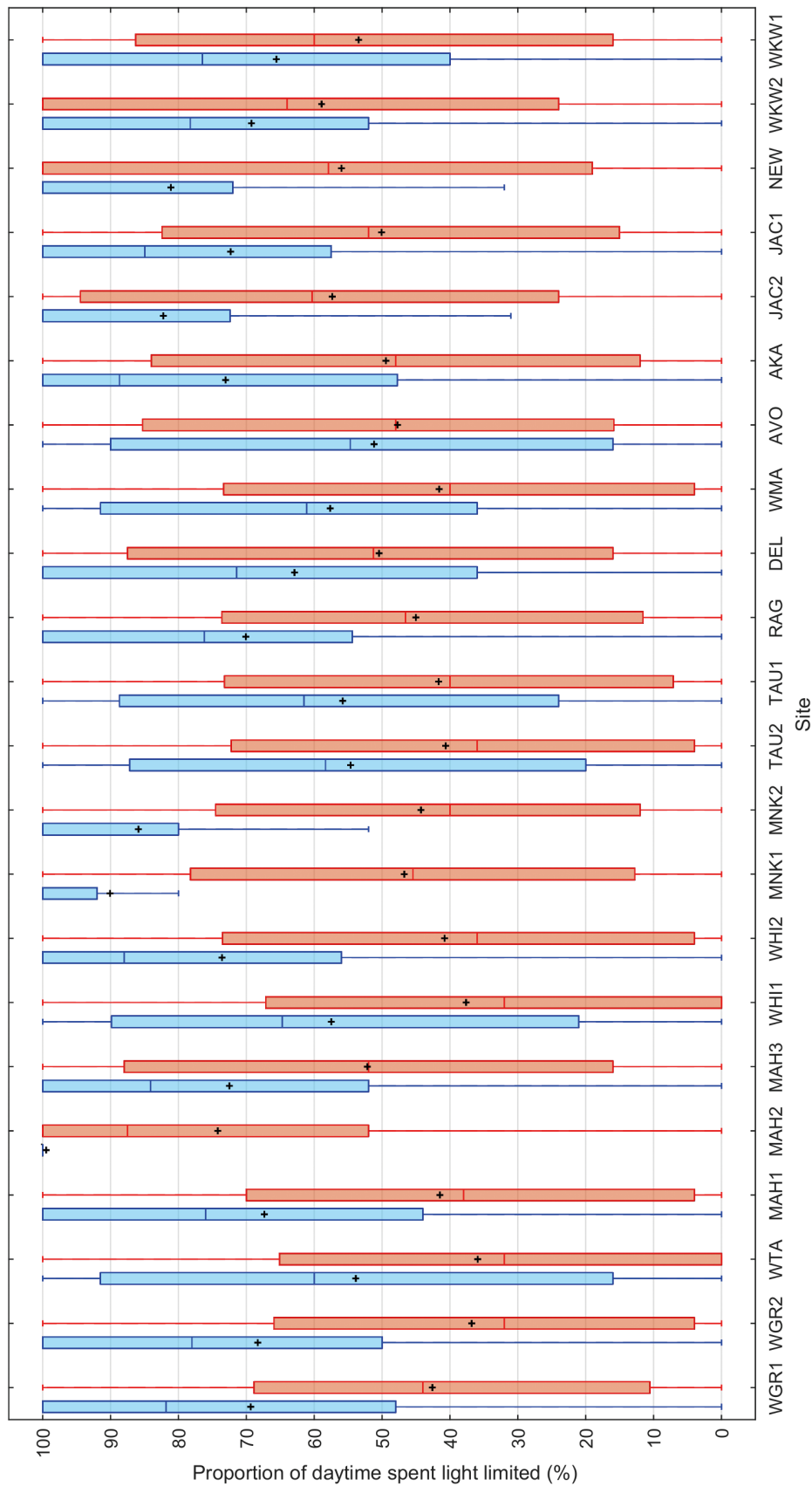


Fig. 4. Estimated proportion of each day over 9 mo that microphytobenthic production was light limited during immersion (blue) and emersion (red) assuming a light saturation value of $258 \mu\text{mol m}^{-2} \text{s}^{-1}$ (see Section 2.3 for details). Boxes represent the 25th and 75th percentiles, and whiskers are the 5th and 95th percentiles. A solid line and black cross within each box denote median and mean, respectively. Sites are ordered by latitude from north to south. Site abbreviations are defined in Table 1

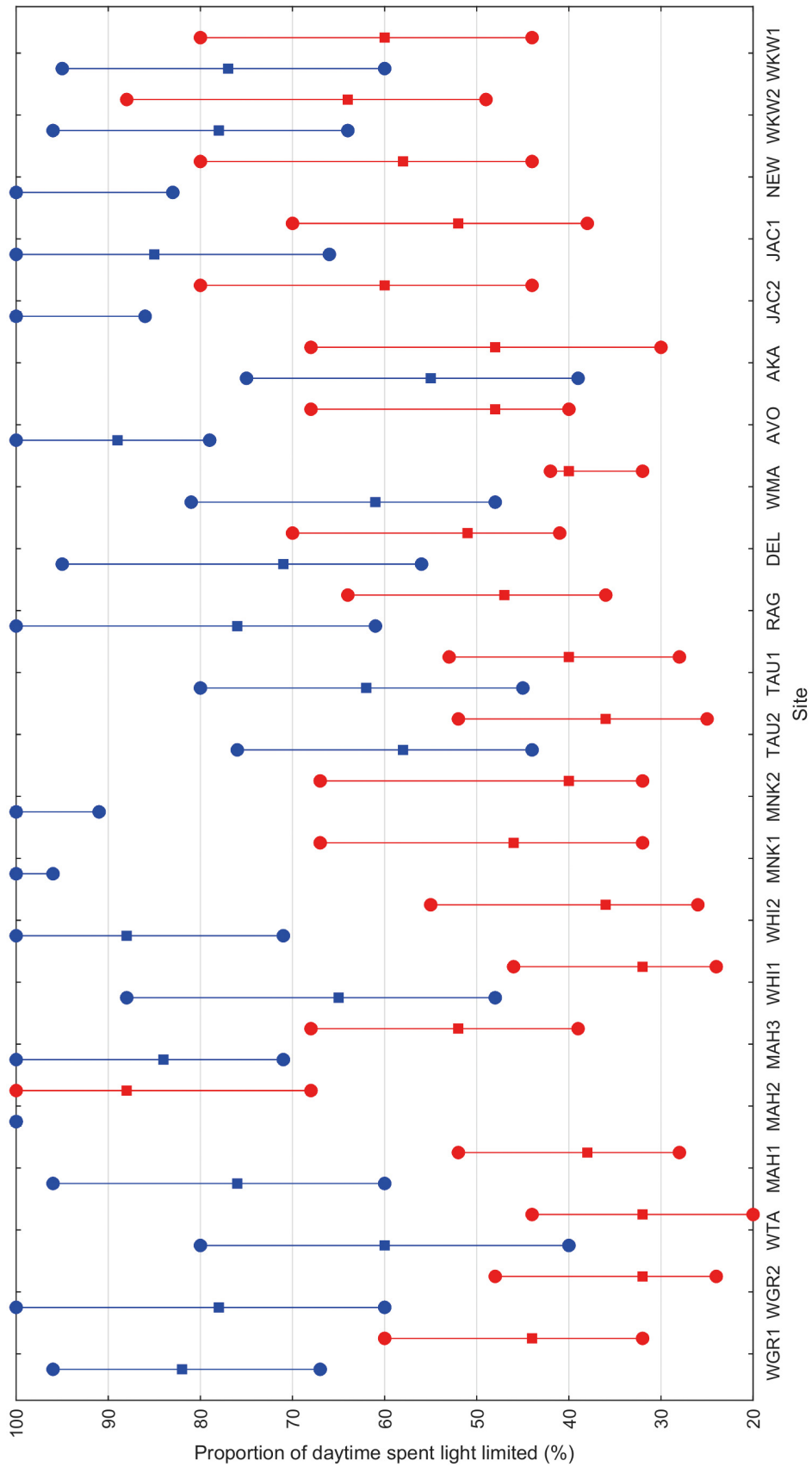


Fig. 5. Variation in the median proportion of the daytime that each estuary was light limited, assuming a light saturation value of 170 (lower point in each line), 258 (centre point) and 424 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (upper point). These values correspond to the 25th, 50th and 75th percentiles of literature light saturation values. Blue and red represent submerged and emerged data, respectively, and sites are ordered by latitude from north to south. Site abbreviations are defined in Table 1

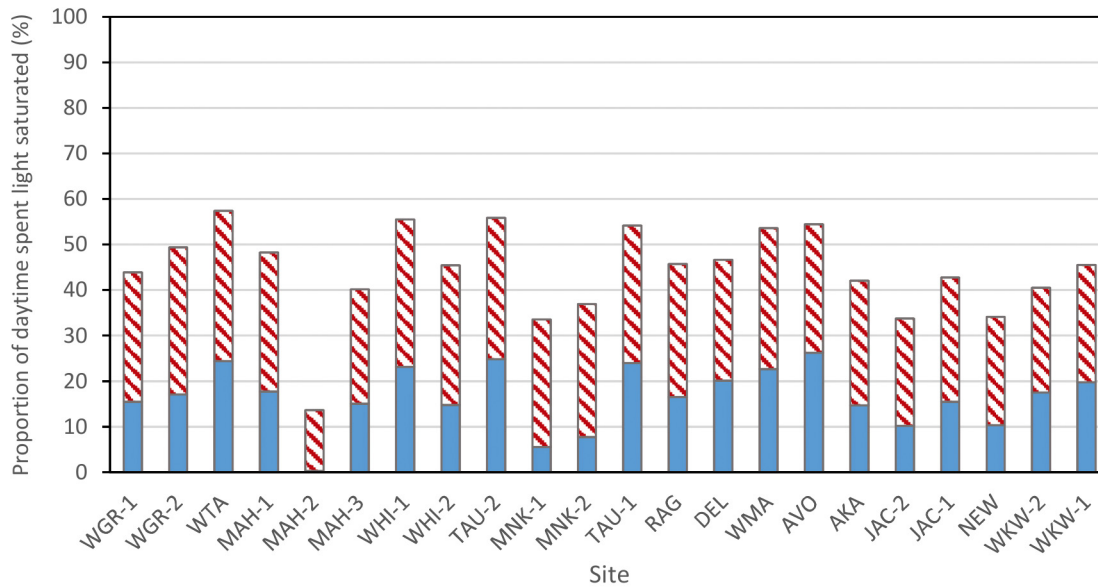


Fig. 6. Proportion of time over 9 mo where benthic primary production was light saturated (based on a light saturation value of $258 \mu\text{mol m}^{-2} \text{s}^{-1}$; see Section 2.3 for details). Daytime is divided into 2 tidal periods: immersion (solid blue bars) and emersion (hashed red bars). Sites are ordered by latitude from north to south. Site abbreviations are defined in Table 1

measure of light limitation, it does allow the novel examination of broad-scale patterns across large spatial and temporal gradients as well as comparisons with estuaries globally.

The literature-derived P-I curves are valuable not only for estimating the onset of light limitation, but also for gaining insight into maximum potential rates of primary production. Our literature review revealed that light saturation was notably lower for subtidal compared to intertidal environments (median 79 vs. $258 \mu\text{mol m}^{-2} \text{s}^{-1}$), which corresponded to a lower rate of maximum gross community production (median 25 and $52 \text{ mg C m}^{-2} \text{ h}^{-1}$, respectively). Moreover, light saturation and maximum gross community production observed in the literature data are positively correlated (Pearson's $r = 0.7$, $p < 0.001$; Fig. S1). Thus, a lower saturation value, while resulting in a decreased percentage of time being light limited, is more likely to correspond to lower maximal rates of primary production; the 2 effects compensate for each other.

Reductions in primary production, as evident in this study, have direct implications for the ecosystem functions delivered by MPB. For highly turbid estuaries, the persistent inhibition of production (those close to 100% light limitation, Fig. 4) is likely to directly modify the transfer of labile organic carbon and thus the transfer of energy within and across ecosystems (MacIntyre et al. 1996), having direct implications for global carbon budgets (Duarte et al. 2005, Bauer et al. 2013). In addition, decreasing light availability is closely coupled to increasing effluxes

of ammonium (NH_4^+) (Pratt et al. 2014), which, in synergy with other modifications to nutrient recycling and transformation (e.g. changes in denitrification rate), can lead to an exacerbation of the eutrophication cycle (Sundbäck et al. 2006) and further reductions in light climate over the longer term. Increasing attenuation of light will therefore have the effect of breaking down closely linked ecosystem processes as MPB photosynthesis becomes inhibited during tidal inundation. While there are many other factors when considering modifications to primary production estimates and comparisons across large spatial gradients (e.g. temperature and nutrient availability), our study highlights the profound impact of high light limitation (as occurs at MAH-2 and MNK). The resulting ecological consequences extend not only to direct effects on primary production, but have cascading ecological impacts in these coastal marine ecosystems, to the point where systems are pushed beyond tipping points (Kemp et al. 2005, Jickells et al. 2016, Christianen et al. 2017).

When light attenuation in the water column inhibits benthic production, intertidal areas can become a refuge for MPB through emerged periods at low tide (Migné et al. 2004). We estimate this may already occur at site MAH-2, where over the 9 mo period, light conditions during immersion were almost continuously below our estimated saturation threshold (Fig. 6), suggesting that MPB within this area are relying on periods of emergence at low tide. Similarly, light only became saturating within MNK-1

and MNK-2 for 6 and 8% of immersion periods, respectively, also suggesting that low tide periods may be contributing significantly to the maintenance of MPB production. This reliance on emersion is already evident for turbid estuaries globally, where low tide production can support and sustain MPB communities (e.g. Guarini et al. 2002, Migné et al. 2004, Yamochi et al. 2017, Drylie et al. 2018). In addition, this light-saturated emerged period can result in intertidal habitats being frequently more productive than their subtidal counterparts (Charpy-Roubaud & Sournia 1990) as supported by our review of literature-based P–I curves (see above). Although productivity can be sustained during emersion, other ecosystem functions are lost (e.g. modification to nutrient recycling through effluxes of ammonium with decreasing light availability; Pratt et al. 2014) and so ecosystem service delivery will still be reduced. Our currently limited knowledge of MPB is impeding our understanding of this compensatory dynamic in relation to other ecosystem services.

The dependence on low tide emergence in estuaries within this study and globally are likely to strengthen if light limitation and water column turbidity continue to increase. In addition, there has already been a 16% decline in worldwide intertidal habitats over the last 30 yr (Murray et al. 2019), a consequence primarily attributed to coastal development and land reclamation (MEA 2005, Blum & Roberts 2009, Field et al. 2014), an inevitable outcome of growing coastal populations worldwide (Airoldi & Beck 2007). Intertidal areas are disproportionately impacted such that many countries have already lost over half of their intertidal habitats (Perkins et al. 2015). Climatic changes will exacerbate these effects, as sea-level rise and stormier seas begin to inundate coastal areas (Nicholls & Cazenave 2010). The most extreme sea-level rise scenario of the Intergovernmental Panel on Climate Change (RCP8.5) predicts a 0.6–1.1 m increase by 2100 (Pörtner et al. 2019), with other estimates of up to 1.4 m (Rahmstorf 2007, Turner et al. 2009, NRC 2012) and exceeding 2 m (Kopp et al. 2017). This in turn will increase the demand for flood and erosion protection (Hallegatte et al. 2013), further driving habitat loss and alterations (Airoldi & Beck 2007). For example, sea defences constrict the ability of the intertidal to shift with SLR, ultimately resulting in the squeezing and reduction of intertidal areas. These significant alterations of important physical, chemical and biological processes unique to intertidal habitats have detrimental implications to benthic community structure and the associated ecosystem functions derived from these habitats (Perkins et al. 2015).

Despite the fact SLR has been described as one of the greatest potential causes of ecosystem disruption and global species extinctions (Noss 2011), we know very little of the ecological implications on intertidal areas. To provide a first-order estimation of the loss of intertidal area with SLR on our study estuaries, we used hypsometry curves (Fig. 7) to determine their sensitivity. Hypsometry curves are calculated using bathymetric grids, and compare the cumulative distribution of surface area with respect to elevation (for more details see Text S1), with the shape of the curve influenced by the curvature of the shoreline, tidal range, net sediment transport and wind-waves (Friedrichs & Aubrey 1996). The change in intertidal area (defined as the area between mean high/low water spring tide) following SLR scenarios from 0.2–1.4 m (Rahmstorf 2007, Turner et al. 2009, NRC 2012, Pörtner et al. 2019) were then calculated (Fig. 8). Assuming the intertidal area does not migrate landward (either restricted due to flood and coastal defences or occurs so rapidly there is a long hysteresis in ecological/morphological recovery), the resulting loss of intertidal area in our focal estuaries would range from 27–94% (Fig. 8). The difference in calculated estimates stems from the slope of the hypsometry curve, such that those estuaries with the most gradual slopes result in the largest losses of intertidal area. This is exemplified within TAU (Fig. 8), where a relatively small increase in sea level can disproportionately result in a large loss of intertidal area. In addition, MAH highlights the non-linear rate of change observed in several estuaries, where a 0.2 m increase in sea level from 0.6 to 0.8 m produced an abrupt (18%) loss of intertidal area. It should be noted that these estimates of intertidal loss are an over-simplification of highly complex and dynamic systems with both landward and seaward influences. For example, it discounts the role of changes to sedimentation rates and biomorphodynamic feedbacks which can build new land (D'Alpaos et al. 2007) and potential changes to sediment supply due to altered storm frequencies and intensities (Seneviratne et al. 2012). Despite its limitations, this analysis does provide a framework to examine the relative extent of intertidal area lost, which is likely to have far-reaching ecological consequences for coastal ecosystems.

When these future predictions of intertidal area are coupled with light limitation estimates, the vulnerability of different estuaries to loss of MPB production can be considered. For example, both TAU sites exhibited a relatively low proportion of light limitation (~60% during immersion), and therefore the

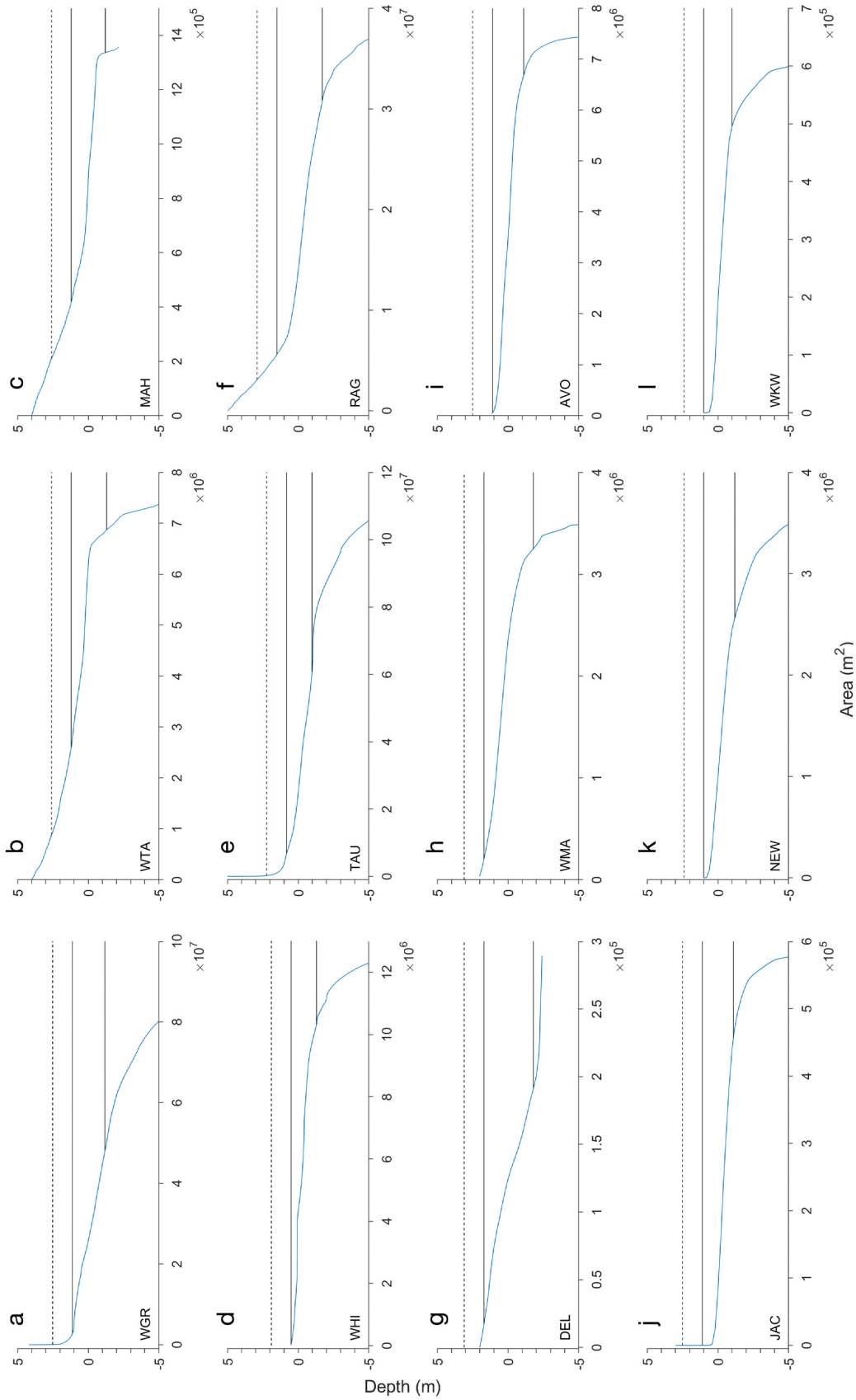


Fig. 7. Estuary hypsometric curves (see Text S1) ordered by latitude (north to south: a–l). The upper and lower solid black lines represent the water level at high and low tide during a spring tide, respectively, and the dashed black line represents a 1.4 m increase in sea level. For locations of each estuary, see Fig. 1. Site abbreviations are defined in Table 1

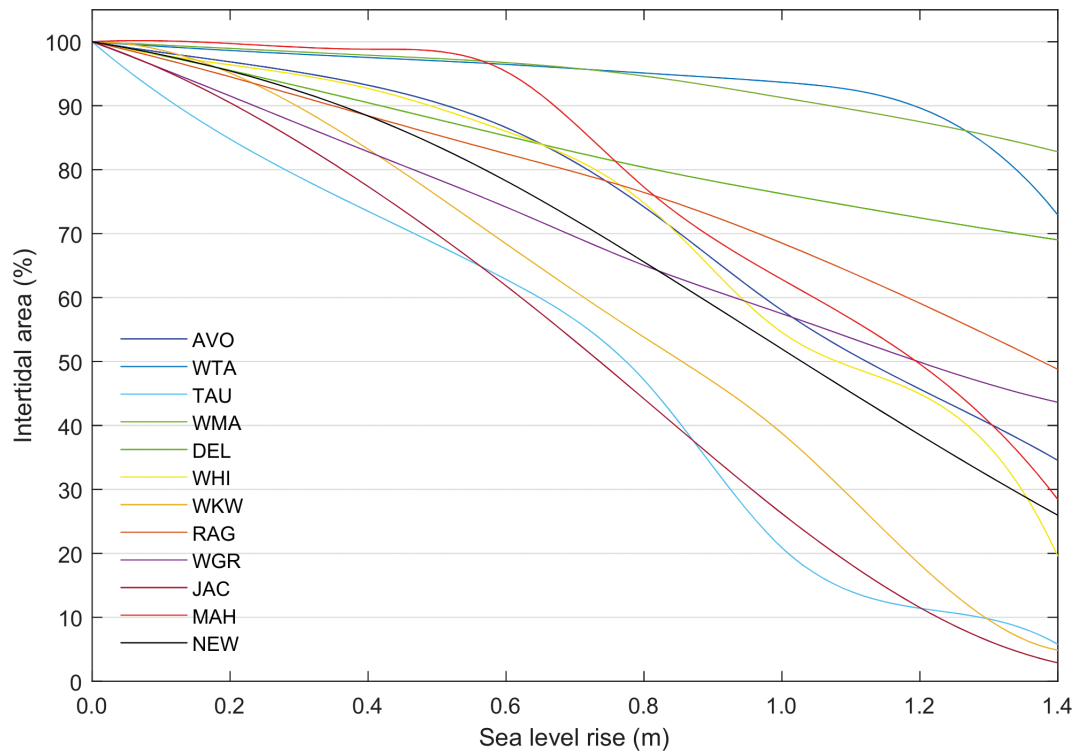


Fig. 8. Calculated change in intertidal area (derived from hypsometric curves shown in Fig. 7) as a function of sea level rise up to 1.4 m (predicted for 2100; Rahmstorf 2007, Turner et al. 2009, NRC 2012). Sites are ordered from highest to lowest median immersed photosynthetically active radiation over the 9 mo study period. Site abbreviations are defined in Table 1

large loss of the intertidal here is least likely to result in significant changes to benthic primary production and ecosystem functionality. Conversely, WHI has a predicted loss of 80% intertidal area, in conjunction with having one of the poorest light climates during immersion at the upper estuarine site (WHI-2, 88% light limitation). For WHI-2 and other sites where high turbidity and large reductions of intertidal area co-occur (e.g. RAG, WGR), vulnerability to the loss and degradation of ecosystem functioning will increase, as emersion periods, which were providing a level of resilience to estuarine ecosystems, become restricted. However, even estuaries with low turbidity may become vulnerable in the future if increases in the frequency and intensity of extreme weather events deliver more land-derived sediment and nutrient inputs increasing water column turbidity (Seneviratne et al. 2012). Ultimately, the reduction in benthic MPB production will lead to a reduced capacity to moderate pollutant loads (NRC 2007), a loss of climate regulating services such as carbon sequestration (Yim et al. 2018) and changes in trophic structure, nutrient cycling and productivity (Dugan et al. 2018). These all feed back within the system, modifying trophic interactions and ecological net-

works, pushing ecosystems closer to tipping points (Scheffer & Carpenter 2003, Thrush et al. 2014, Selkoe et al. 2015).

5. CONCLUSIONS

Using light measurements conducted across a large latitudinal gradient and a literature compilation of P–I curves, our findings demonstrate that light attenuation within estuaries can substantially limit MPB primary production. Considering that water column turbidity is a widespread and global stressor, that our study estuaries incorporate a range of estuarine topography and the generality in overall patterns, we suggest these results are not only relevant to barrier-enclosed coastal lagoons such as those used in this study, but also to other coastal systems where MPB are the dominant primary producers. As a consequence of high light limitation observed at some sites, benthic productivity can become entirely reliant on periods of emersion, resulting in reductions of overall productivity and the associated ecosystem functions and services provided by MPB. This will influence the vulnerability of estuaries, through

the potential reduction of intertidal areas via both SLR and land reclamation practices. The health and functioning of an estuary under future global change is therefore likely to be closely coupled to light climate reaching the sediment surface but also to the proportion of intertidal area within an estuary. A deeper understanding of how MPB respond to future local and global stressors in a changing climate is critical to prevent the ecological collapse of these fundamental coastal ecosystems on which humanity relies.

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