Spatial Synchrony in Intertidal Benthic Algal Biomass in Temperate Coastal and Estuarine Ecosystems

Daphne van der Wal,* Annette Wielemaker-van den Dool, and Peter M. J. Herman

Netherlands Institute of Ecology (NIOO-KNAW), Centre for Estuarine and Marine Ecology, P.O. Box 140, 4400 AC Yerseke, Netherlands

ABSTRACT

Microphytobenthos plays a vital role in estuarine and coastal carbon cycling and food webs. Yet, the role of exogenous factors, and thus the effects of climate change, in regulating microphytobenthic biomass is poorly understood. We aimed to unravel the mechanisms structuring microphytobenthic biomass both within and across ecosystems. The spatiotemporal distribution of the biomass of intertidal benthic algae (dominated by diatoms) was estimated with an unprecedented spatial extent from time-series of Normalized Differential Vegetation Index (NDVI) derived from a 6-year period of daily Aqua MODIS 250-m images of seven temperate, mostly turbid, estuarine and coastal ecosystems. These NDVI time-series were related to meteorological and environmental conditions. Intertidal benthic algal biomass varied seasonally in all ecosystems, in parallel with meteorology and water quality. Seasonal variation was more pronounced in mud than in sand. Interannual varia-

tion in biomass was small, but synchronized year-to-year biomass fluctuations occurred in a number of disjointed ecosystems. Air temperature explained interannual fluctuations in biomass in a number of sites, but the synchrony was mainly driven by the wind/wave climate: high wind velocities reduced microphytobenthic biomass, either through increased resuspension or reduced emersion duration. Spatial variation in biomass was largely explained by emersion duration and mud content, both within and across ecosystems. The results imply that effects on microphytobenthic standing stock can be anticipated when the position in the tidal frame is altered, for example due to sea level rise. Increased storminess will also result in a large-scale decrease of biomass.

Key words: microphytobenthos; NDVI; remote sensing; inundation; spatial scales; synchrony.

INTRODUCTION

Benthic algae are a vital link in carbon cycling in shallow waters (Gattuso and others 2006); the

annual productivity of benthic microalgae alone is estimated to contribute about 500 million tons of carbon globally (Cahoon 1999). The major part of the benthic microalgae inhabit intertidal sediments in estuarine and coastal ecosystems (Heip and others 1995; Cahoon 1999). They constitute a primary carbon source for food webs (Miller and others 1996; Herman and others 1999), and influence sediment dynamics by forming a sediment stabilizing biofilm (Holland and others 1974).

Intertidal sediments in estuarine and coastal ecosystems experience fluctuations in temperature, irradiance, desiccation, nutrients, grain-size, and activity and grazing by benthic fauna, resulting in variability in microphytobenthic biomass and species composition at different temporal scales (Admiraal and Peletier 1980; Underwood 1994; Blanchard and others 1997). Intertidal zones also show large spatial heterogeneity for many of these factors (for example, irradiance as a function of emersion duration in turbid waters, and sediment grain-size), and so a large spatial variation in microphytobenthic biomass is also expected (Pinckney and Zingmark 1993; MacIntyre and others 1996; Underwood and Kromkamp 1999; Guarini and others 2008).

Given their global importance, estuarine and coastal water bodies are a major focus of concern regarding the potential impacts of anthropogenic climate change (Harley and others 2006). Observed and projected climate trends include changes in (air and sea) temperature, sea level, tidal range, precipitation, river discharge and turbidity, and storm frequency and intensity (Bates and others 2008), all of which may potentially affect intertidal microphytobenthic biomass and primary production.

Thus, there is a need to unravel the factors structuring microphytobenthic biomass, so that the effects of climate change can be better predicted. We hypothesize that the key to unraveling these factors is the extent of synchrony in microphytobenthic biomass across ecosystems. Spatial synchrony in populations, that is, the coincident changes (temporal coherence) in abundance of geographically disjointed populations, may arise from three primary mechanisms: dispersal among populations, trophic interactions with populations of other species that are themselves spatially synchronous (such as benthic macrofauna) or mobile, and congruent dependence of population dynamics on a synchronous exogenous (random) factor (such as temperature) (Liebhold and others 2004). Thus, when microphytobenthic biomass fluctuates in the same way in different ecosystems, it will be governed largely by factors that are effective at such a large geographical scale, whereas any local departure will point to the influence of locally operating factors (Beukema and Essink 1986).

Advances in remote sensing allow a synoptic estimation of intertidal microphytobenthic biomass over large spatial scales (for example, Combe and others 2005; Van der Wal and others 2008), but to date very few studies have taken a multi-temporal basin-wide or inter-ecosystem approach. In contrast, in the marine (Behrenfeld and others 2006)

and terrestrial (Pettorelli and others 2005) realm, satellite remote sensing is widely used to assess changes in the biomass of photo-autotrophs over vast areas. A common measure for photo-autotrophs is the Normalized Differential Vegetation Index, NDVI, computed from reflectance in the red (R_R) and near-infrared (R_{NIR}) part of the electromagnetic spectrum, that is: NDVI = $(R_{NIR} - R_R)/(R_{NIR} + R_R)$. Photo-autotrophs absorb most of the incoming light, notably in the red. Thus, NDVI gives higher values with increasing biomass, cover or health (Tucker 1979). In the absence of macrophytes, NDVI is a good proxy for chlorophyll-*a* (Chl-*a*) and microphytobenthic biomass in intertidal sediments (Kromkamp and others 2006; Van der Wal and others 2008). Retrieval of NDVI from moderate resolution satellite sensors, such as Aqua MODIS (Huete and others 2002), enables microphytobenthic biomass to be monitored simultaneously in multiple ecosystems. Such information can also facilitate the incorporation of benthic algae into models of carbon and nitrogen cycling in coastal and estuarine areas.

This article addresses the spatiotemporal variation of intertidal benthic algae, derived from a 6-year daily time-series of Aqua MODIS 250-m imagery. The study is aimed at (1) determining the extent of synchrony in microphytobenthic biomass across ecosystems and the coupling of temporal variation in microphytobenthos and exogenous factors (meteorology and water quality) and (2) determining the extent of spatial structuring of microphytobenthos by emersion duration and sediment type, both within and across temperate estuarine and coastal ecosystems.

METHODS

Study Sites

Seven estuarine and coastal water bodies in the Netherlands and United Kingdom were selected (Figure 1; Table 1), all with extensive intertidal areas and all experiencing a semi-diurnal tidal regime. The Dutch sites include the Westerschelde (site WES) and the Ems-Dollard (EMS), two eutrophic, turbid, macrotidal estuaries, and the Oosterschelde (OOS), an estuary that is relatively clear and saline due to construction of dams in the upper estuary and a storm surge barrier at the mouth, as well as the western Wadden Sea (site WAD), a eutrophic turbid mesotidal basin bordered by a series of barrier islands. The three exposed and turbid sites in east England (Devlin and others 2008) include the macrotidal open coast mudflats
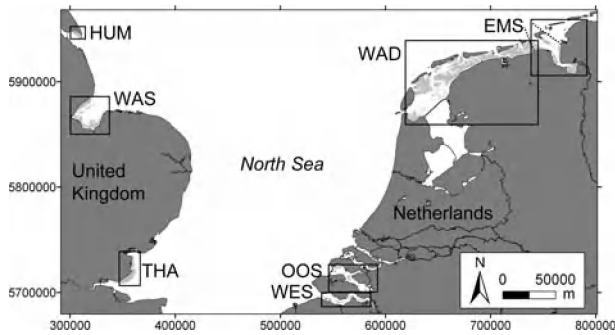
Figure 1. Study sites: The Westerschelde (WES), Oosterschelde (OOS), Wadden Sea (WAD), and Ems-Dollard (EMS) in the Netherlands, and the Thames (THA), Wash (WAS), and Humber (HUM) in the United Kingdom. *Light gray* areas indicate intertidal areas above Mean Low Water Spring (MLWS). Coordinate system is in UTM 31/WGS84 (m).

and sandflats of the Thames estuary (THA), the Wash (WAS), a macrotidal embayment, and Spurn Bight at the mouth of the macrotidal Humber estuary (HUM). The seven sites are not nutrient-limited for microphytobenthos (Nienhuis 1992; Aldridge and Trimmer 2009).

The sediments are dominated by benthic micro-algae, in particular diatoms (Admiraal and Peletier 1980; Heip and others 1995). Benthic macroalgae (for example, *Enteromorpha* sp. and *Ulva* sp.) occur in all sites, mainly attached to suitable substrate such as empty shells or shellfish beds. Nienhuis (1992) presented a carbon budget of primary producers and estimated that benthic macroalgae contribute less than 10% of the benthic algae in site OOS, less than 5% in site WAD and even less in sites WES and EMS. Macroalgal cover in the British sites is comparably low (for example, Aldridge and Trimmer 2009).

Time-Series of NDVI from MODIS 250 Satellite Images

A total of 2,179 daily composite images (September 2002-2008) from Aqua MODIS (EOS PM) were distributed by the Land Processes Distributed Active Archive Center (LP DAAC), located at the USGS Earth Resources Observation and Science (EROS) Center (http://www.lpdaac.usgs.gov). The Aqua MODIS Surface Reflectance Daily L2G Global 250-m SIN grid product (MYD09GQ.005) contains surface reflectance with 250-m resolution in a red band R_R (620–670 nm, central wavelength 645 nm) and a near-infrared band R_{NIR} (841–876 nm, central wavelength 859 nm). Equatorial crossing time is 13:30 for Aqua, but the daily products contain the best observations over a 24-h period (in practice acquired between 9:35 and 14:05 UTC) with respect to solar zenith angle, view angle and cloud cover. The data are atmospherically corrected using aerosol and water vapor information derived from MODIS data and taking into account the directional properties of the observed surface, and corrected for adjacency effects. Images (reprojected to UTM/WGS84) were used in conjunction with the associated MOD09GA quality information products. Pixels with highest quality reflectance data (for example, solar zenith angle < 85°) were selected using the 500-m resolution quality assessment (QC_500), and pixels with clouds/cirrus, cloud shadow, pixels adjacent to clouds, and pixels with fire, snow or ice were flagged using the 1-km resolution quality assessment (state_1 km). For pixels that were not flagged, NDVI was calculated in a Geographical Information System (ESRI ArcGIS), provided R_R was greater than 0% and R_{NIR} was greater than 2%.

Although we used only high-quality surface reflectance data, the NDVI will still contain some

Table 1. Site Characteristics

Site	WES	OOS	WAD	EMS	THA	WAS	HUM
Longitude (°E)	3°50′	4°00′	5°40′	7°00′	1°00′	0°15′	0°05′
Latitude (°N)	51°20′	51°35′	53°20′	53°25′	51°35′	52°55′	53°35′
Intertidal area (km²)	70	50	990	180	120	170	30
Spring tidal range (m)	4.4	3.1	2.0	2.6	3.9	4.9	4.2
Mud (%), intertidal only	13	5	17	40	–	–	–
Kd (m^{-1})	3.15	0.90	2.27	4.17	–	–	–
Secchi depth (m)	0.44	1.60	0.69	0.56	–	–	–
Salinity	23.4	31.2	27.7	21.9	–	–	–
DIN (mg/l)	1.562	0.379	0.383	1.366	–	–	–
P (mg/l)	0.092	0.035	0.029	0.071	–	–	–
Si (mg/l)	1.114	0.374	0.665	1.768	–	–	–

See "Materials and methods" for sources. Water quality variables are averaged over September 2002–2008.

noise. Underestimation of NDVI can be due to residual cloud cover and residual atmospheric contamination; both effects increase with optical path length (Huete and others 2002). Overestimation of NDVI at large solar or view angles due to anisotropic effects such as shadow-casting and multiple scattering, as reported for many vegetation types (Van Leeuwen and others 1999; Pettorelli and others 2005) can be neglected in our study, as the surface of an intertidal flat can be assumed Lambertian.

Supratidal areas were excluded using a land/water mask with a 500-m buffer. Seagrass (*Zostera* sp.) meadows (notably in sites EMS, WAD, and THA) and perennial saltmarshes (for example, *Spartina* sp.) were excluded based on vegetation maps and aerial photographs. Low-density stands of annuals (for example, *Salicornia* sp.) were not excluded, and no distinction between benthic macroalgae and benthic microalgae could be made.

NDVI values (with NDVI > 0 to exclude water) were binned per month for each pixel and subsequently averaged per site.

Ground-Truthing

Ground-truthing the monthly averaged NDVI of 250-m satellite image pixels at the appropriate spatio-temporal scale requires an extensive in situ data set. In situ Chl-*a* data from the period 2002–2005 (Rijkswaterstaat 2006) were available for ground-truthing at site WES only. Every 1–3 months, the top 1 cm of the sediment was sampled (4 cm^2 surface) at approximately 90 well distributed (but fixed) intertidal stations (n = 2439 samples in total), and Chl-*a* content (in μg/g) of the samples was determined using HPLC techniques. For each campaign, satellite-derived NDVI depended significantly on in situ Chl-*a* (for example R^2 = 0.47, SE = 0.0297, $F_{1,45}$ = 39.512, P < 0.0001, for May 2005). Monthly site-averaged NDVI also depended significantly on monthly site-averaged Chl-*a* (NDVI = 0.00450 × Chl-*a* + 0.0285, R^2 = 0.52, SE = 0.0149, $F_{1,22}$ = 24.143, P < 0.0001). Moreover, monthly site-averaged NDVI and Chl-*a* exhibited a similar seasonal variation, with a maximum in June. Thus, spatial patterns and temporal (interannual and seasonal) trends in Chl-*a* could be significantly represented by NDVI.

Time-Series of Meteorological and Water Quality Variables

Meteorological time-series included monthly averages of mean and maximum hourly wind velocities, maximum wind gust, mean, minimum and

maximum daily air temperature, global radiation, sun duration and surface air pressure and days of air frost (Royal Netherlands Institute of Meteorology, http://www.knmi.nl) for sites WES and OOS (weather station Vlissingen) and sites WAD and EMS (station De Kooij, Den Helder), and monthly averages of mean, minimum and maximum daily air temperature, sun duration and days of air frost (UK Met Office, http://www.metoffice.gov) for site THA (Met Office district East Anglia) and sites WAS and HUM (Met Office district East and Northeast England).

Monthly averages of significant wave height Hs in the North Sea (Rijkswaterstaat Waterbase, http://www.waterbase.nl) were used for sites WES, OOS, and THA (North Sea station Euro Platform) and sites WAD, EMS, WAS, and HUM (North Sea station K13).

In situ water quality time-series (Rijkswaterstaat Waterbase, http://www.waterbase.nl) of the Dutch waters included Secchi depth, light extinction coefficient (Kd), nutrients [dissolved inorganic nitrogen (DIN), orthophosphate (P) and silicate (Si)], and salinity in the surface water at approximately four fixed monitoring stations per site, averaged per month, per site.

Emersion Duration and Sediment Type

Emersion duration was approximated for each pixel by the number of unclouded images in which the pixel is exposed (that is, has an NDVI > 0) as a percentage of the total number of unclouded images. Recent elevation data (available for all sites except WAS) were combined with information on tidal levels to qualitatively validate the retrieval of emersion duration from the satellite images.

Sediment data were available for the Dutch sites (for example, Rijkswaterstaat Sedimentatlas, http://www.waddenzee.nl), comprising surface samples collected in the period 1990–2008 in sites WAD and EMS (7502 samples in total), site WES (1,418 samples) and site OOS (1025 samples). Mud (particles < 63 μm) percentages were determined from laser particle sizer analysis. Mud percentages at the sample points were interpolated in a GIS by an inverse distance power 2 algorithm, and a distinction was made between muddy (that is, ≥20% mud) and sandy (<20% mud) sediments. For the British sites, a broad distinction between mud and sand was taken from recent Landranger Ordnance Survey maps (scale 1:50000) and used in a qualitative way only.

Data Analysis

ANOVA was carried out to test whether monthly averaged NDVI depended on the categorical predictors Year, Month, Site and the first-order interaction terms (each year starting in September to guarantee a complete ANOVA design). As ANOVA requires the residuals of the factor levels to be independent, model residuals of the monthly time-series were checked for autocorrelation at each site; no significant (temporal) autocorrelation was found.

Normal (that is, average) monthly values of NDVI, meteorological and water quality variables were calculated over the 6-year period. Time-series of monthly anomalies of all variables were defined as the departure from these normal monthly values. The impact of meteorology and water quality on NDVI was tested by Pearson product moment correlations. Synchrony was demonstrated by correlations of (anomalies of) NDVI between sites.

The impact of sediment type and emersion duration on NDVI was quantified using ANOVA (effects site, sediment type (sand/mud), emersion (in 5 classes), and sediment × emersion, on NDVI averaged per pixel over the full period).

A 5% significance level was applied to all statistical tests.

RESULTS

Seasonal and Year-to-Year Variation in Microphytobenthos

NDVI time-series show a striking seasonal cycle (Figure 2). This seasonal variation is significant for all sites (one-way ANOVA per site). NDVI is lowest in December. NDVI peaks in June, but in sites WAD, OOS, and HUM maximum NDVI occurs in September and in site EMS in April. The blooms also differ in magnitude in each site (Figure 2).

ANOVA confirms differences in NDVI between month ($F_{11,330} = 59.51$, $P < 0.001$), between sites ($F_{6,330} = 100.88$, $P < 0.001$), and between month × sites ($F_{66,330} = 3.17$, $P < 0.001$); but not between years ($F_{5,330} = 0.99$, $P = 0.424$) and not between month × year ($F_{55,330} = 1.34$, $P = 0.065$) and year × sites ($F_{30,330} = 0.91$, $P = 0.600$). A post hoc Tukey HSD test reveals that NDVI is lowest in sites WAD, THA, and WES, intermediate in EMS and WAS and highest in sites HUM and OOS.

Synchrony in Microphytobenthos

The strongest correlations in monthly NDVI are found between sites WAD and EMS ($r = 0.79$,
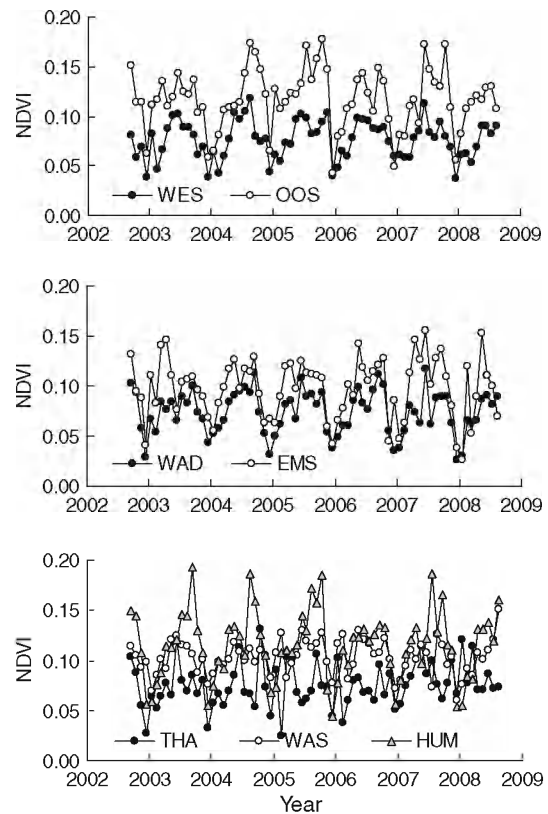

Figure 2. Time-series of monthly mean NDVI for the seven sites.

$n = 72$, $P < 0.001$), but cross-correlations are also significant between other sites, confirming seasonal synchrony. The exception is NDVI in site THA, significantly correlating with NDVI in site OOS and WES only.

The monthly *anomalies* of NDVI also show significant cross-correlation between all Dutch sites, demonstrating interannual synchrony, except between WAD and OOS (Table 2). The strongest correlations are between WAD and EMS, and between OOS and WES; both sets of sites are situated closest to each other. There is no cross-correlation between the Dutch and British sites (except for a negative correlation of THA with WAD and EMS) and there is no significant cross-correlation between the British sites (Table 2).

Correlations of the anomalies are generally stronger in the winter half-year (October–March) than in the summer half-year (April–September). For example, $r = 0.74$, $n = 36$, $P < 0.001$ for the correlation between NDVI anomalies in site WAD and EMS in winter. Moreover, correlation between NDVI anomalies in site WAS and HUM is significant in winter ($r = 0.50$, $n = 36$, $P = 0.002$), pointing to year-to-year synchrony between the

Table 2. Year-to-Year Synchrony in NDVI: Correlations of Monthly NDVI Anomalies Between Sites

Site	WES	OOS	WAD	EMS	THA	WAS	HUM
WES (Westerschelde)		0.47*	0.32*	0.31*	−0.19	0.03	0.03
OOS (Oosterschelde)	0.47*		0.22	0.30*	−0.07	0.04	0.06
WAD (Wadden Sea)	0.32*	0.22		0.58*	−0.31*	0.13	0.02
EMS (Ems-Dollard)	0.31*	0.30*	0.58*		−0.25*	−0.07	0.01
THA (Thames)	−0.19	−0.07	−0.31*	−0.25*		−0.14	−0.11
WAS (Wash)	0.03	0.04	0.13	−0.07	−0.14		0.12
HUM (Humber)	0.03	0.06	0.02	0.01	−0.11	0.12	

Significant correlations (P < 0.05) are marked (*).

two most northern British sites. In contrast, correlations between sites WAD and THA and between sites EMS and THA are neither significant in the winter half-year nor summer half-year. In the summer half-year, the strongest correlations of NDVI anomalies are found between sites WAD and EMS ($r = 0.47$, $n = 36$, $P = 0.004$) and between sites WES and OOS ($r = 0.42$, $n = 36$, $P = 0.010$).

Impact of Meteorology and Water Quality on Microphytobenthos

Obviously, time-series of monthly NDVI are significantly correlated with variables with a seasonal component, including a positive correlation with temperature, global radiation, sun hours and salinity and Secchi depth and a negative correlation with wind velocity, significant wave height, days of air frost, Kd, and some nutrients. NDVI has the strongest correlation with temperature (for exam-

ple, $r = 0.79$, $n = 72$, $P < 0.001$ in site WES) and global radiation (for example, $r = 0.73$, $n = 72$, $P < 0.001$ in site WES).

In contrast, monthly *anomalies* of both NDVI and meteorological and water quality variables are generally not well correlated (Tables 3, 4), suggesting that year-to-year variation in benthic algae is not well explained by these exogenous factors. However, anomalies of NDVI and wind velocity (and wave height) are negatively correlated in a number of sites, particularly in the upper intertidal zone; this effect is strongest in site EMS. Most Dutch sites also show a significant positive correlation between anomalies of NDVI and surface air pressure. Anomalies of NDVI and Secchi depth are positively correlated for site WAD. In site WES, temperature best explains year-to-year variation in NDVI (but maximum wind gust is also a significant factor). In the British sites WAS and HUM, (minimum) temperature and days of air frost most sig-

Table 3. Impact of Exogenous Factors on Year-to-Year Variation in NDVI in the Dutch Sites: Correlation of Monthly Anomalies of NDVI and Anomalies of Meteorology and Water Quality

Variable	WES		OOS		WAD		EMS	
	All	High	All	High	All	High	All	High
Wind velocity, mean (m/s)	−0.10	−0.18	−0.20	−0.23*	−0.16	−0.21	−0.26*	−0.32*
Wind velocity, max (m/s)	−0.14	−0.23	−0.23	−0.27*	−0.15	−0.22	−0.30*	−0.34*
Wind velocity, max gust (m/s)	−0.14	−0.24*	−0.25*	−0.27*	−0.16	−0.23	−0.33*	−0.37*
Global radiation (J/cm^2)	−0.06	0.16	−0.07	0.01	−0.20	−0.03	0.09	0.05
Sun (hours)	−0.11	0.14	−0.01	0.06	−0.15	−0.00	0.09	0.11
Temperature, mean (°C)	0.22	0.33*	0.05	0.09	0.07	0.12	0.12	0.08
Temperature, min (°C)	0.24*	0.30*	0.08	0.10	0.10	0.13	0.11	0.05
Temperature, max (°C)	0.22	0.36*	0.07	0.12	0.05	0.13	0.16	0.13
Air frost (days)	−0.02	−0.03	0.07	0.07	−0.13	−0.14	−0.05	−0.08
Surface air pressure, mean (hPa)	0.06	0.17	0.22	0.23*	0.06	0.25*	0.34*	0.34*
Kd (m^{-1})	−0.03	−0.09	−0.08	−0.10	−0.16	0.03	0.02	−0.02
Secchi depth (m)	0.06	0.14	0.12	0.09	0.28*	0.26*	0.03	−0.02
Significant wave height North Sea (m)	−0.09	−0.23	−0.19	−0.21	−0.11	−0.18	−0.23*	−0.35*

Significant correlations (P < 0.05) are marked (*). Distinction between all areas, and upper intertidal only (high: emersion duration ≥ 50%).

Table 4. Impact of Exogenous Factors on Year-to-Year Variation in NDVI in the British Sites: Correlation of Monthly Anomalies of NDVI and Anomalies of Meteorology

Variable	THA		WAS		HUM	
	All	High	All	High	All	High
Sun (hours)	0.09	−0.03	−0.12	−0.06	−0.23	−0.15
Temperature, mean (°C)	0.11	0.11	0.24*	0.37*	0.13	0.20
Temperature, min (°C)	0.09	0.07	0.31*	0.41*	0.22	0.25*
Temperature, max (°C)	0.11	0.14	0.15	0.28*	0.03	0.12
Air frost (days)	−0.10	−0.01	−0.30*	−0.31*	−0.26*	−0.24*
Significant wave height North Sea (m)	0.03	0.11	−0.14	−0.25*	0.05	−0.03

Significant correlations ($P < 0.05$) are marked (*). Distinction between all areas, and upper intertidal only (high: emersion duration $\geq$ 50%).

nificantly explain interannual variation in benthic algae, although site WAS is also affected by anomalies in wind/wave climate (Table 4).

The effect of wind/wave climate occurs throughout the year (that is, for all months), but is strongest in the winter half-year. For example, correlation of anomalies of mean wind velocity and NDVI is only significant in the winter half-year for the highest shores in site WAD ($r = -0.35$, $n = 36$, $P = 0.038$). The effect of temperature is also significant in both winter and summer, except for the effect of minimum temperature in site HUM and days of air frost in site WAS and HUM, which are only significant in the winter half-year.

We did not obtain higher correlation coefficients when applying a time lag of one season between anomalies of NDVI and exogenous factors. For example, no significant correlation was found between average temperature anomalies in winter and NDVI anomalies in the subsequent spring: a hotter or colder winter did not lead to a change in microphytobenthic biomass in spring. However, the available number of years is (too) limited for such a time-lag analysis.

Impact of Emersion Duration and Sediment Type on Microphytobenthos

Highest values for NDVI are generally found in the upper intertidal flats (Figures 3, 4). Extremely high values of NDVI in the eastern part of site OOS are associated with benthic macroalgae and mussel bed cultures (Figure 3). NDVI increases with emersion
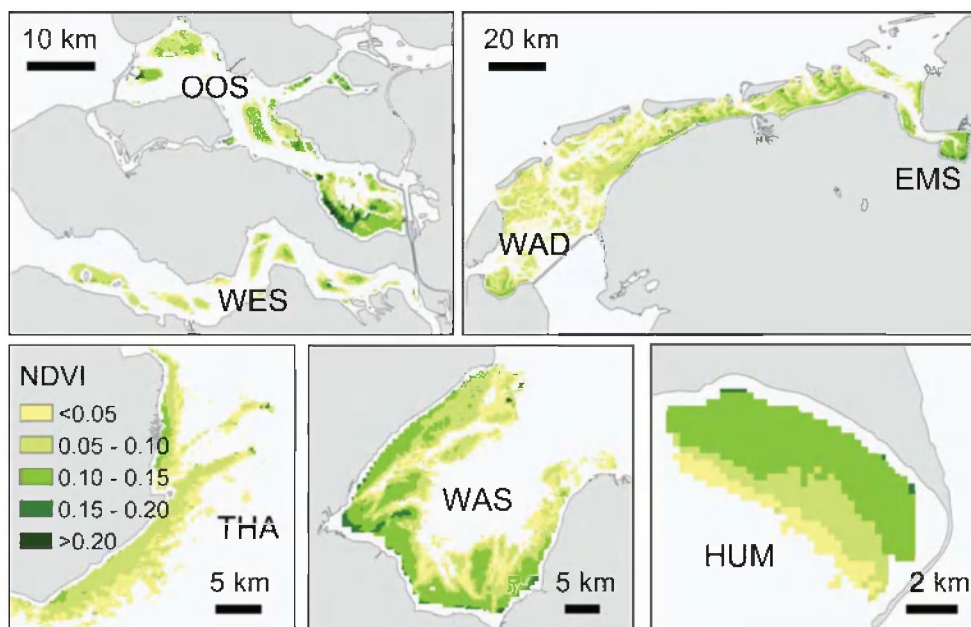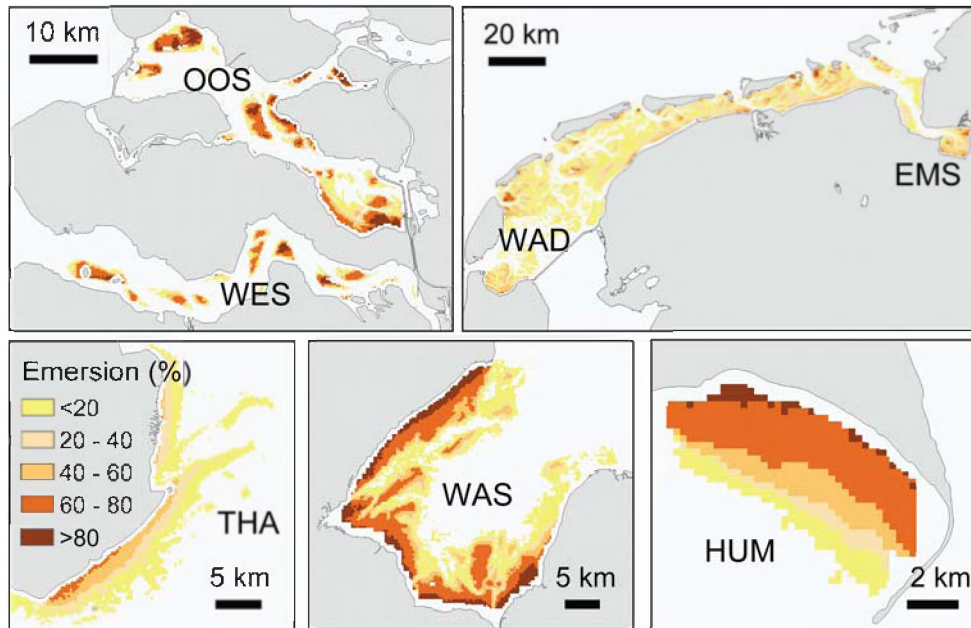

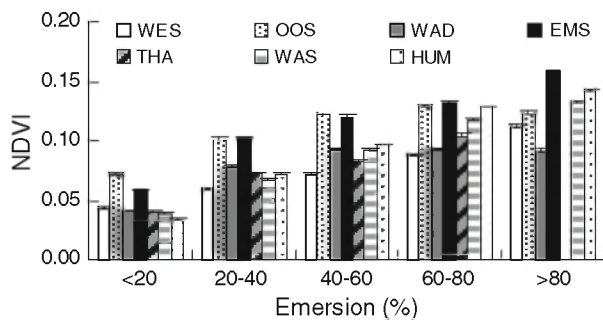Figure 3. Spatial variation in long-term mean NDVI.

Figure 5. Relationship between long-term mean ($\pm$SE) NDVI and emersion duration for the seven sites.

duration in all sites (Figure 5), and for a given emersion duration class NDVI increases with mud content at most sites (Figure 6).

An ANOVA model was constructed to disentangle the effects of emersion duration and sediment type on NDVI. Mean NDVI depends on site ($F_{6,40364}$ = 883, $P < 0.001$), and on emersion ($F_{4,40364}$ = 9315, $P < 0.001$), sediment type ($F_{1,40364}$ = 2101, $P < 0.001$) and their interaction ($F_{4,40364}$ = 120, $P < 0.001$). The model explains 62% of the variation (R^2 = 0.62, $F_{15,40364}$ = 4389, $P < 0.001$).

NDVI is not only higher in mud than in sand, but the peak bloom is also more pronounced in muddy sediments, with a few exceptions (such as site WAS) (Figure 7). Given similar sediment, NDVI increases with emersion duration, and seasonal variation is in some sites more pronounced in the upper intertidal zone, but the effect is minor when compared to the effect of sediment type (Figure 7). There is no clear evidence for a temporal shift in

bloom with increasing emersion duration or mud content.

Ecosystems with short mean emersion duration (such as sites THA and WAD) generally have a low long-term mean NDVI, whereas sites that are exposed longer (such as HUM) have higher long-term mean NDVI values (Figure 8A). The relationship between emersion duration and NDVI is significant in sand (Figure 8C), but not in mud (Figure 8B). Note that a large variation in mud content may be present within the sediment category 'mud'. Mud content in site EMS for example is much larger than in the other Dutch sites (Table 1). Regression equations of NDVI and emersion duration are not significantly different for muddy and sandy sediments (tested with a homogeneity of slopes model, and subsequent test for offset differences), except when a paired test is carried out (slope higher in mud than in sand). Corrected for emersion duration, sediment type and their interaction using ANOVA on a per pixel basis, residual NDVI is positive for sites OOS and EMS (that is, NDVI is higher than can be expected based on sediment type and emersion duration) and negative for sites WES and THA.

DISCUSSION

Satellite-Derived NDVI as a Proxy for Microphytobenthic Biomass

NDVI is used as a proxy for benthic Chl-a and in particular for intertidal microphytobenthic biomass. Ground-truthing in the Westerschelde showed a
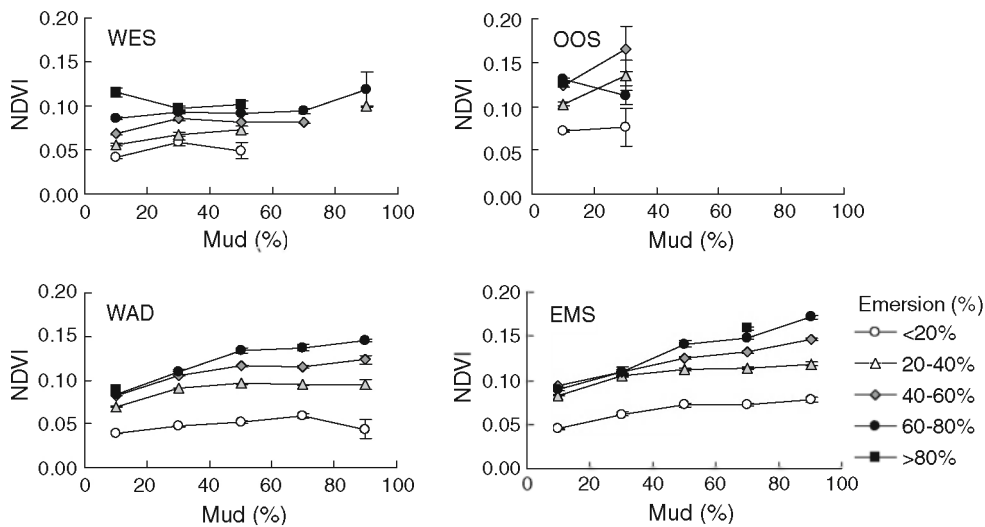
Figure 6. Long-term mean (±SE) NDVI as a function of mud content and emersion for the Dutch sites.
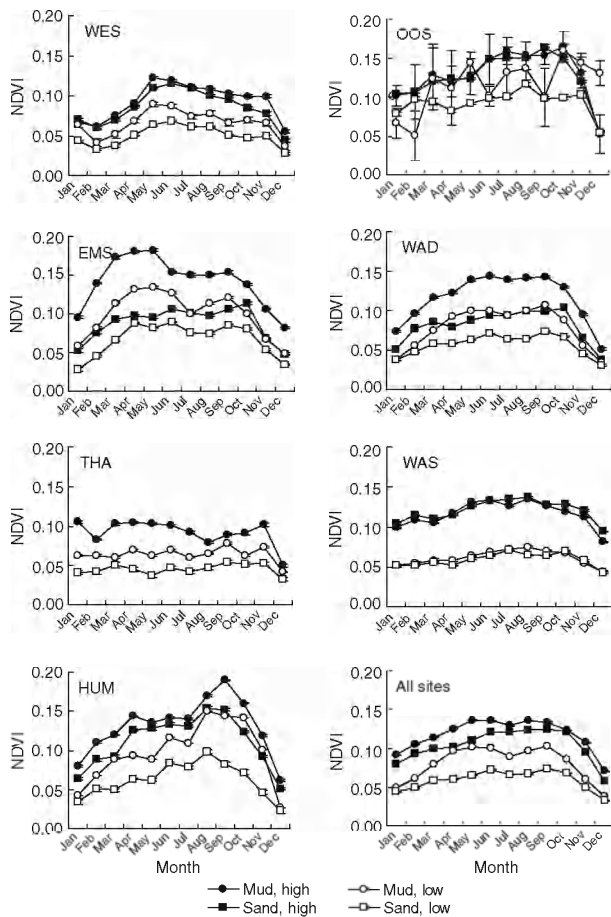

Figure 7. Seasonal variation in normal monthly (±SE) NDVI depending on sediment type (mud/sand) and emersion (low: < 50% emersion, high: ≥50% emersion).

significant coefficient of determination of about 50% between NDVI and Chl-a, both in space and in time. Correlations between in situ Chl-a and NDVI

derived from in situ or airborne sensors reported in the literature are comparably low (for example, Murphy and others 2005; Van der Wal and others 2008) or slightly higher (for example, Kromkamp and others 2006). Although there may be more effective spectral indices to retrieve Chl-a (for example, Murphy and others 2005; Serôdio and others 2009), performance of NDVI is found to be consistent within and across (temperate) estuaries (Kromkamp and others 2006).

The moderate correlation between NDVI and Chl-a in the sediment can be partly attributed to a mismatch in spatial support. In our study, each ground sample represents 4 cm^2 only, whereas each satellite pixel takes into account spatial variation in benthic algal biomass within an area of 250 by 250 m. Moreover, a number of factors may confound the satellite signal. At the subpixel scale, mixels with surface water will inevitably reduce NDVI. Low-density *Salicornia* stands will increase the NDVI in summer in a limited number of high shore places. In addition, shellfish beds and mussel cultivation plots may yield an increased NDVI locally; for example, mussel beds cover less than 1% of the intertidal area in site WAD (Beukema and Dekker 2007). Benthic algae consist of both microphytobenthos and macroalgae. However, even in the site with the highest abundance of macroalgae, that is site OOS, macroalgae contribute less than 10% and microphytobenthos more than 90% to the annual primary production of benthic algae (Nienhuis 1992). Thus, bare sediment and microphytobenthic biomass with varying biomass dominate all sites and NDVI is generally proportional to microphytobenthic biomass.

The satellite sensor can only detect Chl-a at the (near-)surface of the sediment, and therefore
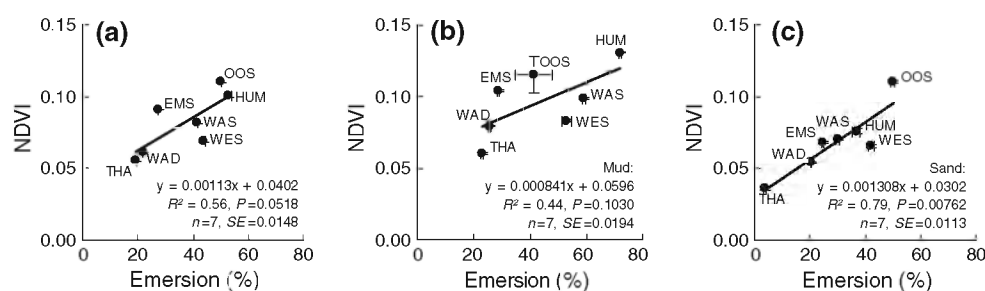
Figure 8. Long-term mean ($\pm$SE) NDVI as a function of mean ($\pm$SE) emersion percentage, for **A** entire sites, **B** muddy sediments only, and **C** sandy sediments only.

underestimates the total standing stock of microphytobenthos as sampled using cores. Light is more effectively absorbed in muddy sediments than in sand (Kühl and Jørgensen 1994), whereas sediment mixing is orders of magnitude higher in sand (Middelburg and others 2000), Chl-a concentration generally has a steep vertical gradient in mud and is relatively constant with depth in sand. A special feature of epipelic diatoms is their ability to migrate within the (mostly muddy) sediment with the tidal cycle (time after emersion) and daylight (solar zenith angle) (Pinckney and Zingmark 1991; Jesus and others 2009). Vertical migration of epipelic diatoms to the surface of the sediment causes an increase in NDVI until about 1 h after exposure, followed by a stabilization of NDVI during daytime emersion (Palmer and Round 1967; Paterson and others 1998). The satellite will capture this more or less stable state in NDVI with regard to daylight, but not necessarily with regard to emersion time. Note that tidal phasing is site-dependent (Serôdio and Catarino 1999). For example, low water springs occur consistently at dawn and dusk in the Thames and Ems estuaries.

Seasonal Variation in Microphytobenthos

We found a significant seasonal pattern in the dynamics of benthic algae in all ecosystems studied. Others have observed that microphytobenthic biomass can vary seasonally as a function of temperature, irradiance, nutrient concentrations, and resuspension, resulting in an increase in spring and/or autumn, and a decrease in summer generally attributed to an increase in grazing by benthic fauna (Admiraal and Peletier 1980; Colijn and Dijkema 1981; Underwood 1994; MacIntyre and others 1996; Blanchard and others 1997), although in some (temperate) ecosystems no seasonal variation is found (for example, Brotas and others 1995; Thornton and others 2002; Méléder and others 2007). Santos and others (1997) attributed the contradictive findings in seasonality to the fact that many in situ studies are based on sampling

schedules of once or twice a month, despite a large daily and weekly/fortnightly variation in microphytobenthos. Our method, binning daily NDVI values per month, allowed an unequivocal study of seasonal variations.

In the open coast intertidal flats of the Thames (seasonal), variations in NDVI were small, suggesting that local factors could be more important in regulating microphytobenthic biomass. Lack of seasonality in microphytobenthic biomass in the nearby Colne estuary was attributed to severe grazing pressure throughout the year (Thornton and others 2002).

Spatial differences in the onset of the microphytobenthic bloom have been attributed to differences in emersion duration, and hence, in turbid waters, irradiance (Admiraal and others 1984), but this effect was not found at the ecosystem scale in our study. Spatial differences in the magnitude and timing of seasonality have also been attributed to species composition of the diatom assemblages (Admiraal and others 1984; Underwood 1994; Sahan and others 2007). Sandy sediments, generally found in more exposed areas, contain proportionally more epipsammic algae (attached to the substrate), whereas muddy sediments, generally dominating areas sheltered from current and wave action, contain more (mobile) epipelic algae (Round 1971; Paterson and Hagerthey 2001), although such assemblage differences also occur in similar sediments (Underwood 1994). Epipelic assemblages show higher seasonal variability in diatom diversity and biomass than epipsammic assemblages (Underwood 1994; Hamels and others 1998; Sahan and others 2007). Our study confirmed that seasonal variation for a given site was largest in mud, and seasonal variation was limited in exposed sites such as those in the Thames and the Wash. Note that NDVI may be sensitive to the background properties of the sediment surface (Huete and others 1985; Combe and others 2005, but see Murphy and others 2005), such as mud content, which may itself show seasonal variation, with highest values typically found in early au-

tumn (Van der Wal and Herman 2007; Van der Wal and others 2008). This effect was not obvious from our results. Mud content can also vary over the years, limiting the applicability of a single sediment survey as used in our study, although broad patterns in sediment characteristics persist for years (Van der Wal and Herman 2007).

Year-to-Year Variation in Microphytobenthos

Interannual changes in benthic algal biomass were small relative to their seasonal dynamics. Part of the year-to-year variation operated on a large spatial scale, in parallel in different ecosystems in the Netherlands, demonstrating regional synchrony. This synchrony was mainly driven by the wind/wave climate: winds/waves had a negative effect on benthic algal biomass, which was most pronounced in the upper intertidal zone. The influence of wind/wave climate on benthic algae biomass can thus be substantial even in tide-dominated estuaries such as the Oosterschelde and Westerschelde. Two mechanisms may be responsible for the negative correlation of wind velocity and NDVI. First, increased inundation due to wave set-up would limit the effective photoperiod (length of time available for photosynthesis). Second, increased wind velocities may induce resuspension. Resuspension of benthic algae by turbulence and shear stress generated by waves and currents and subsequent transport by currents can be substantial in wave-dominated estuaries and lagoons (Demers and others 1987; De Jonge and Van Beusekom 1995), but also in very shallow waters in tide-dominated estuaries (Baillie and Welsh 1980; Lucas 2003). Field observations show that this can drastically reduce microphytobenthic biomass, generally followed by a recovery period of one or more weeks (Colijn and Dijkema 1981; Admiraal and others 1984; Underwood 1994; Blanchard and others 1997; De Brouwer and others 2000).

Apart from wind/wave climate, temperature anomalies in the 6-year period studied were a significant driver for anomalies in NDVI. Low temperatures (and days of air frost) accounted for regional synchrony in algal biomass in the winter half-year in the two most northern (coldest) British sites. This is in accordance with most previous studies that show a positive effect of temperature on algal growth up to a maximum temperature (Blanchard and others 1997), although other studies demonstrate little effect of temperature (Admiraal and Peletier 1980) or a more complex regulation by temperature, for example by influencing grazing pressure (Thompson and others 2004).

In the Thames, anomalies in meteorology and NDVI were not correlated, in accordance with the limited seasonality in benthic algal biomass found.

Spatial Variation in Microphytobenthos

Microphytobenthic biomass varies across spatial scales. At very small spatial scales (centimeters), patchiness of microphytobenthos is generally attributed to interspecies interactions, notably grazing (Saburova and others 1995; Murphy and others 2008). Variability on intermediate scales (centimeters to tens of meters) has been associated with the interplay of sediment, microtopography, and diatoms (Plante and others 1986; Saburova and others 1995; Blanchard and others 2000). The limited number of in situ studies carried out at the whole ecosystem scale demonstrated the presence of patterns in microphytobenthic biomass at these large spatial scales (tens of meters to kilometers) (Guarini and others 1998). In a study in the Tagus estuary in Portugal, Brotas and others (1995) showed that approximately 62% of the variability of microphytobenthic biomass at this scale could be explained by sediment type and elevation.

Our study highlighted the large scale patterns in microphytobenthic biomass and showed that the position in the tidal frame (emersion duration) and sediment type largely explained their spatial variability within ecosystems. Our study also demonstrated, for the first time, that these factors explain spatial variability across ecosystems (thus, at a scale of about 100–1000 km). A similar amount of variance was explained within and across the ecosystems, and explained variance was comparable to that reported by Brotas and others (1995) for the Tagus estuary. At still larger spatial scales, latitude effects (for example, temperature gradients and day length) may become more important.

The increase in NDVI with increasing emersion duration may be associated with lower water contents for sediments on the higher shores, facilitating algal growth (Underwood and Paterson 1993). However, it also suggests that light is a limiting factor for benthic algal growth in all sites. Less light attenuation in the Oosterschelde could explain the larger NDVI values when corrected for emersion duration and sediment type, across the entire tidal frame (combined with the higher proportion of benthic macroalgae). Note that in such clear waters, positive NDVI values may occur even if there is overlying water, making the estimates of benthic algae biomass and the emersion maps unreliable here.

Our study also confirmed the results of in situ studies, reporting lower biomasses of microphytobenthos in sand than in mud (MacIntyre and others 1996). This can be partly explained by a difference in microphytobenthic species composition and their life traits. In addition, sands tend to be lower in nutrients and resuspension losses and grazing pressure may be higher (Underwood and Paterson 1993; De Jong and De Jonge 1995; Underwood and Kromkamp 1999; Herman and others 2001), all contributing to a lower microphytobenthic standing stock.

CONCLUSIONS

The satellite-derived time-series of NDVI have provided information on the spatiotemporal distribution of benthic algae with an unrivalled spatial extent. The results demonstrate an interannual regional synchrony (superimposed on a seasonal cycle) in intertidal microphytobenthic biomass across a number of ecosystems, mainly driven by the wind/wave climate and to some extent by temperature, and reveal that the long-term averaged biomass of benthic algae can be well explained by emersion percentage and sediment type, both within and across ecosystems. The results imply that effects on microphytobenthic biomass and primary production can be anticipated when the position of the mudflats and sandflats in the tidal frame is altered, for example due to sea level rise. In addition, increased storminess will result in a large-scale decrease of benthic algae biomass, either through resuspension or through a reduction of the effective emersion duration.

ACKNOWLEDGMENTS

OPEN ACCESS

REFERENCES

Admiraal W, Peletier H. 1980. Influence of seasonal variations of temperature and light on the growth rate of cultures and natural populations of intertidal diatoms. Mar Ecol Prog Ser 2:35–43.

Admiraal W, Peletier H, Brouwer T. 1984. The seasonal succession patterns of diatom species on an intertidal mudflat: an experimental analysis. Oikos 42:30–40.

Aldridge JN, Trimmer M. 2009. Modelling the distribution and growth of 'problem' green seaweed in the Medway estuary, UK. Hydrobiologia 629:107–22.

Baillie PW, Welsh BL. 1980. The effect of tidal resuspension on the distribution of intertidal epipelic algae in an estuary. Estuarine Coast Mar Sci 10:165–80.

Bates BC, Kundzewics ZW, Wu S, Palutikof JP (Eds). 2008. Climate change and Water. Technical Paper IPCC. Geneva: IPCC Secretariat.

Behrenfeld MJ, O'Malley RT, Siegel DA, McClain ChR, Sarmiento JL, Feldman GC, Millignan AJ, Falkowski PG, Letelier RM, Boss ES. 2006. Climate-driven trends in contemporary ocean productivity. Nature 444:752–5.

Beukema JJ, Essink K. 1986. Common patterns in the fluctuations of macrozoobenthis species living at different places on tidal flats in the Wadden Sea. Hydrobiologia 142:199–207.

Beukema JJ, Dekker R. 2007. Variability in annual recruitment success as a determinant of long-term and large-scale variation in annual production of intertidal Wadden Sea mussels (*Mytilus edulis*). Helgol Mar Res 61:71–86.

Blanchard GF, Guarini J-M, Gros P, Richard P. 1997. Seasonal effect on the relationship between the photosynthetic capacity of intertidal microphytobenthos and temperature. J Phycol 33:723–8.

Blanchard GF, Paterson DM, Stal LJ, Richard P, Galois R, Huet V, Kelly J, Honeywill C, de Brouwer J, Dyer K, Christie M, Seguignes M. 2000. The effect of geomorphological structures on potential biostabilisation by microphytobenthos on intertidal mudflats. Cont Shelf Res 20:1243–56.

Brotas V, Cabrita T, Portugal A, Serôdio J, Catarino F. 1995. Spatio-temporal distribution of the microphytobenthic biomass in intertidal flats of Tagus Estuary (Portugal). Hydrobiologia 300–301:93–104.

Cahoon LB. 1999. The role of benthic microalgae in neritic ecosystems. Oceanogr Mar Biol Annu Rev 37:47–86.

Colijn F, Dijkema KS. 1981. Species composition of benthic diatoms and distribution of chlorophyll a on an intertidal flat in the Dutch Wadden Sea. Mar Ecol Prog Ser 4:9–21.

Combe J-P, Launeau P, Carrère V, Despan D, Méléder V, Barillé L, Sotin C. 2005. Mapping microphytobenthos biomass by non-linear inversion of visible-infrared hyperspectral images. Remote Sens Environ 98:371–87.

De Brouwer JFC, Bjelic S, De Deckere EMGT, Stal LJ. 2000. Interplay between biology and sedimentology in a mudflat (Biezelingse Ham, Westerschelde, The Netherlands). Cont Shelf Res 20:1159–77.

De Jong DJ, De Jonge VN. 1995. Dynamics and distribution of microphytobenthic chlorophyll-a in the Western Scheldt estuary (SW Netherlands). Hydrobiologia 311:21–30.

De Jonge VN, Van Beusekom JEE. 1995. Wind and tide induced resuspension of sediment and microphytobenthos in the Ems estuary. Limnol Oceanogr 40:766–78.

Demers S, Therriault J-C, Bourget E, Bah A. 1987. Resuspension in the shallow sublittoral zone of a macrotidal estuarine environment: wind influence. Limnol Oceanogr 32:327–39.

Devlin MJ, Barry J, Mills DK, Gowen RJ, Foden J, Sivyer D, Tett P. 2008. Relationships between suspended particulate material, light attenuation and Secchi depth in UK waters. Estuar Coast Shelf Sci 79:429–39.

Gattuso J-P, Gentili B, Duarte CM, Kleypas JA, Middelburg JJ, Antoine D. 2006. Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and their distribution to primary production. Biogeosciences 3:489–513.

Guarini J-M, Blanchard GF, Bacher C, Gros P, Riera P, Richard P, Gouleau D, Galois R, Prou J, Sauriau PG. 1998. Dynamics of spatial patterns of microphytobenthic biomass: inferences from a geostatistical analysis of two comprehensive surveys in Marennes-Oléron Bay (France). Mar Ecol Prog Ser 166:131–41.

Guarini J-M, Sari N, Moritz C. 2008. Modelling the dynamics of the microalgal biomass in semi-enclosed shallow-water ecosystems. Ecol Model 211:267–78.

Hamels I, Sabbe K, Muylaart K, Barranguet C, Lucas C, Herman P, Vyverman W. 1998. Organisation of microbenthic communities in intertidal estuarine flats, a case study from the Molenplaat (Westerschelde estuary, the Netherlands). Eur J Protistol 34:308–20.

Harley CDG, Hughes AR, Hultgren KM, Miner BH, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L, Williams SL. 2006. The impacts of climate change in coastal marine systems. Ecol Lett 9:228–41.

Heip CHR, Goosen NK, Herman PMJ, Kromkamp J, Middelburg JJ, Soetaert K. 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanogr Mar Biol Annu Rev 33:1–149.

Herman PMJ, Middelburg JJ, Van de Koppel J, Heip CHR. 1999. Ecology of estuarine macrobenthos. Adv Ecol Res 29:195–240.

Herman PMJ, Middelburg JJ, Heip CHR. 2001. Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. Cont Shelf Res 21:2055–71.

Holland AF, Zingmark RG, Dean JM. 1974. Quantitative evidence concerning the stabilization of sediments by marine benthic diatoms. Mar Biol 27:191–649.

Huete A, Didnan K, Miura T, Rodriguez EP, Gao X, Ferreira LG. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sens Environ 83:195–213.

Huete AR, Jackson RD, Post DF. 1985. Spectral response of a plant canopy with different soil backgrounds. Remote Sens Environ 17:37–54.

Jesus B, Brotas V, Ribeiro L, Mendes CR, Cartaxana P, Paterson DM. 2009. Adaptations of microphytobenthos assemblages to sediment type and tidal position. Cont Shelf Res 29:1624–34.

Kromkamp JC, Morris EP, Forster RM, Honeywill C, Hagerthey S, Paterson DM. 2006. Relationship of intertidal surface sediment chlorophyll concentration to hyperspectral reflectance and chlorophyll fluorescence. Estuaries Coasts 29:183–96.

Kühl M, Jørgensen BB. 1994. The light field of microbenthic communities: radiance distribution and miscroscale optics of sandy coastal sediments. Limnol Oceanogr 39:1368–98.

Liebhold A, Koenig WD, Bjørnstad ON. 2004. Spatial synchrony in population dynamics. Annu Rev Ecol Evol Syst 35:467–90.

Lucas C. 2003. Observations of resuspended diatoms in the turbid tidal edge. J Sea Res 50:301–8.

MacIntyre HL, Geider RJ, Miller DC. 1996. Microphytobenthos: the ecological role of the 'secret garden' of unvegetated shallow water marine habitats. I. Distribution, abundance and primary production. Estuaries 19:186–201.

Méléder V, Rincé Y, Barillé L, Gaudin P, Rosa P. 2007. Spatiotemporal changes in microphytobenthos assemblages in a macrotidal tidal flat (Borgneuf Bay, France). J Phycol 43:1177–90.

Middelburg JJ, Barranguet C, Boschker HTS, Herman PMJ, Moens T, Heip CHR. 2000. The fate of intertidal microphytobenthos carbon: an in-situ 13C labelling study. Limnol Oceanogr 45:1224–34.

Miller DC, Geider RJ, MacIntyre HL. 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats II. Role in sediment stability and shallow-water food webs. Estuaries 19:202–12.

Murphy RJ, Tolhurst TJ, Chapman MG, Underwood AJ. 2005. Estimation of surface chlorophyll-a on an emersed mudflat using field spectrometry: accuracy of ratios and derivative-based approaches. Int J Remote Sens 26:1835–59.

Murphy RJ, Tolhurst TJ, Chapman MG, Underwood AJ. 2008. Spatial variation of chlorophyll on estuarine mudflats determined by field-based remote sensing. Mar Ecol Prog Ser 365:45–55.

Nienhuis PH. 1992. Eutrophication, water management and the functioning of Dutch estuaries and coastal lagoons. Estuaries 15:538–48.

Palmer JD, Round FE. 1967. Persistent, vertical migration rhythms in benthic microflora. VI. The tidal and diurnal nature of the rhythm in the diatom *Hantzschia virgata*. Biol Bull 132:44–55.

Paterson DM, Hagerthey SE. 2001. Microphytobenthos in contrasting coastal ecosystems: biology and dynamics. In: Reise K, Ed. Ecological comparisons of sedimentary shores. Heidelberg: Springer. p 105–21.

Paterson DM, Wiltshire KH, Miles A, Blackburn J, Davidson I, Yates MG, McGrortym S, Eastwood JA. 1998. Microbiological mediation of spectral reflectance from intertidal cohesive sediments. Limnol Oceanogr 43:1207–21.

Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker CJ, Stenseth NC. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends Ecol Evol 20:503–10.

Pinckney J, Zingmark RG. 1991. Effects of tidal stage and sun angles on intertidal benthic microalgal productivity. Mar Ecol Prog Ser 76:81–9.

Pinckney J, Zingmark RG. 1993. Biomass and production of benthic microalgae communities in estuarine habitats. Estuaries 16:887–97.

Plante R, Plante-Cuny M-R, Reys J-P. 1986. Photosynthetic pigments of sandy sediments on the north Mediterranean coast: their spatial distribution and its effect on sampling strategies. Mar Ecol Prog Ser 34:133–41.

Rijkswaterstaat. 2006. Monitoring van de effecten van de verruiming 48'/43' (MOVE). Report RIKZ/2007.003.

Round FE. 1971. Benthic marine diatoms. Oceanogr Mar Biol Annu Rev 9:83–139.

Saburova MA, Polikarpov IG, Burkovsky IV. 1995. Spatial structure of an intertidal sandflat microphytobenthic com-

munity as related to different spatial scales. Mar Ecol Prog Ser 129:229–39.

Sahan E, Sabbe K, Creach V, Hernandez-Raquet G, Vyverman W, Stal LJ, Muyzer G. 2007. Community structure and seasonal dynamics in diatom biofilms and associated grazers in intertidal mudflats. Aquat Microb Ecol 47:253–66.

Santos PJP, Castel J, Souzasantos LP. 1997. Spatial distribution and dynamics of microphytobenthos biomass in the Gironde estuary (France). Oceanol Acta 20:549–56.

Serôdio J, Catarino F. 1999. Fortnightly light and temperature variability in estuarine intertidal sediments and implications for microphytobenthos primary productivity. Aquat Ecol 33:235–41.

Serôdio J, Cartaxana P, Coelho S, Vieira S. 2009. Effects of chlorophyll fluorescence on the estimation of microphytobenthos biomass using spectral reflectance indices. Remote Sens Environ 113:1760–8.

Thompson RC, Norton TA, Hawkins SJ. 2004. Physical stress and biological control regulate the producer-consumer balance in intertidal biofilms. Ecology 85:1372–82.

Thornton DCO, Dong LF, Underwood GJC, Nedwell DB. 2002. Factors affecting microphytobenthic biomass, species composition and production in the Colne Estuary (UK). Aquat Microb Ecol 27:285–300.

Tucker CJ. 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sens Environ 8:127–50.

Underwood GJC. 1994. Seasonal and spatial variation in epipelic diatom assemblages in the Severn estuary. Diatom Res 9:451–72.

Underwood GJC, Paterson DM. 1993. Seasonal changes in diatom biomass, sediment stability and biogenic stabilization in the Severn estuary. J Mar Biol Assoc UK 73:871–87.

Underwood GJC, Kromkamp J. 1999. Primary production by phytoplankton and microphytobenthos in estuaries. Adv Ecol Res 29:93–153.

Van der Wal D, Herman PMJ. 2007. Regression-based synergy of optical, shortwave infrared and microwave remote sensing for monitoring the grain-size of intertidal sediments. Remote Sens Environ 111:89–106.

Van der Wal D, Herman PMJ, Forster RM, Ysebaert T, Rossi F, Knaeps E, Plancke YMG, Ides SJ. 2008. Distribution and dynamics of intertidal macrobenthos predicted from remote sensing: response to microphytobenthos and environment. Mar Ecol Prog Ser 367:57–72.

Van Leeuwen JD, Huete AR, Laing TW. 1999. MODIS vegetation index compositing approach: a prototype with AVHRR data. Remote Sens Environ 69:264–80.