

# Diatom-based tidal-level transfer functions as an aid in reconstructing Quaternary history of sea-level movements in the UK

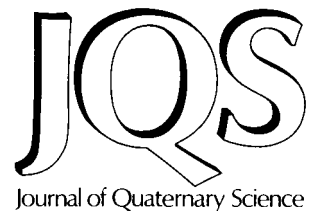
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**ABSTRACT:** This research analyses the diatom assemblages recorded from six UK coastal sites and relates these diatom assemblages to tidal levels. The relationship between diatom assemblages and tidal levels is examined statistically in order to develop a diatom-based tidal-level transfer function. The results suggest that there is highly significant correlation between the diatom assemblages and water levels from mean high water of neap tides to highest astronomical tide ( $p = 0.01$ , 99 random permutations). A weighted average (WA) transfer function is thus established, and the predictive ability of this transfer function is highly satisfactory. Finally, this transfer function is applied successfully to estimate palaeotidal-levels from fossil diatom data recorded in late Holocene coastal sequences. Copyright © 1999 John Wiley & Sons, Ltd.



**KEYWORDS:** diatoms; transfer function; saltmarsh; tidal flat; water level.

## Introduction

Although the general ecology of many coastal diatoms is known (e.g. Hendey, 1964; McIntire and Moore, 1977; Denys, 1991–2; Vos and de Wolf, 1993), the understanding of the habitat preferences, particularly in coastal saltmarshes where terrestrial and marine systems intersect, is limited (Zong, 1997). Previous investigations of diatom distribution across coastal saltmarshes include the work of Carter (1932–33), Round (1960), Riznyk (1973), Whiting and McIntire (1985), Hall and Fisher (1985) and Sullivan (1975, 1978, 1982). There are, however, differing opinions regarding the influence on diatom distributions of altitude relative to the tidal frame. The works of Nelson and Kashima (1993), Hemphill-Haley (1996), Shennan *et al.* (1995, 1996), Zong (1997) and Zong and Horton (1998) suggest a strong vertical zonation of diatom species. This concept implies that all environmental variables that determine diatom distribution are related to tidal submergence, which, in turn, is correlated with altitude of the marsh surface. Accordingly, sedentary organisms of saltmarshes are distributed in clearly identifiable

vertical zones. In contrast, other research has suggested that additional environmental factors also influence diatom distributions. These include the level of nutrients and pH (Denys, 1991–2), type of substrate (Chapman, 1941) and water salinity (Juggins, 1992, Vos and de Wolf, 1993).

The comprehensive ecological classifications of coastal diatoms, particularly for salinity and life form (e.g. Denys, 1991–2; Vos and de Wolf, 1993) have been widely used for diatom-based sea-level studies (e.g. Haggart, 1986; Long, 1992; Plater and Shennan, 1992; Robinson, 1993; Shennan *et al.*, 1995, 1996; Zong and Tooley, 1996; Zong, 1992). In these studies, diatom data were used only to validate sea-level index points, rather than reconstructing palaeo-sea-level. As a result, the indicative meaning of sea-level index points was defined only qualitatively by assessing the relationship between macrofossil remains such as *Phragmites* roots and stems, sediment types and their associated water levels (Shennan, 1982, 1986). Clearly, the quality of these studies relies on the precision of palaeo-sea-level reconstructions, and can be enhanced by a better understanding of the contemporary diatom distributions across upper intertidal zones from where sea-level data are derived.

To develop a new generation of high-resolution sea-level reconstructions we need to quantify the indicative meaning. This study develops a transfer function based on the relationship between diatom assemblages and altitudinal data collected from coastal sites within the UK. For a transfer function to be developed for altitude, the variable should explain a significant part of the total variation of the diatom data. Therefore, the objectives of this study are as follows.

1. To test the hypothesis that diatom assemblages are related

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to altitude. To facilitate comparisons between coastal sites that have different altitudes compared with the tidal frame, the altitudinal data were expressed as a standardised water-level index (SWLI). This is the function of local mean tide level (MTL) and mean highwater of spring tides (MHWST).

2. To create a training set containing a wide range of contemporary coastal environments to ensure that most fossil assemblages have a modern analogue. This will enable the production of a transfer function that is applicable to the user community on a regional scale and enables a range of former sea-levels from a variety of sedimentary environments to be reconstructed without the need for a local or seasonal surface study, which is beyond the scope of most investigations of fossil sequences.

## Site description

The investigations were carried out from 1993 to 1997 at a number of coastal sites in the UK. Three criteria have been used for site selection: differential tidal range, a clear vegetational succession and, most importantly, environmental conditions that are similar to those of fossil sites around the UK from which most sea-level data are obtained. As a result, six sites were selected, with three from estuarine environments, two from coastal embayments and one from a lagoonal site. The six sites under current investigation cover all three 'natural types' of saltmarsh in Britain as defined by Adam (1978). The location and general features of the six sites are shown in Fig. 1 and Table 1, respectively. The morphological and sedimentary details along the sampling transects and the description of the vascular-plant vegetation zones are illustrated in Fig. 2 and Table 2.

### Sites from estuaries

The first site investigated is from the eastern shore of the Nith estuary across a saltmarsh approximately 150 m wide. The lower edge is bounded by a small cliff approximately 1 m in height, and the upper end, passing into a narrow upland zone, is bounded by a coastal road. The small cliff accounts for the absence of a traditional pioneer marsh zone at this site. The river Nith is one of the main rivers draining from southern Scotland into the Solway Firth. Its position in the inner Solway Firth accounts for its macrotidal environment, with a spring tidal range of ca. 7.25 m. This has led to the development of very extensive intertidal sand and mudflats at the mouth of the Nith estuary extending many kilometres into the Solway Firth itself. The high freshwater output of the Nith combined with the large tidal amplitude produces a wide range in salinity within the estuary (5‰ to 25‰).

The second site, Roudsea Marsh, is located towards the head of the Leven estuary, northern part of Morecambe Bay. The marsh lies within a small embayment along the southwest border of a group of small hills of 10 m to 30 m high, which are covered by mixed deciduous forest. Solid rock outcrops occur at the northern and southern ends of the marsh. Hydrologically, the marsh is influenced mainly by discharges of freshwater from the Windermere catchment, and sea water from Morecambe Bay and the Irish Sea. Water

salinity during high spring tides varies between 5‰ to 25‰ (Zong, 1997), with a tidal range of 8.3 m (referring to Heysham Tide Gauge).

The third site is Cowpen Marsh, which is located within the Tees estuary, northeast coast of England, and has a mesotidal range of 4.6 m during spring tides. The majority of the estuarine intertidal flat has been reclaimed during the last two centuries mainly for industrial developments. The remaining saltmarsh under current study is confined within Greatham Creek, which is drained through Seal Sands into the mouth of the Tees estuary. The marsh displays a succession from mudflat through low marsh to high marsh. Salinity varies greatly (15‰ to 25‰) (Horton, in press) between tides as a result of the high volume of freshwater output from the Tees catchment.

### Coastal embayments

The fourth site is located on the west coast of Scotland. Kentra Bay, ca. 4 km<sup>2</sup> in size, is protected from waves by rocky outcrops and a narrow entrance. The floor of the bay is filled with fine-grained sediments and exposed entirely during low tides. On the northeastern fringe of Kentra Bay, the marsh is only 120 m wide but covers a range of environments from tidal flat, through pioneer, low and high marshes, to raised bog (upland) from which acidic runoff drains through the marsh into the bay. The amount of freshwater running into the Bay is minimal and seems to have little effect on the salinity of the incoming tides, which is usually as high as 33‰. The predicted range of spring tides is 4.4 m.

The fifth site was selected in Tramaig Bay of Jura, southwest Scotland. Tramaig Bay is a small, semi-circular tidal basin on the northeast coast of the Isle of Jura, protected by solid outcrops with a narrow inlet connecting to the Sound of Jura. The southern part of the basin displays an undisturbed continuum from pioneer saltmarsh through to mature freshwater fen, which is flat and poorly drained. This feature is mirrored on the northern side of the basin. However, the transition from upland to tidal flat over a distance of less than 20 m on the western side of the basin is interrupted by a narrow estate road. Although the basin is affected by a microtidal regime (ca. 1.6 m range at spring tides), it is completely isolated from the Sound, and a standing pool of saline water is left within the basin during low water of spring tides. Owing to the small output of freshwater from the upland, salinity within the basin is very close to that of sea water, with little variation between tides (>30‰).

### Lagoonal site

Thornham Marsh is the final site. It is located on the North Norfolk coast and is composed of extensive intertidal sand and mudflats, with a tidal range of 6.4 m. The saltmarsh studied has developed near the west end of shingle barriers. This saltmarsh is approximately 1 km in width and covers a wide range of environments, including mudflat and low, middle and high marshes. Freshwater input from the adjacent upland and the Fenland area produces a wide range of salinity in Thornham Marsh (15‰ to 25‰).

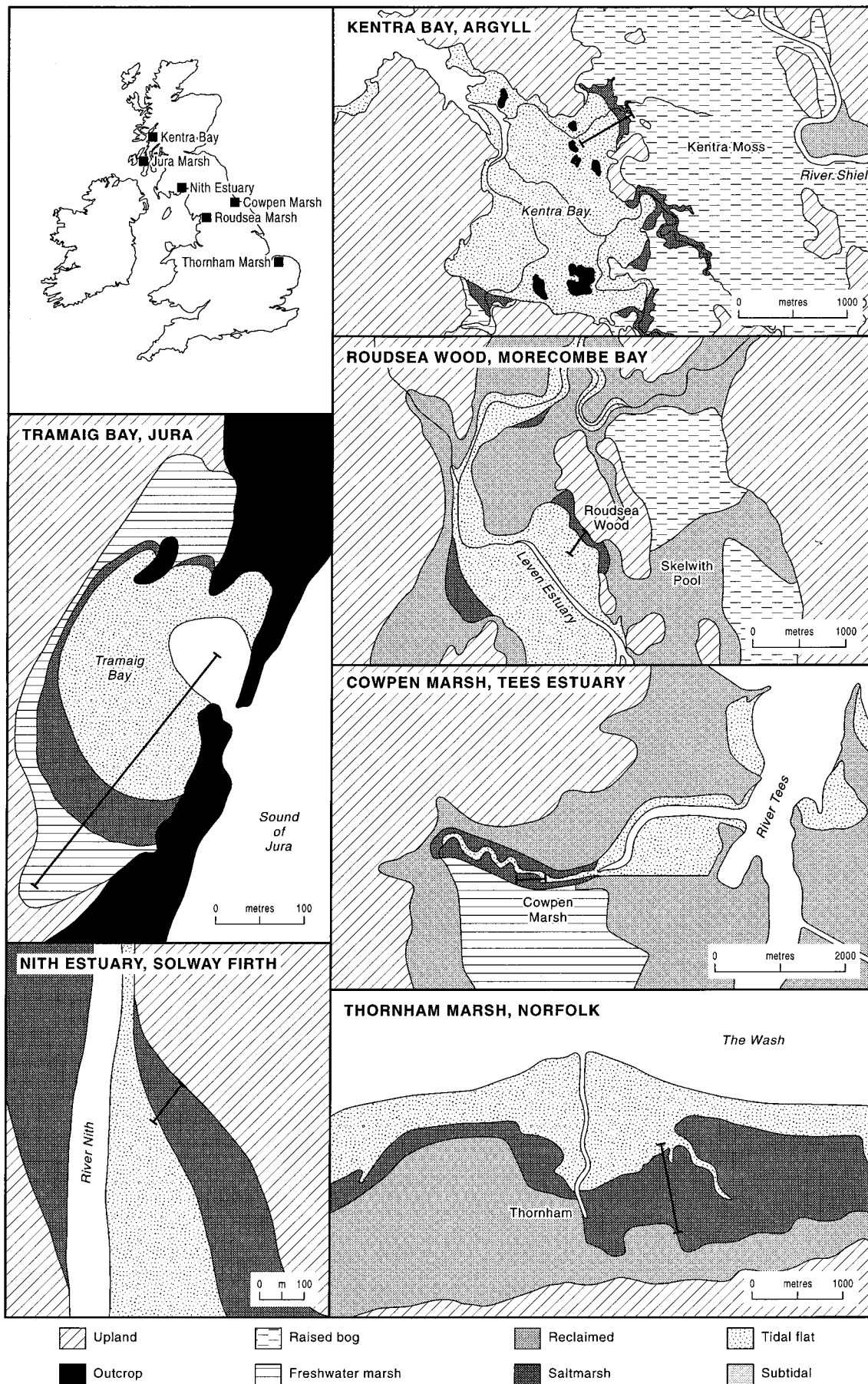
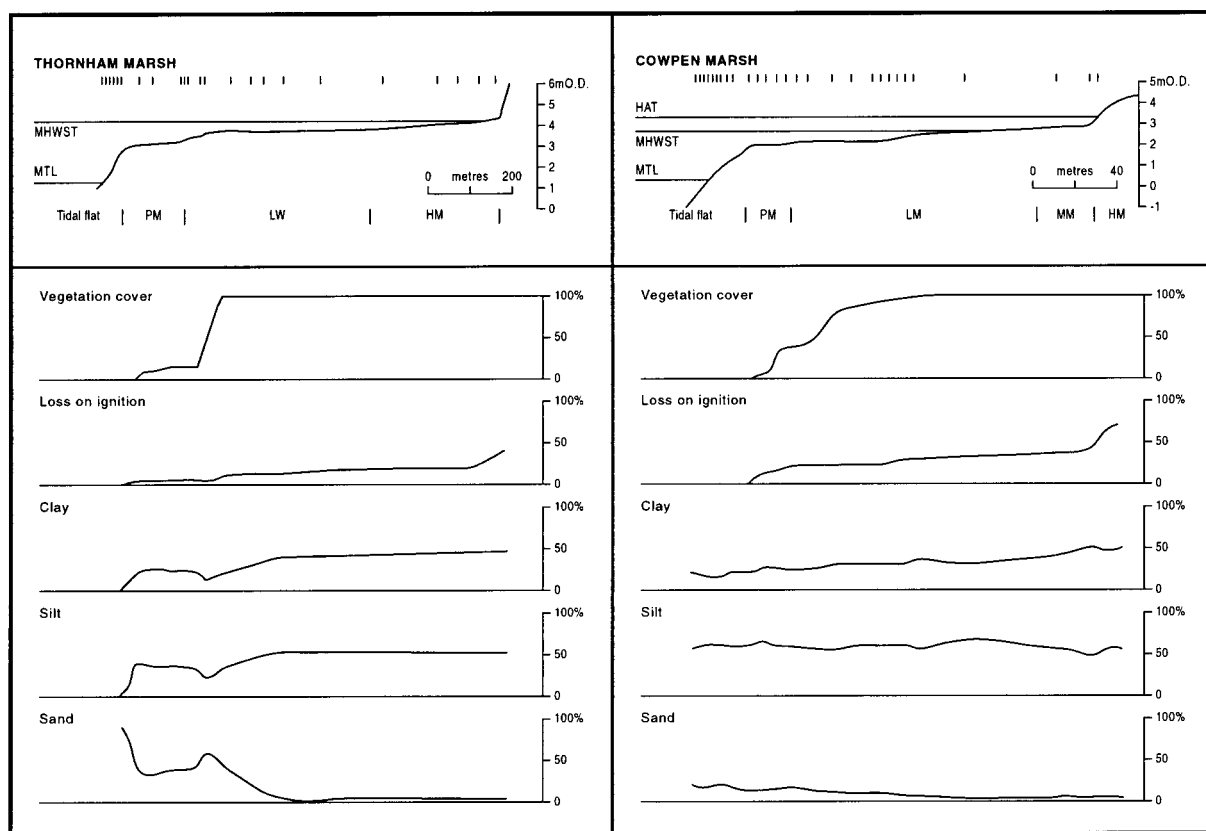


Figure 1 Location of the six coastal sites and details of each sampling transect.

**Table 1** Characteristics of the six coastal sites

Location	Tide (MHWST m OD)	Salinity (‰)	Site description
Kentra Bay, Morar	Meso (2.38)	>30	A sizeable embayment with a narrow entrance and little freshwater input
Tramaig Bay, Jura	Micro (0.98)	>30	A small embayment with a narrow entrance and little freshwater input
Nith Estuary, Solway	Macro (4.29)	5–25	East shore around the mid-reach of the Nith estuary
Roudsea Marsh, Morecambe Bay	Macro (4.70)	5–25	East shore adjacent to Roudsea Wood Nature Reserve at the top of the estuary
Cowpen Marsh, Tees estuary	Meso (2.65)	15–25	Within a small tidal creek connecting to the Tees estuary
Thornham Marsh, The Wash	Macro (3.35)	15–25	At the west end of the barrier system along the Norfolk coast

**Figure 2** Environmental variables measured from the six sites with an indication of sampling locations across each transect and reference water levels.

## Materials and methods

In order to represent the environmental gradient of interest, cross-marsh transects were arranged at each site from mud-flat, through low and high marshes, to upland above the local highest astronomical tide (HAT) (where possible). Sampling intervals were determined according to vegetation zones. At each sampling point, two samples were collected: an approximate 5 cm<sup>3</sup> volume (5 cm<sup>2</sup> surface sample by 1 cm thick, for diatom analysis); and an approximate 30 cm<sup>3</sup> volume (30 cm<sup>2</sup> surface sample by 1 cm thick, for substrate analysis). The samples were wrapped in plastic bags and

refrigerated for laboratory analyses, respectively. All sampling points were levelled relative to Ordnance Datum (the national datum for the UK).

## Diatom samples

Sediment samples were mixed in order to average seasonal effects, and a subsample was selected and prepared by normal procedures (Palmer and Abbott, 1986). It is likely that, in these relatively high-energy environments, the surface diatom assemblages at any sampling points are likely to be

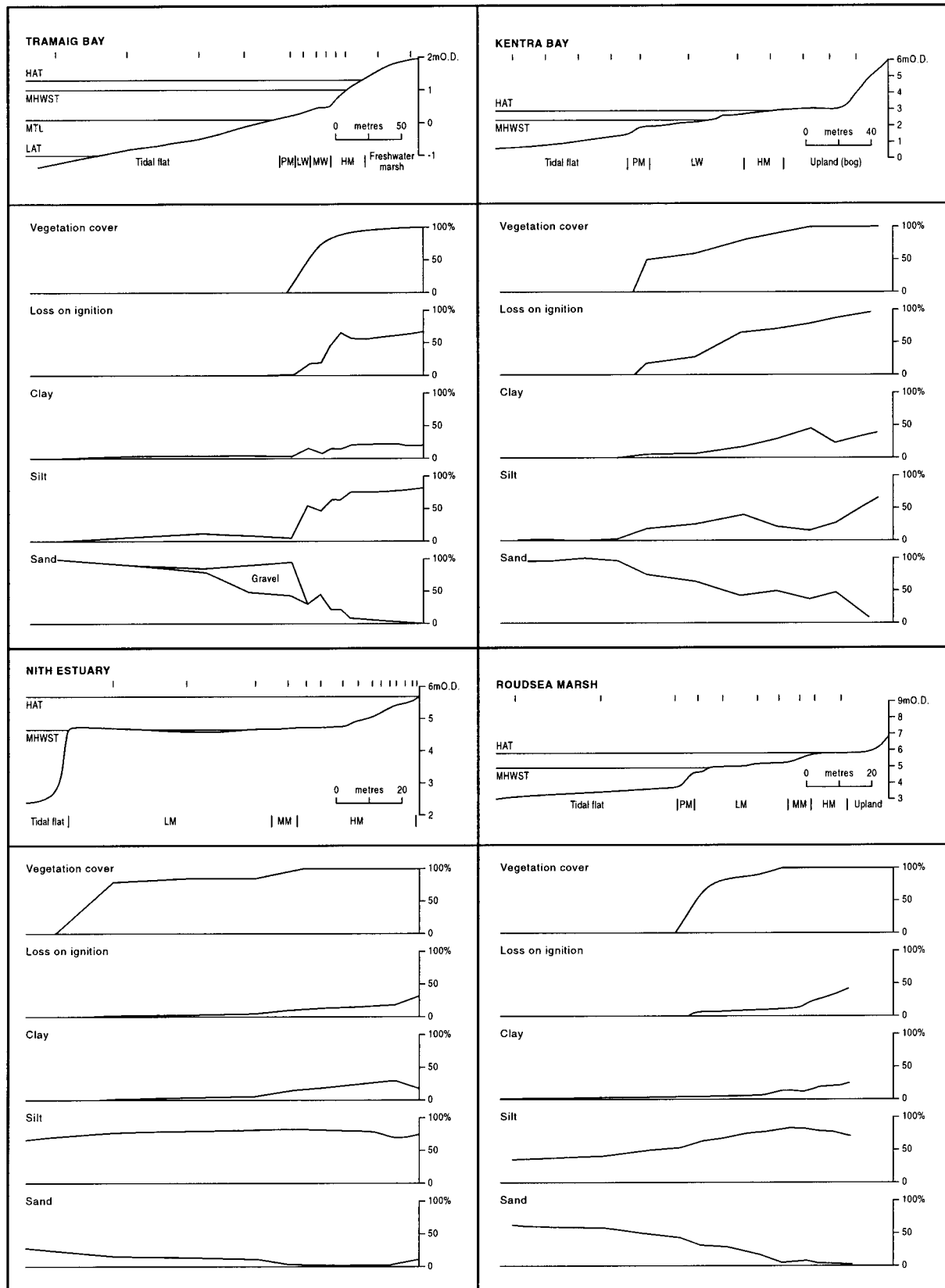


Figure 2 Continued.

a mixture of locally produced taxa and transported taxa. This, however, is not a problem because this study assumes that a mixture of allochthonous and autochthonous diatom valves would occur in sediments that accumulated in the past (Zong, 1997). Therefore, in this study, no attempt is made to separate the allochthonous component from the diatom assemblages.

All samples are composed of fine-grained sediments and diatom preservation is generally very good. As a result, a minimum count of 300 diatom valves was possible for all samples. All diatom valves were identified by reference mainly to Hendey (1964) and van de Werff and Huls (1958–66). Nomenclature of diatom species followed Hartley (1986), and their ecological classifications were based on

**Table 2** Vegetational zones of the six coastal sites

Marsh transect	Pioneer marsh	Low marsh	Mid-marsh	High marsh
Kentra Bay <sup>a</sup>	<i>Salicornia maritima</i> , <i>Armeria maritima</i>	<i>Puccinellia maritima</i> , <i>Plantago maritima</i> , <i>Armeria maritima</i>	Absent	<i>Puccinellia maritima</i> , Gramineae
Tramaig Bay <sup>b</sup>	<i>Spartina maritima</i>	<i>Puccinellia maritima</i> , <i>Armeria maritima</i>	<i>Puccinellia maritima</i> , <i>Glaux maritima</i> , <i>Armeria maritima</i>	<i>Juncus maritimus</i> , <i>Puccinellia maritima</i> , <i>Festuca ovina</i>
Nith Estuary	Absent	<i>Spartina Maritima</i> , <i>Aster tripolium</i> , <i>Triglochin maritima</i> , <i>Plantago maritima</i> , <i>Suaeda maritima</i>	<i>Juncus maritimus</i>	<i>Phragmites communis</i>
Roudsea Marsh <sup>c</sup>	<i>Spartina maritima</i> , <i>Suaeda maritima</i>	<i>Puccinellia maritima</i> , <i>Plantago maritima</i> , <i>Armeria maritima</i> , <i>Aster</i> <i>tripolium</i> , <i>Glaux</i> <i>maritima</i>	<i>Juncus maritimus</i> , <i>Festuca ovina</i> , <i>Plantago</i> <i>maritima</i> , <i>Puccinellia</i> <i>maritima</i>	<i>Phragmites communis</i> , <i>Atriplex sp.</i> , <i>Potentilla</i> <i>anserina</i>
Cowpen Marsh	<i>Salicornia europaea</i> , <i>Festuca ovina</i>	<i>Salicornia europaea</i> , <i>Festuca ovina</i> , <i>Plantago</i> <i>maritima</i> , <i>Aster</i> <i>tripolium</i> , <i>Suaeda</i> <i>maritima</i>	<i>Festuca ovina</i> , <i>Plantago</i> <i>maritima</i> , <i>Suaeda</i> <i>maritima</i> , <i>Limonium</i> <i>vulgare</i>	<i>Elytrigia atheria</i> , <i>Atriplex sp.</i>
Thornham Marsh	<i>Salicornia europaea</i> , <i>Suaeda maritima</i>	<i>Plantago maritima</i> , <i>Spergularia marina</i> , <i>Limonium vulgare</i>	<i>Elytrigia atherica</i> , <i>Spergularia marina</i> , <i>Puccinellia maritima</i>	Absent

<sup>a</sup>Upland vegetation includes *Agrostis sp.*, *Calluna vulgaris*, Gramineae and *Carex sp.*

<sup>b</sup>Freshwater marsh is composed of *Irish pseudacorus*, Gramineae, *Alnus glutinosa*, *Juncus sp.*, *Salix sp.* and *Rumex sp.*

<sup>c</sup>Upland vegetation includes *Betula sp.* and *Alnus glutinosa*.

Denys (1991–2) and Vos and de Wolf (1993). The diatom counts were converted as a percentage of total diatom valves counted (% TDV). The dominant diatom taxa (exceeding 10% TDV) are listed in Table 3.

## Substrate

Apart from altitude, the level of nutrients and pH, vascular-plant vegetation cover, water salinity and type of substrate are, to some extent, influential over the distribution of diatoms. Towards the landward end of the intertidal zone, where freshwater diatoms dominate the assemblages, most of the dominant diatom species recorded from contemporary estuarine marshes are eutrophic, reflecting the eutrophication of the estuarine water, possibly due to human activities in the catchment areas (Zong and Horton, 1998). Both eutrophic and oligotrophic taxa are recorded in high numbers from marshes of such coastal embayments as Kentra Bay where little human disturbance in its catchment (the raised bog) is evident although the saltmarsh itself has been grazed occasionally (e.g. Shennan *et al.*, 1995). As most of the marine and brackish water diatoms are not associated with a specific range of trophic conditions (Denys, 1991–2), this environmental variable is not included in this study.

The pH level of the ground-water can, to some extent, be influential. For example, the acidic runoff from the raised bog in Kentra Moss has supported the domination of *Eunotia valida*, an acidophilous taxon, in the diatom assemblages recorded around the altitude of the local HAT (e.g. Zong

and Horton, 1998). The pH level is not considered here, however, because coastal water is mostly neutral in acidity.

Vascular-plant vegetation cover is important due to the light requirements for the photosynthesis of diatoms. The diatom assemblages, however, are not always correlated to vascular-plant vegetation communities, and in fact, the epiphytic component within the diatom assemblages recorded from saltmarshes is very low (e.g. Nelson and Kashima, 1993; Hemphill-Haley, 1996; Zong, 1997). Thus, the percentage coverage of vascular plants was recorded from each site in order to characterise the sedimentary environment (Fig. 2), but is not taken as one of the environmental variables.

Water salinity along an estuary increases from its upper reach to the mouth. Strong correlation between diatom assemblages and the changes in water salinity along the Thames has been recorded (Juggins, 1992). Based on his data, Juggins (1992) developed a diatom-based salinity transfer function, which was applied to reconstruct palaeowater-salinity. However, along a cross section from tidal flat to saltmarsh, particularly in the upper intertidal zone, water salinity varies greatly according to tidal cycles and the seasons rather than tidal levels (Underwood, 1994). During each observation, little variation in water salinity across marsh transects was recorded (e.g. Zong, 1997; Horton, 1997). In this study, therefore, water salinity is not included.

Finally, substrate type in coastal environments seems more closely related to most diatom taxa. For example, the high frequencies of epipellic diatoms are associated with fine-grained (silt and clay) sediments, whereas sandy substrate is related to episammic taxa (e.g. Nelson and Kashima, 1993; Zong, 1997; Zong and Horton, 1998). It is therefore

**Table 3** Dominant diatom taxa (exceeding 10% TDV) recorded from the six coastal sites with their salinity classes indicated

	Tidal flat	Around MHWST (low marsh) <sup>a</sup>	Around HAT (high marsh) <sup>a</sup>	Upland
Kentra Bay	<i>Achnanthes delicatula</i> (B) <i>Delphineis surirella</i> (B) <i>Amphora marina</i> (B) <i>Opephora pacifica</i> (A)	<i>Achnanthes delicatula</i> (B) <i>Navicula flantica</i> (A) <i>Caloneis westii</i> (B) <i>Diploneis interrupta</i> (B) <i>Navicula peregrina</i> (B)	<i>Navicula pusilla</i> (D) <i>Pinnularia microstauron</i> (D) <i>Nitzschia fruticosa</i> (D)	<i>Eunotia valida</i> (E)
Tarmaig Bay	<i>Achnanthes delicatula</i> (B) <i>Cocconeis scutellum</i> (A) <i>Opephora pacifica</i> (A) <i>Navicula forcipata</i> (A) <i>Amphora marina</i> (B) <i>Navicula digitoradiata</i> (B)	<i>Achnanthes delicatula</i> (B), <i>Cocconeis scutellum</i> (B), <i>Navicula phyllepta</i> (B), <i>Navicula cari</i> var. <i>cincta</i> (C), <i>Eunotia exigua</i> (E), <i>Tabellaria flocculosa</i> (E)		<i>Navicula pupula</i> (D) <i>Eunotia exigua</i> (E) <i>Tabellaria flocculosa</i> (E)
Nith Estuary		<i>Delphineis surirella</i> (B) <i>Navicula phyllepta</i> (B) <i>Achnanthes delicatula</i> (B) <i>Navicula halophila</i> (B) <i>Navicula peregrina</i> (B) <i>Navicula salinarum</i> (B)	<i>Hantzschia amphioxys</i> (D) <i>Nitzschia fruticosa</i> (D) <i>Navicula mutica</i> (C) <i>Nitzschia tryblionella</i> (C) <i>Achnanthes delicatula</i> (B)	
Roudsea Marsh	<i>Delphineis surirella</i> (B) <i>Navicula flantica</i> (A) <i>Caloneis aemula</i> (B) <i>Odontella rhombus</i> (A)	<i>Navicula cari</i> var. <i>cincta</i> (C) <i>Navicula halophila</i> (B) <i>Delphineis surirella</i> (B)	<i>Diploneis ovalis</i> (D) <i>Achnanthes minutissima</i> (D) <i>Navicula pygmaea</i> (B) <i>Nitzschia fruticosa</i> (B) <i>Navicula mutica</i> (C) <i>Navicula viridula</i> (D)	
Cowpen Marsh	<i>Navicula phyllepta</i> (B) <i>Paralia sulcata</i> (A) <i>Navicula halophila</i> (B)	<i>Navicula halophila</i> (B) <i>Achnanthes delicatula</i> (B) <i>Navicula cari</i> var. <i>cincta</i> (C) <i>Nitzschia frustulum</i> (C) <i>Amphora marina</i> (B) <i>Navicula digitoradiata</i> (B)	<i>Navicula halophila</i> (B) <i>Navicula cryptocephala</i> (C) <i>Navicula mutica</i> (C) <i>Achnanthes minutissima</i> (D) <i>Nitzschia dubia</i> (C)	
Thornham Marsh	<i>Navicula digitoradiata</i> (B) <i>Achnanthes delicatula</i> (B) <i>Opephora pacifica</i> (A) <i>Navicula retusa</i> (A) <i>Trachyneis aspera</i> (A)	<i>Navicula digitoradiata</i> (B) <i>Nitzschia dubia</i> (C) <i>Denticula subtilis</i> (B) <i>Nitzschia tryblionella</i> (C)	<i>Navicula halophila</i> (B) <i>Nitzschia frustulum</i> (C) <i>Nitzschia hungarica</i> (C)	

<sup>a</sup>In most case, diatom assemblages associated with pioneer marsh are commonly grouped into either the tidal-flat zone or the low-marsh zone owing to its transitional nature. The same situation occurs in mid-marsh assemblages. A, polyhalobous; B, mesohalobous; C, oligohalobous halophile; D, oligohalobous indifferent; E, halophilous.

important to examine the effects of substrate type on intertidal diatom distribution. To characterise the diatom substrate, grain size and loss on ignition (LOI) were measured, and the results were included in the canonical correspondence analysis. The grain size and LOI analyses were performed following the methods proposed by Folk (1965) and Ball (1964), respectively.

### The relationship between diatom assemblages and altitude

The hypothesis that diatom assemblages are related to altitude is explored by canonical correspondence analysis (CCA) of diatom and environmental data from the coastal sites. Detrended canonical correspondence analysis (DCCA) of

the diatom assemblages has produced gradient lengths that indicate the unimodal nature of the diatom abundance data. Thus, unimodal-based methods such as CCA were used. Canonical correspondence analysis is a relatively new multi-variate technique that relates community composition to known variations in the environment (ter Braak, 1986, 1987; ter Braak and Verdonschot, 1995). Canonical correspondence analysis is used to extract synthetic environmental gradients from ecological data sets. The gradients are the basis for succinctly describing and illustrating the different habitat preferences (niches) of taxa via an ordination diagram.

The independence and relative strength of the major environmental gradients were estimated using a series of partial CCAs (see Borcard *et al.*, 1992) to separate the total variation in the diatom data into components representing: first, the unique contributions of individual environmental variables; second, the contribution of covariances between variables; and third, the unexplained variance. The statistical significance of the partial CCAs was determined using a Monte Carlo permutation test. The CCA analyses used the CANOCO program, release 3.12, (ter Braak, 1988, 1990).

The diatom assemblages, LOI and grain size from each coastal site used an identical taxonomy and constituents. Thus, the data sets were combined. However, the altitudes of each station from the six sites differ with respect to tidal range and were, therefore, reconstructed as a standardised water-level index (SWLI) using equation (1)

$$x_{ab} = [(A_{ab} - MTL_b) / (MHWST_b - MTL_b) \times 100] + 200 \quad (1)$$

where  $x_{ab}$  is the SWLI of station/tide level  $a$  at site  $b$ ;  $A_{ab}$  is the measured altitude (m OD) of station/tide level  $a$  at site  $b$ ;  $MTL_b$  is the mean tide-level (m OD) at site  $b$ ; and  $MHWST_b$  is the mean high water spring tide at site  $b$ . The addition of the constant (200) ensures that all reconstructed values within the training set are positive. For example  $x_{ab} = 300$  if the measured altitude of  $A_{ab}$  equals  $MHWST_b$ . Conversely,  $x_{ab} = 200$  if the measured altitude of  $A_{ab}$  equals  $MTL_b$ . Only diatom taxa that reach 5% of the total sum were included (following Fritz *et al.*, 1991).

## Diatom-based transfer functions

The second objective of this study was to express the value of SWLI as a function of a diatom assemblage. This operation is termed a transfer function (ter Braak, 1987) and the construction thereof is described as calibration (Birks, 1995). The transfer function will be applicable at a regional scale and enable a range of SWLIs from a variety of sedimentary environments to be reconstructed.

Numerous transfer functions have been developed to quantitatively reconstruct palaeoenvironmental variables. Some of these have a stronger ecological and/or statistical basis than others. Thus, some methods are more appropriate than others for quantifying the indicative meaning. The fundamental distinction between existing methods concerns the underlying taxon–environment response model (Birks, 1995). Detrended CCA of the training set with SWLI as the only environmental variable has produced a gradient length of 3.84 standard deviation units. This indicates a unimodal nature for the diatom abundance data with respect to SWLI. Thus, unimodal-based methods of regression and calibration were used.

This study developed diatom-based transfer functions using

weighted averaging (WA) regression and calibration with inverse and classical deshrinking (e.g. Birks *et al.*, 1990; Birks, 1995; Jones and Juggins, 1995; Gasse *et al.*, 1997). Weighted averaging was chosen in preference to WA partial least-squares (ter Braak and Juggins, 1993; Line *et al.*, 1994) because of the high noise level of the data (Line *et al.*, 1994; Horton, 1997).

Weighted-averaging and tolerance-downweighting WA transfer functions for SWLI were developed using the program CALIBRATE, release 0.70 (Juggins and ter Braak, 1992, 1997). The performance of the transfer functions was assessed in terms of root-mean square of the error of prediction (RMSEP) and squared correlation ( $r^2$ ) of observed versus predicted values. The RMSEP and  $r^2$  indicate the overall performance of the model, where the former indicates prediction errors and the latter measures the strength of the relationship of observed versus predicted values. This allows comparisons among transfer functions (Gasse *et al.*, 1995).

The two parameters were calculated as both 'apparent' measures in which the whole training set was used to generate the transfer function and assess the predictive ability, and jack-knifed or 'leave-one-out' measures (ter Braak and Juggins, 1993). Jack-knifing generates a prediction error (RMSEP<sub>jack</sub>) that is a measure of the overall predictive abilities of the training set. However, it does not provide sample-specific errors for each fossil sample (Birks, 1995). Bootstrapping can be used to derive a standard error of prediction (SE<sub>pred</sub>) (Birks *et al.*, 1990; Line *et al.*, 1994). The SE<sub>pred</sub> for an environmental variable in the past can vary from sample to sample depending upon the composition of the fossil assemblage and, thus, the presence or absence of taxa with a particularly strong signal for the environmental variable of interest (Birks, 1995). The SE<sub>pred</sub> was estimated using 1000 cycles with inverse and classical deshrinking regression. This computer intensive procedure used the program WACALIB, release 3.3 (Line *et al.*, 1994).

## Results and discussion

### Diatom assemblages

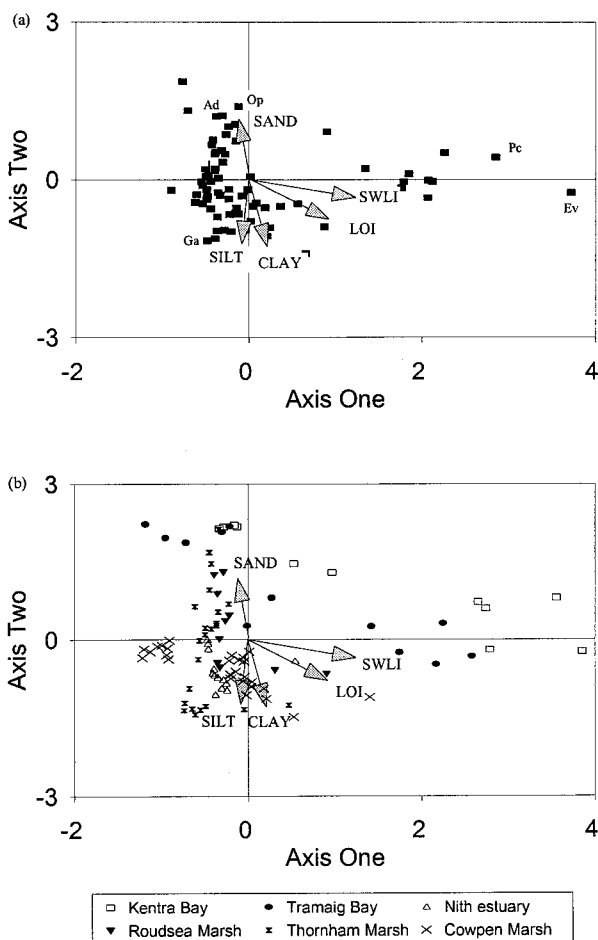
From all six sites, a total of 153 diatom taxa were identified, with 73 taxa exceeding 5% TDV. Along the transects, diatom assemblages are divided according to the morphological and vegetational zones (Table 3). In each transect, there is a clear transition from a marine–brackish diatom group associated with tidal-flat conditions, through the low-marsh environments where a mixed diatom community is found, to a group dominated by freshwater and salt-tolerant freshwater taxa in relation to the high-marsh conditions. Diatom assemblages associated with the pioneer marsh are transitional in nature, thus commonly grouped into either the tidal-flat zone or the low-marsh zone. Similarly, diatom samples related to the mid-marsh are grouped into either the low-marsh zone or the high-marsh zone. Owing to the small tidal range in Tramaig Bay, the diatom assemblages from low and high marshes are grouped together. In Kentra Bay and Tramaig Bay, the transects extend further into upland communities with no marine and brackish taxa present (Table 3).

There is a certain degree of variation in diatom species composition between sites (Table 3). On the tidal flats, *Achnanthes delicatula* and *Opephora pacifica* are common in Kentra Bay, Tramaig Bay and Thornham Marsh, none of

which are within an estuary where abundant freshwater inflow is evident. In contrast, *Delphineis surirella*, *Navicula phylepta* and *N. halophila* are recorded from Roudsea Marsh and Cowpen Marsh, both within an estuary. On the low marshes, brackish taxa dominate the assemblages in Kentra Bay, Tramaig Bay and Nith Estuary, whereas such oligohalobous halophile species as *Navicula cari* var. *cincta*, *Nitzschia frustulum* and *N. dubia* seem important in Roudsea Marsh, Cowpen Marsh and Thornham Marsh. On the high marshes, *Navicula pussila* and *Pinnularia microstauron* appear abundant in Kentra Bay, whereas *Tabellaria flocculosa* is found in Tramaig Bay. As the oligohalobous component dominates the assemblages in Nith Estuary and Roudsea Marsh, *Navicula halophila*, a brackish species, and some oligohalobous halophile taxa are characteristic in Cowpen Marsh and Thornham Marsh. These differences seem to reflect the between-site differences in substrate, tidal hydrology, sea-water salinity and ground-water acidity.

### Canonical correspondence analysis results

The CCA sample–environment and species–environment biplots are shown in Fig. 3. The CCA axes one (eigenvalue = 0.60) and two (eigenvalue = 0.36) explain 12.9% of the



**Figure 3** The CCA biplots of (a) diatom species–environment and (b) sample–environment. Species abbreviations: Ad = *Achnanthes delicatula*; Ev = *Eunotia exigua*; Ga = *Gyrosigma acuminatum*; Op = *Opephora pacifica*; Pc = *Pinnularia microstauron*. Environmental abbreviations: LOI = loss on ignition; SWLI = standardised water level index. Only diatom taxa that reach 5% TDV are included.

total variance in the diatom data (Table 4). These two axes represent 59.7% of the species–environment relationship. The lengths of the environmental arrows approximate their relative importance in explaining the variance in the diatom data and their orientation shows their approximate correlations to the ordination axes and to other environmental variables. Intrasite correlations of environmental variables with axes one and two show that SWLI and LOI are correlated with axis one and that the sand, silt and clay fractions are correlated with axis two (Fig. 3). The CCA axis one, therefore, reflects the major gradient from high marsh plotted on the right (high SWLI and LOI) to tidal flats plotted on the left (low SWLI and LOI). The CCA axis two reflects the grain-size gradient from sand fraction (top) through to silt and clay fractions (bottom).

On the species–environment biplot the position of species projected perpendicularly on to the environmental arrows approximate their weighted average optima along each environmental variable (Fig. 3). Therefore, the species characteristic of a particular environment may be identified. For example, *Eunotia valida* and *Pinnularia microstauron* are related to high and middle marsh with high SWLI and LOI, and *Opephora pacifica* and *Achnanthes delicatula* are associated with tidal flat with low SWLI and LOI.

The five environmental variables account for 21.6% of the explained variance in the diatom data (Fig. 4a). Partial CCAs (Fig. 4b) show that the total explained variance is composed of 23.3% (SWLI), 19.7% (LOI), 5.2% (sand fraction), 5.2% (silt fraction) and 5.1% (clay fraction). The associated Monte Carlo permutation tests indicate that each of these gradients accounts for a significant portion of the total variance in the diatom data ( $p = 0.01$ , 99 random permutations). Therefore, statistically significant transfer functions quantifying the relationship between contemporary diatom assemblages and SWLI can be developed. However, 41.5% of the total explained variance of diatom data is accounted for by intercorrelations between environmental variables and, thus, a transfer function for SWLI cannot be considered to be completely independent from other variables. This is to be expected because Horton (1997) showed strong relationships of altitude (ca. SWLI) versus substrate, the LOI in particular. Subsequently, for palaeoenvironmental reconstructions, it must be assumed that the joint distribution with SWLI in the training set is the same as in the fossil set (Le and Shackleton, 1994; Birks, 1995).

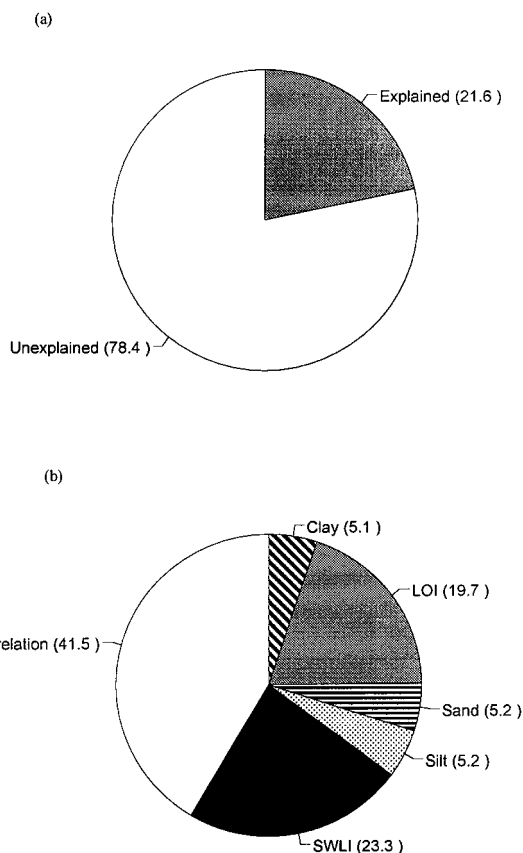
One striking fact raised by CCA is the large amount of unexplained variation: over 78% total variation of the diatom data remain unexplained. Whether this is due to some overlooked factor (e.g. between-site variation in diatom composition) or to a large amount of stochastic variations remains unclear. Nevertheless, the explained percentage is considerably greater than those found in many other biological data sets with a large number of samples with many zero values (Gasse *et al.*, 1995; Jones and Juggins, 1995). Furthermore, partial CCAs indicate that statistically significant transfer functions can be developed for SWLI.

### Diatom-based tidal-level transfer function

Weighted averaging transfer functions were developed for SWLIs based upon 73 taxa from 88 samples (Table 5). Tolerance-downweighted WA appears to perform marginally better than ordinary WA when apparent and jack-knifed errors are considered, i.e. prediction errors (RMSEP) are lower and squared correlations ( $r^2$ ) are higher (Table 6).

**Table 4** Summary of CCA results from diatom assemblages of contemporary coastal sites

Axis	1	2	3	4	Total inertia
CCA Eigenvalues	0.597	0.361	0.275	0.168	7.415
Species–environment correlations	0.908	0.905	0.848	0.748	
Cumulative percentage variance:					
of species data	8.1	12.9	16.6	18.9	
of species environment relationship	37.2	59.7	76.8	87.4	
Sum of all unconstrained eigenvalues					7.415
Sum of all canonical eigenvalues					1.604

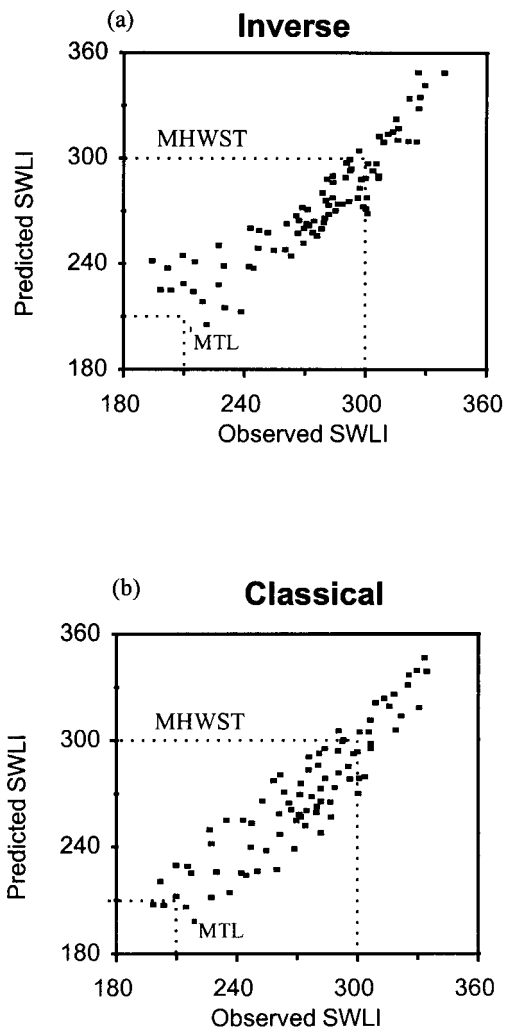


**Figure 4** Pie charts showing the total variation (%) of the diatom training set in (a) explained and unexplained portions and (b) components representing the unique contributions of standardised water level index (SWLI), loss on ignition (LOI), clay, silt, sand and intercorrelation among gradients.

Therefore, tolerance-downweighted WA is more appropriate to this study. Bootstrapped estimates of the standard error for ordinary and tolerance-downweighted WA are higher than the equivalent apparent or jack-knife errors, highlighting the importance of using a method of cross-validation to estimate the likely error when the transfer function is applied to unknown fossil samples.

The relationship between observed and diatom-predicted SWLI shows the relative performance of the tolerance-downweighted WA transfer functions for inverse ( $r_{jack}^2 = 0.71$ ) and classical ( $r_{jack}^2 = 0.72$ ) deshrinking regression (Fig. 5). The former scatter graph (Fig. 5a) has greater accuracy in the mid-range of SWLI, whereas the latter (Fig. 5b) has greater accuracy at high and low SWLIs.

The coefficients of WA transfer functions have a direct



**Figure 5** Scatter plots showing the relationship of the observed standardised water level index (SWLI) versus diatom-predicted SWLI for (a) inverse and (b) classical deshrinking regression. The reference water levels of MHWST and MTL are shown.

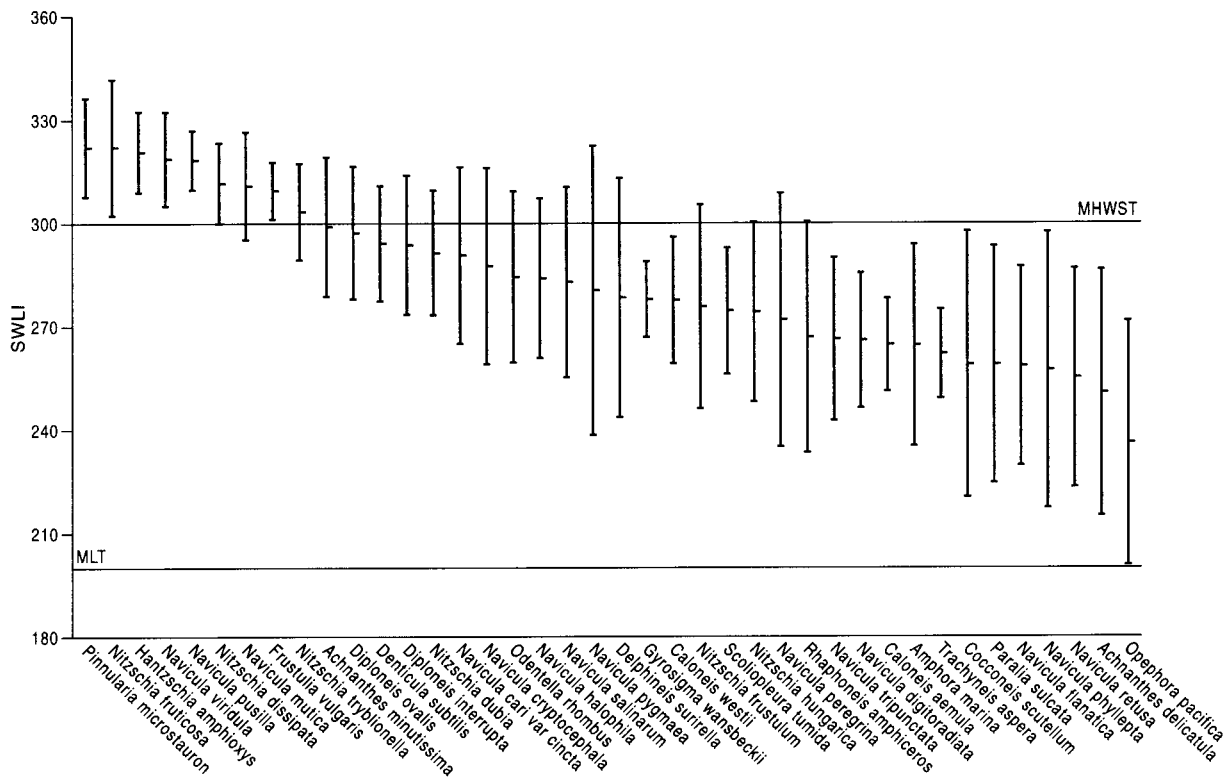
ecological interpretation as species' optima and tolerance to SWLI (the optima and tolerances are not rescaled on the basis of deshrinking regression). For example, Fig. 6 shows species that are commonly found within tidal flat and low marsh environments (e.g. *Opephora pacifica*, *Achnanthes delicatula*, *Navicula retusa*, *N. phyllepta* and *N. flantica*) have the lowest SWLI optima. Species that dominate high saltmarsh and supratidal environments (e.g. *Pinnularia microstauron*, *Nitzschia fruticosa*, *Hantzschia amphioxys*, *Navicula viridula* and *N. pussila*) have the highest SWLIs, with optima well above 300.

**Table 5** Summary of statistics (after data screening) of the training set used to develop ordinary weighted averaging (WA) and tolerance-downweighted WA (Tol-WA) transfer functions for SWLI

Variable	Number of samples	Number of species	Method	Regression coefficients			
				Inverse		Classic	
				b0	b1	b0	b1
SWLI	88	73	WA	-233.63	1.85	177.11	0.36
			Tol-WA	-228.35	1.79	167.33	0.41

**Table 6** Statistics summarising the performance of ordinary weighted averaging (WA) and tolerance-downweighted WA (Tol-WA) transfer functions for SWLI

Method	Deshrinking	RMSEP	r <sup>2</sup>	RMSEP <sub>jack</sub>	r <sup>2</sup> <sub>jack</sub>	SE <sub>pred</sub>
WA	Inverse	16.02	0.80	21.38	0.65	22.09
Tol-WA	Inverse	11.54	0.90	19.45	0.71	20.53
WA	Classical	20.78	0.80	23.58	0.65	24.32
Tol-WA	Classical	18.23	0.91	21.38	0.72	21.98



**Figure 6** Diatom species optima (weighted average) and tolerances (weighted standard deviation) for standardised water level index for all taxa exceeding 10% TDV. The optima and tolerances are not rescaled on the basis of deshrinking regression. The reference water levels of MHWST and MTL are shown.

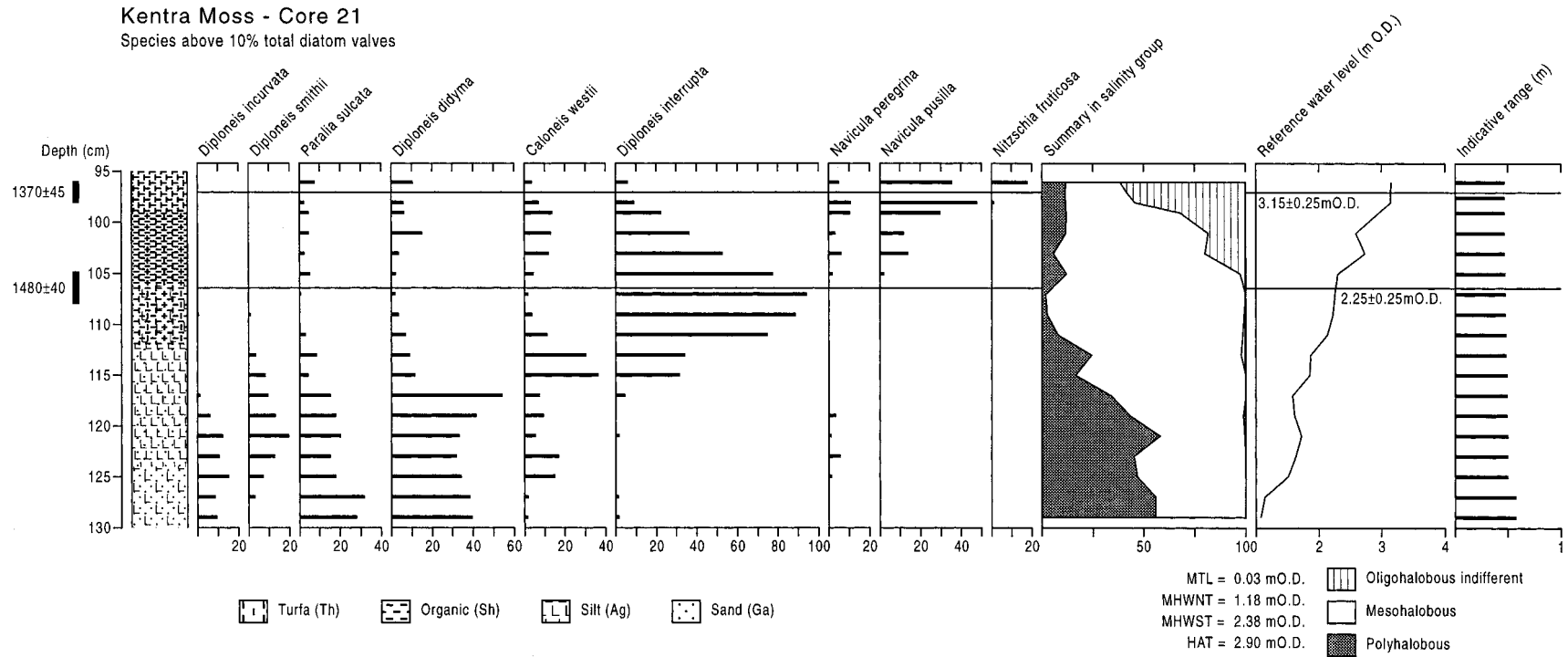
These optima can now be used to infer the SWLI from fossil diatom assemblages using the calibration formula:

$$\text{initial } x_i = \sum_{k=1}^m y_{ik} u_k \left| \sum_{k=1}^m y_{ik} \right. \quad (2)$$

where  $y_{ik}$  is the abundance of taxon  $k$  in fossil sample  $i$ ;  $u_k$  is the WA optimum for taxon  $k$  ( $k = 1, \dots, m$  diatom species);

and initial  $x_i$  is the initial predicted value of SWLI for the fossil sample  $i$ .

In WA environmental reconstructions, averages are taken twice, once in WA regression and once in WA calibration. This results in shrinkage of the range of predicted values towards the mean of the environmental gradient. The correction of this simple linear 'deshrinking' can be achieved via inverse or classical regression (Birks *et al.*, 1990; ter Braak



**Figure 7** The diatom frequencies obtained from core 21, Kentra Moss (after Shennan *et al.*, 1995). The surface altitude is reconstructed based on the computed standardised water-level index (SWLI) and shown as reference water level (m OD). The indicative range of the reconstructed surface altitude, and the radiocarbon dates (expressed in <sup>14</sup>C yr BP) and MHWST are also shown.

and Juggins, 1993). Inverse regression has the advantage of minimising RMSEP in the training set (ter Braak and van Dam, 1989; Martens and Naes, 1989) but at the cost of introducing bias at the end points (ter Braak and Juggins, 1993; Gasse *et al.*, 1995). Classical regression deshrinks more than inverse regression (Martinelle, 1970) and it takes values further away from the mean of the training set (Birks, 1995). Therefore, the choice of inverse or classical deshrinking regression depends upon the part of the gradient of interest.

The regression coefficients shown in Table 5 should be used to deshrink the initial values to give final estimates of the diatom-predicted SWLI using either inverse deshrinking:

$$\text{final } x_i = (b_0 + b_1) \times \text{initial } x_i \quad (3)$$

or classical deshrinking:

$$\text{final } x_i = (\text{initial } x_i - b_0) \times b_1 \quad (4)$$

where  $b_0$  is the intercept and  $b_1$  is the slope of the linear regression.

## Application to fossil sequences

The transfer function is applied to establish the history of changes in tidal level based on fossil sequences obtained from Kentra Moss (Shennan *et al.*, 1995). Core 21, 1.30 m long, was extracted from ca. 200 m landward from the contemporary marsh in Kentra Bay. The core comprises sandy silt in its lower section (1.30–1.12 m below ground surface, see Fig. 7), which is overlain by saltmarsh sediments (1.12–0.95 m) and gradually becomes fully terrestrial at the upper part of the core. From 18 horizons across the lower section of the core, 9 diatom taxa were recorded exceeding 10% TDV, showing a decrease in water salinity according to their salinity preference, which was interpreted to be the result of sea-level falling (Fig. 7). Above 0.95 m, no diatom taxa were found. Two sediment samples were taken from 1.05 to 1.08 m and 0.96 to 0.98 m for radiocarbon dating. Based on the qualitative assessment of the diatom data, the horizon with a date of  $1480 \pm 40$   $^{14}\text{C}$  yr BP had an indicative meaning of  $2.60 \pm 0.20$  m OD, and the indicative meaning of the horizon dated to  $1370 \pm 45$   $^{14}\text{C}$  yr BP was  $2.75 \pm 0.20$  m OD (Shennan *et al.*, 1995).

The SWLIs are reconstructed using WA transfer functions. The SWLIs are subsequently back-transformed relative to OD and expressed in metres. The back-transformation is dependent on the local tidal range. This continuous curve of the reconstructed tidal levels indicates a gradual rise in tidal level from approximately local MTL at 1.29 m to a level slightly above the local highest astronomical tide (HAT) at 0.97 m. From this curve, reconstructed tidal levels of  $2.25 \pm 0.23$  m OD and  $3.15 \pm 0.25$  m OD are given to the dated sedimentary horizons at 1.06 m and 0.96 m, respectively.

The biostratigraphical data indicate that the tidal levels calculated using a diatom-based transfer function are more precise than the qualitative assessments. According to Fig. 6, *Diploneis interrupta* occurs optimally only a little below the reference water level, MHWST. Thus, an altitude of 2.25 m OD for the horizon at 1.06 m is believed to be more realistic than the value (2.60 m OD) given by Shennan *et al.* (1995). Furthermore, because the optimal distributions of *Nitzschia fruticosa* and *Navicula pusilla* are slightly above the HAT, the altitude of 3.15 m OD for the horizon at 0.96

m also seems more accurate than the 2.75 m OD derived from the qualitative assessment.

However, caution should be exercised when applying such transfer functions because several characteristics within the contemporary data may affect the accuracy of sea-level reconstructions. First, there is an uneven spatial sampling within the contemporary data with respect to SWLI. The majority of sites are found above mean high-water neap tide (MHWNT) and therefore predictions for reference water levels below MHWNT maybe unreliable. Second, WA transfer functions calibrate the diatom data to one environmental variable (SWLI). By considering one variable only, this ignores the effects of other variables and may give misleading results (Le, 1992; Huntley, 1993). These factors are responsible for the majority of variations between observed and predicted SWLIs. Nevertheless, the magnitude of uncertainty in palaeotidal-level reconstruction using the transfer function is much smaller than those based on qualitative approaches (e.g. Zong, 1998).

## Conclusions

This study presents a method of estimating former sea levels based upon the contemporary relationship between relative sea-level and diatom assemblages. This study concludes that:

1. Canonical correspondence analysis using the training set of combined diatom distributions from six coastal sites shows a strong and highly statistically significant relationship with altitude. There is, however, a relatively high intercorrelation between variables. Thus, the altitudinal gradient cannot be considered completely independent.
2. In order to facilitate comparisons between areas that have different altitudes compared with the tidal frame, altitudinal data should be expressed as a standardised water-level index (SWLI). This is the function of local MTL and MHWST. A predictive transfer function has been developed for SWLI using weighted averaging calibration with inverse and classic deshrinking regression. Statistical measures assessing the performance of this model suggest that precise reconstructions of former sea-levels are possible (inverse  $SE_{\text{pred}} = 20.53$  SWLI; classic  $SE_{\text{pred}} = 21.98$  SWLI). The transfer function has important implications for developing a new generation of high-resolution sea-level reconstructions from sequences of sediments down-core.

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