

# Live benthic diatoms from the upper continental slope: extending the limits of marine primary production

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**ABSTRACT:** Discovery of obligate benthic diatoms living as deep as 191 m substantially extends the known depth range of these primary producers and holds significant implications for oceanic productivity and biogeochemical cycling. Species of the epipsammic, monoraphid genus *Cocconeis* dominated the  $\geq 35$  species of living benthic diatoms identified from the North Carolina continental margin in samples collected at bottom depths from 67 to 191 m. A total of 126 species were identified from prepared samples, more than 90 % of which are obligate benthic forms. Mid-day, near bottom, photosynthetically active radiation values recorded at the 191 m site averaged  $0.106 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ , representing about 0.028 % of surface incident radiation and resulting from a water column attenuation coefficient of  $0.0446 \text{ m}^{-1}$ . The presence of active benthic microalgae in these extremely low light conditions suggests the development of special light-harvesting adaptations including elevated levels of the blue-light absorbing accessory pigment, fucoxanthin. Extending the limit of benthic microalgal production to upper slope depths offshore from North Carolina increases the estimated total benthic primary production in that area of the continental margin by about 14 %. At present, extrapolating potential increases in benthic microalgal biomass and production resulting from extending the depth limits of viable benthic microalgae to a larger, global, oceanic scale is limited by paucity of data.

**KEY WORDS:** Diatoms · Benthos · Continental slope · Light flux · Pennales

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## INTRODUCTION

The volume of the world's oceans capable of supporting primary production remains to be firmly established, thus limiting our ability to model accurately important biogeochemical processes, including the biological oceanic carbon pump and oceanic productivity harvestable by humans. Recent studies in deep, poorly illuminated habitats substantially extend the known depth ranges and photosynthetic capabilities of the oceanic primary producer community compared with older notions of the limits of the euphotic zone, compensation depth and compensation light

intensity. The depth receiving 1 % of surface incident radiation has typically been cited as the average compensation depth and the lower limit of the euphotic zone, although deviations from this figure to as low as 0.1 % surface incident radiation are acknowledged (Falkowski 1988, Falkowski & Raven 1997). Some oceanic phytoplankton populations, in particular *Prochlorococcus*, are now known to grow at depths of 120 to 160 m, at light fluxes averaging 0.04 % ( $0.02 \% \pm \text{SD}$ ) of surface incident radiation, and to display exceptional photosynthetic efficiencies,  $\alpha^{\text{B}}$ , averaging  $0.107 \text{ mgC (mg chlorophyll [chl] a)}^{-1} \text{ h}^{-1}$  ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ )<sup>-1</sup>, biomass-normalized photo-

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synthetic rates,  $P^B$ , between 0.48 and 3.84 mgC (mgchl a)<sup>-1</sup> h<sup>-1</sup>, and saturating light intensity,  $E_k$ , as low as 9.2  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Johnson et al. 1999, 2002). Benthic macroalgae, although limited to neritic zones in the ocean, have demonstrated a similar ability to colonize relatively deep, poorly illuminated substrates (Markager & Sand-Jensen 1992). Foliose macroalgae have been reported down to 157 m and 0.06% surface incident radiation, and crustose forms down to 268 m and 0.0005% surface incident radiation (Littler et al. 1985, Markager & Sand-Jensen 1992).

Much less is known, however, about the ecological limits of another assemblage of primary producers important in neritic oceanic ecosystems, the benthic microalgae, particularly the limits of their depth distribution, adaptation to low light levels and, therefore, their depth and geographical ranges in the global ocean. Few measurements of benthic microalgal production at depths below 20 m, very few records of benthic microalgal chl *a* at depths below 60 m, and only 2 reports from below 100 m worldwide are published (Cahoon 1999). Limited field studies of benthic microalgal distributions, and assessments of their photophysiology under low light conditions (Steele & Baird 1968, Brotas & Catarino 1995, MacIntyre & Cullen 1995, Meyercordt & Meyer-Reil 1999, Cahoon 1999, 2006, K uhl et al. 2001), suggest the potential for depth and light limits similar to those of phytoplankton and benthic macroalgae. Several lines of evidence suggested that a productive benthic microflora might be present at substantial depths offshore from North Carolina, USA. A distinctly benthic microalgal assemblage containing >100 epipsammic and epipelagic diatom species to depths of 35 m off the coast of North Carolina was described by Cahoon & Laws (1993). Significant concentrations of chemically intact chl *a* have been reported from sediments in outer shelf and upper slope habitats in several locations globally and, offshore from North Carolina, to depths as great as 222 m (Table 1, Fig. 1; Cahoon et al. 1990, 1992, Cahoon 1999). The presence of culturable diatoms and intact chl *a* to depths of 2000 m off Cape Hatteras (Cahoon et al. 1994) suggested at least the potential of benthic microalgae originating in shallower depths to colonize deep benthic habitats. Previous studies also indicated the potential for photophysiological adaptation to very low light fields dominated by shorter

wave lengths at depth (Cahoon et al. 1992). Estimates of light flux in waters offshore from North Carolina using surface and bottom incident irradiation (Cahoon & Cooke 1992), and a 0.1% light level minimum for net autotrophic production (Falkowski 1988), predicted that benthic microalgal growth could occur to depths of ~90 m (Cahoon & Laws 1993), below which benthic microalgae would disappear or enter into a resting spore stage. However, until now we were unable to document the presence of living vegetative cells of obligate benthic microalgae (epipsammic and epipelagic diatoms) in outer shelf or upper slope habitats. This study investigated the taxonomic composition and depth distribution of benthic diatoms from continental margin sediments in Onslow Bay of the Atlantic coast offshore from North Carolina at depths of 67 to 191 m (Fig. 1). Extending the distribution limits of benthic microalgae within continental margin habitats will have significant implications for understanding oceanic production and biogeochemical cycles.

## MATERIALS AND METHODS

Remotely operated vehicle (ROV) and CTD sampling instruments were deployed in Onslow Bay in October 2003 from RV 'Cape Hatteras' to sample water column properties and sediments, respectively, along 2 transects: (1) a 3.93 km long transect ('2003 I') of 8 sites on the outer shelf starting 96 km from shore (33° 12.730' N, 77° 22.499' W) at depths between 67 and 121 m, and (2) a 9.75 km long transect ('2003 II') of 6

Table 1. Distribution of benthic microalgal chl *a* (means or ranges) versus depth in coastal sediments at depths  $\geq 40$  m from previous studies

Depth (m)	Chl <i>a</i> (SD) (mg m <sup>-2</sup> )	Location	Source
40	60–360	McMurdo Sound, Antarctica	Dayton et al. (1986)
40	57–219	Seranilla Bank	Bunt et al. (1972)
40	9.9	Nosy-B�e, Madagascar	Plante-Cuny (1978)
41	25.1 (13.1)	North Carolina, USA	Cahoon & Cooke (1992)
41.3	6.4–15.3	Long Island Sound, USA	Sun et al. (1994)
45	18.5 (9.9)	North Carolina, USA	Cahoon et al. (1992)
55	10.4	Nosy-B�e, Madagascar	Plante-Cuny (1978)
60	27–39	Key Biscayne, USA	Bunt et al. (1972)
60	17	Discovery Bay, Jamaica	Bunt et al. (1972)
60	16.4	Nosy-B�e, Madagascar	Plante-Cuny (1978)
63	36.2 (18.8)	North Carolina, USA	Cahoon et al. (1992)
83	30.4	Nosy-B�e, Madagascar	Plante-Cuny (1978)
96	10.6 (6.3)	North Carolina, USA	Cahoon et al. (1992)
114	22.1 (5.0)	North Carolina, USA	Cahoon et al. (1992)
131	8.8 (6.9)	North Carolina, USA	Cahoon et al. (1992)
142	15	North Carolina, USA	Cahoon et al. (1990)
157	9.2 (10.3)	North Carolina, USA	Cahoon et al. 1992)
194	4.4 (3.6)	North Carolina, USA	Cahoon et al. (1992)
222	1.5 (1.3)	North Carolina, USA	Cahoon et al. (1992)

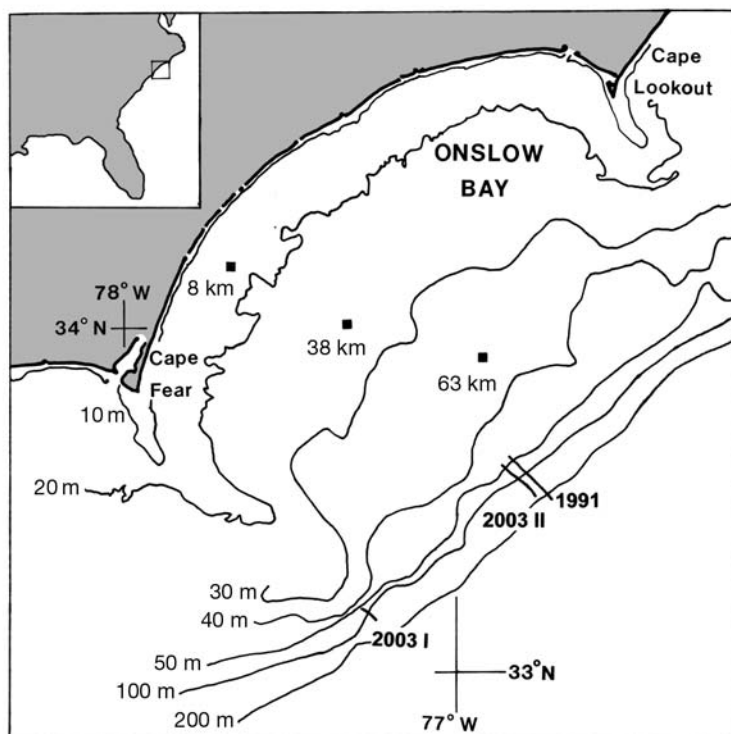


Fig. 1. Location of sampling sites in Onslow Bay, North Carolina, showing 1989 sites from which benthic microflora taxonomic composition was determined (8, 38 and 63 km sites at depths of 20, 33 and 35 m, respectively; Cahoon & Laws 1993. Depth contour positions are approximate), 1991 ROV transect yielding chl *a* and pigment composition data (depth range: 45 to 222 m; Cahoon et al. 1992), and 2003 transects (I and II; this study). Inset shows study area in southeastern USA

sites on the outer shelf to upper slope starting 111 km from shore (33° 36.275' N, 76° 51.797' W) at depths between 93 and 191 m (Fig. 1, Table 2). Each ROV deployment or dive represents a sampling site, and each ROV deployment was accompanied by a CTD cast. Two sites (3 and 4) were duplicate adjacent locations that were sampled by ROV, but not with separate CTD casts. Vertical profiles of conductivity (converted to salinity in psu), temperature (°C), depth (m) and light flux (photosynthetically active radiation [PAR], 400–750 nm, as  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) were measured at each site using a SeaBird SBE 911*plus* CTD with a Paroscientific digiquartz pressure transducer (accuracy  $\pm 0.008\%$ ) and a Biospherical QSP-200L  $4\pi$  PAR sensor at a scan rate of 24 Hz. The CTD casts were halted ~5 to 10 m from the bottom, so actual bottom depths at sampling sites were obtained from the pressure sensor mounted on the ROV (accuracy  $\pm 0.25\%$ ). Light attenuation coefficients,  $k$ , were calculated using averaged surface (<2 m depth) PAR values,  $I_0$ , obtained while the CTD was equilibrated prior to descending and from averaged PAR values,  $I_d$ , at its maximum depth,  $d$ , and the formula  $k = \ln(I_d/I_0)/d$ .

We used a SuperPhantom II ROV equipped with a Tri-Scoop 1000 rotary sampler (Brown et al. 1992) and real-time video control of sample collection activities for site selection and sediment sampling activities. The Tri-Scoop 1000 sampler collected surface sediment samples of approximately 300 ml in volume and 5 cm in depth in 3 separate automatically closing sample cups at up to 3 locations 10 to 100 m apart per dive. Once on board, sediment samples from properly sealed sample cups were taken directly into the ship-board laboratory for microscopic examination using bright field microscopy to determine the presence of live diatom cells (defined as cells containing visible chloroplasts and/or exhibiting motility). Sub-samples of sediment from all 14 sites were placed in screw-cap bottles, wrapped in aluminum foil, and kept refrigerated until examined further in the shore-based laboratory. Species identification and enumeration of live diatom cells were conducted at the shore-based laboratory immediately following the conclusion of the cruise approximately 48 h after collection of the last sample.

Wet slides were prepared from refrigerated raw sediment samples from each site and all live diatom cells were identified. Live cells were counted from Sites 1 and 14. Representative live cells of each species were photographed using a Nikon Coolpix 995 digital camera affixed to an Olympus BH2 microscope at

Table 2. ROV sampling site depths and locations in Onslow Bay, North Carolina, October 2003

Date	Depth (m)	Latitude (N)	Longitude (W)
16 October 2003			
1	69.8	33° 12.730'	77° 22.499'
2	73.7	33° 11.700'	77° 23.107'
3	82.6	33° 11.501'	77° 23.325'
4	79.9	33° 11.456'	77° 23.54'
5	91.8	33° 11.102'	77° 25.109'
6	89.0	33° 11.123'	77° 25.257'
7	102.4	33° 10.906'	77° 24.680'
8	121.0	33° 10.551'	77° 23.882'
17 October 2003			
9	93.6	33° 36.275'	76° 51.797'
10	104.8	33° 35.829'	76° 51.589'
11	114.9	33° 35.425'	76° 51.331'
12	122.6	33° 34.813'	76° 51.178'
13	133.5	33° 34.077'	76° 50.702'
14	191.2	33° 32.801'	76° 47.401'

1250× magnification. Live diatom species are notoriously difficult to identify to species level because the diagnostic morphology of the silica frustule is obscured by cytoplasm. Live diatom species were identified based on size, shape, observable frustule morphology and position of plastids within each cell. In addition, photographs of live cells were compared with light and scanning electron photomicrographs of cleaned specimens from the same samples. We relied on monographs by Hustedt (1955), Hendey (1964), John (1983), and Round et al. (1990) to assist with identifications.

A portion of each sample was processed to produce cleaned material for species identification by light and scanning electron microscopy (SEM). We placed 5 cm<sup>3</sup> of each sediment sample in 50 ml deionized water to which 10 ml of 30% hydrogen peroxide and 0.1 g potassium dichromate were added to remove organic matter. Following 3 rinses with deionized water, 7 ml of 37% HCl were added to the sample along with 50 ml of supernatant to remove carbonates. Following the reaction each sample was rinsed again 3 times with deionized water, diluted to 400 ml total volume, stirred thoroughly and split for light microscope or SEM preparation.

Cover slip preparation of sediment suspensions for light microscope slides followed the settling technique of Laws (1983). Three 22 mm cover slips were made for each sample. The prepared cover slips were mounted on slides using a naphrax/toluene solution and progressively heated until evaporation of the toluene was complete. Excess naphrax was pressed out to remove bubbles and scraped off. Light microscope slides were examined at 1250× using ribbon transects traversing the entire cover slip and cell counts were done using the ribbon counting method described in Laws (1983). Photographs were taken at magnifications necessary to distinguish the morphological features of individual diatom species, and identifications were made using the monograph references cited previously. Measurements of frustule dimensions (length along apical, trans-apical, and pervalvar axes) and observations of frustule ornamentation were made for 5 species of pennate diatoms identified as living at these deep sites for comparison with frustule morphometrics of the same species sampled from intertidal habitats in a previous study (Hilterman 1998).

SEM mounts were prepared by vacuum-filtering a portion of each cleaned sample through one Whatman 5 µm Millipore® cellulose nitrate membrane disc and 2 Whatman 0.4 µm Millipore® cellulose nitrate membrane discs. Discs were dried for 24 h at 24°C, cut into rectangular pieces and mounted on standard aluminum stubs. Three stubs were prepared with 0.4 µm discs and one with a 5 µm disc from each sample. Mounted stubs were sputter-coated with platinum

palladium using a Cressington 208 HR sputter coater and Cressington MTM 20 thickness controller to a thickness of 6 nm. Samples were then viewed using a Philips 1L XL-305 FEG SEM. Twenty-one ribbon transects were analyzed at 1250× on each SEM stub to determine taxonomic content. Photographs and species identifications were performed at various magnifications on the SEM.

## RESULTS

Real-time video imagery from ROV deployments demonstrated the presence of larger scale bottom features, including sand waves and ridges up to 1.3 m high oriented north–south at 122 m deep and east–west at 134 m deep, as well as various benthic macrofauna, including echinoderms, polychaetes, crustaceans and fishes. Near-bottom visibility as assessed from the ROV's video system consistently exceeded 20 m. A sediment surface layer of microalgae could frequently be observed, particularly when sampling activities exposed lighter sub-surface sediment that contrasted with brown-colored microalgal growth. The substrate at shallower sites consisted of poorly sorted coarse-grained quartz sands and shell hash, gradually becoming finer with depth to well-sorted fine to very fine quartz sands and quartzose muds at the deepest sites.

Water clarity and light flux to the bottom were sufficient to provide adequate visibility for ROV operations at all but the deepest site, where artificial lighting

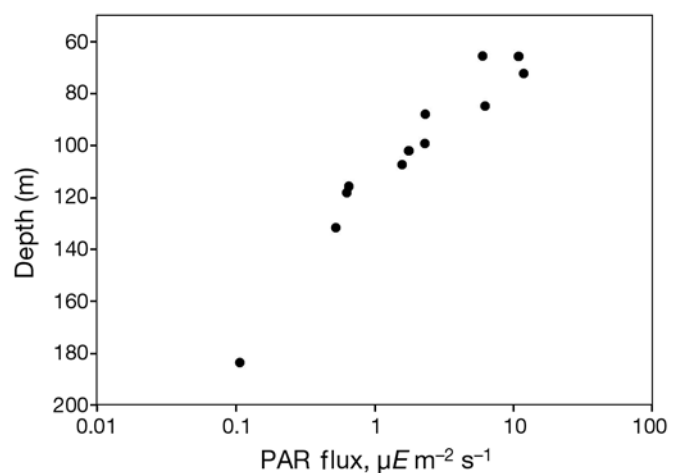


Fig. 2. Values of PAR observed (uncorrected for time of day effects on surface incident PAR flux) at near-bottom depths at each of 12 sites (excluding ROV Sites 4 and 5) in Onslow Bay, 16–17 October 2003 (transects 2003 I and 2003 II, Fig. 1). Linear regression yielded the relationship:  $\log(\text{near-bottom PAR}) = 2.086 - 0.0177(\text{depth})$ ;  $r^2 = 0.925$ ;  $F = 123.9$ ;  $df = 1, 10$ ;  $p < 0.0001$



became necessary. Attenuation coefficients ( $k_{\text{PAR}}$ ) based on cast-average surface (<2 m depth) and near-bottom irradiance values yielded estimates of 0.0497 (4.97% attenuation  $\text{m}^{-1}$ ) at the 67 m site, and 0.0446 (4.46% attenuation  $\text{m}^{-1}$ ) at the 191 m site (Fig. 2). Measured light flux at the 183.5 m depth at the deepest location, ROV sampling site no. 14, was 0.106  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , approximately 0.028% of surface light flux. Surface conditions were calm with clear skies, and sampling operations took place during mid-morning and mid-afternoon hours, probably yielding observed PAR flux values at or near their daily maxima for days of the year 289 to 290. Maximal PAR fluxes to the bottom at solar zenith or in mid-summer would probably have been somewhat higher than observed, but surface wave action or cloudiness would substantially lower those fluxes.

Living diatom cells were observed in sediment samples from all 14 sites upon shipboard microscopic analysis immediately following collection (Table 3, Fig. 3). We observed living cells of at least 35 species of diatoms in the raw sediment samples (Tables 3 & 4). Ribbon counts of individual living cells from Sites 1 (shallowest) and 14 (deepest) showed that more than 99% were of obligate benthic species, most of which were pennate forms less than 30  $\mu\text{m}$  in length (Table 4). The obligate benthic, epipsammic genus *Cocconeis* (Fig. 3) comprised 77% of individual living cells recorded from Sites 1 and 14 (Table 4). Lesser numbers of living cells of the genera *Fallacia* and *Amphora* (Fig. 3), as well as *Nitzschia* and *Navicula*, were also found. We noted dormant or resting spores in several samples, but did not quantify these. Several specimens of *Nitzschia* and *Navicula* from the deepest site displayed characteristic directed linear motion parallel to the apical axis further attesting to the active live nature of this deep microflora. An online photographic archive of all living species observed can be found at [http://dl.uncw.edu/digilib/biology/protists/taxonomy%20and%20systematics/MEPS\\_Diatoms/](http://dl.uncw.edu/digilib/biology/protists/taxonomy%20and%20systematics/MEPS_Diatoms/).

Analysis of diatom species in cleaned material from Sites 1 to 10 and Site 14 revealed 126 diatom species in at least 29 genera (Table 5). In Table 5 we categorize

Table 3. Live diatom taxa recorded at each site (depth indicated in brackets)

<p><b>Site 1 (69.8 m)</b>  <i>Achnanthes</i> cf. <i>A. delicatula</i>  <i>Actinoptychus splendens</i>  <i>Amphora</i> cf. <i>A. coffaeiformis</i>  <i>Cocconeis</i> cf. <i>C. disculus</i>  <i>Cocconeis</i> cf. <i>C. distans</i>  <i>Cocconeis</i> cf. <i>C. placentula</i>  <i>Fallacia</i> cf. <i>F. forcipata</i>  <i>Navicula</i> cf. <i>N. digitoconvergens</i>  <i>Navicula</i> sp. A  <i>Nitzschia</i> cf. <i>N. frustulum</i>  <i>Nitzschia</i> cf. <i>N. hybridaeformis</i>  <i>Nitzschia</i> cf. <i>N. panduriformis</i>  <i>Nitzschia</i> cf. <i>N. pellucida</i></p>	<p><b>Site 7 (102.4 m)</b>  <i>Cocconeis</i> cf. <i>C. disculus</i>  <i>Cymatosira</i> cf. <i>C. belgica</i>  <i>Diploneis</i> cf. <i>D. aestuarii</i>  <i>Navicula</i> sp. B  <i>Nitzschia</i> cf. <i>N. panduriformis</i>  <i>Nitzschia</i> sp. B  <i>Pleurosigma</i> cf. <i>P. distinguendum</i></p>
<p><b>Site 2 (73.7 m)</b>  <i>Actinocyclus</i> sp. A  <i>Cocconeis</i> cf. <i>C. disculus</i>  <i>Cocconeis</i> cf. <i>C. distans</i>  <i>Cymatosira lorenziana</i>  <i>Cymatosira</i> cf. <i>C. belgica</i>  <i>Grammatophora</i> cf. <i>G. marina</i>  <i>Paralia sulcata</i></p>	<p><b>Site 8 (121 m)</b>  <i>Diploneis</i> sp. indeterminate  <i>Nitzschia</i> sp. A</p>
<p><b>Site 3 (82.6 m)</b>  <i>Cymatosira</i> cf. <i>C. belgica</i>  <i>Diploneis</i> cf. <i>D. smithii</i>  <i>Coccinodiscus</i> sp. A</p>	<p><b>Site 9 (93.6 m)</b>  <i>Campylosira</i> sp. A  <i>Cocconeis</i> sp. A  <i>Diploneis</i> cf. <i>D. bombus</i>  <i>Pleurosigma</i> sp. indeterminate  <i>Nitzschia</i> sp. indeterminate</p>
<p><b>Site 4 (79.9 m)</b>  <i>Amphora</i> cf. <i>A. coffaeiformis</i>  <i>Cocconeis</i> cf. <i>C. disculus</i>  <i>Thalassiosira</i> sp. A</p>	<p><b>Site 10 (104.8 m)</b>  <i>Amphora</i> sp. indeterminate  <i>Cymatosira</i> cf. <i>C. lorenziana</i>  <i>Navicula</i> sp. B  <i>Nitzschia</i> cf. <i>N. panduriformis</i></p>
<p><b>Site 5 (91.8 m)</b>  <i>Cocconeis</i> cf. <i>C. disculus</i>  <i>Cymatosira</i> cf. <i>C. belgica</i>  <i>Diploneis</i> cf. <i>D. aestuarii</i>  <i>Navicula</i> sp. B  <i>Nitzschia</i> cf. <i>N. hybridaeformis</i>  <i>Nitzschia</i> cf. <i>N. closterium</i>  <i>Nitzschia</i> sp. A  <i>Thalassiosira</i> sp. B</p>	<p><b>Site 11 (114.9 m)</b>  <i>Navicula</i> sp. A  <i>Nitzschia</i> sp. indeterminate  <i>Paralia</i> cf. <i>P. sulcata</i></p>
<p><b>Site 6 (89.0 m)</b>  <i>Diploneis</i> cf. <i>D. aestuarii</i>  <i>Navicula</i> sp. B  <i>Nitzschia</i> cf. <i>N. panduriformis</i>  <i>Pleurosigma</i> cf. <i>P. distinguendum</i>  Raphid pennate indeterminate</p>	<p><b>Site 12 (122.6 m)</b>  <i>Diploneis</i> cf. <i>D. aestuarii</i>  <i>Navicula</i> sp. A</p>
	<p><b>Site 13 (133.5 m)</b>  <i>Grammatophora</i> cf. <i>G. marina</i>  <i>Pleurosigma</i> cf. <i>P. marinum</i>  <i>Triceratium?</i> sp. indeterminate</p>
	<p><b>Site 14 (191.2 m)</b>  <i>Actinoptychus</i> cf. <i>A. splendens</i>  <i>Cocconeis</i> cf. <i>C. disculus</i>  <i>Diploneis</i> cf. <i>D. chersonensis</i>  <i>Navicula</i> sp. A  <i>Nitzschia</i> cf. <i>N. brevisrostris</i>  <i>Nitzschia</i> cf. <i>N. closterium</i>  <i>Nitzschia</i> cf. <i>N. panduriformis</i></p>

all of the observed diatom taxa into 4 broad groups that have taxonomic and life-mode significance. These are (1) centric, which are largely planktonic or tycho-pelagic (alternately suspended and resting on the substrate); (2) araphid pennate, many of which are chain-forming and can be benthic, tychopelagic or planktonic; (3) monoraphid pennate, most of which are epipsammic or epiphytic; and (4) biraphid pennate, which are typically epipelagic and motile (see Table 5). Of all identified species 113 are obligate benthic pennate forms (epipsammic, epipelagic, and/or epiphytic; Cahoon & Laws 1993). At least 4 species found in cleaned and live material could be considered tycho-

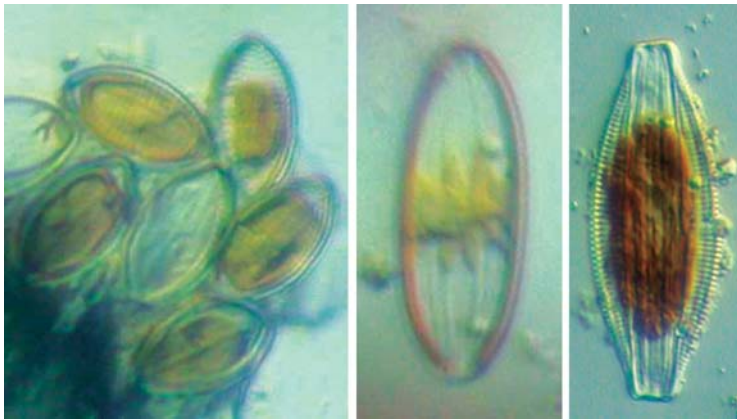


Fig. 3. (left to right) *Cocconeis disculus* (length = ca. 16  $\mu\text{m}$ ), *Fallacia forcipata* (length = 24.5  $\mu\text{m}$ ) and *Amphora coffaeiformis* (length = 23.5  $\mu\text{m}$ ). All specimens photographed in white polarized light

pelagic, *Cymatosira belgica*, *C. lorenziana*, *Grammatophora marina* and *Paralia sulcata*. *Actinoptychus splendens*, a large robust centric species (>50  $\mu\text{m}$  diameter), and several species of *Coscinodiscus* and/or *Thalassiosira* were the only planktonic diatoms noted, accounting for only 1% of the valves identified in cleaned material. Qualitative analysis of cleaned material also revealed that the obligate benthic, epipsammic genus *Cocconeis* constituted the largest number of valves observed in cleaned material. Qualitative analysis of valve density in both freshly collected raw material and cleaned material indicated that, although live diatoms and dead valves were found at all 14 sites, the density of live specimens and valves decreased with increasing depth.

A morphometric comparison of 5 species found live and relatively abundant at Sites 1 and 14 with specimens of the same species previously documented at 2 shallow intertidal sites (Hilterman 1998) was conducted to determine if deep water specimens showed significant morphological differences from their shallow water counterparts. The comparison showed that there were some significant morphometric differences between specimens of the same species sampled in the 2 different habitats, but no consistent patterns of size or shape that would distinguish the deep water organisms from the intertidal microflora (Table 6).

## DISCUSSION

The presence of living obligate benthic diatoms in sediments extending into upper continental slope habitats is strong evidence that benthic primary productivity may be much more important than previously thought. Previous reviews assumed that productive

benthic microalgae were limited to depths above 50 (Charpy-Robaud & Sournia 1990) or 60 m (Cahoon 1999). The exceptional clarity of the continental margin waters off North Carolina, with strong influence from the Gulf Stream, contributes to the ability of benthic diatoms to grow at such great depths, but adaptation to exceptionally low light flux must also be considered. Given that we measured light fluxes at near-bottom depths under almost ideal conditions (calm seas with minimal surface albedo, clear sky, mid-day illumination), perhaps novel photo-adaptation genotypes and phenotypes may be expressed by diatoms living in these habitats.

Several factors indicate an autochthonous origin for benthic diatoms in North Carolina slope habitats, in addition to the distinctly

benthic nature of this microflora. First, the dominant diatom genus, *Cocconeis*, found in the live and cleaned deep water material, is an obligate benthic epipsammic monoraphid form that permanently attaches to the surface of sand grains using adhesive mucus secreted through the raphe valve, so transport of this type of diatom requires movement of the sediment itself. Scarcity of planktonic forms at all 14 sites suggests that settling phytoplankton provide no significant inputs to the benthic assemblage. The physical forcing required to move even fine-grained sands from shallower waters into the deeper shelf/slope waters in Onslow Bay is rarely present except during major storms. Similarly, the relatively low frequency of tychopelagic forms in the deep microflora is not consistent with allochthonous inputs, as would be expected if physical forces drove significant transport from shallower habitats. Major storms that generate currents strong enough to move sand in this region typically only resuspend sediment by oscillatory near-bottom wave

Table 4. Live cell counts from sampling Sites 1 (67 m) and 14 (191 m)

Taxon	Site 1	Site 14
<i>Actinoptychus splendens</i>	0	2
<i>Amphora coffaeiformis</i>	24	0
<i>Cocconeis disculus</i>	359	36
<i>Cocconeis distans</i>	27	0
<i>Cocconeis placentula</i>	9	0
<i>Diploneis chersonensis</i>	0	3
<i>Navicula</i> sp. A	15	0
<i>Navicula digitoconvergens</i>	17	0
<i>Nitzschia frustulum</i>	6	0
<i>Nitzschia panduriformis</i>	36	18
<i>Nitzschia pellucida</i>	7	0
Total	500	59

Table 5. Complete list and occurrence for all taxa identified in raw and cleaned materials. Abbreviations for cell morphology: C = centric, AP = araphid pennate, MP = monoraphid pennate, BP = biraphid pennate. Abbreviations for life habit: p = planktonic, uben = unspecified benthic, epsm = epipsammic, epel = epipelagic, ephy = epiphytic, es/ep = epipsammic/epiphytic, tpl = tychopelagic

Species	Morphology	Life habit	Site no.	Species	Morphology	Life habit	Site no.
<i>Achnanthes brevipes</i>	MP	es/ep	4	<i>Eunotogramma marinum</i>	C	epsm	2–7
<i>A. delicatula</i>	MP	es/ep	1, 2, 5, 8	<i>E. rostratum</i>	C	epsm	2–7
<i>A. danica</i>	MP	es/ep	1, 5	<i>Fallacia forcipata</i>	BP	epel	1, 7, 14
<i>A. hauckiana</i>	MP	es/ep	1, 4, 7, 10	<i>F. litoricola</i>	BP	epel	1, 4, 8
<i>A. kolbei</i>	MP	es/ep	1, 6	<i>F. plathii</i>	BP	epel	3
<i>A. manigera</i>	MP	es/ep	6	<i>F. vittata</i>	BP	epel	5
<i>A. pseudobliqua</i>	MP	es/ep	3, 8	<i>F. sp. A</i>	BP	epel	2
<i>A. reidensis</i>	MP	es/ep	1, 2	<i>F. sp. B</i>	BP	epel	5
<i>A. taeniata</i>	MP	es/ep	3	<i>F. sp. C</i>	BP	epel	3
<i>A. tenera</i>	MP	es/ep	1	<i>F. sp. D</i>	BP	epel	2, 4
<i>Actinocyclus sp. A</i>	C	p	2	<i>F. sp. E</i>	BP	epel	3
<i>Actinoptychus splendens</i>	C	p	1, 14	<i>F. sp. F</i>	BP	epel	2, 5
<i>Amphora beaufortiana</i>	BP	epel	1, 2	<i>Fragilaria brevistriata</i>	AP	uben	2–4, 6
<i>A. coffaeiformis</i>	BP	epel	1–4, 8, 14	<i>F. hyalina</i>	AP	uben	2
<i>A. costata</i>	BP	epel	4	<i>F. tabulata</i>	AP	uben	3, 4, 9
<i>A. delicatissima</i>	BP	epel	6	<i>F. sp. A</i>	AP	uben	1, 2
<i>A. exigua</i>	BP	epel	4, 5	<i>F. sp. B</i>	AP	uben	1
<i>A. granulata</i>	BP	epel	1–3	<i>F. sp. C</i>	AP	uben	1
<i>A. helenensis</i>	BP	epel	5, 7	<i>F. sp. D</i>	AP	uben	1, 4, 5, 7
<i>A. ovalis</i>	BP	epel	1–4	<i>Grammatophora marina</i>	AP	es/ep	2–7, 14
<i>A. pannucea</i>	BP	epel	5	<i>Lyrella sp. A</i>	BP	epel	3
<i>A. pseudoholsatica</i>	BP	epel	3	<i>Mastogloia angusta</i>	MP	epsm	1
<i>A. subcuneata</i>	BP	epel	1, 2	<i>M. lanceolata</i>	MP	epsm	8
<i>A. tenerima</i>	BP	epel	2	<i>M. pseudoelegans</i>	MP	epsm	2
<i>A. sp. A</i>	BP	epel	4	<i>Melosira moniliformis</i>	C	p	1–4
<i>A. sp. B</i>	BP	epel	3	<i>Navicula abunda</i>	BP	epel	1
<i>A. sp. C</i>	BP	epel	2	<i>N. cancellata</i>	BP	epel	2, 6
<i>A. sp. D</i>	BP	epel	9	<i>N. digitoconvergens</i>	BP	epel	1
<i>Biddulphia regina</i>	C	p	5, 6	<i>N. diploonoides</i>	BP	epel	1, 6
<i>Biremis lucens</i>	BP	epel	1, 2	<i>N. diversestriata</i>	BP	epel	1
<i>Campylosira sp. A</i>	C	epsm	9	<i>N. ergadensis</i>	BP	epel	5
<i>Cocconeis californica</i>	MP	epsm	1, 3, 5–7, 9	<i>N. humii</i>	BP	epel	1, 7
<i>C. convexa</i>	MP	epsm	1, 6	<i>N. menisculus</i>	BP	epel	3, 4
<i>C. dirupta</i>	MP	epsm	1–4	<i>N. muraliformis</i>	BP	epel	5
<i>C. disculus</i>	MP	epsm	1–10, 14	<i>N. nummularia</i>	BP	epel	1, 3–5
<i>C. distans</i>	MP	epsm	1, 2, 5–7, 14	<i>N. palpebralis</i>	BP	epel	6, 10
<i>C. distantula</i>	MP	epsm	1, 3, 5, 8	<i>N. paul-schulzii</i>	BP	epel	1, 4, 5
<i>C. granulifera</i>	MP	epsm	2, 3	<i>N. reinhardtii</i>	BP	epel	6
<i>C. hoffmanni</i>	MP	epsm	1, 2, 4	<i>N. riparia</i>	BP	epel	2, 5
<i>C. peltoides</i>	MP	epsm	1, 5	<i>N. subhamulata</i>	BP	epel	1
<i>C. pinnata</i>	MP	epsm	2, 6	<i>N. sp. A</i>	BP	epel	1, 9, 11, 12, 14
<i>C. placentula</i>	MP	epsm	1, 2, 10	<i>N. sp. B</i>	BP	epel	5–7, 10
<i>C. scutellum</i>	MP	epsm	1, 2, 4–6	<i>N. sp. C</i>	BP	epel	1, 5
<i>C. sp. A</i>	MP	epsm	1, 2, 6, 9, 10	<i>Nitzschia amphibia</i>	BP	epel	3
<i>C. sp. B</i>	MP	epsm	1, 2, 7	<i>N. angulares</i>	BP	epel	3, 5, 8, 10
<i>C. sp. C</i>	MP	epsm	3, 4, 6, 7, 9	<i>N. brevistriata</i>	BP	epel	2, 14
<i>Coscinodiscus sp. A</i>	C	p	3	<i>N. closterium</i>	BP	p	5, 14
<i>Cymatosira belgica</i>	C	epsm	2, 3, 5, 7	<i>N. constricta</i>	BP	epel	4
<i>C. lorenziana</i>	C	epsm	1–5, 7, 8, 10	<i>N. frustulum</i>	BP	epel	1, 2, 14
<i>Delphineis karstnii</i>	AP	epsm	1, 5	<i>N. hybridaeformis</i>	BP	epel	1, 3, 5, 10
<i>D. surrirella</i>	AP	epsm	1, 4, 6, 10	<i>N. incurva</i>	BP	epel	3, 4
<i>Diploneis aestuarii</i>	BP	epel	1–10, 12, 14	<i>N. marginata</i>	BP	epel	1
<i>D. bombus</i>	BP	epel	5, 8–10	<i>N. panduriformis</i>	BP	epel	1–10, 14
<i>D. chersonensis</i>	BP	epel	4, 8, 10, 14	<i>N. pellucida</i>	BP	epel	1
<i>D. decipiens</i>	BP	epel	5, 10	<i>N. sp. A</i>	BP	epel	1, 5, 9
<i>D. smithii</i>	BP	epel	3, 7, 9	<i>N. sp. B</i>	BP	epel	3, 4, 7
<i>D. sp. A</i>	BP	epel	8	<i>N. sp. C</i>	BP	epel	7
<i>Entomoneis kjellmanii</i>	BP	epel	1	<i>N. sp. indeter.</i>	BP	epel	9, 11

(Table continued on next page)

Table 5 (continued)

Species	Morphology	Life habit	Site no.	Species	Morphology	Life habit	Site no.
<i>Odontella aurita</i>	C	p/ephy	6	<i>P. sp. indeter.</i>	BP	epel	9
<i>Opephora pacifica</i>	AP	es/ep	1, 2	<i>Thalassiosira decipiens</i>	C	p	9
<i>Paralia sulcata</i>	C	tpl	2, 12	<i>T. sp. A</i>	C	p	1, 5, 6
<i>Parlibellus adnatas</i>	BP	epel	5	<i>T. sp. B</i>	C	p	5
<i>Petronis altisima</i>	BP	epel	3	<i>Trachysphenia accuminata</i>	AP	ephy	1
<i>Pinnularia lanceolata</i>	BP	epel	5	<i>Trachyneis sp. A</i>	BP	epel	1
<i>P. sp. A</i>	BP	epel	4	<i>Triceratium sp. A</i>			13
<i>Plagiogramma pygmaeum</i>	C	uben	1	Unknown sp. A			1, 3
<i>Pleurosigma</i>	BP	epel	5–9, 10, 14	Unknown sp. B			2
<i>distinguendum</i>				Unknown sp. C			3
<i>P. marinum</i>	BP	epel	1, 6, 13	Unknown sp. D			2
<i>P. rostratum</i>	BP	epel	3				

forcing, but do not last long enough to produce significant horizontal transport (Wren & Leonard 2005). Hurricane Isabel, a Category 2 hurricane, transited the study area approximately 1 mo prior to this sampling effort, 17–18 September 2003, but analyses from moorings in Onslow Bay showed that water transport was primarily southwestward, parallel to the coast and shelf break and reversed rapidly northeastward as the eye of the storm passed the area (Bingham 2007). Near-bottom current velocities and durations appear inadequate to have transported benthic microalgae from shelf habitats into slope habitats. Moreover, persistence of a living benthic microflora in slope habitats more than 1 mo after Hurricane Isabel indicates that off-shelf transport was not the source of the diatom assemblage we describe from this sampling effort. Down-slope mass wasting is probably not significant due to the low gradient in the area (<4%), unlike the

situation north of Cape Hatteras, where rapid down-slope transport of viable diatoms to very deep depths has been documented (Cahoon et al. 1994). Though a slight current affected ROV operations during the 2003 cruise, velocities were not great enough to move sediment (<0.3 m s<sup>-1</sup>), as observed directly in video images obtained by the camera affixed to the ROV (McGee 2005).

Second, a previous finding of enhanced fucoxanthin:chl a ratios of benthic microalgal assemblages from a deep, low light location compared with a shallower location in Onslow Bay suggested either selection for an assemblage with enhanced cellular content of the blue-light harvesting pigment, fucoxanthin, or *in situ* chromatic adaptation to lower light levels dominated by shorter wavelengths in deeper water (Cahoon et al. 1992). HPLC analyses (Klein & Sournia 1985) of acetone extracts of sediments collected by divers in

Table 6. Morphometric comparisons of axis lengths of 20 diatom frustules of each species found live at deep sites (D, this study) and 20 frustules of the same species from intertidal habitats (I) in coastal North Carolina (Hilterman 1999) using 1-way ANOVA (df = 1,38 for all comparisons; ns = not significant at p < 0.05). Morphology characteristics: M = monoraphic, B = biraphic, U = unoccluded, H = hymenate

Species Morphology	Axis		
	Apical	Trans-apical	Pervalvar
<i>Cocconeis disculata</i> M, U	ns	ns	ns
<i>Fallacia forcipata</i> B, U	D > I <i>F</i> = 6.39, <i>p</i> = 0.0157	D > I <i>F</i> = 15.63, <i>p</i> = 0.003	D > I <i>F</i> = 9.43, <i>p</i> = 0.0039
<i>Navicula sp. A</i> B, U	D > I <i>F</i> = 11.37, <i>p</i> = 0.0017	I > D <i>F</i> = 17.41, <i>p</i> = 0.0002	I > D <i>F</i> = 13.77, <i>p</i> = 0.0007
<i>Nitzschia frustulum</i> B, H	ns	ns	D > I <i>F</i> = 13.62, <i>p</i> = 0.0007
<i>Nitzschia panduriformis</i> B, U	D > I <i>F</i> = 14.96, <i>p</i> = 0.0004	D > I <i>F</i> = 26.03, <i>p</i> < 0.0001	D > I <i>F</i> = 25.19, <i>p</i> < 0.0001



shallow water (<35 m) and by ROV in deeper waters yielded mean peak area fucoxanthin:chl *a* ratios of 1.86:1 ( $n = 3$ ,  $SD = 0.32$ ) from samples collected at 33 m with ambient light flux of  $81.3 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  and 5.08:1 ( $n = 5$ ,  $SD = 0.86$ ) from samples collected at 63 m with ambient light flux of  $2.34 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Cahoon et al. 1992). Altered light-harvesting physiology supports the argument for distinct microalgal assemblages, consistent with our taxonomic observations. Such adaptation to life in deep, low-light environments is more likely to confer advantages than the inconsistent patterns of morphometric characteristics observed in benthic diatoms from deep habitats.

The presence of live active diatoms in sediments at depths to 191 m, and at <0.03% surface incident radiation, significantly extends the potential limits of benthic primary production. We made a preliminary estimate of potential daily production in the outer continental shelf and upper slope regions of Onslow Bay for the depth range from 41 m, the deepest previous production measurement in Onslow Bay (Cahoon & Cooke 1992), to 191 m, the new depth limit for benthic microalgal production. Using previous estimates of chl *a* biomass distribution in this depth range of approximately  $15 \text{ mg chl } a \text{ m}^{-2}$  (Cahoon et al. 1990), a value for  $P^B$  of  $0.8 \text{ mgC (mg chl } a)^{-1} \text{ h}^{-1}$  (Cahoon & Cooke 1992), and a production day length of 10 h we derive a value on the order of  $120 \text{ mgC m}^{-2}$ . This production estimate is approximately 50% of the average gross daily benthic production in the portions of Onslow Bay <41 m deep (Cahoon & Cooke 1992), but the steeper continental margin portion accounts for only 28% more area than the shelf portion of Onslow Bay (<55 m deep), yielding an increase in total estimated benthic production for Onslow Bay of ~14%. Extrapolations of benthic microalgal biomass and production to larger scales from Onslow Bay, which has had more thorough spatial sampling than any comparable continental margin ecosystems, are limited by paucity of data (Table 1; Cahoon 1999). Clearly, further study of the depth distributions of living benthic microalgae in continental margin ecosystems is warranted, particularly in light of the contribution to benthic food chains, sediment–water interactions and net carbon fluxes in continental margin habitats this community may support.

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