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Cold-water coral growth under extreme environmental conditions, the Cape Lookout area, NW Atlantic

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Abstract

The Cape Lookout cold-water coral area off the coast of North Carolina forms the shallowest and northernmost cold-water coral mound area on the Blake Plateau in the NW Atlantic. Cold-water coral habitats near Cape Lookout are occasionally bathed in the Gulf Stream, which is characterised by oligotrophic warm water and strong surface currents. Here, we present the first insights into the mound distribution and morphology, sedimentary environment and coral cover and near-bed environmental conditions as recorded by bottom landers from this coral area. The mounds occur between 320–550 m water depth and are characterised by high acoustic backscatter indicating the presence of hard structure. Three distinct mound morphologies were observed, (1) a mound with a flattened top at 320 m, (2) multi-summited mounds with a tear drop shape in the middle part of the area and (3) a single mound at 540 m water depth. Echosounder profiles show the presence of a strong reflector underneath all mound structures that forms the base of the mounds. This reflector cropped out at the downstream side of the single mound and consists of carbonate slabs. Video analysis revealed that all mounds are covered by *Lophelia pertusa* and that living colonies only occur close to the summits of the SSW side of the mounds, which is the side that faces the strongest currents. Off mound areas were characterised by low backscatter and sediment ripples, indicating the presence of relatively strong bottom currents. Two bottom landers were deployed amidst the coral mounds between December 2009 and May 2010. Both landers recorded prominent features near the seabed as well as in the overlying water column. The period between December and April was characterised by several events of increasing temperature and salinity, coinciding with increased flow and near-bed acoustic backscatter. During these events temperature fluctuated by up to 9°C within a day, which is the largest temperature variability as measured so far in a cold-water coral habitat. Warm events, related to Gulf Stream meanders, had the duration of roughly one week and the current during these events was directed to the NNE. The consequences of such events must be significant given the strong effects

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boxcores and made video recordings of the epifauna and fish fauna using a tethered video system. Furthermore, near-bed environmental conditions were recorded by long-term mooring deployments (December 2009–June 2010).

1.1 Geological and oceanographic setting of the study area

5 The Cape Lookout CWC area is situated on the northern part of the Blake Plateau (Fig. 1), which forms a continuation of the Bahama Bank carbonate province (Pratt et al., 1964). The Blake Plateau is a broad flat area, which is bounded in the East by the very steep Blake Escarpment and the Blake-Bahama basin. The Blake Plateau consists of a layer of more than 14 km of sedimentary rocks deposited since the Cre-
10 taceous (Sheridan, 1976). At present, the Blake Plateau is a sediment-starved region (Pinet et al., 1981; Pinet et al., 1985) and sediments mainly consist of foraminiferal ooze and pteropod fragments (Pratt et al., 1964; Pinet et al., 1985). In general, material finer than silt is absent and rippling in the sediments as shown on bottom photographs im-
15 plies that considerable sorting, reworking and redeposition took place (Gorsline, 1963; Pratt, 1963). Towards the shelf the sediment becomes enriched in quartz and the boundary between the two sedimentological zones is characterised by deposits rich in glauconite and phosphate (Gorsline, 1963). During the Quaternary, sediment depo-
20 sition and erosion were mainly steered by the Gulf Stream. During sea-level lowstands the Gulf Stream moved offshore, whilst at present, the pathway of the Gulfstream is more inshore (Pratt, 1963; Pinet et al., 1985; Hill et al., 2010).

Stetson (1962) described that numerous coral banks are present at the northeastern portion of the Blake Plateau, and in subsequent years, many more CWC habitats have been discovered (Neumann et al., 1977; Paull et al., 2000; Reed, 2002; Ross and Quattrini, 2007; Partyka et al., 2007). This includes the Cape Lookout coral mounds,
25 which form the northernmost CWC mounds on the Blake Plateau.

The CWC habitats on the Blake Plateau are occasionally flushed by the Gulf Stream (Blake et al., 1994; Ross and Quattrini, 2009), which is characterised by oligotrophic and warm waters with strong currents. The Gulf Stream is an important agent of heat

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transport to the poles and flows from the Florida Straits over the Blake Plateau (between 100 and 800 m water depth) to Cape Hatteras as a meandering jet. Here, the Gulf Stream separates from the coast and flows to the north east (Matsumoto et al., 2003). While flowing over the Blake Plateau and the Cape Lookout coral mounds the Gulf Stream meanders, causing relatively cool continental shelf waters to be temporarily replaced by warmer Gulf Stream water (Bane et al., 1981).

Biological production on the shelf is strongly influenced by this interaction between the Gulf Stream and adjacent shelf waters (Lee et al., 1991; Garciamoliner et al., 1994; Ryan et al., 1999; Leterme et al., 2008). During meandering, eddies are formed and shed off on both sides of the Gulf Stream; those inshore of the Gulf Stream propagate northwards at an average speed of 4 ms^{-1} . The inshore wavelike meanders and eddies amplify north of the Strait of Florida and downstream of the Charleston Bump, after which the features dissipate more off shore between 33°N and 36°N . Cyclonic cold core eddies occur when the meander of the Gulf Stream is in an off shore position. They move to the north at the same speed as the meander and have the same size (Bane et al., 1981; Glenn et al., 1994). Upwelling in cold core eddies uplifts the density structure of the front and transports nutrients into the euphotic zone. It is suggested that phytoplankton and bacterioplankton production is strongly influenced by the upwelling intrusion events, which might form an important food source for the CWC habitats on the Blake Plateau (Lee et al., 1991; Leterme et al., 2008).

2 Methods

2.1 Multibeam

An extensive bathymetric survey with a hull mounted Kongsberg EM 302 multibeam echosounder on the RV Pelagia was conducted between 31 May and 4 June 2010. The system consisted of a 30 kHz echosounder with an 1° opening angle for the transmitter and a 2° angle for the receiver and uses 135 beams with a maximum coverage

sector of 150° (depth range 10–7000 m). This results in a swath width of 5 times the water depth between 500 and 1000 m water depth. The transmit fan is split into at maximum 9 individual sectors that can be steered independently to compensate for ship's roll, pitch and yaw to get a best fit of the ensonified line perpendicular to the ship's track and thus a uniform coverage of the sea bed. The motion of the vessel was registered by a Kongsberg MRU-5 motion reference unit and the ship position and heading was determined by GPS. Data acquisition was conducted using the Kongsberg Seafloor Information System software. The sound velocity profile was calculated from salinity, pressure and temperature data recorded by a Seabird 911+ CTD system immediately prior to the survey. Bathymetric data were processed using Neptune (Kongsberg) and CFloor (Geocap AS). Backscatter maps of the research area were created using Fledermaus Geocoder which show the amount of backscatter as greyscales. Regions with high backscatter are depicted as light areas. The amount of backscatter depends on a variety of factors like the angle of incidence (for which the data are compensated), the sediment composition and the roughness of the seafloor.

2.2 Predictive habitat mapping

A regional scale predictive habitat map was developed with the aim of providing an indication of the relative suitability of the south east USA region for *L. pertusa*. Two models were produced using the Maxent software (Phillips et al., 2006); using default parameters following (Davies et al., 2011; Maxent version 3.3.3k), an increasingly popular method for predicting suitable habitat for data-poor species in the deep ocean (i.e., Davies et al., 2011; Yesson et al., 2012). The environmental variables utilised were initially partitioned into broad groups (bathymetry, biological production, carbonate chemistry, chemical, geological, oxygen, physical oceanography, terrain variables and other), one variable from each group was retained for the production of the final model based on highest training gains for models built from a single variable following a similar approach presented by Yesson et al. (2012) (full details of each variable and gain scores are provided in Table S1). Two models were produced, the first incorpo-

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rated a substrate type layer constructed from point sample data (see Table S1), whilst the second model was built without substrate type as this layer greatly constrained the spatial extent of the model due to poor data coverage. Species data were acquired from previously published records collated by Davies and Guinotte (2011), for the sediment-constrained model 154 records were used to train the model and 65 for the production of test statistics, 179 were used to train the non-sediment model and 76 for test statistics.

2.3 Echosounder

Several 3.5 kHz penetrating echosounder lines were recorded using the RV Pelagia echosounder system across and along different mound structures to gain insight into the internal geometry of the mounds. This system consisted of an ORETech 3010 transceiver and a hull mounted 12 transducers array. The analogue data were digitised with a CodaOctopus DA1000 system running the Coda Geosurvey software and were processed using RadexPro with amplitude correction and Stolt F-K migration.

2.4 Sediment sampling

Sediment samples were taken with a NIOZ designed cylindrical boxcorer equipped with a stainless steel cylindrical box of 50 cm in diameter and 55 cm in height and a trip valve sealing the core after penetration. A camera system attached to the frame allowed video-guided sampling. The surface of each box core was photographed on recovery and a detailed description of the species composition and sediment characteristics was taken.

2.5 Moored equipment

Two benthic landers were deployed at Cape Lookout during a cruise with the RV Cape Hatteras (operated by Duke-UNC Oceanographic Consortium) in December 2009. Both landers were successfully retrieved in June 2010 with the RV Pelagia and each

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lander obtained 6 months of near-bed environmental conditions. The ALBEX lander was deployed in the northern part of the study area at the tail of a mound cluster in 417 m of water at 34°20.941' N, 75°46.756' W. The BOBO lander was positioned amidst a cluster of mounds at 480 m depth at 34°12.680' N, 75°52.204' W (Fig. 1).

The ALBEX lander consisted of an aluminium tripod equipped with a 3-D (2 MHz) acoustic Nortek-AS current meter, a Seabird SBE37 CTD, and a Wetlabs combined optical backscatter sensor and fluorometer. All instruments were mounted 2 m above the seafloor. The ALBEX lander additionally carried a Teledyne RDI 300 kHz upward-looking Acoustic Doppler Current Profiler (ADCP) that measured horizontal currents up to 170 m above bottom for the entire period. The BOBO lander consisted of an aluminium tripod that extended 4 m above bottom, creating a clear area underneath the lander for current velocity and acoustic backscatter measurements, which were measured by a downward looking Teledyne RDI 1200 kHz ADCP mounted at 2 m above bottom. For this deployment the BOBO lander was equipped with an SBE 16+ CT sensor mounted at 3 m above bottom, a combined Wetlabs optical backscatter sensor and fluorometer. All equipment on both landers was programmed to record at 15 min intervals.

Both landers were equipped with a Technicap PPS 4/3 sediment trap with a 0.05 m² aperture. Sediment traps were equipped with a rotating carousel of 12 bottles of 250 mL. Each bottle collected material for 14 days, and samples were preserved in a pH buffered HgCl₂ solution in seawater, which was collected from the deployment site. All samples were split with a rotor splitter and 2 splits were freeze-dried after which total matter was weighed and mass fluxes were calculated. All sediment trap samples of the BOBO lander were analysed for organic carbon, nitrogen content and ²¹⁰Pb. Detailed descriptions of the methods can be found in Mienis et al. (2012).

In addition to the landers, a mooring was deployed in December 2009 at a depth of 550 m at 34°16.023' N/75°45.9216' W outside the cold-water coral area. The mooring was composed of a bottom weight (660 kg), 2 acoustic releases and a Valeport current meter (160 m above bottom).

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2.6 Tethered video imaging and analysis

Video-recordings of the coral habitats in the Cape Lookout CWC area were made using a tethered camera system attached to the boxcorer frame. The camera system consisted of a digital video camera (Sony™), hard disk, power-supply, modem, lights, and a set of parallel green laser pointers set 30 cm apart (Oktopus™). Live video images were transferred to the ship by the modem via the conductive core of the wire holding the boxcorer frame. This connection enabled the winch operator to keep the camera system at more or less constant distance from the seafloor assisted by the distance marks made by lasers. A total of 8 video surveys were made along transects in a SSW to NNE direction crossing coral mounds that were visible on the multibeam map. The length of each transect varied between 1.4 and 4.8 km and started and ended in an off-mound position thereby covering coral as well as non-coral habitats. The video records were used to ground-truth both reef and sedimentary structures observed on the multibeam data and echosounder profiles and to make a general description of the distribution of corals, invertebrate epifauna and fishes in relation to these structures.

Operations with the tethered camera system were hampered by the strong surface currents of the Gulf Stream that had repercussions for the quality and the amount of detail that could be extracted from the resulting video. Because of this, only a few organisms could be identified to species or genus levels with the majority identifiable to taxonomic levels up to phylum. To describe the fauna along each transect, transects were initially divided into sections of 50 m length, and the presence/absence of groups of organisms in these sections was noted. Fishes were enumerated with a distinction between cartilaginous (Chondrichthyes) and bony fishes (Osteichthyes). Simultaneously the predominant substratum in each 50 m sections was assigned to one of the following operational categories: (1) soft sediment, (2) sediment partly to densely covered with coral rubble and/or dead framework, (3) well developed (3-D) but predominantly dead framework with scattered live branches, (4) well developed framework with coalescent live branches, (5) stones/hard rock. Video sections in each transect were subsequently

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grouped according to predominant substratum, and organism counts were summed and averaged over the number of sections in each group.

3 Results

3.1 Predictive habitat mapping

5 The predictive models revealed that the southern parts of the eastern US slopes (Florida, Georgia and South Carolina coasts) contained the majority of suitable habitat for *L. pertusa* relative to the north of North Carolina (Fig. 2). Both the sediment-constrained (Fig. 2a) and non-sediment (Fig. 2b) models performed well with high test AUC scores (0.951 and 0.942, respectively), low omission rates (8 % and 7 %, respectively) and high test gains (2.070 and 1.852, respectively). The sediment-constrained model performed better than the non-sediment constrained model even though the contribution of the sediment layer was low (test gain 0.337 and AUC 0.690 for a model constructed of only sediment type). Based on the regularised training gain, the most important variable was depth for both models, followed by aragonite saturation and dissolved oxygen concentration. The variable that decreased the gain the most when omitted, and therefore contains information not present in other variables, was particulate organic carbon concentration for the non-sediment constrained model and current speed for the sediment-constrained model. However, sediment type decreased the gain by almost an equal amount.

3.2 Distribution of mounds and mound morphology

A total area of 750 km² with a water depth ranging between 240 and 1540 m was mapped with the multibeam echosounder (Figs. 1 and 3). Up to ten large (> 30 m high) and several small CWC mound structures were observed between 320 and 550 m water depth. Mound structures were characterised by high backscatter, which can be related to the presence of living coral colonies and coral debris as was observed in

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video images (bright areas in Fig. 3b). Off mound areas had low backscatter values (darker areas in Fig. 3b) and are largely characterised by sandy sediment. Current ripples were often observed in video images from off mound areas, indicating high near-bed flow velocity. In the study area three distinct mound morphologies were observed, which appeared related to water depth and can be broadly grouped into upper, mid and deep parts of the mound area. The shallowest mound, which was present at 320 m water depth had a flattened top and was up to 40 m high (Fig. 4a). Mounds situated in the intermediate part of the area were characterised by a tear-drop shape and all had an erosional gully at the SSW (up-current) side and a sediment moat at the NNE (down-current) side of the mound. These mounds had an irregular and rugged topography with multiple summits that are up to 40 m high. All mounds in the intermediate part of the study area are oriented in a SSW–NNE direction (Fig. 4b). The deepest mound at 520 m water depth in the area had a different morphology and can be described as a single mound of 0.5 km in diameter and up to 70 m high. The single mound was characterised by very steep slopes and an erosional moat at the NNE side (Fig. 4c).

Echosounder surveys crossing the different mound structures revealed that all mounds had a chaotic and almost transparent internal acoustic facies pattern (Fig. 4). Beneath each mound there was a strong reflector that formed the base of the structures. On the down-current side of the deepest mound this reflector cropped out at the surface and video data showed that it was related to a hard substrate formed by carbonate slabs (Figs. 4c and 6).

3.3 Video data analysis

The distribution of faunal groups within each classified habitat type is summarised in Fig. 5, and the representative features of each habitat are shown in Fig. 6. All transects started and ended in off mound habitat (Fig. 1), which in most cases consisted of rippled sand with a coarse or gravelly character and numerous burrows (possibly of squat lobsters). Boxcores taken in these off mound habitats are characterised by well-

sorted foraminiferal sand with pteropod fragments. Several of the mounds, i.e. transects 31, 39, and 45, were surrounded by a moat that was also visible on the multibeam and echosounder data (Figs. 3 and 4). Video recordings from the elevated parts of mounds revealed predominantly dead coral framework with occasional thickets of living coral (Fig. 6). Live framework was most abundant on the upper (SSW) slopes facing into the Gulf Stream current. In between the coral thickets, patches of softer and finer sediment with coral rubble were visible which was also observed in boxcore samples taken on top of the mound. These samples consisted, down core, of sediment, coral (*L. pertusa*) and shell debris characteristic of organic mound build up. The deepest mound (transect 45) had the most extensive patches of live coral framework on its upstream side and also had a different structure of the mound tail. Whilst the other mounds had tails consisting of sediment mixed with *L. pertusa* rubble, the tail of transect 45 was bare of sediment exposing slabs of hard ground (Fig. 6).

A common feature of all video transects was the presence of large numbers of planktonic organisms near the bottom such as euphausiids and jellyfish. On several occasions the view of the camera was blocked by euphausiids that were attracted by the lights of the camera upon arrival at the seafloor. Transect 5 did not cross a mound as did the other transects. There were marked differences with respect to distribution of taxa including live coral framework between transects. For example, anthozoans (*Actinoscyphia* sp.) and asteroids (*Brisingidae*) were only widespread (and abundant) on the shallowest transect 30 while this was the case for galatheids (*Munida* sp.) on transect 39, and hydrocorals on transect 45. Sponges were not abundant and were only observed on the multi summited mounds in the middle part of the area. Live coral framework was only observed at the mound structures, and was most common on transect 45 and least present on transect 30. Transects also differed with respect to abundance of fishes with the deepest transect 45 having highest number of fishes per 50 m of video (Fig. 7). Average fish numbers of the 50 m sections of the videosurveys were not only relatively high in the coral framework of transect 45 but also across the mound tail with its exposed hard ground.

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3.4 Overlying circulation

The 300 kHz upward looking ADCP mounted on the ALBEX lander measured horizontal currents up to 170 m above bottom. There was a very different character to velocities before mid-April 2010 and afterwards (Fig. 8). Pulses of strong NNE flow occurred in mid-December 2009, early January 2010, mid-February 2010 and early and mid-March 2010. These pulses coincided with increasing water temperatures of up to 15.8 °C. In early April a sustained SSW flow of 4 ms⁻¹ was present, whereas a weaker flow was observed after mid-April and persisted until the recovery of the landers in June. Average current speed was 2.9 ms⁻¹ to the NNE and 1.3 ms⁻¹ to the SSW, whereby a NNE flow was slightly more common over the deployment time period. The average vertical structure of the current varied with current direction, with nearly constant vertical shear of the horizontal current over the lower 100 m above bottom during NNE flow and a 40 m thick bottom boundary layer overlain by vertically homogeneous flow speed during SSW flow.

Elevated values of acoustic backscatter were observed in December 2009, February 2010 and from mid-April to late May 2010 (Fig. 9). Furthermore, a daily migration is obvious in the acoustic backscatter. The location of these signals, well removed from the seafloor and the ocean surface, the acoustic frequency (300 kHz) and the observed daily migration suggest zooplankton as the most likely signal source.

3.5 Near-bed environmental conditions

The records collected by the two bottom landers and mooring are similar in appearance and display the same warm events also recorded by the upward looking ADCP. The lander records before April 2010 were characterised by six pronounced events consisting of peaks in temperature up to 15.2 °C and salinities rising to 36.05, coinciding with increased flow and acoustic backscatter, which is likely related to resuspension of sediments (Fig. 8). During these events the current was directed to the NNE and bottom water temperatures increased with up to 9.5 °C within a day (5.8–15.2 °C), while

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salinity rose from 34.87 to 36.05. These warm water events lasted roughly one week. Minimum temperatures (5.56–8.33 °C) occurred in May 2011 when currents were relatively weak and directed to the SSW. The similarity between measurements by the two landers indicates that events are not local in scale but apply to the wider area (Fig. 8).

This is further substantiated by the match between the lander temperature records and that obtained by the mooring, deployed in 550 m water depth.

The fluorescence records on both landers were similar (Fig. 8), showing one prominent but short peak in early March, on the onset of a warm event. Acoustic and optical backscatter demonstrate different patterns. Acoustic backscatter increases with each warm event (Fig. 10), whilst optical backscatter only shows prominent peaks in December and February. High backscatter peaks correspond to high mass fluxes as collected with the sediment trap (Fig. 11b and f). The event in February completely filled a sediment trap bottle on the ALBEX lander. During both periods of high mass flux, organic carbon values were low, as well as ^{210}Pb values, which indicates resuspension of aged or degraded material (Fig. 11d–f).

Vector plots of displacement show the transport direction and magnitude of water at both lander locations during the deployment period (Fig. 1). Directions of water transport at both deployment sites have a mainly SSW–NNE orientation, which corresponds with the elongation of the mound structures in the middle part of the area. Strongest currents have an orientation in a NNE direction. The transport direction of water at the ALBEX site is likely influenced by topographic steering of water between the different summits of the mound structure, as it was deployed on the down-current side of a mound structure in the intermediate part of the research area.

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4 Discussion

4.1 Mounds

The Cape Lookout CWC area is mainly characterised by multi-summitted CWC mounds that have a teardrop morphology and are oriented in a SSW–NNE direction. Single mound structures were only observed in the shallowest and deepest part of the mound area. All structures have an erosional moat at their up current site, indicating the presence of a very strong NNE directed current in the area, and a sediment tail at the down-current side of the mounds that mainly consists of coral rubble. This same mound morphology was described by Quattrini et al. (2012) for a large CWC mound (Cape Fear mound) located about 80 km southwest of the Cape Lookout mounds. The impression that the mounds are subject to a regime with strong currents is confirmed by the presence of current ripples visible on video transects made in off mound areas, which were also observed during earlier studies on the Blake Plateau (Pratt, 1963). Current ripples had orientations that suggest a predominant NNE transport direction, which can be related to the current direction of the Gulf Stream. The mounds were dominated by the framework-forming scleractinian coral *L. pertusa*, whilst hydrocorals were also found on the deepest single mound in the area (Fig. 4c). Living CWC colonies were mainly found on the SSW sides of mounds. Similar mound structures have been found in the Florida Strait (Grasmueck et al., 2006; Correa et al., 2012), on the continental margin of Norway (e.g., Stjernesund and Traena, Freiwald et al., 1997; Tong et al., 2013) and Tisler reef (Lavaleye et al., 2009; Guihen et al., 2013). In all these areas elongated reef structures and a strong uni-directional current are present. Several studies have indicated that near-bed currents and turbulence are one of the most important factors influencing coral growth (White et al., 2005; Dorschel et al., 2007; Duineveld et al., 2007; Mienis et al., 2007; Davies et al., 2009). Strong currents will influence the (food) particle encounter rate, which is highest at the current facing sides of the mounds in the Cape Lookout area and elsewhere (Purser et al., 2010). Consequently, mounds

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and reefs in these areas are likely growing against the currents in a more horizontal manner creating relatively low structures.

A distinct difference was observed not only in mound morphology between the different depth zones with coral mounds, but also in faunal abundance and diversity. Living *L. pertusa* colonies were not observed on the shallowest single mound, but were instead most abundant on the deepest single mound. In general faunal abundance increased whenever coral framework was present, but also increased with water depth (Fig. 6). Most fishes were present on and around the deepest single mound in the area possibly because of the abundance of other prey (Fig. 7, transect 45). However, we have to take into account that the sample sizes for a variety of depths was limited.

The reflection pattern acquired by echosounder profiles of the mounds off Cape Lookout is similar to previously published seismic data of mounds in the north east Atlantic (Akhmetzhanov et al., 2003; Van Weering et al., 2003a; Mienis et al., 2006). They mainly show chaotic and transparent reflection patterns (Popenoe, 1994), indicating that the mound structures are completely made of cold-water corals and sediments that have been baffled within the coral framework. Underneath the mounds a strong reflector was observed that seems to form the base of all mounds near Cape Lookout. This reflector cropped out behind the deepest mound in the area and video images showed the reflector to be carbonate slabs. CWC mounds on the Blake plateau have developed in a generally erosional regime where pre-Holocene to Cretaceous strata are often exposed (Pinet et al., 1981, 1985; Popenoe, 1994). A similar cemented pavement was also observed by Paull et al. (2000) at the seafloor on the Florida-Hatteras slope. One of the requirements for CWC growth is the presence of a stable substrate for settlement. Mounds in the Porcupine Seabight and on the Rockall Trough margins all seem to have initiated on top of a firmground (Van Rooij et al., 2003; Mienis et al., 2006; Huvenne et al., 2009b). The distribution of the coral mounds near Cape Lookout could be related to sites where the hard ground was exposed during the initial settlement of cold-water corals.

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Compared to CWC mounds on the Irish margin that can be kilometres long and wide and up to 360 m high, the mounds off Cape Lookout are relatively small. This can be either interpreted as the initial phase of mound growth in the area or as an indication that corals are living under stressed conditions, giving rise to a low rate of mound development. Mound growth is mainly due to coral colonies that baffle sediment. If coral growth is outpacing sedimentation, mound structures can form but if the corals are frequently stressed and do not outpace sedimentation then mounds will become relatively limited in size (De Haas et al., 2009; Dorschel et al., 2009).

Retarded coral growth due to stressful conditions seems the most plausible explanation for the small dimensions of the Cape Lookout mounds. Firstly there is evidence of erosion in the form of moats and exposed hardrock. Secondly coral ages seem to be higher than in E. Atlantic areas with mound development. Coral fragments collected at mounds from the Blake Plateau were dated with ages > 20 kyr and very recent datings of CWC fragments from the Cape Lookout even show ages older than 123 kyr (De Matos, personal communication, 2013). This shows that cold-water corals were already present before the Holocene as opposed to coral reefs found on the Norwegian margin that show rapid development during the Holocene (Freiwald et al., 1997; Lopez Correa et al., 2012). Thirdly, the predictive models (Fig. 2) also suggest that this is a stressful area for corals, as the northern US shelf appears less suitable for coral growth than further south along the Florida margin. Finally, the in-situ measurements by the landers showed recurring temperature peaks which are outside the range frequently reported for *L. pertusa* (see below) (Roberts et al., 2006; Davies et al., 2011).

4.2 Environmental conditions

Cold-water corals off Cape Lookout live in an area that is characterised by extreme environmental conditions, which are mainly related to the occasional presence of the Gulf Stream. A clear difference was observed in current velocities before and after April 2010. Before April 2010, several strong pulses of NNE flow were observed, which coincided with increasing temperatures and high near-bed acoustic backscatter values.

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After mid April 2010, current velocities were much lower and minimum temperatures were observed. Sea-surface temperature data obtained from satellite imagery at the end of the first strong NNE pulse (Fig. 12) suggest that the Gulf Stream was atop the mooring and mooring sites during this time and presumably during other times of strong NNE flow. The more-shoreward position of the Gulf Stream at the lander locations at that time was due to a wavelike Gulf Stream meander progressing towards the NE. The crest of the meander was directly over the mooring site on 17 December 2009. Two SST images from March show the effect of the transition from NNE to SSW flow (Fig. 12). A deflection (an almost right angle turn) of the Gulf Stream developed at the end of April, which we associate with a period of stronger SSW flow (Fig. 12). It appears that this deflection moved slowly downstream, but the general location of the Gulf Stream remained offshore of the mooring site from this time until the end of the deployment. Other SST images are consistent with the Gulf Stream remaining well offshore of Cape Lookout until the recovery of the moored instrumentation (Fig. 12).

Regular coastward meanders of the Gulf Stream lead to a rapid rise in bottom water temperature of up by 9 °C and salinity by up to 1.18, which are the largest temperature and salinity variabilities so far measured directly within a CWC habitat. The metabolic consequences of these pulses must be significant given the strong effects of temperature on the respiration of cold-water corals and particularly *L. pertusa*. For example, a rise of almost 10 °C in temperature will lead to a more than five-fold increase in coral respiration ($Q_{10} = 5.4\text{--}7.8$) (Dodds et al., 2007). Prolonged periods of high temperatures will require an equivalent increase in food availability to account for the increased basic demand of corals and other benthic organisms in the region. Naumann et al. (2013) have evaluated the effect of changing temperatures on the physiology of the two most common framework building coral species. Their experiments showed that respiration and calcification rates of *L. pertusa* were less affected by changes in temperature compared to *Madrepora oculata*. Furthermore, *L. pertusa* needed a shorter acclimation time, which might be favourable in light of the large temperature fluctuations as observed off Cape Lookout. Additionally, Brooke et al. (2013) demonstrated

that *L. pertusa* may have a somewhat higher temperature tolerance than was previously reported with an upper lethal boundary near 15°C (Brooke et al., 2013). This might explain why only *L. pertusa* was commonly present on CWC mounds on the Blake Plateau (Neumann et al., 1977; Paull et al., 2000; Reed et al., 2006; Quattrini et al., 2012). However, enhanced metabolic activity must be compensated for by energy intake. Therefore, particle supply and quality play an equally important role in the distribution of *L. pertusa* (Duineveld et al., 2004; White et al., 2005; Mienis et al., 2007; Davies et al., 2009).

According to earlier studies vertical instabilities along the westward boundary of meanders give rise to filaments and eddies with associated nutrient entrainment and enhanced plankton production (Lee et al., 1991; Garciamoliner et al., 1994; Matrai et al., 1996; Ryan et al., 1999, 2001; Leterme et al., 2008). In six months only a single fluorescence peak was recorded (early March 2010) near the sea-bed that coincided with a passing meander. Otherwise, no increase of fluorescence was observed during the warm water events near the seabed. This peak in fluorescence could be related to a spring bloom that occurs in winter due to deep dense water mixing (Leterme et al., 2008) or to shelfbreak upwelling in response to wind stress during unstratified periods (Ryan et al., 1996). During many of the warm events the benthic community could experience food stress due to enhanced metabolic demands and the lack of fresh, high quality food in the form of phytodetritus. This may explain the boxcore and video observations showing relatively low proportions of live coral and scarcity of epifauna, especially of large macrosponges as compared to coral habitats in the E Atlantic (Rockall Bank, Porcupine Seabight, Norwegian reefs) (Van Soest et al., 2007). By contrast, CWC habitats in the E Atlantic have a rich sponge fauna (Van Soest et al., 2007), as well as some reefs in the Western Atlantic, e.g., in the Jacksonville, Cape Canaveral and Florida areas (Partyka et al., 2007).

Lack of phytodetritus could be compensated for by other food sources. Cold-water corals can also feed on zooplankton or nutrients derived from zooplankton (e.g. faeces) (Duineveld et al., 2007; Kiriakoulakis et al., 2007; Becker et al., 2009). Cold-water

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corals have also been shown to capture live prey (Hovland et al., 1999). The increased mid water column acoustic backscatter values recorded by the lander ADCP in the December, February, April to May time period, may point to either greater abundance of scatterers (zooplankton) or a change in the scatterers (e.g. different species). Furthermore, the view of the tethered camera was on several occasions blocked by large numbers of euphausiids attracted by the light. It is possible that these could provide an alternative food source for corals and perhaps other benthic fauna. Given the extreme nature of conditions at Cape Lookout, and the differences with other coral habitats, food-supply studies are particularly needed to provide further insight into the tolerance and prospects of the local CWC communities.

Gulf Stream meanders coincided with current velocities of up to 6 ms^{-1} and increased near-bed acoustic backscatter at both lander locations. These increases indicate resuspension of relatively coarse particles, given that the current meters on the landers are more sensitive to larger ($160\text{--}320 \mu\text{m}$) particles (Mienis et al., 2012). The instantaneous increases in the acoustic backscatter up to 35 m above the seafloor, at the onset of warm events when the current speed increases (Fig. 9), could represent local erosion of the seafloor in off mound areas and deposition of large amounts of sediment on the coral mounds. Sediment in off mound areas consists of relatively coarse carbonate sand. This was also shown by the large amounts of sediment that were collected in the sediment trap as compared to other coral areas (Mienis et al., 2009, 2012). The ^{210}Pb and organic carbon data show that during resuspension events mainly old or degraded material is being resuspended. Such erosion and deposition could explain our observation of partly buried and sediment-filled framework on top of the mounds. These resuspension events, which last up to a week might form another stressor affecting coral growth. Although cold-water corals can handle high sediment load for prolonged periods (Brooke et al., 2009; Larsson et al., 2013), the abrasive nature of sand in combination with strong currents can have a negative effect on living cold-water colonies that are present on the Gulf Stream facing flanks of the mounds. During these periods corals will likely not be able to feed (Purser et al., 2010).

5 Conclusions

Cold-water corals off Cape Lookout live under extreme environmental conditions that potentially limit coral and therefore mound growth. Largest temperature and salinity fluctuations known so far for cold-water coral areas were measured in the Cape Lookout CWC habitat. These large temperature and salinity variations are likely to influence the metabolism of the cold-water corals and associated benthic species on the mounds. Furthermore, corals regularly experience abrasive sand storms that occur during each time the Gulf Stream enters the area. Meandering of the Gulf Stream in and out of the research area is the main driver of the near bed processes near Cape Lookout and influences the whole mound area as events were observed at all lander and mooring stations. Upwelling in cold core eddies and increased productivity in these eddies was not observed near the seabed. Only one major fluorescence peak was observed, which might form a food source for the species. Another additional food source might be zooplankton or nutrients derived from zooplankton, which was highly abundant during April and May 2010.

Supplementary material related to this article is available online at <http://www.biogeosciences-discuss.net/10/18925/2013/bgd-10-18925-2013-supplement.pdf>.

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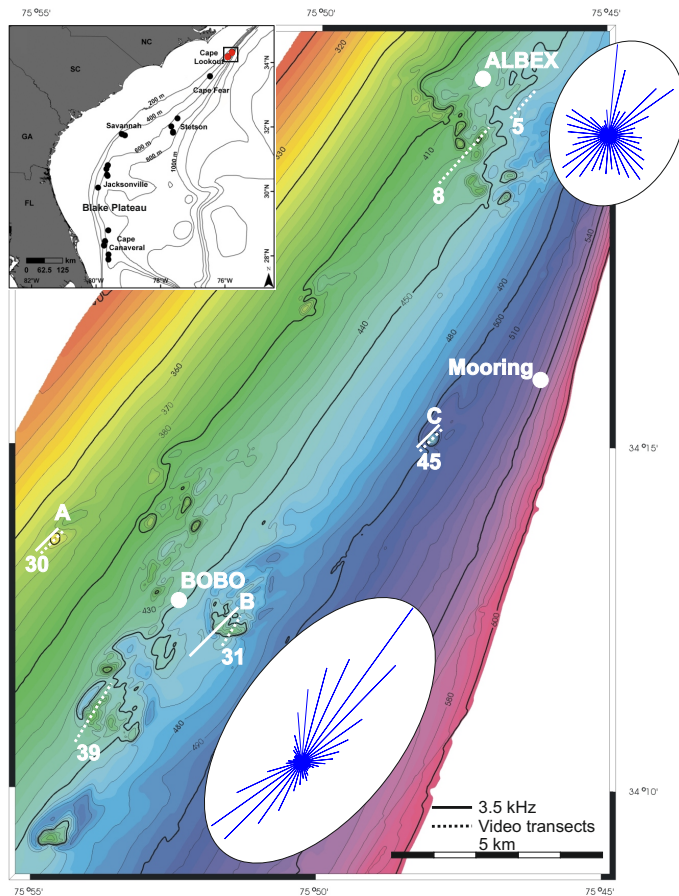


Fig. 1. Multibeam bathymetry map of the research area with 3.5 kHz profiles, video-transects mooring and lander locations indicated. Vector plots of displacement (ellipses) relative to the lander position show the direction and magnitude of the transport of water. Inset shows the general CWC areas that have been recorded in the West Atlantic.

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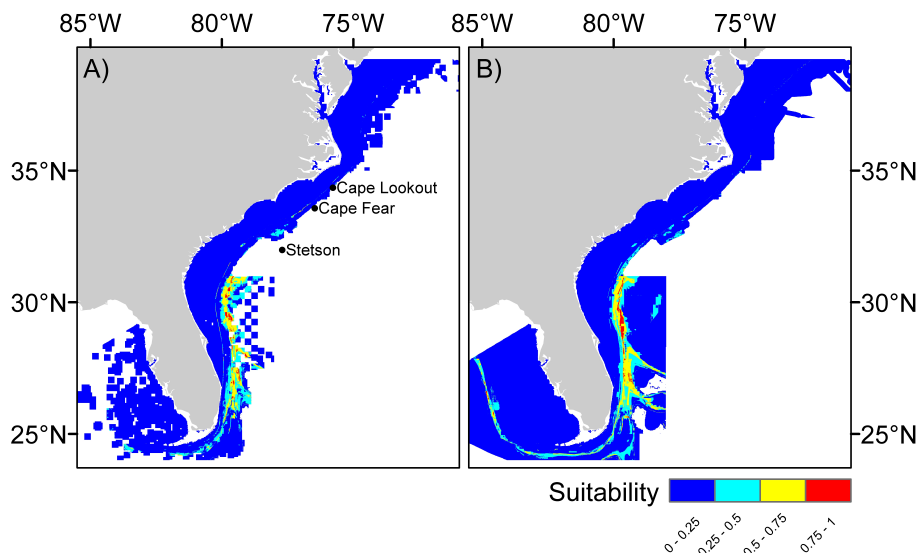


Fig. 2. Habitat suitability models for *L. pertusa* in the southeastern US shelf, **(A)** a model created using sediment type and **(B)** a model without sediment incorporated. The larger area of the non-sediment layer is a result of the limited sediment data available for the region. Higher suitability values indicate that the area is more suitable for coral occurrence but do not mean that corals will be found there as there may be other variables constraining occurrence that are not used in the model.

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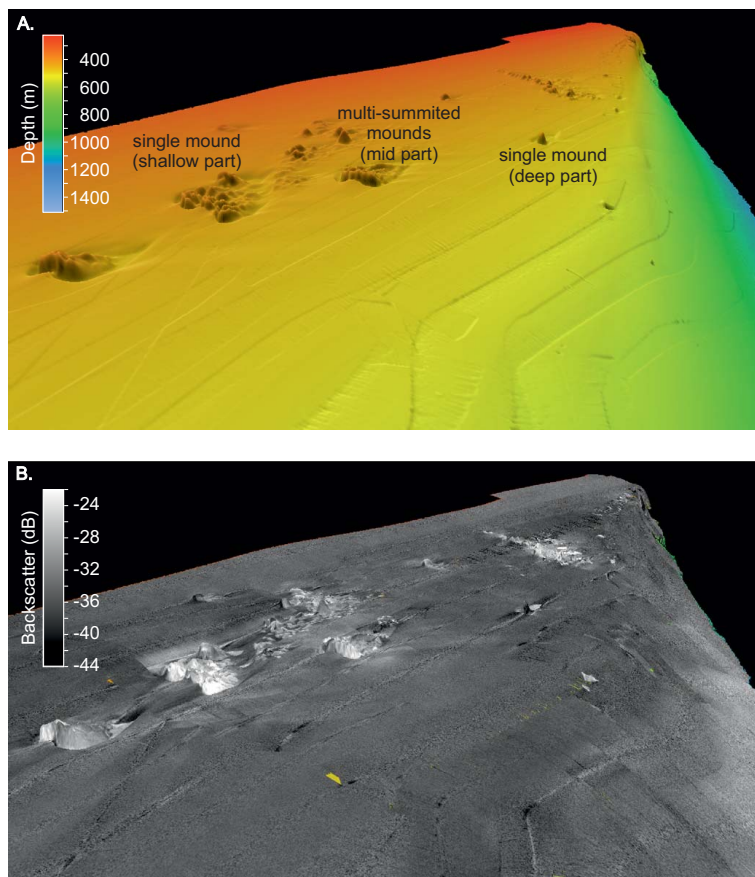


Fig. 3. 3-D Multibeam bathymetry **(A)** and backscatter map **(B)** of the research area. Different mound morphologies were observed on the shallow, mid and deep part of the mound area. Mounds are characterised by high backscatter (bright areas).

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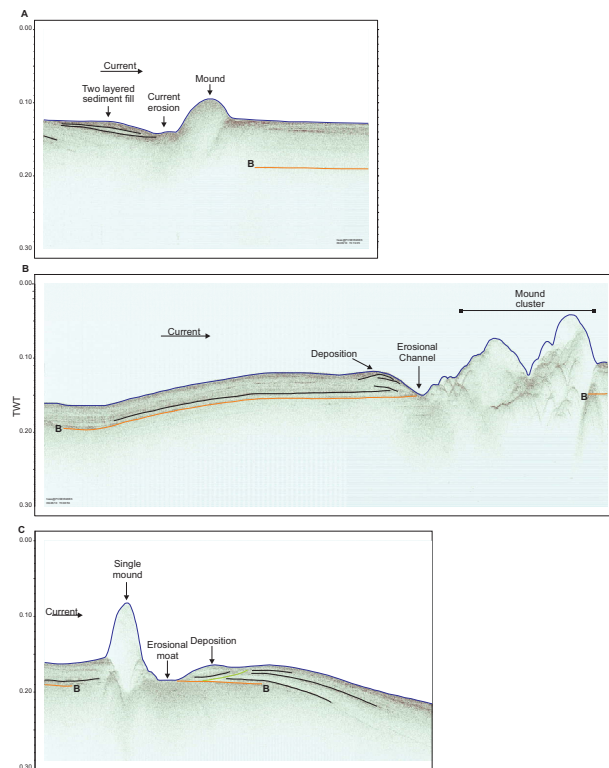


Fig. 4. 3.5 kHz lines (positions of lines are shown in Fig. 1) recorded in a SW–NE direction **(A–C)**, showing the different mound types in the upper, mid and deep part of the Cape Lookout CWC area. **(A)** single mound at the upper slope **(B)** multi summited mounds in the mid slope area **(C)** single mound in the deep area. Underneath the mounds a strong reflector was observed that forms the basement of the mounds (orange line).

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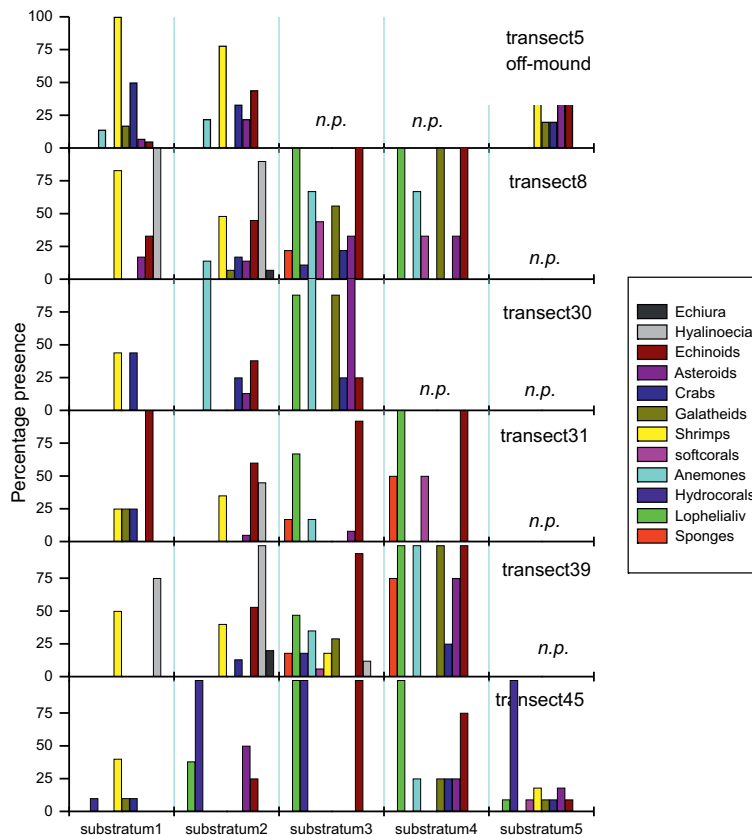


Fig. 5. Faunal assemblages of the video transects for each of the five recognized substrata (1 = soft sediment, 2 = sediment partly to densely covered with coral rubble and/or dead framework, 3 = well developed (3-D) but predominantly dead framework with scattered live branches, 4 = well developed framework with coalescent live branches, 5 = stones/hard rock). The abundance of each faunal group is indicated as a percentage of presence at the 50 m sections of the whole videotranssect. The locations of the transects are indicated in Fig. 1.

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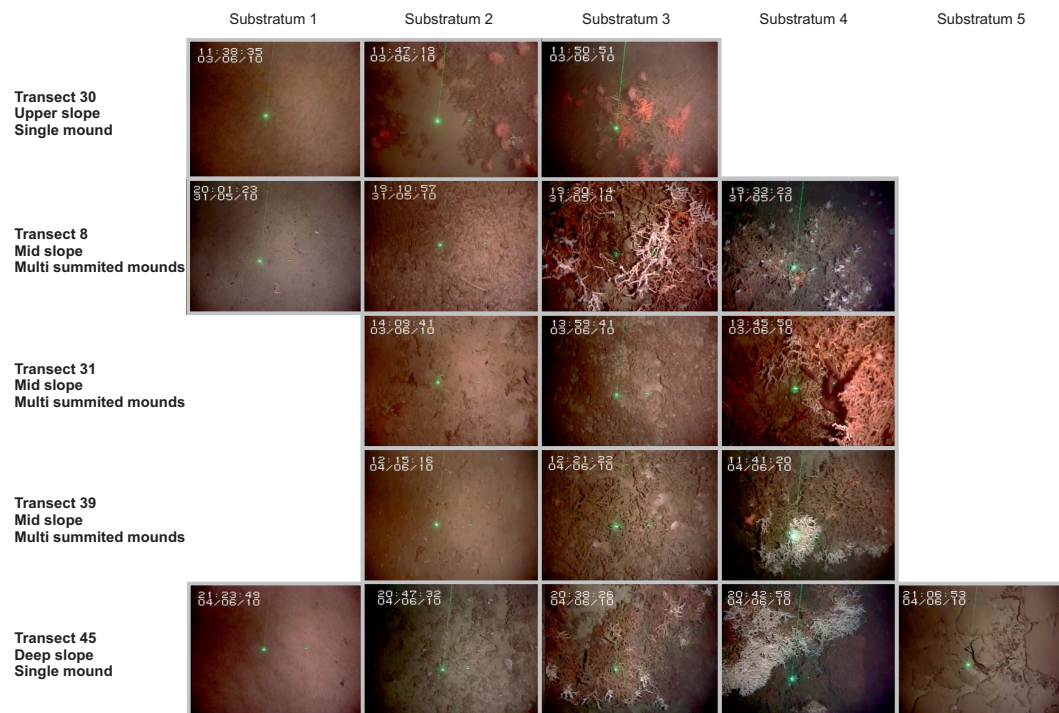


Fig. 6. Still images taken from the video transects characterising different substratum types. For explanation of the substrata numbers see Fig. 5.

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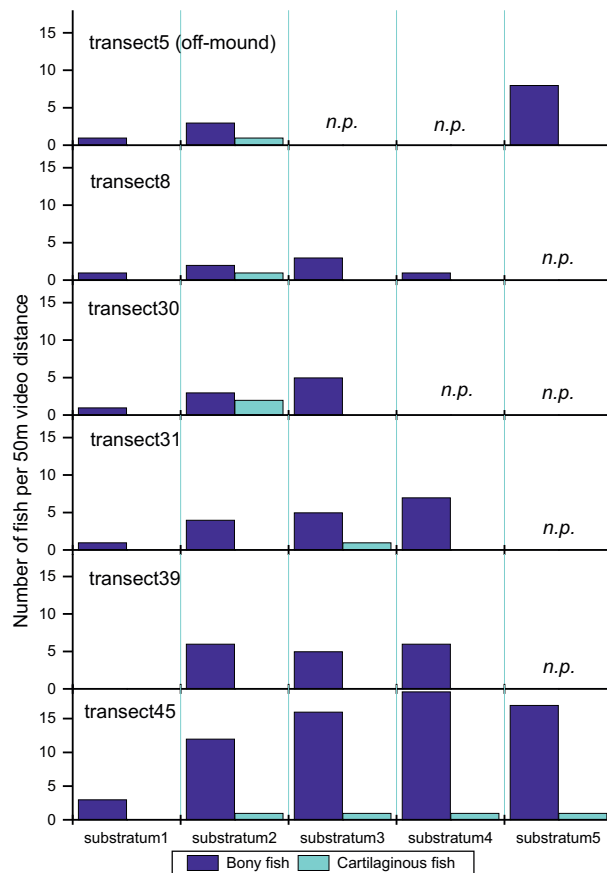


Fig. 7. Average fish abundance as counted for each 50 m section along the video transects for each substratum. For explanation of the substrata numbers see Fig. 5.

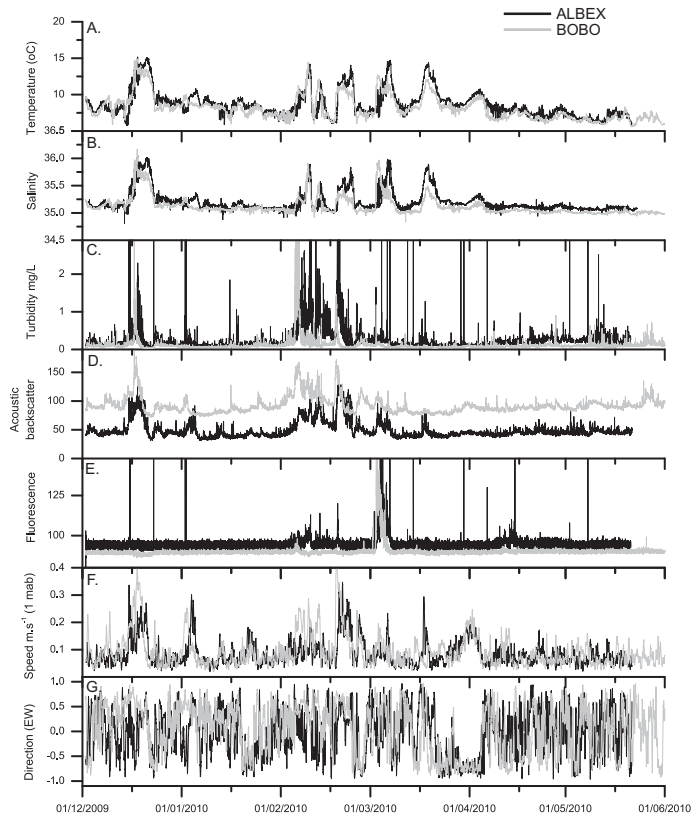


Fig. 8. Six month records (December 2009–May 2010) from instruments mounted on ALBEX and BOBO benthic landers. **(A)** temperature **(B)** salinity. **(C)** turbidity calculated from optical backscatter. **(D)** acoustic backscatter **(E)** fluorescence in relative units. **(F)** current speed at ALBEX deployment site at height of 2 m (black line) and at 40 m (grey line) above bottom. **(G)** current direction at ALBEX deployment site. For A-E the ALBEX data are shown as black lines, while for BOBO as grey lines.

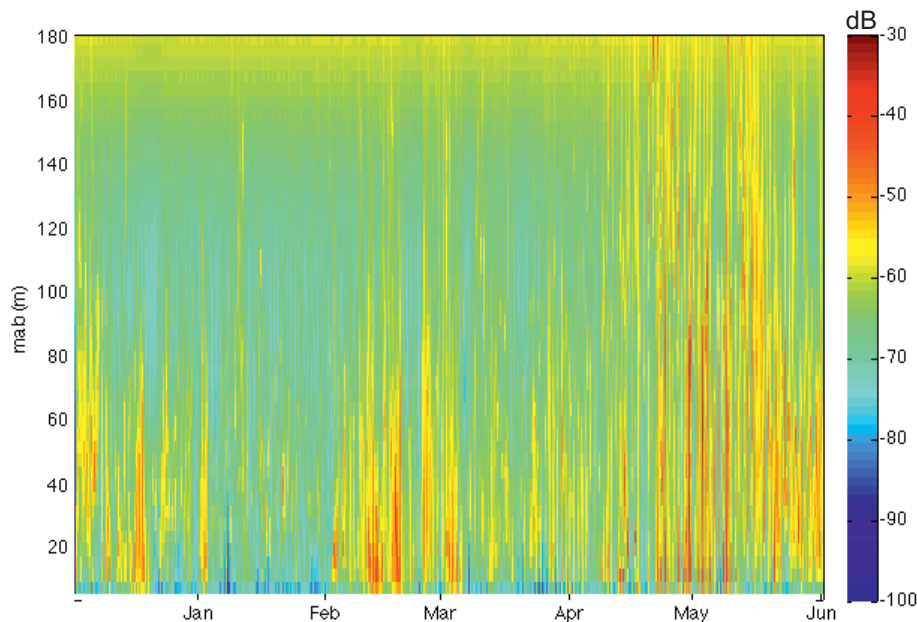


Fig. 9. Acoustic backscatter from the upward looking ADCP on ALBEX lander, expressed as backscatter strength in dB, following (Deines, 1999). Orange colors mean more backscatter (e.g. caused by zooplankton).

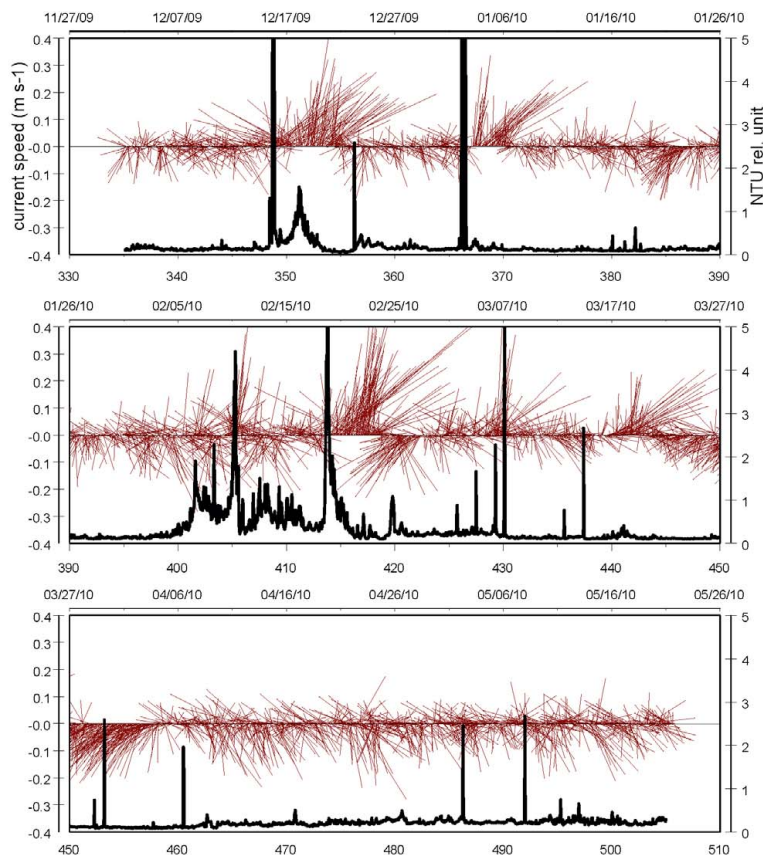


Fig. 10. Current speed and direction (stick plot), in combination with turbidity during 6 month deployment. The lower x-axis gives days since 1 January 2009, while the upper x-axis gives the true dates.

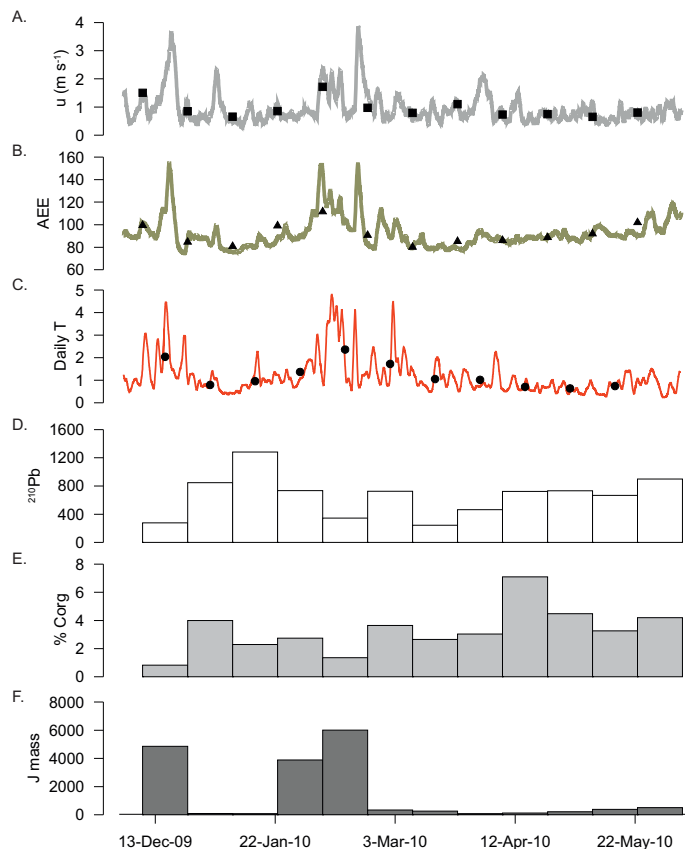


Fig. 11. Record of daily (line) and 16 days average (dots) of fluctuations of **(A)** current speed, **(B)** acoustic backscatter, **(C)** temperature (daily ΔT). **(D)** organic carbon (%), **(E)** ²¹⁰Pb (Bq g⁻¹), **(F)** total mass flux (mg m⁻² day⁻¹).

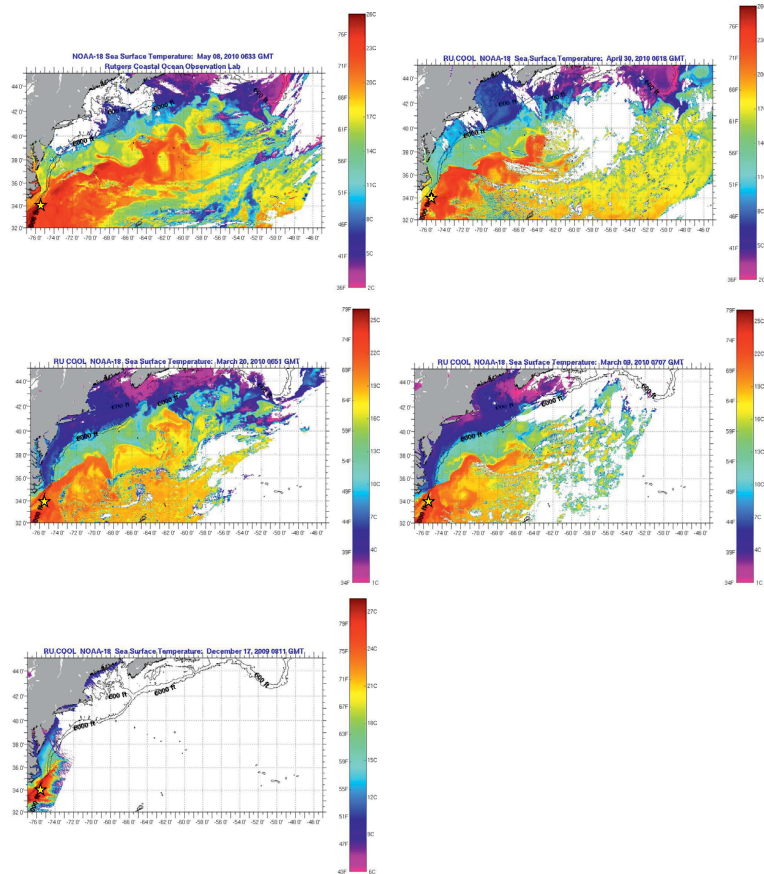


Fig. 12. SST satellite images of sea surface temperature distribution in the NW Atlantic on 17 December 2009, 9 and 20 March, 31 April and 8 May 2010 (http://marine.rutgers.edu/mrs/sat_data/). The position of the Gulf Stream and its influence on the study area off central North Carolina is clearly visible.