

# COLD-WATER CORALS ON THE TISLER REEF

PRELIMINARY OBSERVATIONS ON THE DYNAMIC REEF ENVIRONMENT



BY MARC LAVALEYE, GERARD DUINEVELD,  
TOMAS LUNDÄLV, MARTIN WHITE, DAMIEN GUIHEN,  
KOSTAS KIRIAKOULAKIS, AND GEORGE A. WOLFF

**ABSTRACT.** During HERMES cruises in spring 2006 and 2007 to a cold-water coral (CWC) reef at the border between Norway and Sweden, we studied effects of the reef on the quality (C/N ratio) of suspended particles. The Tisler reef is situated on top of a southeast-northwest-oriented sill forming the connection between the Kosterfjord and the open Skagerrak. In spring 2006, two benthic landers equipped with sediment traps, current meters, and turbidity sensors were deployed at the northwest and southeast edges of Tisler reef. The unidirectional northwest currents during the deployment enabled comparison of the quality of particles before and after crossing the reef. Before the onset of the 2006 spring bloom, particles trapped at the northwest reef edge had a more degraded character than those at the southeast edge. When the spring bloom swamped the study area with fresh phytoplankton, cross-reef distinctions in particle quality disappeared. In spring 2007, near-bottom suspended particles were collected with submersible pumps during one part of a tidal cycle. Analysis revealed a difference in composition of suspended particulate matter along the reef, with highest quality at the northwest edge where particles were delivered, and lower quality at the middle and southeast edge of the reef. Results from both cruises show that particles passing over Tisler reef are subject to preferential removal of nitrogen, indicating that even a relatively small reef such as Tisler has an impact on the biochemistry of its environment. This evidence suggests that, globally, CWC reefs are hotspots of mineralization activity in the ocean.

## INTRODUCTION

The occurrence of the scleractinian cold-water corals *Lophelia pertusa* and *Madrepora oculata* is strongly dependent on environmental variables, specifically those related to (1) water depth (i.e., below the photic zone from 50–1000 m at high latitudes and up to 4000-m water depth at low latitudes; Roberts et al., 2006), (2) water temperature (4–12°C; Dodds et al., 2007), (3) availability of hard substrata for colonization (Wilson, 1979; Mortensen et al., 2001; Freiwald, 2002; Freiwald et al., 2004), and (4) suitable food supply. These variables are, in turn, dependent on the productivity of surface waters,

hydrodynamics, and particulate organic matter (POM) supply (i.e., food) to deeper waters (Duineveld et al., 2004; Freiwald et al., 2004; Mortensen and Mortensen, 2005; White et al., 2005; Kiriakoulakis et al., 2004, 2007), or even availability of zooplankton prey (Kiriakoulakis et al., 2005). Cold-water corals are also dynamic ecosystems associated with high species diversity and richness (Roberts et al., 2006, and references therein) and highly elevated respiration (as compared with similar open slope environments with no coral; D. van Oevelen, Netherlands Institute for Ecology, *pers. comm.*, 2008). There is a need for a quantitative approach to

determine the hydrodynamics, POM supply (carbon, nutrients), and respiration of the corals and associated fauna (O<sub>2</sub> uptake) so that we can better understand the environmental services that cold-water coral reefs provide, in terms of carbon and nutrient remineralization.

Within the EC-funded HERMES consortium, a multidisciplinary collaboration was initiated to shed more light on some of these issues, and ultimately to provide quantitative data that will make it possible to create realistic mathematical models describing the functioning of cold-water coral ecosystems. The main study area selected was Kosterfjord/Hvaler (Northeast Skagerrak; Figure 1), where several *Lophelia* reefs have been found in the coastal deep-water channels. The advantages of this particular location are that it is close to the facilities of the Tjärno Marine Biological Laboratory (TMBL, University of Gothenburg), it is protected from the ocean so that relatively small vessels can be used to reach and work on it, and its water depth is relatively shallow (< 200 m), allowing easy operation of the TMBL remotely operated vehicle (ROV). Furthermore, TMBL has produced detailed maps of coral distribution in the study area as part of the HERMES project and its predecessor, the Atlantic Coral Ecosystem Study (ACES). Thus, the Kosterfjord/Hvaler area was an ideal site for intense observations on cold-water corals and in situ experimentation.

The specific objective of this part of our study was to assess the seasonal variability of environmental forcing on the Tisler reef community. Having insight into the magnitude and time scales of the forcing factors (current regime, turbidity, salinity, O<sub>2</sub> concentrations, POM fluxes,

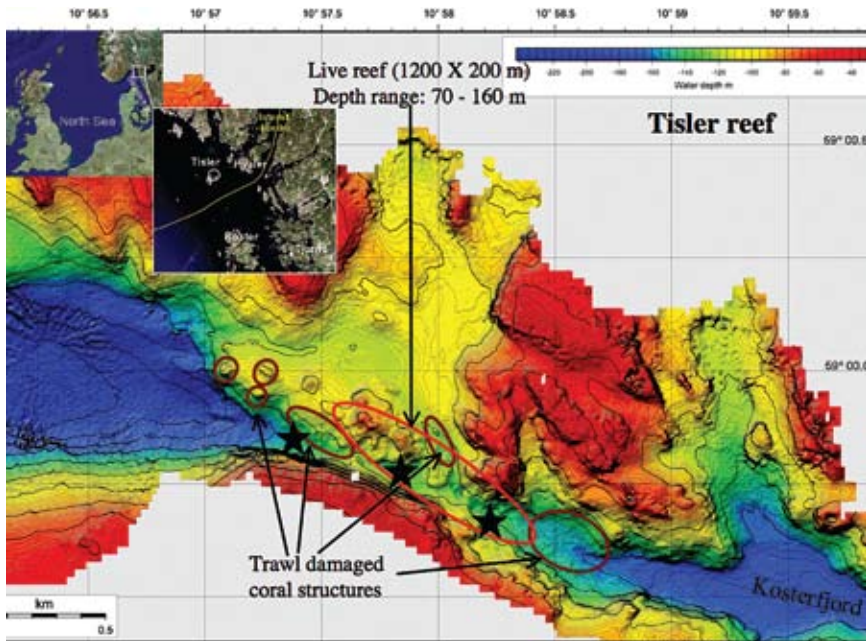
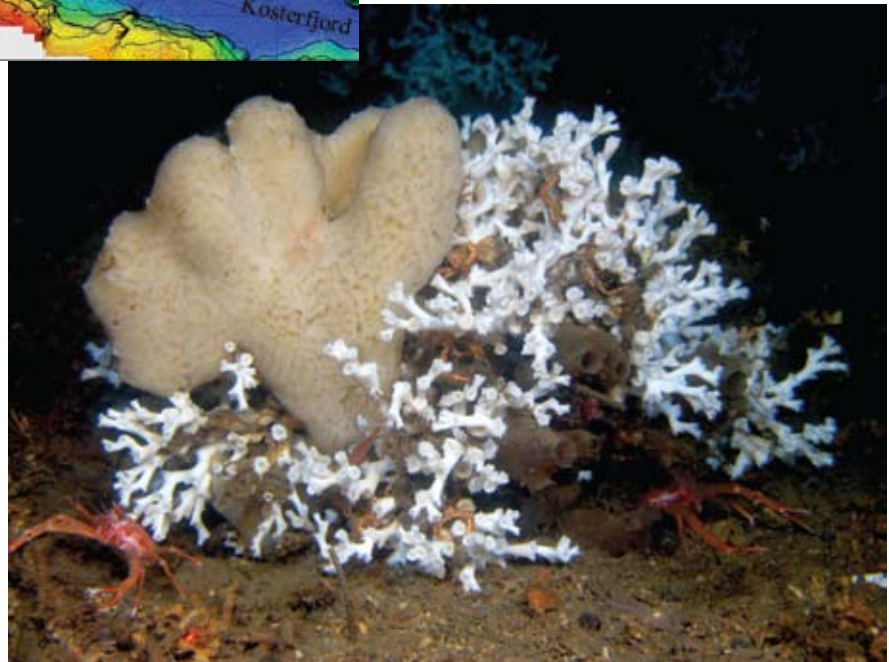


Figure 1. Bathymetry of the Tisler reef. Black stars show the sampling locations (i.e., southeast and northwest edges, and the middle of the reef). Large ellipse indicates live coral area; smaller ellipses indicate areas with trawl damage.

Figure 2. Example of the coral community at Tisler reef showing a mixed patch of *Lophelia pertusa*, sponges, and tunicates, with *Munidopsis serri-cornis* (squat lobster) between coral branches and *Munida rugosa* (squat lobster) in front of coral.



and POM quality) enables appropriate study of functional aspects of the community. Functional aspects that will be included in a subsequent part of the study are the oxygen and biochemical fluxes and turnover of biomass and species. Here, we provide a first report on the results of field studies undertaken in the spring seasons of 2006 and 2007, which were designed to confirm that the *Lophelia* reefs do indeed occupy a highly dynamic environment; we were specifically looking for in situ evidence of a “reef effect” influencing POM fluxes through the reef system.

## METHODOLOGY AND APPROACH

Our studies concentrated on the largest reef, located east of the Tisler islands and situated in the sill area of the Kosterfjord deep-water connection to the open Skagerrak (the submarine border between Norway and Sweden; Figure 1). The reef was first discovered and documented in 2002 (<http://www.tmbi.gu.se/resdev/projects/CUD/rov/survey.html>).

It is thousands of years old, and the living parts of the reef extend 1200 x 200 m laterally over a depth range of 70–155 m, making it one of the largest and shallowest inshore reefs. It contains several color varieties of *Lophelia pertusa*.

The ROV dives and video surveys conducted in the current project showed the Tisler reef to be inhabited by a rich community. The squat lobster *Munidopsis serri-cornis* appeared to be one of the most abundant megafauna organisms

(6.7 ind. m<sup>-2</sup> of *Lophelia pertusa*) on the video footage (Figure 2). *M. serri-cornis* was observed entering into symbiotic relationships with *Lophelia*, feeding on particles attached to the coral framework and hiding in cavities between branches (Berov, 2007). In the smaller nearby Säcken reef, 47 taxa were identified in the video (Jonsson et al., 2004).

Thorough ROV documentation of the area revealed that large, dead coral structures are present in the distal parts of the

reef, with indications of trawl damage (Figure 1), suggesting that the living reef once was about twice its present size. As of late 2003, Norwegian fishery regulations protect the reef from trawling. An additional advantage of the Tisler reef for our experiments is that it is located in a long gully, forcing the currents in a northwest-southeast direction, which makes it easier to measure a possible reef effect on the quality and quantity of particles in the near-bottom water.

Collaborative studies on the Tisler reef were conducted between late March and early May 2006 and in April/May 2007. These periods were chosen to coincide with the spring phytoplankton bloom. Two ships were used to collect samples and to deploy and recover equipment. R/V *Nereus* deployed and recovered the Royal Netherlands Institute for Sea Research (NIOZ) landers and the National University of Ireland, Galway (NUIG) moorings plus acoustic Doppler current profilers (ADCPs). The main task of R/V *Lophelia* was to deploy smaller items using a remotely operated vehicle (SPERRE *SUB-Fighter 7500 DC*) and to visually inspect the placement, deployment, and recovery of the heavy instruments. The ROV was equipped with online video, photographic equipment, a flexible arm with manipulator, a conductivity-temperature-depth (CTD) sensor, and a sonar system to locate

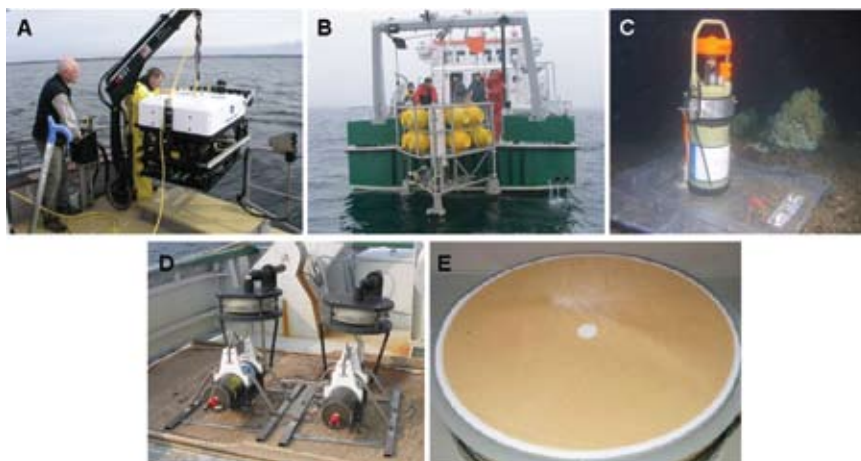


Figure 3. Examples of equipment deployed at the Tisler reef. (A) Remotely operated vehicle. (B) Lander being deployed from support ship R/V *Nereus*. (C) Recording current meter RCM9. (D) Stand-alone in situ pump (SAPS) in special bottom frame. (E) Loaded SAPS filter.

equipment in murky water (Figure 3A).

Near-bed currents, fluorescence, and turbidity at both ends of the coral reef were measured during a 24-day deployment of ALBEX (Autonomous Lander for Biological Experiments) benthic landers (Figure 3B). Currents were measured at 0.85 m above the bottom with a Nortek Aquadopp three-dimensional acoustic current meter. Fluorescence and turbidity were measured at the same height with Seapoint fluorometric and optical backscatter sensors connected to a custom-built data-logging device. The landers also held a Technicap PPS3/4 sediment trap with 12-vial carousel, which collected the sinking POM ( $POM_{sink}$ ). The trap opening was about 2.5 m above the seafloor, and the 12 vials were exposed

in sequence for two days each, covering the period April 1–23, 2006. Mercury chloride was used to preserve the contents of the trap. The samples were divided in half with a Folsom plankton splitter, and poured over CA (Cellulose acetate and pre-ashed GF/F 0.7  $\mu m$ ) filters. These samples were then freeze-dried and weighed for mass flux prior to analyses of organic carbon, nitrogen, and lipid biomarkers. Finally, each lander was equipped with an underwater video system composed of an analog Sony-TR2000E handycam, timer, and battery pack contained in a custom-built aluminium housing, and a Deep-Sea Power and Light underwater light.

To measure the physical oceanographic data, an array of equipment

---

**Marc Lavaleye** ([lava@nioz.nl](mailto:lava@nioz.nl)) is a researcher in the Department of Marine Ecology, Royal Netherlands Institute for Sea Research, Den Burg (Texel), The Netherlands. **Gerard Duineveld** is a researcher in the Department of Marine Ecology, Royal Netherlands Institute for Sea Research, Den Burg (Texel), The Netherlands. **Tomas Lundalv** is a researcher at the Sven Loven Centre of Marine Sciences-Tjarno, University of Gothenburg, Stromstad, Sweden. **Martin White** is Lecturer, Department of Earth and Ocean Sciences, National University of Galway, Galway, Ireland. **Damien Guihen** is PhD Candidate, Department of Earth and Ocean Sciences, National University of Galway, Galway, Ireland. **Kostas Kiriakoulakis** is Senior Research Fellow, Department of Earth and Ocean Sciences, University of Liverpool, Liverpool, UK. **George A. Wolff** is Professor, Department of Earth and Ocean Sciences, University of Liverpool, Liverpool, UK.

was deployed to cover the reef from late March 2006 to September 2007 (data presented in this paper are for spring 2006 and 2007 only). Equipment included:

1. Low-frequency (300-kHz) ADCPs to measure overlying water column dynamics (Figure 3C).
2. High-frequency ADCPs for near seabed dynamics and estimates of resuspended material.
3. Sea-Bird SBE37 Microcat sensors for temperature and salinity measurements in the benthic boundary layer.
4. Bottom-mounted Aanderaa recording current meters (RCM9s), equipped with turbidity and oxygen optodes for near-seabed time series at 80 cm above the seabed (0.8 mab).
5. A short-term deployment of a Nortek velocimeter for direct estimates of turbulent dissipation and Reynolds stress near the seabed.

Stand-alone pump systems (SAPS; Challenger-Oceanic; Figure 3D) were used for sampling suspended POM ( $POM_{\text{susp}}$ ) at and near the Tisler reef in April–May 2006 and 2007. In 2007, the SAPS systems were mounted in a bottom frame with the inlet at 1 mab (Figure 3D) and deployed at the Tisler reef on April 29. Eleven samples spread over three stations (at both ends and in the middle of the reef, with an equal distance between stations of about 750 m) were collected through one tidal cycle. The pre-baked (400°C, 4 h) SAPS filters (29 cm diam. GF/F; Figure 3E) were freeze-dried on return to the laboratory. Analyses of organic carbon and nitrogen were then performed on all freeze-dried samples according to Kiriakoulakis et al. (in press).

## RESULTS AND DISCUSSION

### Flow Characteristics

Typically for the region, tidal currents are small, with semi-diurnal tidal amplitudes of 5–10  $\text{cm s}^{-1}$ , representing neap and spring tide values, respectively. These values rarely exceeded the mean (tidally averaged) residual flow strengths (Figure 4). Tidally averaged residual currents can exceed 30  $\text{cm s}^{-1}$  at times, and flow predominantly across the sill in either direction (northwest toward the open Skagerrak, or southeast toward the inner Kosterfjord) (Figure 4b). These residual flows were generally driven by density, or through wind-driven sea level height differences across the sill region. Results from the lower-frequency ADCP located near the sill indicated that the currents were amplified in the vicinity of the shallowest part of the sill region. The reef region is, therefore, a dynamic one

despite the lack of strong tidal currents, with near-seabed currents of sufficient strength to resuspend material and produce the large organic matter fluxes that are a prerequisite for such an ecosystem.

An example of the importance of density forcing occurred during the spring 2006 field campaign when measurements were made over time periods of contrasting flow dynamics (Figure 4a). At the start of the measurements (end of March), flow was relatively weak and directed to the northwest. On April 24, however, flow reversed to the southeast and increased significantly in magnitude, particularly close to the seabed. Analysis of temperature and salinity data from the two CTD Microcat moorings deployed during this time (Figure 5) suggests that during April, the bottom water was freshened and cooled by seasonal inshore melt water. This water

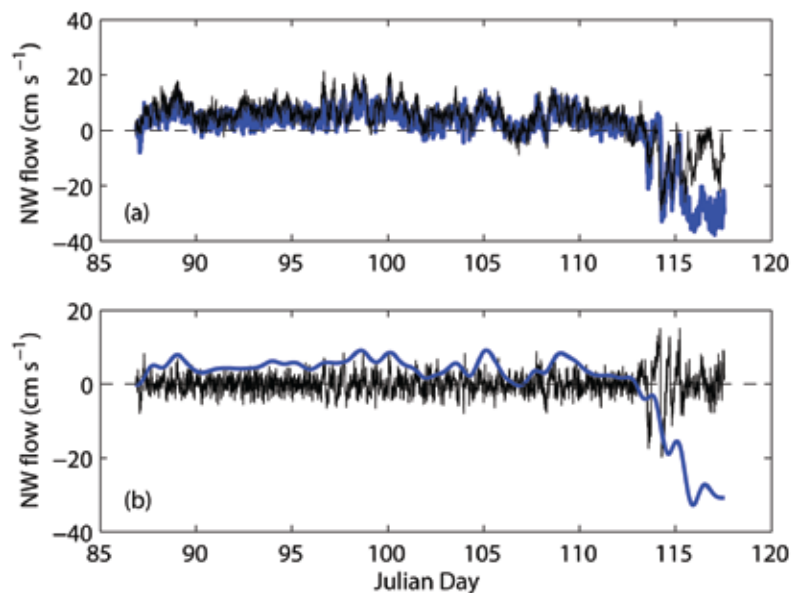


Figure 4. Time series of (a) northwest-directed current at 4 mab (blue) and 24 mab from the spring 2006 LF ADCP deployment at the sill. In (b), the 4-mab data are shown after application of a 27-hr filter for the low (blue) and high (black) components to separate residual and tidally dominated flows.

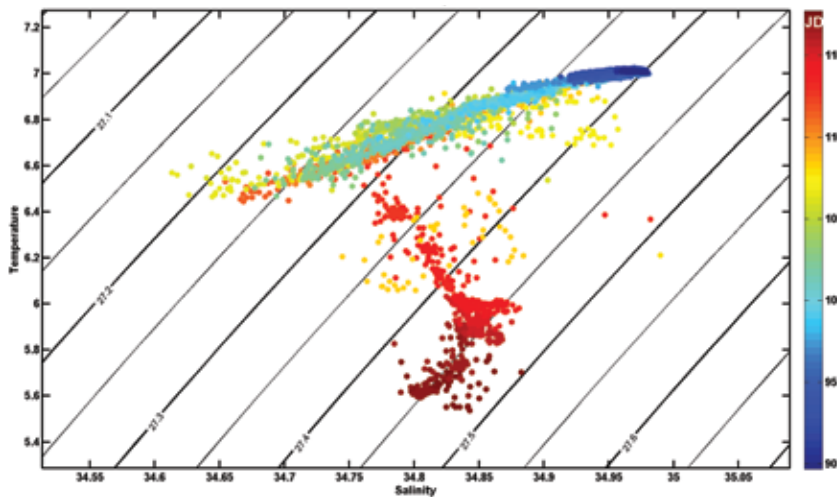
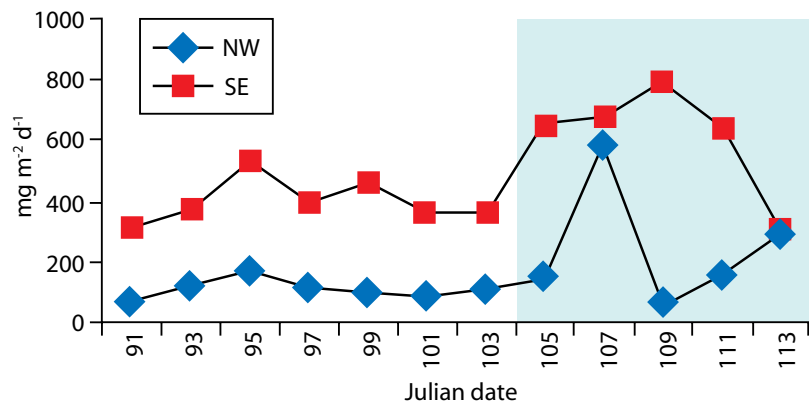


Figure 5. Temperature-salinity diagram for the measurements made at the northwest end of the Tisler reef at 130-m water depth, March 31, 2006–April 28, 2006. Density contours are shown in black and individual T-S points are color coded by time (Julian Day 2006, indicated by the color bar).

Figure 6. Particulate organic carbon fluxes (from sediment traps) to the northwest (NW) and southeast (SE) edges of the “living” reef in spring 2006.

Total organic carbon fluxes



influx resulted in a reduction in water density at the sill. After April 24, a rapid change to colder and more saline water ensued, associated with the reversal in currents. It is inferred that the flow reversal was a result of the reduction in density at the sill, which allowed deep water (cold, relatively high salinity) from the open Skagerrak to flow back into the inner Kosterfjord region after the period of flow to the northwest out of the Kosterfjord.

The weak tidal amplitudes affect the residence time of water parcels over the reef. Tidal amplitudes of 5–10 cm s<sup>-1</sup> result in horizontal tidal period excursions of 800–1600 m. Therefore, for tidal currents alone, water will not be moved over distances greater than the extent of the reef. The addition of residual currents, however, can move water unidirectionally over the reef. A residual current of 3.5 cm s<sup>-1</sup> will advect a water parcel by 1.6 km horizontally during one semi-diurnal period (~ 12.4 hrs). Thus, at times of low residual flow (< 5 cm s<sup>-1</sup>), the residence time of the water in contact with the reef increases significantly. This

observation has obvious biogeochemical implications for the utilization of organic material in the bottom boundary layer and subsequent community respiration and carbon cycling.

#### Sinking POM (POM<sub>sink</sub>-Benthic Lander Sediment Traps) in Spring 2006

Sinking particulate organic carbon (POC<sub>sink</sub>) and particulate nitrogen (PN<sub>sink</sub>) fluxes were invariably low in the first half of April (April 1–13, 2006) but increased (more than doubled) toward the end of the month (Figure 6, POC only). These measurements coincided with the onset of a phytoplankton bloom and its export to the seafloor. During

the early part of the instrument deployment, POC<sub>sink</sub> and PN<sub>sink</sub> fluxes were significantly higher on the southeast edge, probably as a result of higher current velocities at the northwest station (data not presented in this paper), leading to slower settling rates for POM<sub>sink</sub> and possibly to resuspension. Molar C/N ratios were significantly higher on the northwest edge in early April (Figure 7), implying that the POM<sub>sink</sub> was more degraded there. These observations may be related to the preferential uptake of N-containing labile organic compounds (e.g., proteins, amino acids) across the reef (reef effect), and/or to the resuspension of old material from the seafloor at the northwest station. The former theory

is consistent with residual water flow to the northwest during this period. In the second half of the month (April 15–23, 2006), the high influx of organic matter to the system “swamped” smaller-scale (reef) effects, and there appears to be no significant difference in the C/N ratios of  $POM_{sink}$  across the reef.

### Suspended POM (SAPS) in Spring 2007

Suspended POC ( $POC_{susp}$ ) concentrations at the Tisler reef were the same order of magnitude as those measured elsewhere at coral reefs or thickets

along the Northwest European margin (Kiriakoulakis et al., 2007) and at two seamounts in the Northeast Atlantic Ocean (Kiriakoulakis et al., in press), that is,  $\sim 1\text{--}4 \mu\text{mol C L}^{-1}$  equivalent to  $\sim 10$  and  $50 \mu\text{g C L}^{-1}$  (Figure 8). These quantities may represent an optimum “food” range: where values are lower, resources may be too scarce to support *Lophelia*, and where values are significantly higher, suspended particulates may smother the coral and lead to its death. Clearly, there are other important environmental variables that govern the presence and absence of coral, but

carbon loading appears to be important.

To assess the relationship between  $POC_{susp}$  and the Tisler reef, we intensively sampled water with a stand-alone pump through part of a tidal cycle in Spring 2007 (April 29) at the southeast and northwest edges and middle of the “living” reef. The proximity of the pump to the seafloor ( $\sim 1$  mab) enabled close monitoring of the suspended particulate characteristics that may interact with the corals. A moored current meter showed no significant changes in current speed or direction ( $\sim 0.3 \text{ m s}^{-1}$ , SSE) during the experiment. Our observations show a clear increasing trend of suspended POC concentrations at the southeast edge and the middle of the reef through the course of the day, which is not apparent at the northwest edge (Figure 9a). Suspended PN concentrations, on the other hand, generally decrease at the southeast edge and the middle of the reef (except at 19:00 h) during the day, whereas they seem to increase at the northwest edge

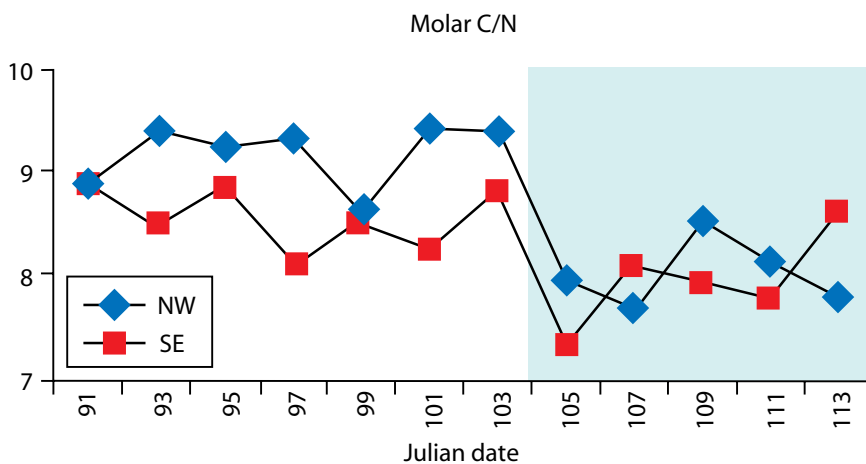


Figure 7. Molar C/N ratios of sinking particulate organic matter (from sediment traps) in spring 2006. NW and SE refer to the northwestern and southeastern edges of the “living” reef.

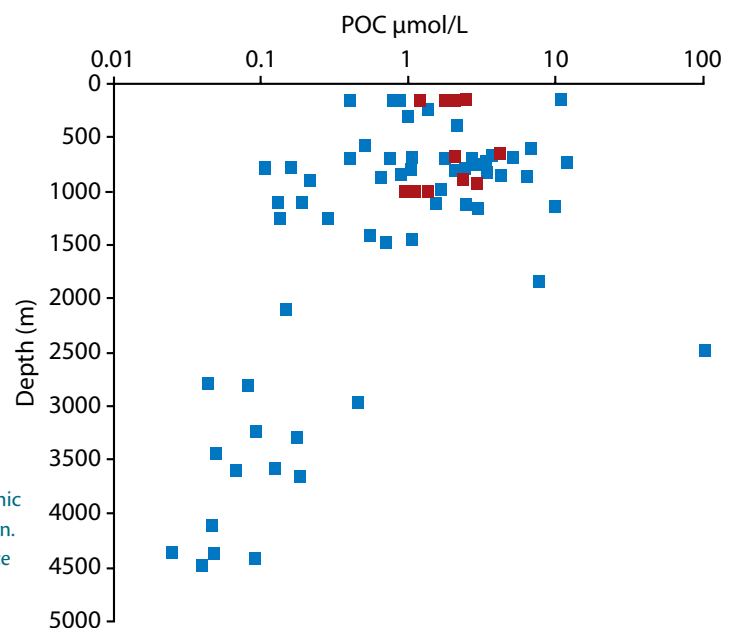


Figure 8. Particulate organic carbon (POC) concentrations in waters collected at the benthic boundary layer in the Northeast Atlantic Ocean. Red and blue squares show presence or absence of *Lophelia pertusa*, respectively (Kiriakoulakis et al., 2004, 2007, in press).

(data not presented in this paper). The middle of the reef seems to have lower  $\text{POC}_{\text{susp}}$  and  $\text{PN}_{\text{susp}}$  concentrations than the edges when sampled consecutively. Molar C/N ratios increase during the day at the southeast edge and middle of the reef, but decrease at the northwest edge (Figure 9b). A common feature of these observations is that the southeast edge and middle of the reef seem to behave similarly, but they behave differently than the northwest edge.

One explanation for the contrasting trends in particle composition at the reef edges is that local differences in hydrodynamic regimes affect the amount and quality of near-bottom suspended particles. Although we found a clear difference in current speed between the northwest and southeast edges of the reef during the atypical period of continuous northwest flow in April 2006, no corresponding measurements were made during the experiment in 2007 when normal tidal patterns had been restored. An alternative explanation, and in our opinion a more likely one, pertains to the origin of the particles. During our 2007 experiment, water was flowing from northwest to southeast across the reef, supplying “new” particles derived from the open Skagerrak at the northwest reef edge. The fact that “new” particles at the northwest edge have not been in contact with the reef (in contrast to those over the middle and southeast edge) underlies the differences in suspended particle composition and the decoupling of trends between the northwest edge and Tisler reef. Because particle residence times are unknown, there should be only cautious comparison of “new” particles with those that have been on the reef for an unknown length of time

(middle and southeast edge). These “older” particles may well have had a different source and initial composition than those collected at the northwest edge. Also, without the data from the northwest edge, the observed trends at the middle and southeast edge provide insight into the effect of Tisler reef. The parallel and gradual increase of  $\text{POC}_{\text{susp}}$  and molar C/N plus the drop in  $\text{PN}_{\text{susp}}$  over the middle and southeast edge during the experiment suggest that the reef “releases” (resuspends?) organic particles that have been subject to preferential removal of labile N-rich compounds (e.g., amino acids, proteins). This loss

in the quality of suspended organic particles during passage over the reef corresponds with the observations that we made in the first half of April 2006 (see above). A third explanation can be drawn if we see the reef as a “filter” for high-quality (low C/N ratio) particles that were transported with a constant speed ( $\sim 0.3 \text{ m s}^{-1}$  at 2 mab) from northwest to southeast during the experiment. The increase in suspended POC during the experiment at all three stations (Figure 9a), but with a time shift of about 1–2 hours between stations, could then be explained by the travel time of particles between stations—which is

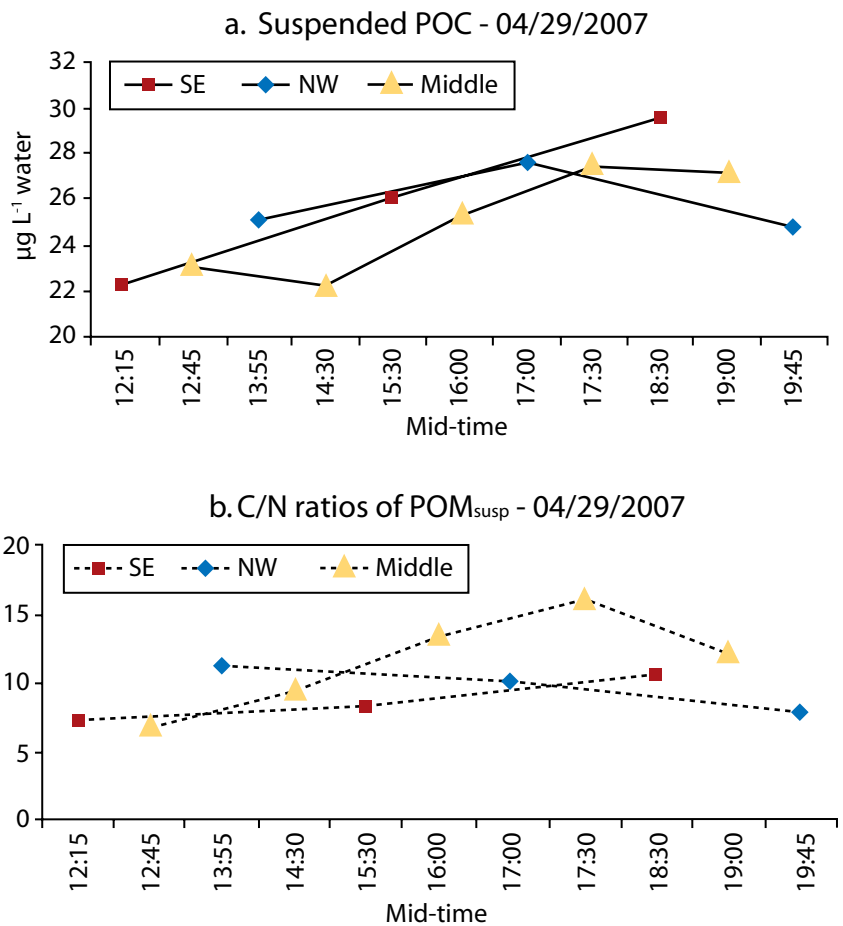


Figure 9. (a) Concentrations of suspended organic carbon at the Tisler reef over a partial tidal cycle on April 29, 2007. (b) Molar C/N of suspended particulate organic matter (POM) of the same samples.




indeed of the same order as the time shift. If the reef filters the high-quality particles out of the water, the C/N ratio will increase and the suspended PN will decrease immediately above the reef. This explanation is consistent with an increase in C/N (Figure 9b) and a decrease in PN (not shown here) of the suspended particles from the northwest to the middle station, accounting for a suspended-particle transport time with a delay of more than one hour between these stations.

## CONCLUSIONS

The Tisler reef environment illustrates and emphasizes the overriding effect of the hydrodynamic regime on the transfer of carbon-rich particles to the reef floor and on the subsequent behavior of the corals. Our preliminary data show the importance and value of obtaining long-time-series data from cold-water coral ecosystems to obtain a deeper understanding of their functioning. The necessity of long-time series is illustrated by observed events, such as the deep-water inflow and extreme temperature events in spring and late 2006, respectively. We observed small-scale variations in water-column characteristics. Individual microhabitats play a significant role in modulating near-seabed currents and turbulence with potentially important consequences for particle residence time, feeding strategies, and hence the distribution of live and dead coral over the whole reef. For example, our experiments in 2006 and 2007, with detailed organic biochemical data for (a)  $POM_{\text{sink}}$  at the northwest and southeast edges of the coral reef, and (b)  $POM_{\text{susp}}$  at the edges and the middle of the reef, show a contrast between the stations, which

we tentatively explain by the physio-biochemical impact of the reef on its immediate environment. The results suggest that this relatively small cold-water coral reef plays a substantial role in carbon sequestration. Likewise, globally, cold-water coral reefs could be hotspots of mineralization activity in the ocean, though this has not yet been quantified.

## ACKNOWLEDGEMENTS

This work was carried out within the integrated project HERMES (Hotspot Ecosystem Research on the Margins of European Seas; EC contract number GOCE-CT-2005-511234), funded by the European Commission's Framework Six Programme. 

## REFERENCES

- Berov, D.N. 2007. Monitoring of environmental variability at a *Lophelia pertusa* cold-water coral in the Tisler reef, Norway. In-situ time-lapse video observation of *Lophelia pertusa*. MSc Thesis, International University of Bremen, 52 pp.
- Dodds L.A., J.M. Roberts, A.C. Taylor, and F. Marubini. 2007. Metabolic tolerance of the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature and dissolved oxygen change. *Journal of Experimental Marine Biology and Ecology* 349:205–214.
- Duineveld, G.C.A., M.S.S. Lavaleye, and E.M. Berghuis. 2004. Particle flux and food supply to a seamount cold-water coral community (Galicia Bank, NW Spain). *Marine Ecology Progress Series* 277:13–23.
- Freiwald, A. 2002. Reef-forming cold-water corals. Pp. 365–385 in *Ocean Margin Systems*. G. Wefer, D. Billett, D. Hebbeln, B.B. Jorgensen, M. Schluter, and T. van Weering, eds, Springer, Berlin.
- Freiwald, A., J.H. Fosså, A. Grehan, T. Koslow, and J.M. Roberts. 2004. Cold-water coral reefs. UNEP-WCMC. Biodiversity Series 22, Cambridge, UK. 84 pp.
- Jonsson, L.G., P.G. Nilsson, F. Floruta, and T. Lundälv. 2004. Distributional patterns of macro- and megafauna associated with a reef of the cold-water coral *Lophelia pertusa* on the Swedish west coast. *Marine Ecology Progress Series* 284:163–171.
- Kiriakoulakis, K., B.J. Bett, M. White, and G.A. Wolff. 2004. Organic biogeochemistry of the Darwin Mounds, a deep-water coral ecosystem, of the NE Atlantic. *Deep Sea Research Part I* 51:1,937–1,954.
- Kiriakoulakis, K., L. Fisher, A. Freiwald, A. Grehan, M. Roberts, and G.A. Wolff. 2005. Lipids and nitrogen isotopes of two deep-water corals from the North-East Atlantic: Initial results and implications for their nutrition. Pp. 715–729 in *Cold-Water Corals and Ecosystems*. A. Freiwald and M. Roberts, eds, Springer, Berlin Heidelberg.
- Kiriakoulakis, K., A. Freiwald, E. Fisher, and G.A. Wolff. 2007. Organic matter quality and supply to deep-water coral/mound systems of the NW European Continental Margin. *International Journal of Earth Science (Geologische Rundschau)* 96:159–170.
- Kiriakoulakis, K., J.C. Vilas, S.J. Blackbird, J. Aristegui, and G. Wolff. In press. Seamounts and organic matter – is there an effect? The case of Sedlo and Seine Seamounts. Part II. Composition of suspended particulate organic matter. *Deep Sea Research Part II*.
- Mortensen, P.B., and L. Buhl-Mortensen. 2005. Deep-water corals and their habitats in The Gully, a submarine canyon off Atlantic Canada. Pp. 247–277 in *Cold-Water Corals and Ecosystems*. A. Freiwald and M. Roberts, eds, Springer, Berlin Heidelberg.
- Mortensen, P.B., M. Hovland, J.H. Fosså, and D.M. Furevik. 2001. Distribution, abundance and size of *Lophelia pertusa* coral reefs in mid-Norway in relation to seabed characteristics. *Journal of the Marine Biological Association of the United Kingdom* 81:581–597.
- Roberts, J.M., A.J. Wheeler, and A. Freiwald. 2006. Reefs of the deep: The biology and geology of cold-water coral ecosystems. *Science* 312(5773):543–547.
- White, M., C. Mohn, H. de Stigter, and G. Mottram. 2005. Deep-water coral development as a function of hydrodynamics and surface productivity around submarine banks of the Rockall Trough, NE Atlantic. Pp. 503–514 in *Cold-Water Corals and Ecosystems*. A. Freiwald and M. Roberts, eds, Springer, Berlin Heidelberg.
- Wilson, J.B. 1979. "Patch" development of the deep-water coral *Lophelia pertusa* (L.) on Rockall Bank. *Journal of the Marine Biological Association of the United Kingdom* 59:165–177.