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Food supply mechanisms for cold-water corals along a continental shelf edge

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Abstract

In recent years it has been documented that deep-water coral reefs of the species *Lophelia pertusa* are a major benthic habitat in Norwegian waters. However, basic information about the biology and ecology of this species is still unknown. *Lophelia* live and thrive under special environmental conditions of which factors such as temperature, water depth, water movement and food supply are important. The present work explores the hypothesis that *Lophelia* forms reefs in places where the encounter rate of food particles is sufficiently high and stable over long periods of time for continuous growth. This is done by relating the distribution of reefs with the results of numerical ocean modelling.

Numerical simulations have been performed with an idealized bottom topography similar to what is found outside parts of the Norwegian coast. In the simulations the model is first forced with an along slope jet and then with an idealized atmospheric low pressure. The model results show that the encounter rates between the particles and the water layer near the seabed are particularly high close to the shelf break. This may indicate that many *Lophelia* reefs are located along the shelf edges because the supply of food is particularly good in these areas.

A sensitivity study of the particle supply in the area close to the seabed for increasing latitude has also been done. This shows that the Ekman transport in the benthic layer tends to create a steady supply of food for benthic organisms near the shelf edge away from the equator.

1. Introduction

The cold-water coral *Lophelia pertusa* (L., 1758) is a Scleratinian coral belonging to the family of Caryo-

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phyllidae. *Lophelia* is the most common habitat-forming, reef-building deep-water coral (Freiwald et al., 2004). The species has a cosmopolitan distribution (Zibrowius, 1980), but the highest densities and the largest reefs have been documented in the North-East Atlantic, especially in Norwegian waters (Fosså et al., 2004). The distribution known so far most probably reflects the intensity of research in the different parts of the world. Globally the bathymetrical distribution is between 39 and 3380 m, but in Norway most reefs are

found in depths of 250–350 m along the continental shelf break, on ridges on the continental shelf, and also on fjord sills (Mortensen et al., 2001; Fosså et al., 2002), see Fig. 1.

Beside their intrinsic natural value, it has been estimated that the biological diversity in the reef habitat is three times higher compared to the surrounding seabed. Almost 800 species are documented to live associated with the *Lophelia* reefs in the North-East Atlantic (Mortensen and Fosså, in press). The reefs are known as good fishing places especially with long-line and gill-nets, but also bottom trawling has expanded into the coral areas and has impacted or damaged a significant part of the reefs in Norwegian waters (Husebø et al., 2002; Fosså et al., 2002).

The recent research in Norway has put much emphasis on mapping and assessment of the fishery impact on the reefs although also many other aspects of the biology and ecology of the reefs have been addressed (e.g. Mortensen, 2000; Fosså et al., 2004). However, fundamental questions such as larval development, growth, feeding, the ecological importance and the important physical factors for the development of reefs are almost unknown (Freiwald et al., 2004; Freiwald and Roberts, 2005).

Lophelia mainly occur on hard bottoms with stones or rock (Dons, 1944; Wilson, 1979; Mortensen et al., 2001; Freiwald, 2002; Freiwald et al., 2004). For the corals along the Norwegian margin, the relatively warm Atlantic inflow also seems to be important. One
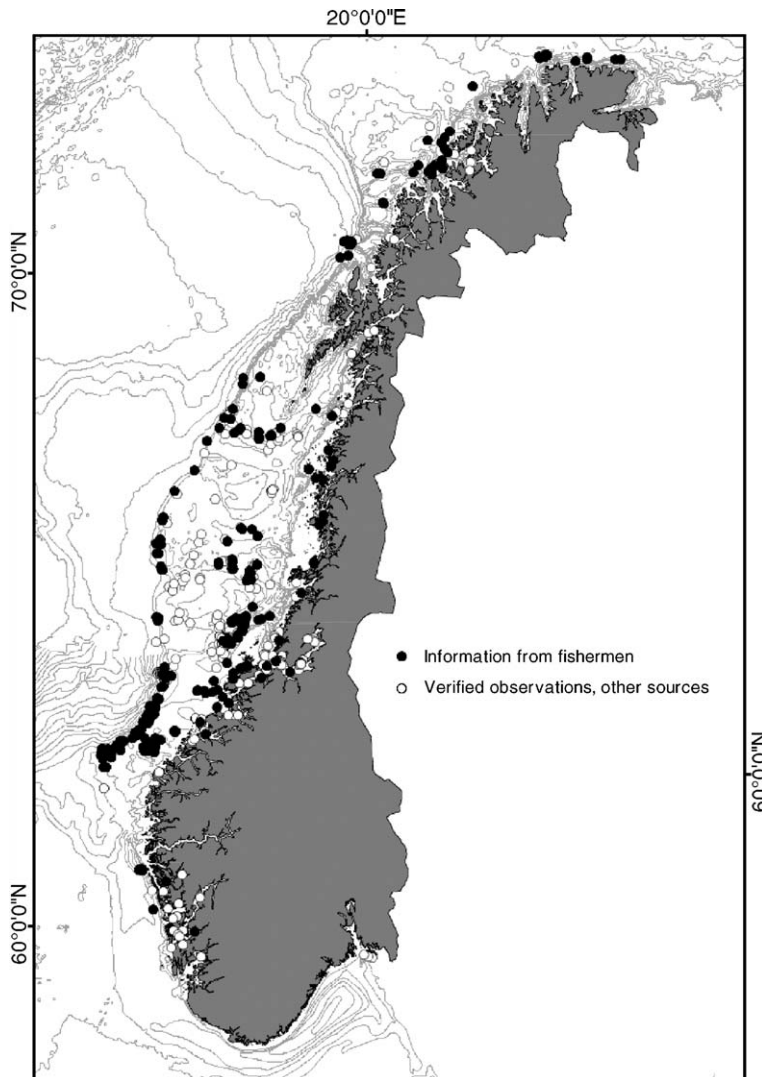

Fig. 1. Distribution of the known coral reefs in Norwegian waters.

of the most decisive factors that controls their location appears to be the seabed topography (Mortensen et al., 2001). Hills, troughs, outcrops, iceberg scour marks and glacial lineaments are all favourite places for *Lophelia* to grow, and in general, many of the places one finds *Lophelia* are known to have comparable strong bottom currents. Roberts et al. (2005) recorded a maximum current speed by the Sula Ridge reef complex in Norway of 0.28 m s^{-1} and 0.70 m s^{-1} on the Galway carbonate mound in Ireland. According to the authors this reinforces speculation about the dependence of these communities on current-swept conditions. Frederiksen et al. (1992), however, suggested an upper tolerance limit of about 1.0 m s^{-1} for *Lophelia* colonies before they tip over.

A sessile benthic animal must rely on food being brought to where it is living. *Lophelia* build large reefs and it has been shown that on the Sula Ridge the corals have most probably lived continuously for almost 10 000 years (see Hovland and Mortensen, 1999). This indicates that the favourable environmental conditions for coral growth may have been stable for the same period of time. Some of the most important factors may be the current regime and the abundance of small zooplankton and other food-particles in the water. Johan Hjort also knew the reefs well and in the book "The Depths of the Ocean" (Murray et al., 1912) he ascribed "The presence of corals like the Lophohelia over great parts of the slope of the Norwegian Sea…"to be the "… most interesting indication of the motion of the organic matter along the sea-bottom". This is a very interesting statement inferring that *Lophelia* relies on food supplied by currents and thus prefers to live in an advective environment (Fosså et al., 2004).

An overview of the role of physical processes along the shelf edge on circulation, exchange of water masses and transport of materials between the shelf and the ocean is given in Huthnance (1995). More site specific studies of exchanges at the oceanic margins have also been performed, see for instance Yanagi et al. (1992) and Huthnance et al. (2002a,b). The physical processes are influenced by the bathymetry and the stratification. The mixing between the shelf and the ocean may be driven by slope currents, tides, and atmospheric forcing (Huthnance, 1995). The focus in many studies has been on physical processes, but ecosystem responses have been investigated, see Monaco et al. (1990).

The aim of this study is to explore the hypothesis that *Lophelia* forms reefs in places where the encounter-rate of food particles is sufficiently high and stable over long periods of time for continuous growth. This is done by relating the distribution of reefs to the results from a numerical model for geophysical fluid flow.

A numerical ocean model has been set up for an idealized shelf sea, see Section 2. The model has first been forced with an idealized jet which imitates the Atlantic inflow along the Norwegian shelf, Section 2.1. Then the model has been forced with a rotating wind instead. This wind forcing mimics the atmospheric low pressure activity which is common along the Norwegian coast, Section 2.2. The sensitivity of the encounter rates between particles and benthic organisms to latitude is studied in Section 2.3.

2. The numerical model

The numerical σ-coordinate ocean model applied in the present study is described in Berntsen (2000) and available from www.mi.uib.no/BOM/. The governing equations are basically the same as for the Princeton Ocean Model (POM) (Blumberg and Mellor, 1987; Mellor, 1996), but the numerical methods are different. For advection of momentum and density a TVD-scheme with a superbee limiter described in Yang and Przekwas (1992) is applied. The model is mode split with a method similar to the splitting described in Berntsen et al. (1981) and Kowalik and Murty (1993). The solution is propagated in time using single time step methods. For the depth-integrated momentum and continuity equations the forward–backward method is applied. In the vertical the Mellor and Yamada (1982) 2–1/2 level scheme is applied to parameterize subgridscale processes. The internal pressure is estimated with the second order central difference scheme applied in POM.

An idealized shelf profile is set up in a rectangular channel, see Fig. 2. The undisturbed depth $h = h(y)$ varies only in the cross shelf direction. The shelf slope has been approximated by a parabolic profile with a sharp corner (singularity) at the shelf edge and with uniform depth on the shelf and in the deep ocean, see Gjevik et al. (2002),

$$
\begin{aligned}
h &= h_s & \text{if } 0 < y < L, \\
h &= h_o - (h_o - h_s)\left(\frac{L + S - y}{S}\right)^2 & \text{if } L \le y \le L + S, \\
h &= h_o & \text{if } L + S < y < L_y.
\end{aligned}
\tag{1}
$$

Here L and S are the widths of the shelf and the shelf slope and h_s and h_o are the depths on the shelf and in the deep ocean, respectively. At $y = 0$ and $y = L_y$ there are vertical walls. The σ-coordinate transformation is given
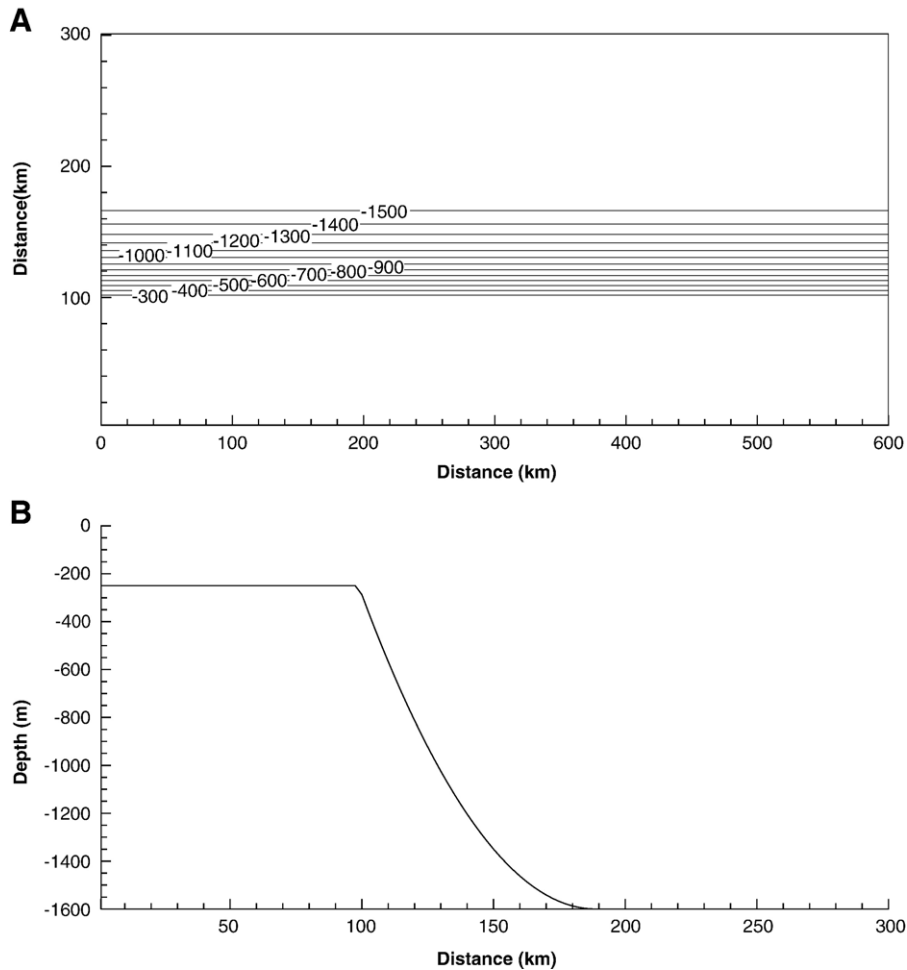
Fig. 2. The shelf profile used in the simulations. The parameters in Eq. (1), which are used to set up the bottom topography are found in Table 1. (A) Horizontal view of the model domain. The depth contours are drawn for every 100 m. (B) Vertical view of the cross shelf.

by

$$\sigma = \frac{z - \eta}{h + \eta}, \tag{2}$$

where z is the vertical coordinate, η is the free surface elevation and h the undisturbed depth. The formula

$$\sigma(KB + 1 - K) = -1 + \frac{K - 1}{KB - 1} - \frac{1}{KB - 1} \frac{\sin\left(\frac{\pi(K-1)}{KB-1}\right)}{\sin\left(\frac{1.25\pi}{KB-1}\right)},$$

$$K = 1, \dots, KB \tag{3}$$

is used to distribute the $KB - 1$ σ layers (Lynch et al., 1995). The thickness of the bottom σ layer on the shelf is 2.0 m and in the deep ocean it is 12.8 m, which means that the layers close to the seabed are well resolved on the shelf and the upper shelf slope. The thickness of the σ layers is then gradually increased towards the surface and the surface σ layer is 14.5 m thick on the shelf and 92.8 m in the deep ocean.

The bottom drag coefficient is computed from

$$C_D = \max\left(0.0025, \frac{0.16}{\left(\ln \frac{z_b}{z_0}\right)^2}\right). \tag{4}$$

Here z_b is the distance of the nearest grid point to the bottom and z_0 is the bottom roughness parameter.

In the along channel direction periodic boundary conditions will allow the particles that imitate the food for the corals to be transported out of the region at one end of the channel and re-enter in the other end. The particles are passive tracers that will drift with the currents according to

$$\overrightarrow{x_p}^{n+1} = \overrightarrow{x_p}^{n} + \Delta t \overrightarrow{u}^{n}. \tag{5}$$

Here $\overrightarrow{x_p}^{n}$ is the location of a particle at time step n, Δt the time step size, and $\overrightarrow{u}^{n}$ the velocity of the water

Table 1
Parameters and values used in this study

Model domain		
	L_x	600 km
	L_y	300 km
Grid size		
	Δy	2.5 km
	Δx	2.5 km
σ-Distribution		
(Eq. (3))	KB	31
Shelf profile		
(Eq. (1))	h_s	250 m
	h_o	1600 m
	L	100 km
	S	90 km
Bottom friction		
(Eq. (4))	z_0	0.01

surrounding the tracer at time step n. Accumulations of particles near the seabed will then indicate places with rich access of food to the benthic organisms. If the particles are closer than 2.0 m from the seabed, they will be taken out of the simulation and the particles last locations will be stored to identify places with a higher particle hit rate than others.

The Norwegian Atlantic Current with the Atlantic Water, dominates the current system along the continental shelf edge off Norway. The tidal forces here are relatively weak, see Orvik et al. (2001) and Orvik and Skagseth (2003). Near the coast the flow is influenced by the Norwegian Coastal Current, and the coastal water masses are located above the Atlantic Water. Outside the shelf edge, the Norwegian Sea Arctic Intermediate Water is found below the Atlantic Water. The interface between these two water masses is typically at 500–600 m depth (Hopkins, 1991). In the present study we are interested in the areas along the shelf edge around depths of 200–300 m. The shelf edge will therefore almost always be in the Atlantic Water and that is why the model is run with constant density.

The simulations are started from rest with no flow, wind or displacement of the surface. During the simulations the viscosity v is kept low and constant. Common parameters and values used as input to the model for all the simulations are found in Table 1. The 3D time step used in the model simulation is 150 s, with 30 2D steps for each 3D time step.

2.1. The jet experiment

In this experiment the focus is on the Atlantic inflow and the model is forced with an along slope jet. In the Norwegian Sea this inflow is known as a topography following jet located outside the shelf break with a mean maximum speed in the core of approximately 0.4 m s^{-1}.

The jet in this experiment is described by a Gaussian current profile (Gjevik et al., 2002)

$$\overline{u}(y) = u_o \exp\left[-\left(\frac{2(y - L_B)}{B}\right)^2\right],\tag{6}$$

where the parameters that define the jet are u_o which is the maximum speed, L_B is the position of the centre, and B the width of the jet.

In order to force the model velocities towards the prescribed Gaussian profile the equation

$$\frac{\partial u}{\partial t} = \frac{1}{\text{TS}}\left(\overline{u}(y) - u\right)\tag{7}$$

is applied where TS is the prescribed timescale. The body force is limited to act only in the region where the velocity of the jet is greater than 0.01 m s^{-1} in the present studies. The parameters used for the jet simulation are found in Table 2.

2.1.1. Results from the jet experiment

The experiment shows that the along slope inflow will set up a vertical circulation of water in the core of the jet. This circulation forces the water to flow down in the shallow part and up in the deeper part of the jet core, see Fig. 3(A). The activity of the jet near the seabed can be seen in Fig. 3(B). The velocities close to the seabed are high and directed towards the ocean floor in the jet. This increases the number of encounters in the upper part of the shelf slope, see Fig. 4, and prevent the particles from hitting the bottom in the deeper part of the shelf slope. The result is sharp peaks where the particles hit the bottom in the jet, and almost no hits in the surroundings, see Fig. 4.

In addition there are particles entering the benthic layer at the shelf break. This is caused by horizontal divergences, $\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y}$, in the bottom layer flow, due to the abrupt change in the topography. The horizontal

Table 2
Parameters for the jet experiment

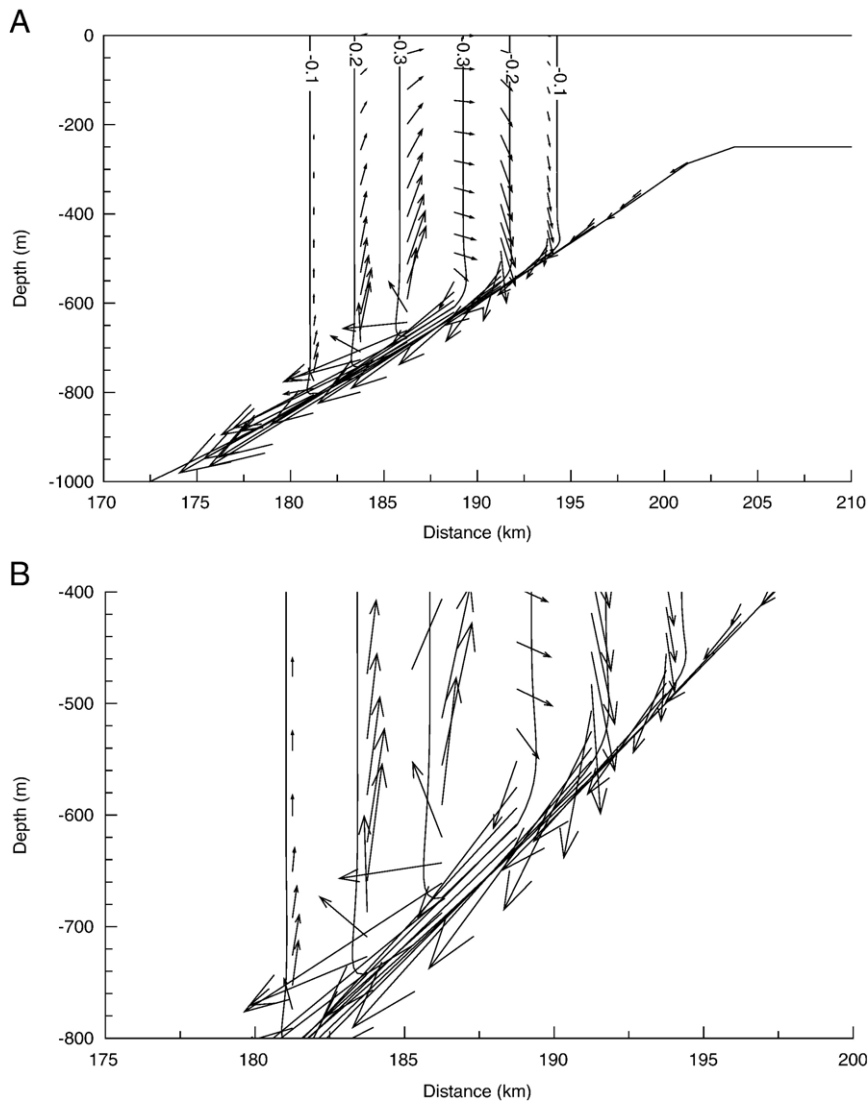| Body force time scale	TS	24 h
Viscosity	v	0.2 m^2 s^{-1}
The jet		
(Eq. (6))	u_o	0.4 m s^{-1}
	B	10 km
	L_B	115 km
Coriolis parameter	f	1.2×10^{-4} s^{-1}

Fig. 3. Modelled currents for the jet experiment. The components of the current vectors are the cross shelf velocities and vertical velocities. In order to indicate the vertical exchanges, the vertical velocities are multiplied by 1000. The along shelf velocity component is shown by contour lines where the contour interval is 0.10 m s^{-1}. (A) The circulation set up by the jet. (B) The activity set up by the jet close to the seabed.

divergences then lead to vertical motion of the particles.

2.2. The rotating wind experiment

In these experiments, an idealized rotating wind is used to force the flow. The wind direction is the same in the whole model domain and is rotating in the anti cyclonic direction with a time period of 3 (TP) days. This wind behaviour is typical for a travelling low pressure at the Norwegian latitudes and imitates low pressures travelling both north and south of the area of interest. The wind is spun up linearly over a 12 h period.

The wind speed in the x- and y-directions at time t is given by

$$(W_x, W_y) = W_{max}(\cos(\omega_{wind}t), \sin(\omega_{wind}t)), \qquad (8)$$

where W_{max} is the maximum wind speed 10 m above the sea surface and ω_{wind} the frequency of the wind rotation in s^{-1}. From the wind speed, the drag (τ_x, τ_y) in x- and y-direction respectively is computed by

$$(\tau_x, \tau_y) = \rho_{air}c_d W_s(W_x, W_y), \qquad (9)$$

see Large and Pond (1981). Here ρ_{air} is the density of the air, ρ_0 is the density of the water, c_d is the drag
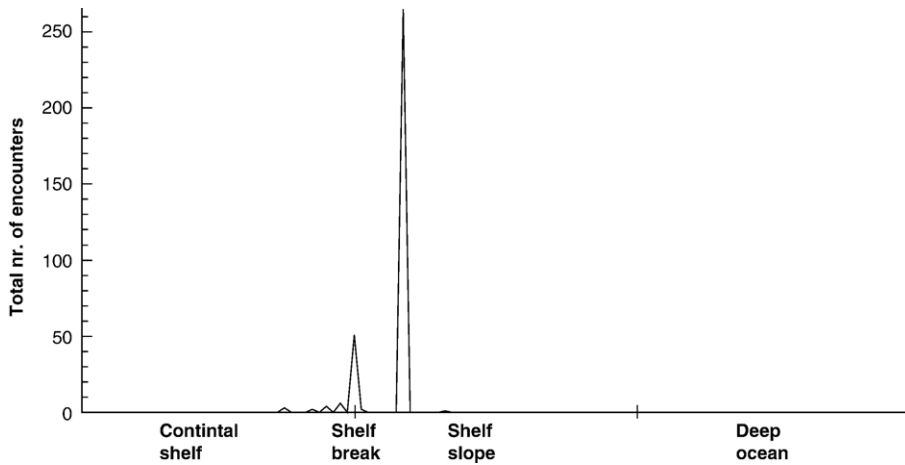
Fig. 4. Total number of encounters across the continental shelf, the shelf break, the shelf slope, and the deep ocean for the jet experiment.

coefficient and $W_s = \sqrt{W_x^2 + W_y^2}$. Values for this simulation are found in Table 3.

2.2.1. Results from the rotating wind experiment

The results show that the wind forcing will set up a surface Ekman transport in the upper layer. When the surface Ekman transport is off the shelf, this will result in up-welling at the inner shelf area. When the surface Ekman transport is towards the shelf, there will be a down-welling in the inner shelf area. During up-welling, deeper water masses are transported towards the shelf, see Fig. 5(A), to conserve volume. On the other hand, transport of deeper water masses off shelf is present during down-welling, see Fig. 5(B). This movement of water masses to and from the shelf will transport particles and matter close to the seabed. The location of the total encounters over a 10 day simulation is shown in Fig. 6. The highest number of encounters is found at the shelf edge and the upper part of the shelf slope.

Fig. 7 shows the horizontal divergence, integrated over the grid cell closest to the bottom $\left(\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y}\right)\Delta x \Delta y$, of the flow at 4 locations near the seabed in the model. The figure shows that flow over abrupt topography will

result in vertical flow that will lead to vertical transport of particles. Dependent on the wind direction, the vertical transport can be directed upward or downward, see Fig. 7. When the vertical transport is up, new water enters the area horizontally (called convergence), and when the vertical transport is down, the water exits the area horizontally (called divergence). However, both divergence and convergence in the flow field can be favourable for the corals, since the convergence and divergence increase the transport of particles, and hence increase the particle encounter rate into the shelf break area.

In this experiment the wind forcing has been of constant magnitude. Stronger wind forcing will give stronger Ekman transport in the surface, which will result in higher velocities close to the seabed due to the Ekman suction. A stronger low pressure will thus result in a higher number of encounters in the benthic layer.

2.3. Sensitivity of encounters relative to increasing latitude (Northern Hemisphere)

To investigate sensitivity of encounter rates to latitude, several simulations have been run where the Coriolis parameter $f = 2\Omega \sin\phi$ has been changed by selecting ϕ from 0° to 90°. Here $\Omega = 7.29 \times 10^{-5}$ rad s^{-1} is the rotation of the earth. In these experiments wind periods of 1 and 3 days have been used.

2.3.1. Results for sensitivity relative to latitude

The model results show that peak values in the number of encounters occur when the wind period matches the natural period of the system, i.e. the wind rotation frequency and the Coriolis frequency are the

Table 3
Parameters for the rotating wind experiment

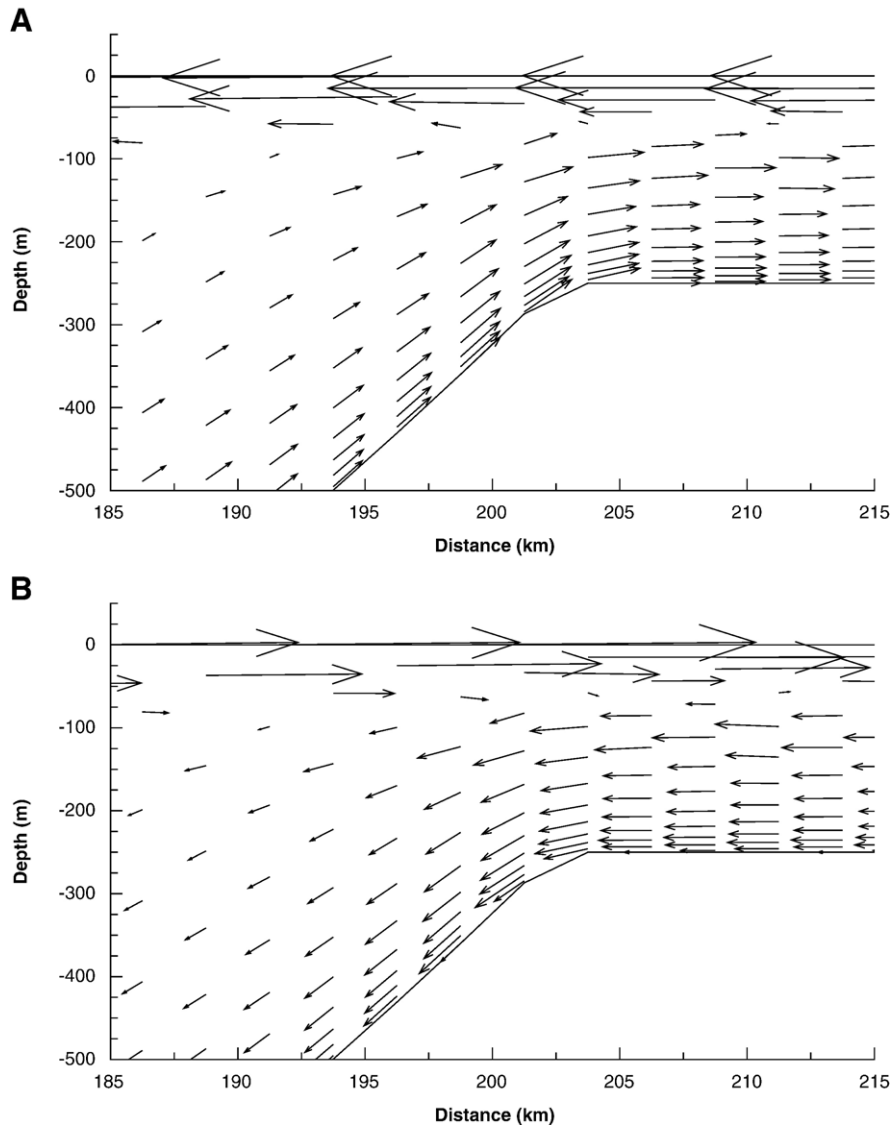|		
Viscosity	ν	5.0 m^2 s^{-1}
The wind		
(Eq. (8))	W_{max}	10 m s^{-1}
	ω_{wind}	$-\dfrac{2\pi}{24 \cdot 3600 \cdot TP}$ s^{-1}
Density		
(Eq. (9))	ρ_{air}	1.3 kg m^{-3}
	ρ_0	1025.0 kg m^{-3}
Wind drag coefficient		
(Eq. (9))	c_d	1.2×10^{-3}
Coriolis parameter	f	1.2×10^{-4} s^{-1}

Fig. 5. Modelled currents for the rotating wind experiment. The components of the current vectors are the cross shelf velocities and vertical velocities. In order to indicate the vertical exchanges, the vertical velocities are multiplied by 1000. (A) Wind towards the south. (B) Wind towards the north.

same. This is a theoretical result that will be mainly of mathematical interest since the wind forcing generally varies in strength, time, etc. Resonance effects of this kind are therefore not very likely to occur in a real ocean.

For latitudes higher than 40°, the number of encounters is relatively constant. This indicates that the food supply in these regions is robust, and peak values in the encounters due to wind forcing at high latitudes are even less likely to appear, see Fig. 8. The number of encounters is dependent on the wind period. Longer wind periods seem to generally give more encounters, probably due to the fact that higher current

speeds are present. This is connected to the time it takes to build up a strong Ekman transport.

3. Discussion

Although we lack detailed observations and experimental work to describe the fundamental niche of *L. pertusa*, it seems that environmental factors such as temperature, salinity, substrate and topography of the seabed are important even though the species can exist under quite large variations within these factors (Rogers, 1999; Mortensen et al., 2001; Freiwald, 2002). For example, the depth distribution is approximately from
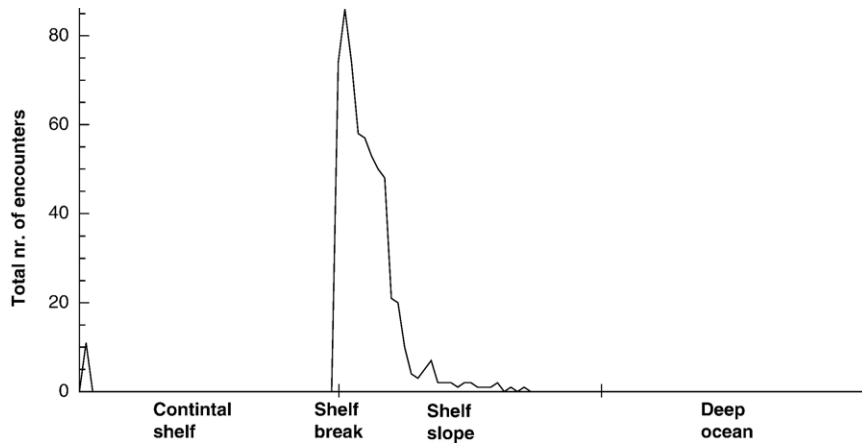
Fig. 6. Total number of encounters across the continental shelf, the shelf break, the shelf slope, and the deep ocean for the rotating wind experiment.

40 to 3400 m and a large geographical range covering many very different oceanic situations like the Barents Sea, the Mediterranean and the Gulf of Mexico. In these environments the condition for production and the food chains are quite different, so the food supply is probably one of the key factors for the location of *Lophelia* reefs.

The feeding of *Lophelia* was studied in aquaria by Mortensen (2001). He showed that *Lophelia* ate flesh from different types of marine animals such as fish, mussels and zooplankton. This indicates that they can

have a varied diet and not specialized to one kind of animal food. Mortensen (2001) also made another observation that can relate to the feeding. There was a higher survival of coral colonies in the section of the aquarium where there was a visible accumulation of sediment. The accumulation of sediment indicates a supply of dead organic matter. The higher survival rate in this part of the aquarium was especially pronounced when the corals were not fed with flesh. On this basis, one may speculate if the corals can survive on dead particulate organic matter. In tropical corals it has been
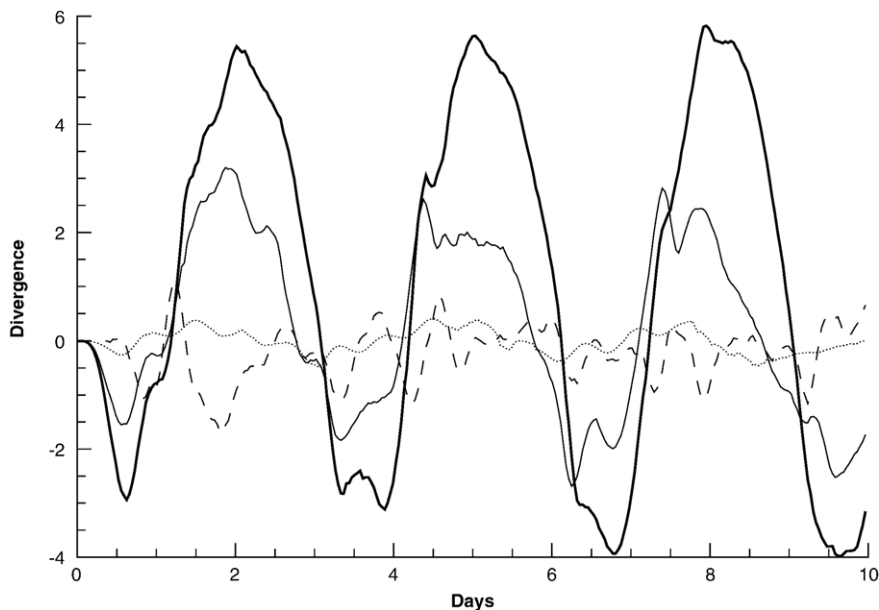

Fig. 7. Computed horizontal divergence in m^2 s^{-1} at 4 locations for the bottom cell. The dashed line is the divergence on the shelf (75.0 km), the thin solid line is at the break (100.0 km), the thick solid line is the first cell outside the shelf break (102.5 km) and the dotted line is at the shelf slope (125.0 km). The numbers are positive when the net flux is out of the bottom cell and negative when the flux is into the bottom cell.
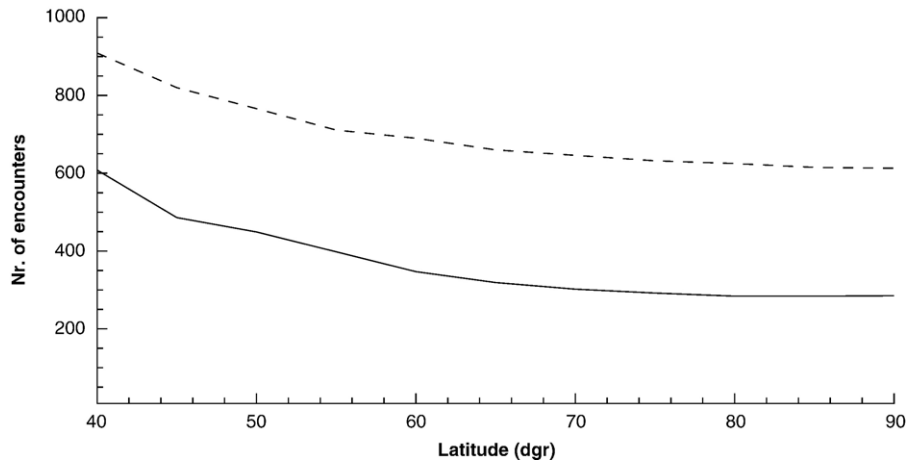
Fig. 8. Number of encounters relative to latitude for 1 day wind period (solid line) and 3 days wind period (dashed line).

shown that small particles of dead organic matter may be important for some species even if they also benefit from the symbiosis with zooxanthellae.

Freiwald (2002) observed in situ on the Sula Reef that *Lophelia*-polyps captured zooplankton such as copepods and swimming cumaceans. Duineveld et al. (2004) used δ^{15}N signatures of coral tissue and potential food such as phytodetritus, amphipods and copepods to explore the place of *Lophelia* in the food chain at 800 m in the Atlantic west of Spain. They concluded that a mixed diet of animals and algae could explain the observed values of δ^{15}N found in the coral tissue, however, most of it originating from animals.

Frederiksen et al. (1992) showed that the occurrence of *Lophelia* around the Faroe plateau coincides with a zone of predicted high particle content near the seabed. They suggested that this was due to breaking of internal waves at the shelf slope resulting in resuspension of bottom material in an area with high primary production in the surface waters.

There is no doubt about the ability of *Lophelia* to catch and eat animals, but there is an uncertainty whether or not, or to what extent, the species can feed on particles of dead organic matter. However, it seems likely, because this may constitute a major carbon source especially during seasons with low production and biomass of zooplankton in the water column.

In general there is a high production on the Norwegian shelf and along the shelf break (see Melle et al., 1993; Skjoldal, 2004). On the shelf break several eddies and small fronts governed by the bottom topography develop (Sætre, 1983) and have an important influence on the distribution of the phyto- and zooplankton as well as on sinking rates of organic material (Melle et al., 1993). The organic material produced in the surface

layers is transported to the bottom by sinking of e.g. phytodetritus and fecal pellets and by vertical migration of zooplankton.

Another mechanism also seems to increase transport down to the bottom. Phytoplankton blooms start on the shelf break during April. At this time of the year the herbivore zooplankton stocks have not developed and a large part of the early primary production is not efficiently grazed. Therefore a significant part of the primary production will probably sink down (Rey, 2004). An indication of this phenomenon was observed in 2003 when high Chl *a* values were observed from the surface and down to the bottom. The sinking is enhanced by the development of a front along the Norwegian shelf break between the North Atlantic Water and the Norwegian Coastal Current (see e.g. Rey, 2004). The front is typically seen as almost vertical isolines of salinity sloping down to the east (against the land) above the shelf break. This situation is not permanent and is to a certain degree broken down during periods of northerly winds. The mechanism can be seen as one of several indicating that the seabed along the shelf edge receives substantial amounts of organic material that can serve as food for the benthic food web. That fronts like this generate local down-welling is well known, see e.g. Luketina and Imberger (1987).

The Norwegian Atlantic Current dominates the flow along the continental shelf edge outside Norway, see Orvik et al. (2001) and Orvik and Skagseth (2003). This inflow will set up an Ekman transport in the lower layer, causing vertical exchanges of water and matter and cross shelf movements of the surrounding water masses. The cross shelf current will then generate a horizontal divergence in the bottom boundary layer at the shelf break and other areas where the bottom topography is

changing rapidly, and create vertical flow. This vertical exchange over uneven topography is probably the most important factor for the transportation of particles either down towards the seabed or in from the surroundings, where benthic organisms can catch them.

In this study, the inflow is not allowed to move in time and space. This means that the horizontal eddy generation (Gjevik, 2002; Davies et al., 2003) and flow on and off the shelf are suppressed. These effects would increase the amount of particles that enter the layer near the seabed close to the shelf break, and would probably also tend to spread out the area where the particles penetrate the bottom layer in the shelf slope to a broader area. The highest number of encounter will then probably be found close to the shelf break and upper shelf slope.

The oceanic flow along the coast of Norway is also strongly influenced by travelling atmospheric low pressure systems, moving mostly towards the northeast (Vikebø et al., 2004). Due to the Ekman veering there will be a flow near the seabed on the shelf towards the shelf edge when the wind is to the north. If the wind is to the south, there will be a flow outside the continental slope towards the shelf edge (Alendal et al., 2005). In both cases, there will be an associated supply of particles in the upper shelf slope and shelf edge area due to horizontal divergence in the layer near the seabed.

In both the Atlantic Inflow and the low pressure simulations, the shelf break and the upper shelf slope are revealed as areas where the supply of particles to the benthic layer will be higher than in the surrounding areas due to geophysical currents. The studies show that the Ekman transport plays a key role in supplying particles to the benthic layer along the shelf edges, due to the horizontal divergence in the bottom flow field. This coupling between a large-scale current system along the Norwegian continental shelf and the distribution of the deep-water reefs formed by L. pertusa may therefore explain why so many coral reefs grow and thrive along the shelf break.

At high latitudes the model results show that the encounter rates are relatively robust to variations in the low pressure activity, which points towards a constant supply of food to benthic organisms located along the shelf edges in these regions. However, this does not exclude low latitude shelf breaks as less suited for corals, since the model results reveal high numbers of encounters here as well.

Our model also indicates why Lophelia prefer to settle on ridges and irregularities on the continental shelf, since uneven topography will enhance the vertical current near the seabed due to the horizontal divergence in the bottom boundary layer. On the shelf there may also be topographically induced currents and turbulence that are important and able to produce a high particle encounter rate close to the bottom. However, large scale phenomena such as low pressure activity and the Atlantic Inflow, will probably still be important for the generation of high velocities close to the seabed. These forces may therefore also be important at the shelf. However, strong currents in themselves will not necessarily produce vertical flow, unless topography is present to force it.

Along the Norwegian shelf slope the tidal effects are relatively weak (Orvik et al., 2001) which means that the wind and the Atlantic inflow are the dominating forces that control the currents. On banks on the continental shelf the Norwegian Coastal Current may be the decisive factor. Closer to the coast, tidal effects are more important. In e.g. fjords, the tide is maybe the most important factor and provides Lophelia with good feeding conditions on fjord sills. To model the food supply for the corals in these areas would demand high spatial resolution and the effects of the stratification must also be considered.

The coral reefs may grow to heights of at least 30 m (Freiwald, 2002). One driving force for such high build-ups can be increased supply of food due to the horizontal divergence in the flow field generated by the reef itself. This hypothesis can be tested by using numerical models with very high spatial resolution, which can resolve the processes around the reefs.

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