Simulation and analysis of flow patterns around the scleractinian coral *Madracis mirabilis* (Duchassaing and Michelotti)

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Three-dimensional morphologies of *Madracis mirabilis* were obtained using X-ray computed tomography scanning techniques. The morphologies were used to simulate the flow patterns around the colony. In the simulations, the thin-branching low-flow morph with a relatively larger branch-spacing was compared with the more compact high-flow morph of *M. mirabilis*. For both morphologies, the inside-colony flow velocities were computed for Reynolds numbers ranging from 154 to 3840. In the high-flow morph, it was found that in the range of investigated Reynolds numbers a stagnant region develops within the colony, whereas in the low-flow morph the stagnant region disappeared. Experiments done under natural conditions suggest that a morph is adapted to a certain external flow velocity and develops a stagnant region below a particular threshold for the external flow velocity. When the external flow velocity exceeds a certain threshold, which is characteristic for the growth form, the core velocity becomes equal to the external velocity. A potential application of a profile of core velocities for a range of Reynolds numbers for a certain morph is the prediction of the optimal external flow velocity for a certain morph, and this can be used to assess the state of the physical (palaeo-) environment.

Keywords: scleractinian corals; hydrodynamics; simulation models

1. INTRODUCTION

Water flow has a strong influence on the growth process of branching scleractinian corals. Veron & Pichon (1976) present several series of growth forms of scleractinians (for example *Pocillopora damicornis* and *Seriatopora hystrix*), which are arranged along a gradient of increasing water movement. Both species show a gradual transformation from a compact shape with a relatively low branch-spacing under exposed conditions, to a thin-branching shape with a relatively larger branch-spacing under sheltered conditions. In the Caribbean coral *Madracis mirabilis* (Kaandorp & Kübler 2001) a similar range is found of compact growth forms with a low branch-spacing gradually changing into more open thin-branching forms with a larger branch-spacing. Two examples of growth forms of the two extremes, the thin-branching low-flow morph collected from a depth of 20 m and the compact hemispherical high-flow morph collected from a depth of 6 m, are shown in figure 1*a,b*, respectively. At the site where our samples were collected, water movement at 6 m depth

is, on average, 2.3 times higher than the site at 20 m depth (Vermeij & Bak 2002). Water flow has a strong influence on the growth process of branching scleractinians. Hydrodynamics affects the distribution of particulate matter in the immediate environment of the coral, as was demonstrated in experiments with branching corals (Sebens *et al.* 1997; Anthony 1999). Furthermore, water movement influences the local concentrations of essential dissolved nutrients, such as phosphate, nitrate (Sorokin 1993) and inorganic carbon (Lesser *et al.* 1994). In studies on the influence of hydrodynamics on particle capture in *M. mirabilis* (Sebens *et al.* 1997), it was demonstrated that branch-spacing is a crucial morphological property. Lesser *et al.* (1994) demonstrated that the morphological plasticity of the skeleton of *P. damicornis* provides a mechanism that minimizes diffusional boundary-layer thickness and maximizes mass transfer through the boundary layer under different flow regimes. High-flow morphs that have relatively small boundary layers can develop relatively more compact growth forms, with still sufficient transfer of dissolved nutrients through the boundary layer.

Earlier experiments with branching corals in flume studies (Chamberlain & Graus 1977) showed that densely packed branching colonies, comparable with *M. mirabilis* colonies, act as a solid body. Water flow (even for rela-

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Figure 1. Surface renderings of CT scans of the coral *Madracis mirabilis*. (a) Thin-branching low-flow morphology, (b) compact high-flow morphology. In both pictures we have defined an xyz -coordinate system. The x -axis corresponds to the horizontal axis, the y -axis corresponds to the vertical axis. Both morphs are visualized on the same scale. The dimensions of the bounding box which can be constructed around the actual objects shown in (a) and (b) in this xyz -coordinate system are $13\text{ cm} \times 8\text{ cm} \times 11\text{ cm}$ and $11\text{ cm} \times 10\text{ cm} \times 6\text{ cm}$, respectively.

tively high flow velocities such as 20 cm s^{-1}) starts to circumvent the colony and a stagnant region develops inside the colony. The authors indicate that the water velocity between the branches of the colony reaches an upper limit, and that this saturation velocity is relatively low when compared with the free fluid velocity. Lesser *et al.* (1994) provide data about flow velocities around *P. damicornis* colonies. For high-flow morphs an external flow velocity of *ca.* 8 cm s^{-1} and inside-colony flows of *ca.* 1 cm s^{-1}

were found. For the low-flow morphs an external flow velocity of *ca.* 3 cm s^{-1} and inside-colony flow of 0.8 cm s^{-1} were reported. Information on the flow pattern within a colony and the formation of boundary layers is crucial in studies on coral mortality due to bleaching events occurring during periods of high sea-surface temperatures, where intricately branched corals are more susceptible to mortality than massive corals (Davies *et al.* 1997; Gates & Edmunds 1999). Nakamura & Van Woesik (2001) provided experimental evidence that the more compact high-flow ($50\text{--}70\text{ cm s}^{-1}$) morphs of the branching scleractinian *Acropora digitifera* show a higher survivorship during a bleaching event than the more open low-flow ($2\text{--}3\text{ cm s}^{-1}$) morphs. It is hypothesized that the open thin-branched corals can disperse fewer metabolic toxins because the mass transfer through the boundary layer is strongly diffusion dominated. Information on the impact of hydrodynamics on the growth process of scleractinians is also very relevant in studies in which models of the growth and form of scleractinians and the influence of the physical environment are developed (Kaandorp & Kübler 2001; Kaandorp & Sloot 2001; Merks *et al.* 2002).

An important limitation in experimental work on the hydrodynamic properties of different coral morphologies is that it is extremely difficult to access relevant local physical environmental parameters, like micro-flow patterns, boundary layers, local absorption of food particles and dissolved material at the coral colony. An important additional option to study these problems is by using simulation models. In this paper, we have simulated the flow patterns around 3D morphologies of *M. mirabilis* obtained using X-ray CT scanning techniques (Kaandorp & Kübler 2001). We compare the flow patterns for a range of Re .

2. MATERIAL AND METHODS

(a) Data acquisition

For the simulations we have used 3D images of the high-flow and the low-flow morphs of the scleractinian *M. mirabilis* (see figure 1). X-ray CT scanning techniques were used for the 3D data acquisition. The CT scan data were stored in DICOM format (a general data format used for medical images). The CT scan data consist of $512 \times 512 \times z$ ($20 \leq z \leq 50$) 3D pixels, the so-called 'voxels'. The slice thickness of the CT scan data is 2.5 mm in the xy direction. Each voxel represents a density value between 0 and 2^{12} , where 0 is the lowest density (the air around the coral skeleton), while high values indicate the calcium carbonate of the coral skeleton. In figure 1, the 3D images are visualized using a surface rendering technique that employs the marching cube technique discussed in Lorensen & Cline (1987). The surface is constructed, approximately, at the boundary between air and the calcium carbonate skeleton of the coral. With this technique, using the original dataset of $512 \times 512 \times z$ voxels, an image is reconstructed with an equal resolution in the x , y and z directions (for details see Schroeder *et al.* 1997). Only the surface of the coral is visualized, without any surface structures such as corallites. On the voxels representing the surface of the corals a triangulated mesh was constructed using the surface rendering technique. This triangulated surface representation is used to map the form onto a lattice of 512^3 voxels, with an equal resolution in the x , y and z directions. In figure 1 the x -axis corresponds to the horizontal axis and the

y-axis to the vertical axis. The actual dimensions of the bounding box around the low-flow morph and the high-flow morph in this xyz -coordinate system are $13\text{ cm} \times 8\text{ cm} \times 11\text{ cm}$ and $11\text{ cm} \times 10\text{ cm} \times 6\text{ cm}$, respectively. The lattice description of the *M. mirabilis* morphologies is used in the simulations to specify the boundary conditions.

(b) Modelling the flow patterns

Branching scleractinians typically have complex-shaped, fractal-like growth forms. Such growth forms impose several problems on the specification of boundary conditions in numerical simulations. Another complication is that the simulation of hydrodynamic processes around complex-shaped, 3D objects requires an enormous computational effort. This can only be done with solving techniques that are suitable for large-scale computing on parallel computers. Similar problems are encountered in studies of flow and diffusion processes in porous media. Relatively recently within computational physics an alternative method for solving the hydrodynamic equations, the lattice Boltzmann method, has been developed. This method has been successfully applied in various case studies with complex-shaped boundary conditions in 3D problems (Heijs & Lowe 1995; Lowe & Frenkel 1996; Kaandorp *et al.* 1996; Koponen *et al.* 1998; Kandhai *et al.* 2002). It has been demonstrated that this method is competitive with conventional methods (e.g. finite-element based methods) for solving the hydrodynamic equations and advection–diffusion problems (Chopard & Droz 1998; Kandhai *et al.* 1999; Succi 2001). The method is well established in computational physics, and the method is potentially a very promising approach for simulating a large range of problems stemming from computational biology.

In this paper we have computed the flow patterns about the 3D images with the lattice Boltzmann method. In Appendix A we give a brief introduction to the lattice Boltzmann method and the parameter settings that we have used in our simulations. For further details we refer to the literature (Chen *et al.* 1992; Ladd 1994; Chopard & Droz 1998; Kaandorp & Kübler 2001; Succi 2001). In this method, space was discretized using a cubic lattice structure. In the simulations, a cubic lattice is used consisting of 256^3 nodes. Although the simulations could be carried out in theory on a 512^3 lattice using the original voxels from the CT scans, we had to downscale the datasets in all dimensions by a factor of 2 for computational reasons. In the simulations we have studied flow patterns for various Re . In the simulations this number was set by varying the parameter ν_{lattice} , the so-called lattice viscosity, in equation (A 4). The simulated flow patterns can be linked to their physical counterparts by using this Re .

In the simulations we have varied the Re from *ca.* 154 to *ca.* 3840. Above the value of 3840 the numerical method tends to become unstable (see Appendix A). For the coral colonies, the Re can be defined as (see Lesser *et al.* 1994)

$$Re = \frac{\langle \mathbf{u} \rangle h}{\nu}, \quad (2.1)$$

where $\langle \mathbf{u} \rangle$ is the average flow velocity, h is the height of the colony and ν is the viscosity of water (0.685×10^{-2} Stokes $\text{cm}^2\text{ s}^{-1}$). Under natural conditions, $\langle \mathbf{u} \rangle$ for *M. mirabilis* can vary between 0 cm s^{-1} and 5 cm s^{-1} , and the height of a *M. mirabilis* can vary between 6 cm and 30 cm. Re under natural conditions for *M. mirabilis* are within the range 100–300 000.

In the simulations we have generated flow patterns in which the flow is in a steady state and where the velocity field is close

to equilibrium. The flow patterns were generated for both the 3D images of the low-flow and high-flow morph shown in figure 1. Two types of boundary conditions were used: at the borders of the lattice periodic boundary conditions are applied, whereas in the nodes adjacent to the nodes representing the 3D image of the coral, solid (no-slip, zero velocity) boundary conditions were used.

3. RESULTS

In figures 2 and 3 some of the results are visualized for respectively the lowest Re (154) and the highest Re (3840) used in the simulations. In all of the experiments the main flow direction corresponds to the x -axis and is directed from the left to the right in both pictures. In figure 2 the results are shown of the simulations done for both the low-flow and high-flow morphs shown in figure 1, where the Re was set to the value 154. In figure 3 similar results are shown for the simulations in which Re was set to 3840. In both figures we show sections through the simulation box along the xz -plane, and the xy -plane, respectively (note that we have applied the xyz -coordinate system as defined in figure 1). In both pictures the flow is visualized by depicting the absolute size of the flow vector, where black indicates a maximal size of the flow vector and white a value near zero. In the simulations we computed the flow patterns for a range of Re varying from 154 to 3840. Within these flow patterns the average flow velocity in the core region of a colony was determined for various Re . The core of the colony was defined as a spherical region with a radius of 1 cm and with its centre positioned at the centre of gravity of the colony. The (spatial) average of the flow velocity was computed by taking the mean value of the flow velocities of the fluid nodes within the core (the nodes representing the object are excluded) and normalized using the flow velocity of the free fluid. The results are summarized in table 1.

4. DISCUSSION

In figure 2 a stagnant region develops in the central region of the colony for both the low-flow and high-flow morphs for a relatively low Re value of (154). In figure 2*b* a few channels with higher flow velocities can be observed between the branches of the low-flow morph. In both morphologies, especially in the high-flow morph, a relatively large boundary layer develops in which the flow velocity is close to zero and where mass transfer between the environment is dominated by diffusion. In the simulations carried out for a high Re (3840), which are shown in figure 3, the distribution of flow velocities around the form shows, especially in the low-flow morph, a highly complex pattern. This result indicates that for higher Re it is not possible to determine only one inside-colony velocity, as was done by Lesser *et al.* (1994). It can be observed in the low-flow morph experiments that there is no longer a stagnant region within the colony, but a complicated pattern of flow channels develops within the colony for a higher Re . In the high-flow morph flow-stagnant regions are formed within the colony even for higher Re . It can be seen in table 1 that the stagnant region in the low-flow morph disappears at Re above *ca.* 1540

Figure 2. Computed flow velocity patterns around the CT scans of the coral *Madracis mirabilis* shown in figure 1. The flow direction is in the x -direction and directed from the left to the right (the same xyz -coordinate system is used as in figure 1). The Re in the simulations was set to 154. In the picture the absolute size of the flow vector is visualized, where black indicates a maximum size of the flow vector and white a value near zero. (a) Low-flow morph, sectioned in the xz -plane, magnitude of flow vectors. (b) Low-flow morph, sectioned in the yz -plane, magnitude of flow vectors. (c) High-flow morph, sectioned in the xz -plane, magnitude of flow vectors. (d) High-flow morph, sectioned in the xy -plane, magnitude of flow vectors.

and the flow velocity in the core region becomes equal to the external velocity in the system. For the high-flow morph the average core flow velocity increases for larger Re , but the stagnant region remains preserved within the range of tested Re . Our observations that in tightly packed high-flow morphs, even for high-flow velocities, stagnant regions develop, which corresponds with the observations done by Chamberlain & Graus (1977). The high-flow morph should therefore be effectively considered as a solid body with flow circumventing the growth form. In the low-flow morph the stagnant regions disappear for higher Re and the flow velocity in the core region becomes equal to the flow velocity of the environment.

Under natural conditions it was found that flow velocity inside the colony reaches an upper limit, which is a relatively low velocity compared with the velocity of the external fluid (Chamberlain & Graus 1977). For high-flow morphs of *P. damicornis* an external flow velocity of *ca.* 8 cm s^{-1} and inside-colony flows of *ca.* 1 cm s^{-1} were found. For the low-flow morphs an external flow velocity of *ca.* 3 cm s^{-1} and inside-colony flow of 0.8 cm s^{-1} were reported by Lesser *et al.* (1994). These observations seem to suggest that morphs are adapted to a certain flow regime, where stagnant regions develop within the colony,

but where the inside-colony flow is still large enough to ensure sufficient mass transfer. Under natural conditions, such as those shown in figure 3*b*, where the stagnant region completely disappears and where the inside-colony flow velocity becomes equal to the external velocity, will normally not occur in low-flow morphologies. Also, the other extreme in which an almost stagnant and diffusion-dominated region develops in high-flow morph as shown in figure 2*d* will normally not be found. The experiments done under natural conditions suggest that a morph is adapted to a certain external flow velocity and that a stagnant region or low-flow velocity region develops within the colony. When the external flow velocity exceeds a certain threshold, which is characteristic for the growth form, the core velocity becomes equal to the external velocity. A potential application of core velocity profiles for a certain morph, such as is shown in table 1, is to predict the optimal external flow velocity for a certain morph and can, for example, be used to assess the state of the physical (palaeo-) environment and environmental conditions by analysing the growth form in a flow simulation.

Several issues have still not been resolved in our simulations. One computational issue is that our method becomes unstable above Re of *ca.* 3840, whereas Re under

Figure 3. Computed flow velocity patterns around the CT scans of the coral *Madracis mirabilis* shown in figure 1. The flow direction is in the x -direction and directed from the left to the right (the same xyz -coordinate system is used as in figure 1). In the picture the absolute size of the flow vector is visualized, where black indicates a maximum size of the flow vector and white a value near zero. The Re in the simulations was set to 3840. (a) Low-flow morph, sectioned in the xz -plane, magnitude of flow vectors. (b) Low-flow morph, sectioned in the xy -plane, magnitude of flow vectors. (c) High-flow morph, sectioned in the xz -plane, magnitude of flow vectors. (d) High-flow morph, sectioned in the xy -plane, magnitude of flow vectors.

Table 1. Ratio of the (spatial) average of the flow velocity $\langle u \rangle$ in a spherical core region with a radius of 1 cm within the colony and the flow velocity of the free fluid. The ratios (and standard deviations) were determined in the colonies from figure 1a (low-flow morph) and 1b (high-flow morph) for a range of Re .

Re	154	307	768	1540	3840
low-flow morph	0.45 ± 0.14	0.67 ± 0.21	0.83 ± 0.28	0.93 ± 0.27	0.99 ± 0.25
high-flow morph	0.04 ± 0.03	0.07 ± 0.04	0.11 ± 0.08	0.16 ± 0.15	0.34 ± 0.24

natural conditions for *M. mirabilis* are within the range of 100–300 000. For obtaining flow patterns above Re 3840 we may need a different numerical method and we need to analyse time-dependent flow patterns. Another computational issue is the size of the simulation box. In this currently reported work we have used a simulation box consisting of 256^3 nodes, while the original dataset contains 512^3 nodes. Because our method is suitable for execution on a parallel computer, we expect that this is only a practical constraint and that we can simply upscale our simulations. Two other important issues still have to be addressed. In our simulations the 3D images are not positioned on a substrate plane, which is a more plausible choice if we want to compare our simulations with actual flow patterns around corals. In the simulations presented in this paper we were especially interested in the relation-

ship between external and internal flow velocities within a small central region in the colony. If we wish to compare the overall flow pattern around the colony with simulated flow fields then it will be important to include the effects of the substrate plane on the flow pattern. Another issue is the quantification of the mass flux of material at the surface of the 3D representation of the corals. We are planning to do this in the near future by combining our flow simulations with a tracer step, with which we can study the advection–diffusion of material through the colony and absorption at the surface of the object, for a certain external flow field.

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APPENDIX A

In the simulations a cubic lattice is used consisting of 256^3 nodes. Each node is connected with 18 other nodes. There are six links with the length of one lattice unit, 12 links with the length of $\sqrt{2}$ units and mass that remains on the link itself (particles that do not propagate to neighbouring links). All parameters and variables in the lattice Boltzmann method are expressed in lattice units. The mean populations of particles move simultaneously from one node to one of the neighbours. The evolution of the lattice is described by the following dynamical rule:

$$n_i(\mathbf{r} + \mathbf{c}_i, t + 1) = n_i(\mathbf{r}, t) + \Delta_i(\mathbf{r}, t, \tau) \quad \text{for } i = 0, \dots, 18, \quad (\text{A } 1)$$

where $n_i(\mathbf{r}, t)$ is the continuous particle distribution function, which describes the number of particles at a node at position $\mathbf{r}$, at time t and with direction $\mathbf{c}_i$, and $\Delta_i(\mathbf{r}, t, \tau)$ is the collision operator describing the changes in n_i due to collisions at the nodes. The parameter τ the lattice viscosity ν_{lattice} can be covaried in the following relation

$$\nu_{\text{lattice}} = \frac{2\tau - 1}{6}. \quad (\text{A } 2)$$

The moments of the particle distribution function $n_i(\mathbf{r}, t)$

$$\begin{aligned} \rho &= \sum_i n_i, \\ \rho \mathbf{u} &= \sum_i n_i \mathbf{c}_i, \\ \Pi &= \sum_i n_i \mathbf{c}_i \mathbf{c}_i, \end{aligned} \quad (\text{A } 3)$$

correspond to the hydrodynamic fields mass density ρ , momentum density $\rho \mathbf{u}$ ($\mathbf{u}$ is the flow velocity at node $\mathbf{r}$), and momentum flux Π . By using the properties of conservation of mass, momentum and symmetry it is possible to compute the post-collision distribution function $n_i(\mathbf{r} + \mathbf{c}_i, t + 1)$ and to approximate solutions of the hydrodynamic equations (see Ladd (1994) for details) and to compute flow patterns about obstacles. The properties of conservation of mass and momentum are based on the two hydrodynamic laws (the continuity equation describing the conservation of mass and the Navier–Stokes equation describing the conservation of momentum). Symmetry is important to avoid spurious conservation laws in a lattice (for example when the particles tend to move especially along the axes of the lattice system). To avoid spurious conservation laws the lattice system should have sufficient isotropy. Two types of boundary conditions are used: at the borders of the lattice periodic boundary conditions are applied, whereas in the nodes adjacent to the nodes representing the obstacle, solid boundary conditions are used. Periodic boundary conditions can be implemented by exchanging the n_i s of the links at the borders of the lattice. Solid boundary conditions can be represented by exchanging the n_i s between the adjacent node and a neighbouring fluid node. The Re in the simulations can be controlled with a parameter ν_{lattice} , representing the lattice viscosity. This parameter can vary (in theory) within the range $0 < \nu_{\text{lattice}} \leq 1/2$. For values of ν_{lattice} close to 0, the lattice Boltzmann can become unstable (Chen *et al.* 1992; Ladd 1994). In the

simulations we have studied flow patterns for various Re by varying ν_{lattice} in

$$Re = \frac{0.1256}{\nu_{\text{lattice}}}, \quad (\text{A } 4)$$

where 0.1 is the (maximum) flow velocity of the free fluid in lattice units and 256 is the characteristic length of the lattice. In the simulations we have varied the Re from ca. 154 ($\nu_{\text{lattice}} = 1/6$) to ca. 3840 ($\nu_{\text{lattice}} = 0.03$). Below the value $\nu_{\text{lattice}} = 0.03$ our numerical method became unstable. In the simulations we have applied 1000 lattice Boltzmann iteration steps to obtain a velocity field; this number of steps is adequate to be close to equilibrium and remove transients.

REFERENCES

- Anthony, K. R. N. 1999 Coral suspension feeding on fine particulate matter. *J. Exp. Mar. Biol. Ecol.* **232**, 85–106.
- Chamberlain, J. A. & Graus, R. R. 1977 Water flow and hydro-mechanical adaptations of branched reef corals. *Bull. Mar. Sci.* **25**, 112–125.
- Chen, S., Wang, Z., Shan, X. & Doolen, G. 1992 Lattice Boltzmann computational fluid dynamics in three dimensions. *J. Statist. Phys.* **68**, 379–400.
- Chopard, B. & Droz, M. 1998 *Cellular automata modeling of physical systems*. Cambridge University Press.
- Davies, J. M., Dunne, R. P. & Brown, B. E. 1997 Coral bleaching and elevated sea-water temperature in Milne Bay Province Papua New Guinea 1996. *Mar. Freshwat. Res.* **48**, 513–518.
- Gates, R. D. & Edmunds, P. J. 1999 The physiological mechanisms of acclimatization in tropical reef corals. *Am. Zool.* **39**, 30–43.
- Heijs, A. W. J. & Lowe, C. P. 1995 Numerical evaluation of the permeability and the Kozeny constant for two types of porous media. *Phys. Rev. E* **51**, 4346–4351.
- Kaandorp, J. A. & Kübler, J. E. 2001 *The algorithmic beauty of seaweeds, sponges and corals*. Berlin: Springer.
- Kaandorp, J. A. & Sloot, P. M. A. 2001 Morphological models of radiate accretive growth and the influence of hydrodynamics. *J. Theor. Biol.* **209**, 257–274.
- Kaandorp, J. A., Lowe, C. P., Frenkel, D. & Sloot, P. M. A. 1996 The effect of nutrient diffusion and flow on coral morphology. *Phys. Rev. Lett.* **77**, 2328–2331.
- Kandhai, D., Vidal, D., Hoekstra, A., Hoefsloot, H., Iedema, P. & Sloot, P. M. A. 1999 Lattice Boltzmann and finite-element simulations of fluid flow in a SMRX static mixer. *Int. J. Num. Meth. Fluids* **31**, 1019–1033.
- Kandhai, D., Hlushkou, D., Hoekstra, A. G., Sloot, P. M. A., Van As, H. & Tallarek, U. 2002 Influence of stagnant zones on transient and asymptotic dispersion in macroscopically homogeneous porous media. *Phys. Rev. Lett.* **88**, 234501–1–234501–4.
- Koponen, A., Kandhai, D., Hellen, E., Alava, M., Hoekstra, A., Kataja, M., Niskanen, K., Sloot, P. M. A. & Timmonen, J. 1998 Permeability of three-dimensional random fiber webs. *Phys. Rev. Lett.* **80**, 716–719.
- Ladd, A. J. C. 1994 Numerical simulations of particulate suspensions via a discretized Boltzmann equation. Part I. Theoretical foundation. *J. Fluid Mech.* **271**, 285–309.
- Lesser, M. P., Weis, V. M., Patterson, M. R. & Jokiel, P. L. 1994 Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): diffusion barriers, inorganic carbon limitation, and biochemical plasticity. *J. Exp. Mar. Biol. Ecol.* **178**, 153–179.

- Lorensen, W. E. & Cline, H. E. 1987 Marching cubes: a high resolution 3D surface construction algorithm. *ACM Computer Graphics* **21**, 163–169.
- Lowe, C. P. & Frenkel, D. 1996 Do hydrodynamic dispersion coefficients exist? *Phys. Rev. Lett.* **77**, 4552–4555.
- Merks, R. M. H., Hoekstra, A. G., Kaandorp, J. A. & Sloom, P. M. A. 2002 Spontaneous branching in a polyp oriented model of stony coral growth. In *Lecture notes in computer science* (ed. G. Goos, J. Hartmanis & J. van Leeuwen), pp. 88–96. Berlin: Springer.
- Nakamura, T. & Van Woesik, R. 2001 Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Mar. Ecol. Prog. Ser.* **212**, 301–304.
- Schroeder, W., Martin, K. & Lorensen, B. 1997 *The visualization toolkit: an object-oriented approach to 3D graphics*, 2nd edn. Englewood Cliffs, NJ: Prentice-Hall.
- Sebens, K. P., Witting, J. & Helmuth, B. 1997 Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). *J. Exp. Mar. Biol. Ecol.* **211**, 1–28.
- Sorokin, Y. I. 1993 *Coral reef ecology*. Berlin: Springer.
- Succi, S. 2001 *The lattice Boltzmann equation: for fluid dynamics and beyond*. Oxford University Press.
- Vermeij, M. J. A. & Bak, R. P. M. 2002 How are coral populations structured by light? Marine light regimes and the distribution of *Madracis*. *Mar. Ecol. Prog. Ser.* **233**, 105–116.
- Veron, J. E. N. & Pichon, M. 1976 *Scleractinia of eastern Australia part I: families Thamasteriidae, Astrocoeniidae, Pocilloporidae*. Canberra: Australian Government Publishing Service.

GLOSSARY

- CT: computed tomography
 DICOM: digital imaging and communications in medicine
 Re: Reynolds number(s)