The Virtual Laboratory

The Algorithmic Beauty of Seaweeds, Sponges and Corals

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DIE FACHBUCHHANDLUNG

Environmentally Driven Plasticity

2.1 The Physical Environment

The two major environmental parameters which have the greatest impact on the growth forms of marine sessile organisms are light, required for photosynthesis, and hydrodynamics. A full discussion of the physics of underwater light distributions and hydrodynamics could easily cover a few textbooks. In Box 2.1 the basic hydrodynamic laws are summarized, together with two dimensionless parameters, the Reynolds number *Re* (2.3) and the Péclet number *Pe* (2.4), which can be used to characterize the impact of the flow on the organism. In Sect. 2.1.1 "Growing and flowing" we will focus on the biomechanical impact of hydrodynamics on the growth process and try to construct a number of laws for the biomechanical impact of hydrodynamics using an engineering approach. In Sect. 4.3 we will return to the topic of hydrodynamics, from a modeling point of view and try to construct a computational method capable of capturing the influence of hydrodynamics in models of growth and form of marine sessile organisms. In Box 2.2 the basic equations, in a highly simplified form, of underwater light distributions are shown. To a certain extent, in contrast with the hydrodynamic equations, these simplified equations can more or less straightforwardly be included in computational models; this will be discussed in Chap. 4.

Box 2.1   *Hydrodynamics*

Flow of water in space can be captured through two fundamental equations:

$$\frac{\partial \rho}{\partial t} + \nabla \cdot \rho U = 0 \tag{2.1}$$

$$\frac{\partial U}{\partial t} = -(U \cdot \nabla)U - \frac{1}{\rho}\nabla P + \nu \nabla^2 U \tag{2.2}$$

In these equations ρ represents the mass density, t the time, U the flow velocity, P the pressure, and ν the kinematic viscosity. The symbols ∇ and ∇^2 are respectively the del and Laplacian operator (in three dimensions respectively: $\partial/\partial x + \partial/\partial y + \partial/\partial z$ and $\partial^2/\partial x^2 + \partial^2/\partial y^2 + \partial^2/\partial z^2$). The first equation (the continuity equation) expresses the conservation of mass, and states that the density can change at a point in space only due to a net in- or outflow of matter. The second equation, the Navier–Stokes equation, expresses the conservation of momentum, and states that the

flow velocity U changes in time in response to convection $(U \cdot \nabla)U$, spatial variations in pressure ∇P, and viscous forces $v\nabla^2 U$

Two important dimensionless parameters, characterizing the flow, are:

$$Re = \frac{\bar{u}l}{v} \, , \tag{2.3}$$

$$Pe = \frac{\bar{u}l}{D} \tag{2.4}$$

The Re parameter is the Reynolds number and is the ratio between the inertial forces $\bar{u}l$ and the viscous forces, where $\bar{u}$ is the average flow velocity and l a characteristic length in the system (for example the height of the organism). High values of Re indicate that the flow becomes turbulent and the flow will not attain a steady state ($\partial U/\partial t = 0$), while the flow will reach a steady state for low Re numbers (laminar flow).

The Pe parameter is the Péclet number and is the ratio between the inertial forces $\bar{u}l$ and the Brownian forces, where D is the diffusion coefficient. The value of D represents, for example, the diffusion coefficient of a suspended food particle. Low Pe numbers indicate that particles are mainly distributed by diffusion, while high Pe numbers indicate that food particles are mainly dispersed through hydrodynamics.

Box 2.2   *Underwater light intensities*

The change of light intensity, due to the attenuation in the water column, is described for monochromatic light by the Lambert–Beer Law:

$$I_d = I_0 e^{-\gamma d} \tag{2.5}$$

where I_d and I_0 are respectively the light intensities at depth d and just below the water surface. The attenuation coefficient γ is the sum of the absorption coefficient and the scattering coefficient. The light absorption depends upon the wavelength of the monochromatic light, minimal absorption takes place in clear water at 465 nm, absorption of blue light increases by the presence of soluble yellow humus-like substances in the water. The scattering coefficient depends upon the amount of suspended particles in the water.

The Lambert-Beer Law gives the light intensity at a certain depth. The amount of light received by a unit area can be calculated by considering the angle of incidence of light, which gives a more detailed description of the local light intensities at the surface of an organism. A (highly simplified) light model (Foley et al. 1990) is described by the equation:

$$I = I_S \cdot \cos \theta \tag{2.6}$$

The light intensity I (W/m²) on a surface is determined by $\cos \theta$, where θ is the angle of incidence between the direction of the light beam and the surface normal and I_S is the intensity of the light source (at a certain depth). In this equation it is assumed that the light source is constant, the light direction corresponds to the vertical, and there is no diffuse reflection from the environment.

2.1.1 Growing and Flowing

Marine sessile organisms, such as macroalgae and colonial animals, risk being dislodged or broken by ambient water currents and waves, yet they also depend on that moving water for transport (reviewed in Koehl 1982, 1986, 1999, Denny 1988, 1999, Vogel 1994). Ambient water motion is responsible for dispersing the spores or larvae, and in many cases the gametes, of sessile organisms. Waste products and sediments are also carried away by moving water. Attached algae and animals depend on moving water for the transport of dissolved materials such as nutrients and gases, while suspension-feeding animals depend on ambient currents to bring particulate food to them, and in many cases to ventilate their filters. Body designs that enhance an organism's interaction with the water flowing around it enhance not only transport, but also hydrodynamic forces.

The first step in studying how sessile organisms interact with the water flowing around them is to determine their hydrodynamic microhabitats (e.g. Koehl 1977a, Denny 1988). Many benthic organisms in deep water and in protected bays and estuaries encounter unidirectional currents or tidal currents that flow in one direction for several hours, and then in the opposite direction. Attached organisms in shallow coastal habitats are also exposed to waves. When a wave passes over an organism on the substratum where water depth is less than one half of the crest-to-crest distance between waves, the water flow along the bottom is back-and-forth with a period of seconds. When fluid flows along a solid surface, such as the substratum or the surface of an organism's body, the layer of fluid in contact with the surface does not slip with respect to it. Therefore, a velocity gradient (the boundary layer) develops in the fluid between the surface and the freestream flow. The greater the distance a fluid flows across a surface, the thicker the boundary layer becomes. In marine habitats, the benthic boundary layer can be a meter or more thick, although the steepest velocity gradient occurs within a few centimeters of the substratum (reviewed in Jumars and Nowell 1984). Although a thin sublayer (mm's thick) of laminar flow occurs along the substratum, water flow in the benthic boundary layer is turbulent, so mass and momentum are mixed between the freestream flow and the bottom by swirling eddies. Since it takes time for a boundary layer to build up when water begins to flow over a surface, the benthic boundary layer in the back-and-forth sloshing water of waves is much thinner than in unidirectional flow (e.g. Denny 1988). Local topography and neighboring organisms can have a profound effect on the water flow encountered by a benthic organism, hence the hydrodynamic microhabitat of an attached animal or plant can be very different from the freestream flow over the site where it occurs (Koehl 1977a, Koehl and Alberte 1988). As a sessile organism grows, it can encounter more rapid water movement as it sticks up higher in the benthic boundary layer and becomes larger relative to its neighbors.

Biomechanical studies have shown that general physical rules that apply across taxa can permit us to understand and predict how organisms interact with their physical environments. Such an approach provides a useful framework for considering the consequences of shape and size on the hydrodynamic forces and on the transport experienced by sessile animals and macrophytes as they grow.

Hydrodynamic forces

UNIDIRECTIONAL WATER CURRENTS.   Drag is the hydrodynamic force tending to push an organism downstream. The drag on macroscopic organisms is due to the pressure difference across the body that occurs when a wake forms behind the organism (form drag), and to the viscous resistance of the fluid in the boundary layer along the surface of the body to being sheared (skin friction drag) (e.g. Vogel 1994). Drag D on a macroscopic body is given by:

$$D = 0.5\, \rho C_D U^2 S \tag{2.7}$$

where D is drag, ρ is the density of the fluid, C_D is the drag coefficient of the body (which depends on its shape and surface texture), U is the water velocity relative to the body, and S is a relevant plan area of the body. The convention for relatively undeformable organisms is usually to use the projected area of the organism at right angles to the flow for S (e.g. Koehl 1977a, Vogel 1994, Denny 1988), whereas the convention for very flexible organisms such as macroalgae is to use the maximum plan area of the thallus (Koehl 1986, Carrington 1990, Gaylord et al. 1994) This simple equation points out important features of any benthic organism that affect the drag it experiences. Since drag is proportional to the square of velocity, as organisms grow and encounter more rapid water motion up away from the substratum, they experience disproportionately larger drag. Any morphological characteristics that decrease the size of the wake that forms on the downstream side of a macroscopic organism reduce drag. Such features include orientation parallel to the flow direction, streamlined shape (i.e. a shape that is long and tapered on the downstream side), and porosity (i.e. gaps between branches or lobes that permit water to flow through the structure) (e.g. Koehl 1977a, Vogel 1994).

Most macroalgae and some colonial animals (e.g. arborescent hydroids and bryozoans; gorgonian sea whips and sea fans, Fig. 2.1) are flexible and are passively reconfigured by ambient water currents into more streamlined shapes as flow velocity increases. Such passive reorientation or reconfiguration of flexible organisms by flowing water reduces the size of the wake

Fig. 2.1. Gorgonian sea fan reconfigured by ambient water current

downstream of a body, thereby reducing form drag (e.g. Koehl 1977a, 1986, Vogel 1984, Koehl and Alberte 1988, Carrington 1990). Vogel (1984) has proposed an index, the "figure of merit" B, to describe the relative reduction in drag experienced by flexible structures as they reconfigure as flow velocity increases, where B is the slope of a log-log plot of speed-specific drag D/U^2 as a function of velocity; the greater the absolute value of the negative slope, the greater the relative drag reduction experienced with an increase in velocity. In addition, if the flexibility of a blade-like sessile organism permits it to be pushed down close to the substratum, the underside of the blade encounters slower flow than the upper surface, thereby reducing the shear and thus the skin friction drag on that surface (Koehl 1986). Although shape can affect the hydrodynamic forces which flexible organisms experience (e.g. Koehl 1977a, Koehl and Alberte 1988, Johnson and Koehl 1994), Carrington (1990) found that a variety of very flexible blade-like, branching, and bushy seaweeds converged onto similar drag coefficients when subjected to high water velocities at which they all were compacted into similar streamlined bundles.

Benthic organisms in a water current can also experience lift, the hydrodynamic force acting at right angles to drag. When water speeds up locally as it moves over and around an obstacle, such as an organism, the local pressure on the organism is lower where the flow along its surface is faster; a pressure difference across the body of an organism can thus develop. Organisms protruding above the substratum are pulled up by lift, and organisms that present an asymmetric shape to the oncoming current are pulled laterally if the water speeds up more to move around one side of the organism relative to the other (Denny 1988, Vogel 1994). Lift (L) is given by

$$L = 0.5\,\rho C_L U^2 S \qquad\qquad\qquad (2.8)$$

where C_L is the coefficient of lift (which depends on shape) and S is a relevant area (usually planiform area normal to the direction in which the lift acts). Thus, as with drag, lift increases as an organism grows, not only because its S increases, but more importantly because it encounters higher water velocities. Even a symmetric structure, such as the cylindrical branch of an animal colony, can experience transient lateral lift, alternating from side to side as vortices are shed in the wake behind it (explained in Denny 1988). If such structures are flexible, they wobble side-to-side as water flows past. Furthermore, if flexible organisms are pushed over by drag, and pulled back up by lift, they can flutter like a flag; the wake behind a fluttering organism can be bigger and the drag force higher than on a body of similar shape and orientation that does not flutter (Koehl and Alberte 1988). When ambient currents encounter a branching structure, such as a coral colony, some of the water flows between the branches, but most of it is diverted above the colony. The lower pressure that occurs above a coral colony as water speeds up to flow over it not only subjects the colony to lift, but also can draw the slowly-moving water between the branches up and out of the colony, thereby reducing the stagnation of flow that can occur in the middle of colonies as they grow larger (Chamberlain and Graus 1977).

WAVES.   Sessile organisms exposed to waves experience back-and-forth water motion. Since the velocity changes with time, the instantaneous lift and drag that the organisms experience (which are proportional to the square

of the instantaneous velocity) also vary with time. In addition to lift and drag, organisms in the accelerating flow in waves also are subjected to the acceleration reaction force (A),

$$A = \rho C_M \frac{dU}{dt} V \qquad\qquad\qquad (2.9)$$

where C_M is the inertia coefficient (which depends on shape), $\frac{dU}{dt}$ is the instantaneous water acceleration, and V is the volume of the organism (Koehl 1977a, Denny 1988). Bodies with shapes that deflect the path of the water moving around them a lot (such as stiff, planar colonies normal to the flow) have higher C_M's than do bodies that do not deflect the flow as much (such as streamlined bodies). Since A depends on the volume of an organism (V is proportional to length^3), a small increase in body length can lead to a very large increase in A. If water is trapped between the branches or blades of an algal thallus or animal colony, the functional volume of the organism that affects A is the volume of that water in addition to the volume of the organism's body (Gaylord et al. 1994). Since A is proportional to the instantaneous water acceleration, it varies with time as the water flows back and forth past an organism; when water is speeding up, A acts in the same direction as drag, but when water is slowing down, it acts in the opposite direction from drag. The instantaneous net force on an organism in waves is the sum of the acceleration reaction, drag, and lift at that instant.

Since the hydrodynamic forces on an organism depend on the magnitude of the velocity and acceleration of the water relative to the organism, a flexible organism that can move along with the water in waves can avoid being pulled by hydrodynamic forces until it is fully extended in the direction of flow and the water moves past it. The longer the organism relative to the distance the water moves before it flows back the other way, the more likely the organism is to avoid flow forces at times when accelerations and velocities are high (Koehl 1999). However, a flexible wave-swept organism moving with the flow can be jerked to a halt if it reaches the end of its rope before the water in a wave begins to flow back in the opposite direction; when this occurs, a brief inertial force (proportional to the mass, and hence to the V, of the organism) pulls on the organism (Denny et al. 1998). The length of a flexible macrophyte or colony relative to the distance X that the water in a wave flows in one direction before stopping and accelerating in the opposite direction can have a profound effect on the forces the organism experiences in waves because it determines when in the wave cycle the organism is jerked to a halt and begins to experience flow relative to its body. As flexible organisms that are short relative to X grow, the total force they experience in waves increases (e.g. Gaylord et al. 1994). However, once organisms grow long enough relative to X that they reach the end of their rope only after the water in a wave has begun to decelerate, further growth does not lead to an increase in force on the holdfast, as demonstrated by experiments with model organisms in an oscillating-flow tank and by measurements of forces on real kelp on waveswept shores (Koehl 1999). Stretchy tethers such as the stipes of kelp can act as shock absorbers whose stretching absorbs mechanical work, thereby permitting the kelp to withstand the transient high loads they encounter in turbulent or wave-swept habitats (Koehl and Wainwright 1977). Mathematical models suggest that the tuning of the time-dependent material properties of stretchy tethers relative to the frequencies at which these structures must

resist high inertial loads in wave-swept environments can have a significant effect on their likelihood of experiencing large forces (Denny et al. 1998).

While some sessile organisms (such as stony corals) are very stiff, and some (such as thin blade-like algae) are very flexible, others (such as sea fans, Fig. 2.1, or stipitate kelp) are of intermediate stiffness. Measurements of hydrodynamic forces experienced in a wave tank by models of organisms of the same blade-like shape, but different flexural stiffnesses, showed that as the stiff models "grew" the peak force increased, whereas as the very flexible models "grew" the force remained low (Koehl 2000). A third type of size-dependent behavior was shown by the models of intermediate stiffness: lengthening increased hydrodynamic forces on short models, had no effect on models of intermediate length, and decreased forces on long models. Since the deflection of the free end of an organism attached to the substratum (like a cantilever) depends on length[4], the longer the models of intermediate stiffness become, the more they bend over and go with the flow (Koehl 2000).

Consequences of Hydrodynamic Forces as Organisms Grow.   Hydrodynamic forces can deform sessile organisms (which can in turn affect performance of functions such as light or food interception), and can break or rip them off the substratum. How much the tissues in a body deform, and whether or not they break, depends not only on the stiffness and strength of the tissues, but also on the stresses to which they are subjected (stress is the force imposed on a material divided by the cross-sectional area of material bearing that force). The stresses within an organism's body when being stretched, bent, or compressed by a hydrodynamic force can be calculated using the same techniques engineers use to calculate the stresses in man-made structures (for details, see e.g. Roark and Young 1975, Wainwright et al. 1976). Such analyses reveal that, not only do the shape and size of attached organisms determine the magnitude of the hydrodynamic forces which they experience when exposed to ambient currents, but shape and size also determine the distribution and magnitude of stresses within their bodies when bearing those forces (e.g. Koehl 1977b, 1986).

Whether organisms grow geometrically (i.e. maintain the same shape as they get bigger) or allometrically (i.e. change shape as they grow) determines whether or not the local stresses in their tissues increase, decrease, or stay the same during their ontogeny. Although the scaling of the proportions of terrestrial and locomoting organisms of different sizes has received much attention, the scaling of attached sessile organisms is less well studied (Denny 1988, 1999, Johnson and Koehl 1994, Koehl 2000). The "safety factor" of a structure is the ratio of the strength of the material composing it to the maximum stress it experiences during its lifetime. Since ambient water flows on sessile organisms often vary with season and since the size, shape, and mechanical properties of their tissues can change with age, the "environmental stress factor" is a biological version of safety factor that relates the ability of organisms at their particular stages in ontogeny to resist breakage relative to the maximum loads that they experience in nature at those stages. For example, the giant kelp *Nereocystis luetkeana* adjusted their shapes and material properties as they grew in different hydrodynamic habitats in such a way that the "environmental stress factor" was the same in all the habitats and was maintained as the kelp grew during the summer months, but de-

creased during the winter, after the kelp had reproduced and when they were subjected to storms (Johnson and Koehl 1994).

Whether or not waves impose a mechanical upper limit to the sizes of attached organisms is still being explored (reviewed by Denny 1999). However, breakability is not necessarily a "bad" feature preventing organisms from succeeding in wave-swept environments if those broken organisms can regrow. For example, when bits of a sessile organism or colony break off, the hydrodynamic forces on the part of the structure that remains can be reduced, hence partial breakage can prevent total destruction (e.g. Black 1976). Furthermore, if the broken-off pieces of an organism or colony can reattach and grow, breakage can be a mechanism of asexual reproduction and dispersal, as has been shown for a number of species of coral (Highsmith 1982).

To be able to include the impact of hydrodynamic forces in simulation models of growth processes, as will be discussed in Sections 4.5 and 4.6, it is required to be able to compute local forces exerted by the fluid on the growing object. In most cases these objects will have a typical complex-shaped and branching geometry and are usually characterized by a rough and fractal-like surface. In (2.8) and (2.9) all morphological details are "hidden" in the coefficients C_l and C_M. In morphological simulations of growth processes, where local hydrodynamic forces are included, in many cases a more microscopic description of forces will be needed to be able (for example) to simulate partial breakage. In Sect. 4.3.1 we will discuss how microscopic estimates can be derived from simulated hydrodynamics about complex-shaped obstacles.
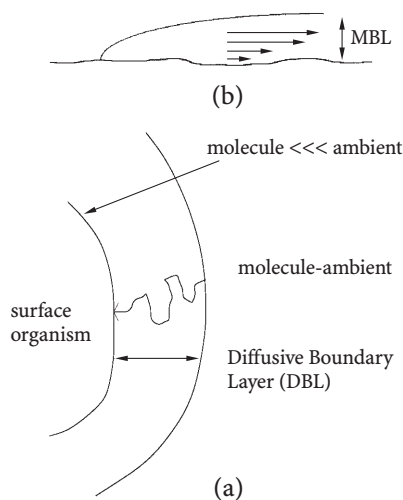
Mass transfer

Boundary layers and mass flux.   Organisms such as corals and seaweeds rely on uptake of nutrients and gases across the surfaces of their tissues. Such an exchange of mass is subject to the physical laws of diffusion and convection which are mediated by both properties of the organism surface and hydrodynamic characteristics of the fluid environment. Mass and heat transfer at surfaces have been addressed rigorously in the engineering literature (White 1988, Kays and Crawford 1993). Engineering correlations have been used successfully to describe mass transfer processes at the seafloor (Dade 1993) and for various organisms and communities (Patterson et al. 1991, Bilger and Atkinson 1992, Baird and Atkinson 1997). As fluid moves over surfaces, momentum is extracted from the fluid through friction and a gradient in flow speed is established over the surface that is called the momentum boundary layer (Fig. 2.2a). Analogously, if mass is transferred at a surface by the uptake of a compound, gas, or ion from the bulk fluid, a gradient in concentration is established over the surface; this is the diffusive boundary layer (Fig. 2.2b). Delivery of mass to the surface by diffusion is described by Fick's 1st Law of Diffusion

$$flux = -D_m \, \mathrm{d}C/\,\mathrm{d}X \qquad (2.10)$$

where D_m is the coefficient of diffusion for the compound, gas, or ion in the fluid and $\mathrm{d}C/\,\mathrm{d}X$ is the concentration gradient over the diffusive boundary layer. As a result, at a constant bulk concentration, flux is inversely proportional to the thickness of the diffusive boundary layer. The relationship

(b)

(a)

Fig. 2.2. (*a*) Diagram of the formation of a momentum boundary layer (*MBL*) as a fluid flows over a surface. The *MBL* is a gradient in velocity from zero at the substratum to 99% of the freestream velocity. (*b*) The diffusive boundary layer (*DBL*) is a gradient in concentration of some molecule of interest, from an ambient concentration far from the surface of an organism to a much lower concentration adjacent to the organism surface where it is taken inside and used in metabolism. Molecule transport across the *DBL* is by diffusion

between the momentum (*MBL*) and diffusive boundary (*DBL*) layers is given by

$$DBL/MBL = Sc^{-0.33} \qquad (2.11)$$

where *Sc* is the Schmidt number, which is the ratio of the diffusivity of momentum to the diffusivity of the compound, gas, or ion in question. For molecules that are relevant to photosynthesis and respiration, values of *Sc* in seawater at 25 °C are 797 for HCO_3^- and 410 for O_2, resulting in diffusive boundary layers that are approximately 1/7 th to 1/10 th, respectively, as thick as the momentum boundary layer.

Momentum and diffusive boundary layer characteristics are related to the type and speed of fluid motion, the distance the fluid moves over the surface, the surface roughness, and the steadiness of the flow (White 1994). Both types of boundary layers decrease as flow speed increases but how they decrease depends on whether the flow is laminar or turbulent. Characteristics of the flow surrounding an object are related to the Reynolds number *Re* (see (2.3)). Fluids with $Re < 10^5$ (over a smooth flat plate) usually are laminar and become turbulent at $Re > 5 \cdot 10^5$. As a fluid flows steadily over a surface, the boundary layer grows and its thickness is a function of the local *Re* (Re_x), defined as $U_\omega x / \nu$, where *x* is the distance downstream from the leading edge of the surface and where $U\omega$ is the freestream flow speed. The thickness of a boundary layer over a smooth flat surface is $\approx 5(Re_x)^{-0.5}$, and in turbulent flow is $\approx 0.37(Re_x)^{-0.2}$. Laminar boundary layers become turbulent when $Re_x > 10^5 - 10^6$. Over smooth surfaces turbulent boundary layers consist of a thin viscous sublayer adjacent to the surface, a transition zone, and an outer region that is fully turbulent. In the presence of surface roughness the viscous sublayer disappears. Unsteady flows (e.g. oscillatory) introduce a temporal component to boundary layer formation and growth and can result in the periodic disruption of established boundary layers (White 1994). All other things being equal, boundary layers (both momentum and diffusive) will be thicker over organisms with smooth, bladelike shapes compared with organisms whose surfaces have projections and/or arehack highly branched.

Diffusive boundary layers may represent a significant resistance to the flux of mass to and from the surfaces of benthic organisms. If the compound, gas, or ion is taken up and used immediately in a metabolic process, then diffusion across the boundary becomes the rate-limiting step and the process is mass transfer limited (Bilger and Atkinson 1992). In this case, the metabolic rate should be a function of flow speed to either the 0.5 (laminar) or 0.8 (turbulent) power (Fig. 2.3).

MODELS OF MASS FLUX.   To make analyses dimensionless, previous approaches to relate rates of mass transfer to fluid motion have used the Sherwood number (*Sh*, Patterson et al. 1991) or the Stanton number (*St*, Bilger and Atkinson 1992). *Sh* is defined as $h_m W / D_m$, where h_m is the mass transfer coefficient, *W* is the characteristic dimension of the organism, and D_m is the coefficient of diffusion for the compound, gas, or ion. The mass transfer coefficient is calculated from the metabolic rate per unit area divided by the concentration gradient $C_b - C_o$ between the bulk fluid C_b and the wall (C_o, site of exchange). *Sh* represents the metabolic rate in a dimensionless form and is the ratio of convection-assisted mass transfer to exchange by
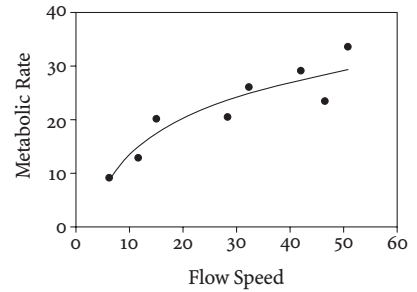

Fig. 2.3. Theoretical relationship between flow speed and the rate of metabolism of mass transfer limited processes. Axis units are arbitrary. The curve fit represents a power function of the form: $MR = aFL^b$

diffusion alone. Sh is related to St as

$$Sh = St\, Sc\, Re \qquad\qquad\qquad (2.12)$$

where:

$$St = m/U_\omega(C_b - C_o) \qquad\qquad\qquad (2.13)$$

where m is the metabolic rate or uptake rate per unit area. As a result, either Sh or St can be used to examine relationships between metabolism and water motion.

These engineering correlations are for mass transfer to hydrodynamically smooth surfaces. However, seaweeds and corals often have projections (e.g. hairs, bullae, calices) on their surfaces.

For rough surfaces, a more appropriate formulation of St is given by Kays and Crawford (1993). Alternatively, in the cases where a detailed estimation is required of the local mass transfer at the surface of complex-shaped growth forms and to be able to include mass transfer in simulation models of growth processes, estimates of the local mass transfer in a simulation of hydrodynamics can potentially be made, by estimating local flow velocities and concentration gradients from a simulation. In Sections 4.3.1, 4.5, and 4.6, methods will be discussed for approximating flow fields and concentration gradients through simulation.

EFFECTS OF THE FLOW ENVIRONMENT ON ORGANISMAL METABOLISM: EXAMPLES. Several previous studies have quantified the effect of increasing water flow on rates of nutrient uptake and rates of organismal and community metabolism (Parker 1981, Carpenter et al. 1991, Patterson et al. 1991). A few studies have also examined how organismal morphology interacts with flow to alter boundary layer dynamics and mass flux (Koehl and Alberte 1988, Hurd et al. 1996, Hurd and Stevens 1997).

Patterson and Sebens (1989) used an engineering approach to examine the effects of water flow on rates of respiration of a temperate species of octocoral (*Alcyonium*) and a species of sea anemone (*Metridium*). For both species they found a positive relationship between water flow and Sh (based on respiration rate), suggesting that mass transfer of gas exchange limits the metabolic rate. They concluded that organism shape, the local flow environment, and the resulting boundary layer dynamics were important determinants of organismal function.

Seaweeds vary in morphology, both within and between species. Koehl and Alberte (1988) investigated the effects of morphological variation in the bull kelp, *Nereocystis luetkeana*, on boundary layer thickness and rates of photosynthesis of low and high flow morphs under different flow environments. *Nereocystis* has strap-like blades that might be expected to develop thick boundary layers under low flow conditions. Their results indicate that variation in blade morphology allows the low flow morph to flap at a lower flow speed, thereby increasing the flow relative to the blade, resulting in higher rates of photosynthesis. The narrow, flat blades of the high flow morph collapse into a bundle more readily, reducing the drag force experienced, but likely also reducing rates of photosythesis due to self-shading and perhaps increased boundary layer thickness between the blades. This study provides a good example of how seaweed morphology is often a trade-off between the costs and benefits of interaction of the thallus with the physical environment.
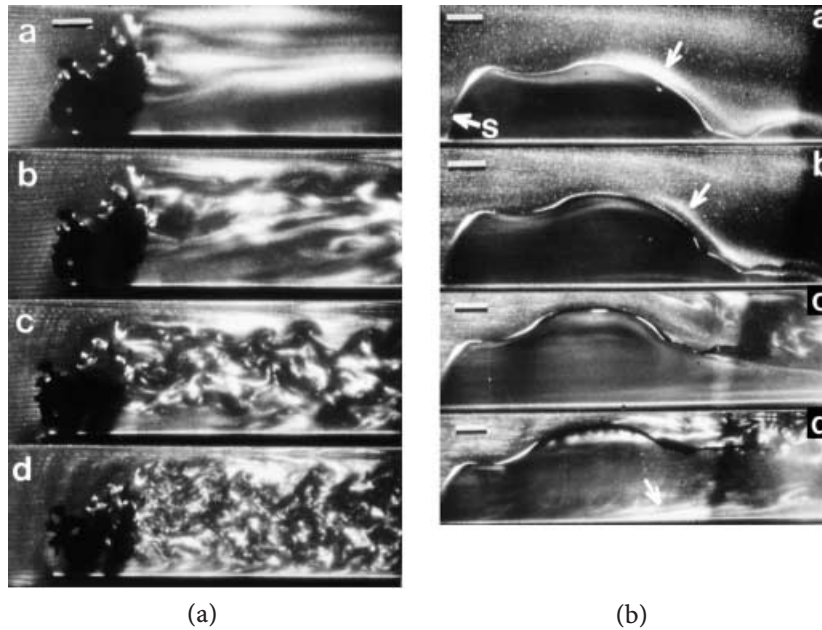
Fig. 2.4. (*a*) Visualized flow around *Fucus gardneri*. (*b*) Visualized flow over *Laminaria setchellii*. In both (*a*) and (*b*) the flow velocity, and consequently turbulence, increases from the top picture to the bottom (pictures after Hurd and Stevens 1997).

(a)   (b)

Patterns of variation in seaweed morphology across flow environments and the resulting effects on metabolic processes have been investigated by Hurd et al. (1996) and Hurd and Stevens (1997). In their initial work, they found that kelp (*Macrocystis integrifolia*) morphology varied between low flow and high flow locations and that nutrient uptake for both forms increased as a function of flow speed. However, estimates of the diffusive boundary layer over the low flow morph blades were no different from those estimated over high flow morph blades, and in this case, changes in blade morphology did not result in higher nutrient uptake at a given flow speed. Hurd and Stevens (1997) used reflective particles and photography to visualize the flow fields around eight taxa of seaweeds that varied in gross morphology, from flat blades (*Laminaria setchellii*) to highly branched thalli (*Gelidium coulteri*), over a range of flow speeds from 0.5 to 5 cm/s. From the photographs (Figs. 2.4a and b) they were able to determine whether the flow over the blades or thalli was laminar or turbulent and concluded that under field flow conditions, it is likely that flow is turbulent over most of the morphologies examined. There were two cases where this conclusion did not apply. Flow over a frond of *Macrocystis* that included multiple blades (the normal condition in the field) was less turbulent than flow over an isolated blade, again suggesting that flow-induced changes in morphology resulting from blades compressing may have important effects on the local flow environment. The second case was for highly-branched thalli where turbulence was reduced and flow always exited the thalli as laminar. For branched thalli, it is the flow environment between branches that determines boundary layer dynamics and these results suggest that boundary layers may be much thicker within the tangle of branches of highly dissected thalli (Carpenter et al. 1991). Given that the demand for nutrients and gases should be related positively to the surface area:volume ratio SA/V of the thallus (Littler and Littler 1980), rates of metabolism of seaweed taxa with high SA/V should be the most flow-dependent. Data collected to date support this prediction (Carpenter et al. 1991, Stewart 1999).

A final example of the effects of flow on organismal metabolism is how uptake of phosphorus by coral reef communities is mediated by hydrodynamic processes (Atkinson and Bilger 1992). Using the *St* number approach outlined above, phosphorus uptake by coral reef benthos (corals, algal turfs, and macroalgae) arranged in a flume over a range of flow speeds indicated that uptake was mass transfer limited and occurred through turbulent boundary layers. Furthermore, Atkinson and Bilger concluded that rates of phosphorus uptake are 6–7 times higher than predicted from theory and this might result, in part, from the fractal nature of coral reef surfaces and their high surface area (of organisms) per planar area.

FLOW, FORM, AND FUNCTION.   The examples given above illustrate the complex relationships between organism morphology, the physical environment, and physiological function (and presumably growth). For seaweeds, some morphologies perform better in particular flow environments with shape and form resulting from a trade-off between the positive and negative effects of water motion. However, the morphology is not constrained entirely by genetics and phenotypic changes in morphology are common.

Size may also have important effects on mass transfer. As the size of an organism increases, the flow environment that it experiences changes. Larger benthic organisms generally extend further from the substratum and away from the benthic boundary layer and experience higher flow that may influence rates of mass transfer. Conversely, larger organisms present more surface area over which local boundary layers can develop, perhaps negating any beneficial effects of growing out of the benthic boundary layer. Combined with the lower SA/V of larger organisms (assuming isometry), the overall ability of larger organisms to take up materials from the surrounding fluid relative to the demand for these materials, may be inversely related to size. Clearly, the interplay between water motion, seaweed morphology and size, and the resulting effects on mass transfer are complex. Attempts to model the growth and form of seaweeds must incorporate, as far as possible, the effects of the flow environment on organismal function, short-term, flow-induced changes in morphology, and the numerous and intimate interactions between morphology and the physical environment.

Particle Capture

Suspension-feeding invertebrates rely, to varying degrees, on the movement of water for the delivery of plankton and other particulate matter to their feeding surfaces. As is the case for the processes of mass flux and momentum transfer, the delivery of food is often strongly affected by the characteristics of water moving past the organism's surface, which in turn can be significantly modified by the organism's shape and position within the benthic boundary layer. Furthermore, particulate capture is also dependent on the size, density, and, in the case of zooplankton, behavior of the food item being captured.

The general theories underlying the mechanisms of particle capture in the marine environment have been thoroughly examined by previous reviews (Rubenstein and Koehl 1977, LaBarbera 1984, Shimeta and Jumars 1991, Wildish and Kristmanson 1997). These mechanisms are often divided into general categories, each reflecting the relative importance of factors such as the relative size of the particle and the filtering apparatus, the density (and thus

momentum) of the particle in the fluid, the difference in charge between the particle and the filter, and the tendency of the particle to sink due to gravity. The size and even species of prey item captured from the water column by a sessile suspension feeder is thus to a large extent determined both by the characteristics of the particle and by the interaction of the filter feeder with the characteristics of the ambient flow environment. Both theoretical and empirical approaches have been undertaken to address the role of organism morphology in driving prey capture by sessile invertebrates. While theoretical approaches can offer considerable insight into the factors most likely to affect particle capture, extrapolation to organisms living in the field can be difficult. In contrast, empirical measurements account for more of this natural variability, but in doing so can reduce our ability to generalize. Both levels of approach are therefore necessary and complementary in order to gain a better understanding of the interactions of coral and sponge architecture with the hydrodynamic environment.

SPONGES.   As active filter feeders, sponges are able to generate currents through the action of flagella, which line the walls of the interior of the sponge. Bacteria and other microscopic food particles are absorbed from the moving water and incorporated into food vacuoles, and then transported into the main body of the cell. As a result of this active filtration, sponges are often able to thrive in areas of low to moderate flow, where more passive feeders are excluded (Reiswig 1974, Leichter and Witman 1997). Nonetheless, the overall morphology and architecture of sponges can also have a significant impact on particle transport. The intake of water, and thus particulate matter, into the sponge occurs through myriad pores called ostia. The fluid then travels through chambers of varying length and complexity to a central chamber, where the water is expelled through a large opening called an osculum. Generally, the total combined surface area of the incurrent pores exceeds that of the exhalant osculum (Bidder 1923, Vogel 1974). The effect of the reduced surface area is thus akin to a jet, and water exiting the sponge is accelerated, reducing the chances that the sponge will refilter the water that it just processed.

Sponges and other sponge-like organisms also benefit from water movement not induced by flagellar action. As water flows around and over the top of a sponge, the fluid is accelerated. This faster-moving water induces a region of lower pressure, which in concert with viscous entrainment within the fluid serves to induce flows out of the top of the sponge, further enhancing the transport of water throughout the organism (Vogel 1974). The movement of water outside the sponge also serves to replenish nutrient- and particle-depleted water, as sponges at high densities can compete for food resources with one another (Buss and Jackson 1981).

CORALS.   While corals display some ciliary activity within the coelenteron, and in some cases have been shown to generate weak currents (Helmuth and Sebens 1993), particle capture is to a large degree dependent on the delivery of zooplankton and particulate matter directly to the coral's tentacles, where the particle is ensnared by a series of harpoon-like nematocysts. The interaction of ambient flow with a coral's morphology thus can have a significant impact on rates of particle capture, as can the presence of neighboring organisms.

Quantifying the interaction of coral morphology with flow is, however, a very complex undertaking, especially given the wide array of flow

(e)

(d)

(c)

(b)

(a)
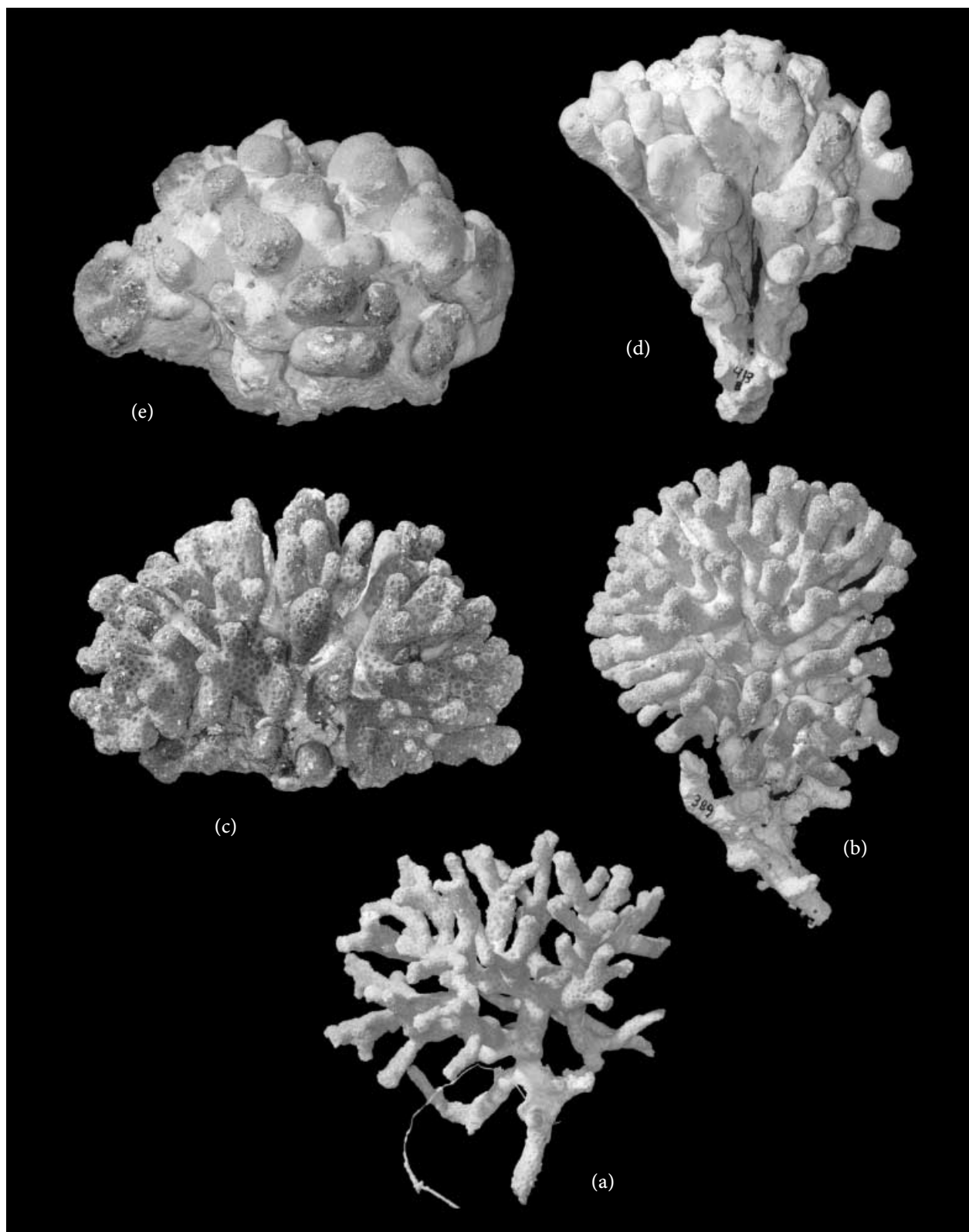
regimes normally found on most coral reefs. Both theoretical and empirical approaches have been undertaken to address this issue. Models of coral feeding under simplified, laminar flow conditions (Abelson et al. 1993) have suggested that the size and type of particle captured is dependent on the height of the organism above the substrate relative to the width of the organism in the direction of flow. Corals which extend above the substrate are expected to feed on finer particles which are resuspended from the bottom, whereas corals which lie close to the bottom were predicted to feed primarily on heavier, bed-load transported particles (Abelson et al. 1993). While this model was supported by measurements conducted using physical models, it has yet to be tested using corals living under more realistic flow conditions.

Empirical measurements of particle capture by corals and other suspension feeding invertebrates have also been employed under both artificial (laboratory flume) and semi-natural (field flume) conditions, and have shown that patterns vary significantly with coral morphology (Heidelberg et al. 1997). Sebens and Johnson (1991) measured rates of feeding by two species of scleractinian corals using brine shrimp cysts as food particles. They found that the branching, cylindrical species of coral, *Madracis decactis* (see Fig. 2.5), showed an increase in particle capture with increasing flow speed. In contrast, a flat species of coral, *Meandrina meandrites*, showed no effect of flow speed on particle capture, due to the tendency of the coral's tentacles to flatten under ever higher flow speeds (Johnson and Sebens 1993). Helmuth and Sebens (1993) examined particle capture by several morphotypes of *Agaricia agaricites*, and found that particle capture in unidirectional flow increased with flow speed up to a velocity of approximately 30 cm/s, but then decreased at flows above this level. Similarly, Sebens et al. (1997) found that feeding by solitary branches of the coral *Madracis mirabilis* (see Fig. 2.5, a cylindrical coral that exists almost exclusively in aggregations of clonemates) experienced maximum rates of food capture at a flow speed of 10–15 cm/s. These studies show that while increasing flow speeds do increase the rates of particle delivery to the coral surface, particle capture efficiency often decreases with increasing flow due to the tendency for a coral's tentacles to flatten under high flows, rendering them unable to capture the particles moving across their surfaces (Patterson 1984, Lasker 1981, Johnson and Sebens 1993, Sebens et al. 1997). Thus, particle capture rates are often highest at intermediate flow speeds, where particle delivery rate is high, but tentacles are still capable of retaining particles.

Some species have apparently been able to at least partially circumvent this limitation through the formation of aggregations in which the spacing between ramets varies as a function of ambient flow (McFadden 1986, Sebens et al. 1997). For example, McFadden (1986) found that under low flow conditions, the presence of neighboring colonies reduced the rate of particle capture by the soft coral *Alcyonium*. However, at higher flow speeds, particle capture rates were enhanced by the presence of neighbors. Sebens et al. (1997) found that branches within aggregations of the cylindrical coral *Madracis mirabilis* were more widely spaced in slower moving water than in areas with higher average water velocities. Feeding trials in a laboratory flume confirmed that particle capture increased with branch spacing in low flows, but decreased with branch spacing in higher flows, suggesting that plasticity in branch spacing represents a means of acclimatizing to the characteristics of the local flow environment. Thus, living in aggregations may

◀ Fig. 2.5a–e. The stony coral *Madracis decactis* collected at different depths, sample (*e*) originates from a depth of 6 m, (*d*) was collected at a depth of 15 m. The stony coral *Madracis mirabilis*, samples (*c*), (*b*), and (*a*), were collected at depths of respectively 6, 8, and 20 m.
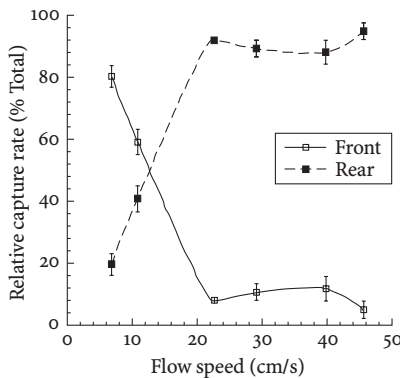
Fig. 2.6. Capture rates of a single branch of a *Madracis mirabilis* colony at the front (upstream) and the rear (downstream) region (after Sebens et al. 1997)

serve as a means of dampening fluctuations in ambient flows (Chamberlain and Graus 1977, Sebens et al. 1997, Helmuth et al. 1997).

Measurements of particle capture by corals have also shown that the location of capture on a colony, and within aggregations, can vary consistently depending on local flow conditions. For example, several studies have shown that particle capture at low flow speeds tends to be highest on upstream regions of colonies. As flow speed increases, areas of maximum capture rate are shifted to the downstream region of the colony or aggregation (Patterson 1984, Helmuth and Sebens 1993, Sebens et al. 1997). In Fig. 2.6 the capture rates of a single branch of a *Madracis mirabilis* colony at the front and rear sites are compared; for high flow speeds the maximum capture rate is shifted to the downstream region of the branch. However, most of these studies were conducted under conditions of unidirectional, low-turbulence flow, and it is unclear whether or not these patterns remain under conditions of highly turbulent flow. Patterson (1984) found highly asymmetrical patterns of particle capture by a soft coral under conditions of laminar flow; however, these differences disappeared under higher levels of turbulence. Hunter (1989) studied feeding by a hydroid under oscillatory flow, and found that patterns in intracolony particle capture disappeared when compared with those observed during feeding in unidirectional flow, but also that capture rates under conditions of alternating flow could not be predicted given measurements in unidirectional flow. While both oscillatory and unidirectional flows occur on coral reefs (Sebens and Johnson 1991, Helmuth and Sebens 1993), the relationship between colony morphology and particle capture under highly complex flow regimes requires much more detailed study before we can explicitly relate patterns in flow over large scales to patterns in food uptake by corals.

2.2 The Case Studies

In this section the different organisms, used as case studies, will be discussed in more detail. Information will be provided regarding the growth processes, which will be later used in the simulation models. This section will focus on the level of organization varying from molecular genetics to the level of the modules and give an overview of the morphological plasticity of each organism.

2.2.1 Case Studies of Environmentally Driven Plasticity: Seaweeds

Seaweeds include a vast variety of evolutionarily distant organisms with the single unifying feature of being macroscopic algae which live in the sea. Their myriad variety of growth forms is produced by a number of very different growth processes which are, in general, associated with different evolutionary lines.

Seaweeds occur in three different divisions, or phyla: reds (Rhodophyta), browns (Phaeophyta), and greens (Chlorophyta). The three groups are not closely related to each other and one, the green algae, are more closely related to land plants than they are to other seaweeds. Red and green seaweeds are evolutionarily ancient, first appearing in the midproterozoic, 1600 million years ago, before the earliest traces of invertebrates. Brown seaweeds are part of a very large and diverse group which includes unicellular algae such

as diatoms which date to 900 million years ago, but the earliest putative brown seaweed appeared only 490 million years ago in the ordovician epoch (Graham and Wilcox 1999).

All three groups include unicellular and multicellular forms, filaments, sheets, balloons and branching structures while each group has, with a few exceptions, a different characteristic mode of producing new growth (Fig. 2.7).
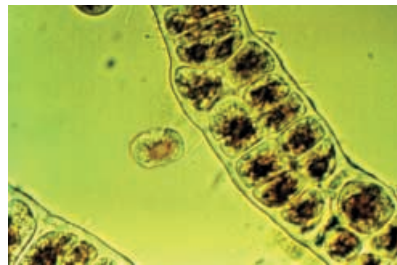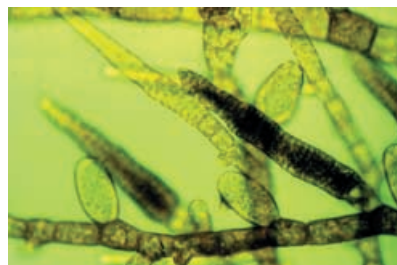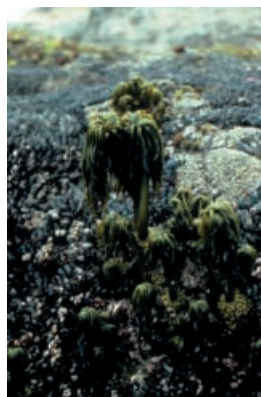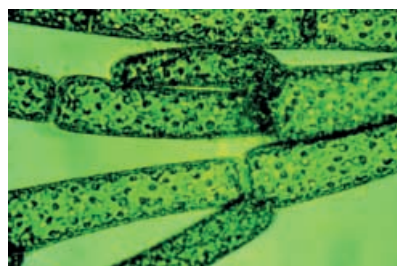

(a)

(b)

(c)

(d)

(e)

(f)

(g)

(h)

(i)

Fig. 2.7. (*a–c*): red seaweeds: (*a*) *Bangia spp.* (*b*) *Mazaella splendens* (*c*) Heteromorphic generations of *Mastocarpus stellatus*. The upright fronds are the haploid phase and the dark colored crust on the rock, in the foreground, is the diploid phase of the same species. (*d–f*): brown seaweeds: (*d*) *Ectocarpus siliculosus* (*e*) *Postelsia palmaeformis* (*f*) *Fucus evanescens* (*g–i*) green seaweeds: (*g*) *Cladophora*, (*h*) *Ulva lactuca* (*i*) *Caulerpa racemosa* (photos (*a*), (*d*), (*g*), and (*i*) courtesy of R. Sheath, C. O'Kelly, J. Graham, and R. Carpenterm, respectively)

Fig. 2.8a–d. Branching red seaweeds. (*a*) *Nitophyllum punctatum* (*b*) *Polysiphonia sp.* (*c*) *Bonnemaisonia asparagoides* (*d*) *Stenogramme interrupta* (after Harvey 1869)

(a)

(b)

(c)

(d)
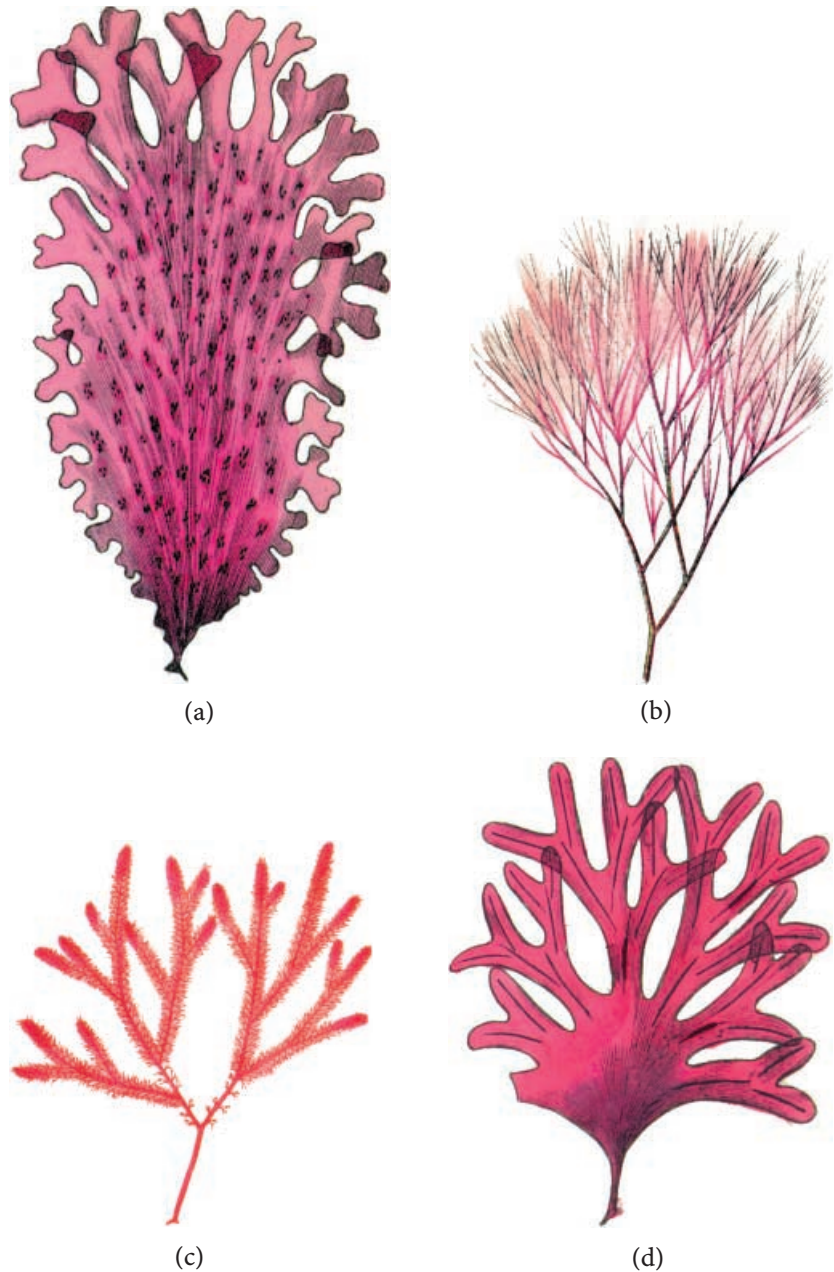
Green seaweeds have diffuse growth, meaning that cell divisions occur all over the thallus as the whole organism grows. Red and some brown seaweeds have apical growth. Like land plants, they grow outward from the edges, or apices. In many of the red seaweeds branching growth forms are found. An example is *Callithamnion roseum* shown in Fig. 1.2, and selected examples of branching red seaweeds are depicted in Fig. 2.8. Most brown seaweeds grow outward from a zone of tissue within the thallus. In the case of kelps, the growth zone is at the base of the blades. Stipe tissue is produced from one edge of the growth zone while frond tissue is produced on the other.