

3.4 The Decomposition Process

So far we have explored a simple linear food chain, supported by photosynthetic production. The losses due to respiration have been built into this sequence in Figure 3.6. We now need to consider the organic losses – the formation and decomposition of organic detritus. This leads to a realization that there is a second base to the food web; a food chain leading from detrital organic material. Although decomposition is seen to be the prerogative of the micro-organisms (the group referred to by ecologists as the **decomposers**), it is a process contributed to by all heterotrophic organisms, from bacteria to whales, although for the reasons discussed in 3.2.1 bacteria and the protists play the dominant role. Decomposition, the breakdown of organic material by heterotrophic metabolism as a consequence of respiration, results in the production of inorganic carbon (as CO_2), nitrogen (as ammonium), and phosphorus (as phosphate), the process is collectively referred to as **remineralization** (or sometimes simply as **mineralization**).

- Decomposition is a process to which all heterotrophic organisms contribute, although the microbiota play a dominant role.

3.4.1 Marine detritus

Although, as we will see later, there is direct release of soluble organic material from marine organisms during feeding and growth, it is convenient to consider the decomposition process as starting from particulate material. The initial stage is the conversion of the insoluble, non-diffusible material (e.g. cellulose, proteins and fats) to low molecular weight material by extracellular hydrolytic enzymes (digestive enzymes). In principle, the first stage must occur outside the cell, in the gut, in vesicles or in the external environment. As the process of hydrolysis is biochemically simple it does not require complex organization. The products

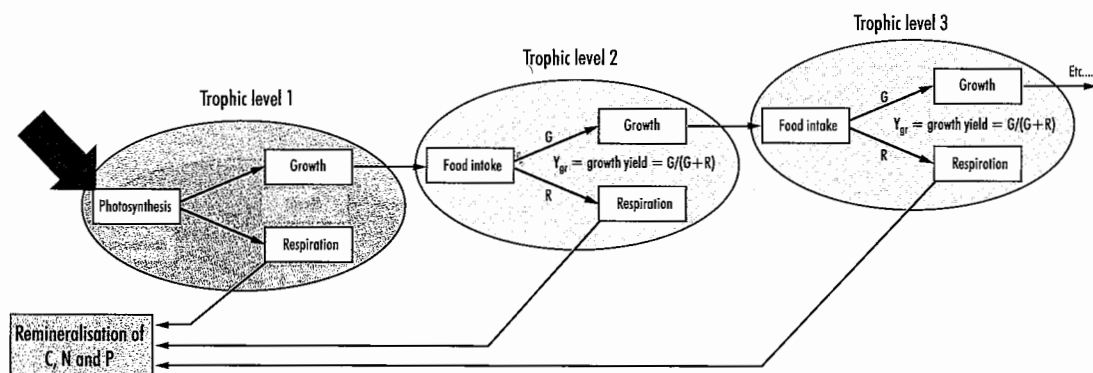


Fig. 3.6 The flow of respired nutrients has been added to Fig. 3.5.

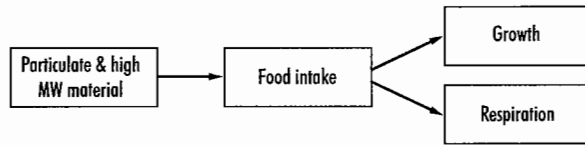


Fig. 3.7 An extended version of Fig. 3.4, showing the two stages in decomposition.

(amino acids, sugars, fatty acids) may now diffuse into the cell, through the gut wall in the case of most metazoans. The subsequent stages of metabolism, and in particular the very final stages (respiration), are complex processes that require a high level of organization that can only occur within the cell. As these events are more or less universal in all heterotrophic organisms, we can now separate the first stage in Figure 3.4 into these two steps (see Fig. 3.7).

No food chain is entirely closed, there is always some wastage of food along the way. This may come as faeces, from incomplete digestion, release of soluble organic material from either the algae or heterotrophic organisms (exudates), or damage of, or incomplete feeding upon, the prey (so called 'munchates') – the odd leg torn off or piece of cell not consumed. This (both soluble and particulate material) is collectively known as **marine detritus** (see Fig. 3.8), the nature and origins of which are dealt with in the following section.

- Hydrolysis is biochemically simple and does not require complex organization.
- Respiration is a complex process that requires a high level of organization that can only occur within the cell.

- No food chain is entirely closed, there is always some wastage of food.

3.4.2 The nature and production of marine detritus

Marine organic detritus is partly composed of the scraps left over from the various meals of the marine heterotrophs. As such it has no particular composition and thus will vary with the type of food organism and the feeding mechanism. Although it may be of poor nutritional value to the organism giving rise to its production, the micro-organisms have the metabolic and nutritional versatility to make a meal out of

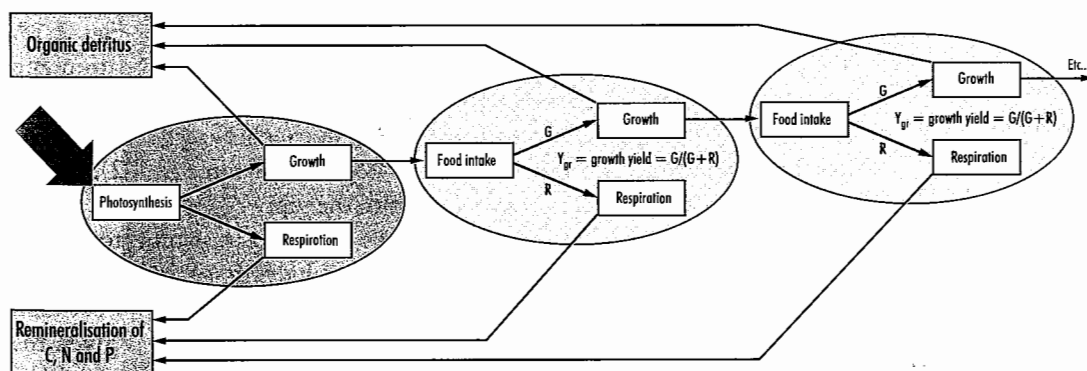


Fig. 3.8 Incorporation of remineralization and detritus formation into Fig. 3.6.

it: indeed 'one person's trash is another's treasure'. In addition to the uneaten remains, there are two additional sources of marine detritus. Various marine organisms secrete mucilage or slough off polysaccharide material during their growth and development; for example, coral are a rich source of mucilaginous material. Appendicularians (a class of chordates also known as larvaceans) surround themselves with a mucilaginous 'house', which contains filtering apparatus with which food is garnered. When the filters become blocked they discard the 'house' and construct a new one, this process takes a few minutes and can be repeated up to a dozen times per day. A quite different source of organic detritus comes from the algae themselves. The mechanism and causes of release of this dissolved organic material are far from clear. It occurs in active as well as moribund cells, so it may be regarded to be a 'normal' part of the metabolism of the algae. It would appear to be high when the cells are under high irradiances and in such situations a metabolic pathway (photo-respiration), closely associated with the primary CO₂ fixation, is known to produce compounds such as glycolic acid, and the amino acids serine and glycine as by-products. However, this is probably only one of a series of processes giving rise to the release of these compounds. The extent of release in actively growing, unstressed cells, is probably in the range of 5 to 15% of photosynthetic production (Chapter 2), but may rise to 50 to 80% if the algae are stressed by high light or low nutrient conditions.

- Marine detritus is in part the scraps from the various meals of the marine heterotrophs.

Table 3.2 Major organic carbon pools sizes in the biosphere.

Pool	Pool size (as mol C)
Oceanic pools	
Dissolved organic material	1×10^{17}
Particulate organic material	3×10^{15}
Marine plankton	1×10^{14}
Fish	5×10^{12}
Terrestrial pools	
Terrestrial plants	5×10^{16}
Soil	2×10^{18}
Global pools	
Fossil fuels	5×10^{17}

Because of its multiplicity of sources and formation mechanisms, marine detritus is a heterogeneous mix of compounds and not readily amenable to detailed chemical analysis. The normal procedure is to divide it into two categories based primarily on size, using fine filters, into so-called dissolved and particulate organic material (DOM and POM). The point of separation is not exact but lies in the region 0.2 to 1 μm , determined by the nature, properties, and loading of the filter used as well as the morphology of the particles themselves. The dissolved organic carbon (DOC) fraction constitutes by far the largest organic pool in the sea, and one of the largest in the planet (see, Fig. 2.19, Table 3.2). DOC has been subject to detailed chemical examination and yet we are only able to characterize 5 to 10%, as simple molecules such as amino acids, simple sugars (hexoses). The remaining 90% of DOC has been identified only into broad categories (Benner 2002). While some of the DOC cycles rapidly within the upper part of the water column, a substantial proportion of the DOC is resistant to decay. ¹⁴C dating of the resistant material gives it a half-life of approximately 6000 years. It was previously thought that this recalcitrant material consisted of complex high molecular weight material and was given the name 'marine humus' but recent work has shown that the material has a molecular weight less than 1000 daltons and thus does not conform

to these earlier notions. A major challenge facing the marine chemist and microbiologists is the chemical nature of this material, it is resistant to decay, and the mechanism of its eventual decay remains unknown. The current view is that its decomposition involves photochemical and microbiological reactions working in consort, but without doubt there is a lot to be learned about this aspect of carbon flow in the oceans.

The particulate organic fraction comprises a melange of small living organisms, bits and pieces left over from the various meals and particulate material created by physicochemical processes from soluble detritus. The material (Fig. 3.9) has the general overall appearance of snowflakes (although it lacks their characteristic symmetry) and is commonly referred to as 'marine snow'. Early bathysphere explorers of the ocean depths reported marine snow to occur at the scale of a terrestrial snow blizzard on occasions. The first step in their creation is the agglutination by shear forces of hydrated mucilaginous fibrils released from the plankton to form transparent exopolymer particles or TEPs (Wotton 2004). The marine snowflakes arise by random collision of TEPs. In the northern Adriatic these flakes can reach massive size (Fig. 3.10). As discussed later in this chapter (3.5.4) they are a habitat for marine micro-organisms and possibly oases in an otherwise nutritional desert. It is thought that these flakes are the main vehicle for the transport of organic matter from the upper ocean to the ocean floor and, as such, a vital step in the carbon cycle of the oceans. The fate of marine snow and the rate at which it is decomposed by its bacterial hitchhikers is critical to the behaviour of the oceans as a potential sink for carbon.

- Marine detritus is a heterogeneous mix of compounds and not readily amenable to detailed chemical analysis.

- DOC constitutes by far the largest organic pool in the sea, and one of the largest in the planet.

- 'Marine snow' has been reported to occur on blizzard scales.

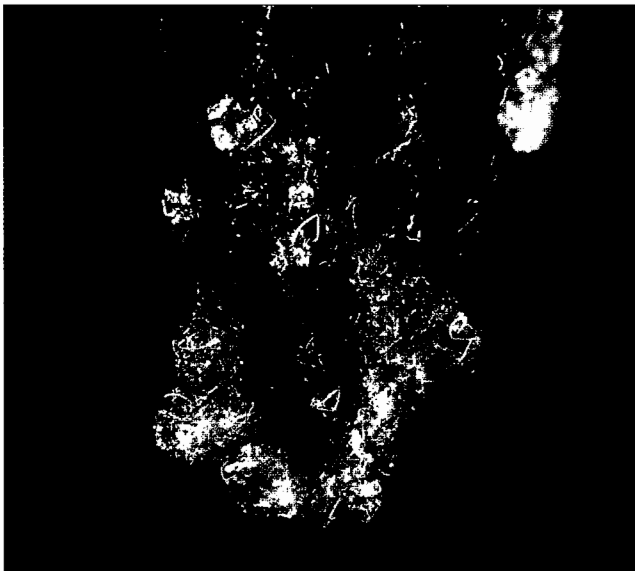


Fig. 3.9 Marine snow particle.
(Photograph: Alice Alldredge.)



Fig. 3.10 A massive marine 'snowflake' in the northern Adriatic. (Photograph: Michael Stachowitsch.)

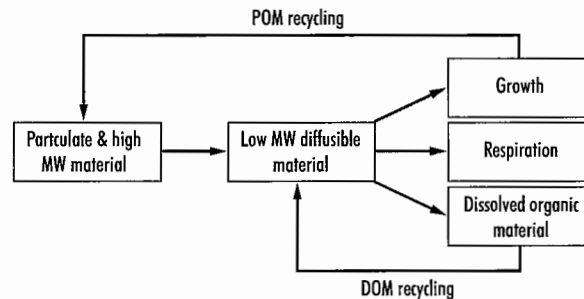


Fig. 3.11 Extension of Fig. 3.7, showing the recycling of particulate and dissolved organic material back into the food chain.

In a simplified form Figure 3.11 builds on Figure 3.7 to show how this 'waste' material will feed back into the food chain. As shown in Figure 3.12 (3.4.3) the flows to the detrital section are multiple. They would appear to equal to 50% of the primary photosynthetic formation of organic material.

3.4.3 The utilization and recycling of marine detritus

Detrital material is potentially a valuable food resource that is utilized by a complex of organisms (the decomposers). To fit this into our developing model of the marine plankton community and explore the consequences of the recycling of organic material, we need to depart from our simple linear food chain, with a single starting point (the photosynthetic autotrophs), to two initially parallel food chains with separate starting points: one based on photosynthesis, and the other starting from detritus, which involves the microbial community. In Figure 3.12 these separate food chains are shown to merge at one point; the reality is more like that depicted in Figure 3.14 – that the whole system is more of a network.

● Detrital material is potentially a valuable food resource.

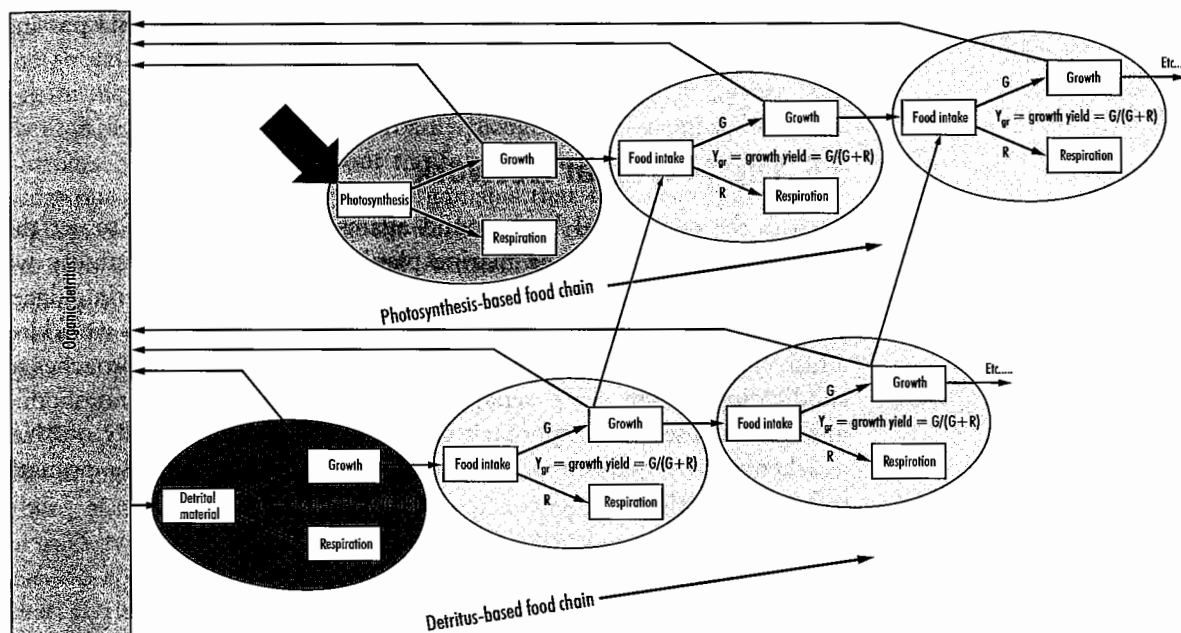


Fig. 3.12 The dual food chain, showing the two starting bases: photosynthesis (the green ellipse) and organic detritus (the red ellipse).

Thus, whereas organic material can only pass through respiration once, a single carbon atom (also a nitrogen or phosphate atom) in organic material can be taken up by marine organisms several times before it is respired. This introduces the concept of **organic recycling** within the plankton community. The consequence of recycling is that the organic material used by the planktonic, or any community, will be greater than the primary introduction of organic material. If we know the fraction recycled (let us call this Y_{det}) it is a simple matter to calculate the total amount of material passing through the food web. If we take a commonly estimated figure of about 50% recycled through each cycle (Nagata 2000), then of the original amount, 50% will be recycled on the first pass, 50% of that (25% of the original) on the second pass, etc, and the total amount passing through will be in this case:

$$1 + 0.5 + 0.25 + 0.125 \dots \text{ or } 0.5^0 + 0.5^1 + 0.5^2 + 0.5^3 + \dots,$$

or expressed more generally:

$$Y_{det}^0 + Y_{det}^1 + Y_{det}^2 + Y_{det}^3 + \dots$$

This is a mathematical series with a surprisingly simple solution:

$$\frac{1}{1 - Y_{det}}$$

Thus if $Y_{\text{det}} = 0.5$, then the total amount of organic material passing through is $1/(1 - 0.5) = 2$.

3.5 The Microbial Network

Such is the conceptual background against which we need to set the organismal biology. In the marine plankton microbial community we have traditionally identified four major categories – bacteria, algae, protozoa, and the larval zooplankton. Comparatively recently we added a fifth category: the marine viruses. There are a number of approaches to subdividing within these separate groups and typically a taxonomic approach is used. The approach used here is based principally on size, as when micro-organisms acquire food, size is in many cases the primary selection criterion.

3.5.1 Trophic components

Viruses

It is only in the late 1980s that we have been aware of the ecological importance of viruses. They are not organisms in the normal sense, but their impact on the marine community as a whole appears to be substantial. They occur in numbers of 10^7 cm^{-3} and they are known to infect organisms from bacteria to seals (Fuhrman 1999). There is evidence that they can play a major role in terminating blooms of coccolithophorids (Chapter 2) and we may expect the same is true for other groups of phytoplankton as well.

- Marine viruses infect organisms from bacteria to seals.

Bacteria

As with viruses the full understanding of the role of bacteria developed late also, in the 1970s and early 1980s (Sherr and Sherr 2000). There is an enormous variety of metabolic types within the bacteria, far greater than any other group of organisms. Here attention will be restricted to two major physiological types: organotrophs and the chemoautotrophic nitrifying bacteria.

- There is an enormous variety of metabolic types within the bacteria.

The former group are the classical heterotrophs, which can use a vast range of organic compounds for their growth. The initial attack on the organic detritus in the natural environment (and unnatural environments such as sewage works) is led by these organisms. It is axiomatic that all material produced naturally, and many novel synthetic organic chemicals, are broken down by this group of organisms. They are termed heterotrophs as they need organic material for their growth; they gain the energy for growth and other activities such as motility from the respiration of the assimilated organic material.

- It is axiomatic that all materials produced naturally are broken down by bacteria.

The other group we need to consider are a highly specialized group, the so called 'nitrifying' bacteria (see also Chapter 2). This group of organisms gain their existence from oxidizing ammonia to nitrite, and then nitrite to nitrate. We can broadly recognize two groups within the nitrifiers, with one carrying out the former reaction and a second carrying out the latter. As they are organisms that utilize inorganic compounds exclusively to provide the carbon and energy for growth, they are accordingly termed **autotrophs**. Autotrophs lack the capability to use organic material for growth and have to produce the organic material themselves by 'fixing' CO₂ as do the algae, and both groups of organisms use the same enzymatic pathways.

Algae

The categorization of algae in this context is in relation to their availability as a source of food. The algae span a zone where the combination of fluid dynamics and size has a considerable bearing on the mechanisms used to collect food. In the case of the smaller algae we enter a realm characterized by a value known as **Reynolds number** (Box 3.1), where the behaviour of particles gives the impression that the water is very

Box 3.1 Life at low Reynolds number – where our intuitions fail

Reynolds number is a coefficient and gives us a scale that allows us to anticipate how a moving organism will experience the fluid physics of its environment. It is calculated from the size of the organism, its rate of movement and a property known as the kinematic viscosity, which is the normal viscosity times the density of the fluid. We occupy high Reynolds numbers, e.g. 10^6 , whereas micro-organisms occupy low numbers, e.g. 10^{-5} . Our everyday experience gives us a poor understanding of the circumstances at low Reynolds number and our intuitions can be very misleading. If we were to experience life at the scale of micro-organisms we would be in for big surprises. Consider the basic component of Reynolds number, the kinematic viscosity. The kinematic viscosity of air is *greater* than water, thus it means that a particle the size of a bacterium falling through the atmosphere would settle faster once it entered the water, not slower as we would experience on our scale. At low Reynolds numbers, the fluid gives the appearance that it is highly viscous, and if we look at organisms under a high powered microscope (when we have entered the world of low Reynolds numbers) we can actually see this phenomenon. Scaled up to the human scale, the environment has a viscosity somewhere between molasses and tarmac. But, in truth the viscosity is the same, but the organisms have virtually no momentum. This lack of momentum means that when micro-organisms cease swimming they stop almost immediately, a bacterium coasts for 10 microseconds, only the length of a hydrogen bond (0.1 nm). On our scale such a deceleration would be lethal, many orders of magnitude worse than driving a Formula One car at full speed into a concrete wall. These properties at small scales have a controlling influence of the mechanisms for motility and feeding of organisms living at these scales. A delightfully entertaining account of life at low Reynolds numbers is given by Purcell (1977).

viscous; although it is important to stress that this is in appearance only, as it is a feature of their **lack of momentum** rather than any change in the viscosity of water. This means that feeding mechanisms that rely upon straining or collecting the particles by sweeping them into funnel-shaped gullets simply do not work for algal flagellates and bacteria; whereas with larger algae it is very effective. There is no sharp boundary but a practical dividing line that lies in the vicinity of 5 μm body size is commonly used. The small phytoflagellates lie below this boundary, the dinoflagellates and many of the diatoms above, while the coccolithophorids span the boundary.

Protozoa

Currently the protozoa are grouped with the algae into a single category: the protista (Sherr and Sherr 2000), although here we deal with them separately. In functional ecology, protozoa are not so much classified by their size as by the nature of their food, although in a broad way this will also reflect their size. Bacterivores essentially define themselves functionally, but they comprise a diverse range of different protistan groups. The common feature is that they are flagellated, collectively known as the **heterotrophic nanoflagellates**, and span a size range of 2–20 μm . In this group, the flagellum serves a dual function by providing motility and as a device for collecting bacteria. It is broad grouping in which the separation between photosynthetic and heterotrophic forms is least clear and a number of species within this collection of phylogenetic groups, the **myxotrophs**, take advantage of both forms of nutrition (see Chapter 2). The other functional groupings are the **microzooplankton protists**, characteristically they fall in the size range 20–200 μm . They include major groupings such as the ciliates and the larger dinoflagellates. These organisms are characteristically herbivores that prey mainly on the smaller phytoplankton. They will also prey upon bacteria, as is so often with these small organisms, sharp functional divisions simply do not exist.

● Modern thinking places the protozoa with the algae into a single category – the protista.

Larval zooplankton

Although taxonomically very distinct from the microzooplankton protists, the larvae of many metazoan plankton are functionally similar to them and the two groups are commonly lumped into a single category, the **microzooplankton** (see also Chapter 6).

3.5.2 How much do we find?

In Figure 3.2, we produced profiles of biomass and activity developed extensively from theory. However theory can only take us so far. Field observations of biomass and calculated surface area are broadly

consistent with the theoretical distribution given in Figure 3.2 (Fig. 3.13 and Table 3.3). The biomass profile shows that there is not a marked difference in biomass between the small and large forms, and the high biomass of phytoplankton is probably in part an artefact as much of the sampling from which these compilations are derived, as have been made during the bloom period. The striking feature is the span of surface areas, dominated by the bacteria (Table 3.3).

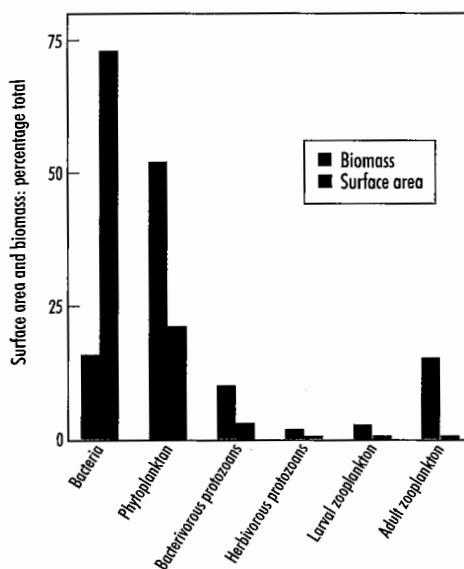


Fig. 3.13 The typical distribution of surface area and biomass of the major planktonic groupings.

Table 3.3 Typical values for abundance and biomass and surface area of the major planktonic types.

	Number (per m ³)	Biomass (mmol C/m ³)	Biomass (%)	Surface area (m ² /m ³)	Surface area (%)
Viruses	c.10 ¹³	–	–	–	–
Bacteria	c.10 ¹² –10 ¹³	1.5	16	1.00	73
Phytoplankton	c.10 ⁸ –10 ⁹	5.0	52	0.30	22
Bacterivorous protozoans	c.10 ¹⁰	1.0	10	0.05	4
Herbivorous protozoans	c.10 ⁶	0.2	2	0.01	1
Larval zooplankton	c.10 ⁵	0.3	3	0.005	0.4
Adult zooplankton	c.10 ³	<u>1.5</u>	16	<u>0.01</u>	1
		<u>9.5</u>		<u>1.37</u>	

3.5.3 Trophic arrangement

We now need to put the pieces together. Figure 3.14 summarizes our current understanding of the major flows within the microbial network and provides a pictorial summary of the statements in 3.5.1. This diagram can be reorganized to give the twin source food chains developed in 3.4.3. As the intensity of the various flows will vary with the location and time of year (considered in 3.7.3), no attempt is made to generalize on them here; this will be done in 3.8. The relative distribution of the biomasses is summarized in Table 3.3, but again these figures vary spatially and temporally and the numbers may only be taken as guides.

3.5.4 Spatial and phase distribution

Popular accounts of the plankton give the impression that a drop of water is teeming with life. Without doubt there are many thousands of individual organisms in a drop of water. Bacteria are present in numbers of a million or more per cubic centimetre, in other words they occur about 100 μm apart. Expressed relative to their body size, they will be on average about 200 body lengths apart, which on a human scale is about 0.5 km apart. Hence, if a drop of seawater is viewed under a high-powered microscope there is less than a one in fifty chance of a bacterium occurring in the field of view.

- If a drop of seawater is viewed under a high-powered microscope there is less than a one in fifty chance of a bacterium being in the field of view.

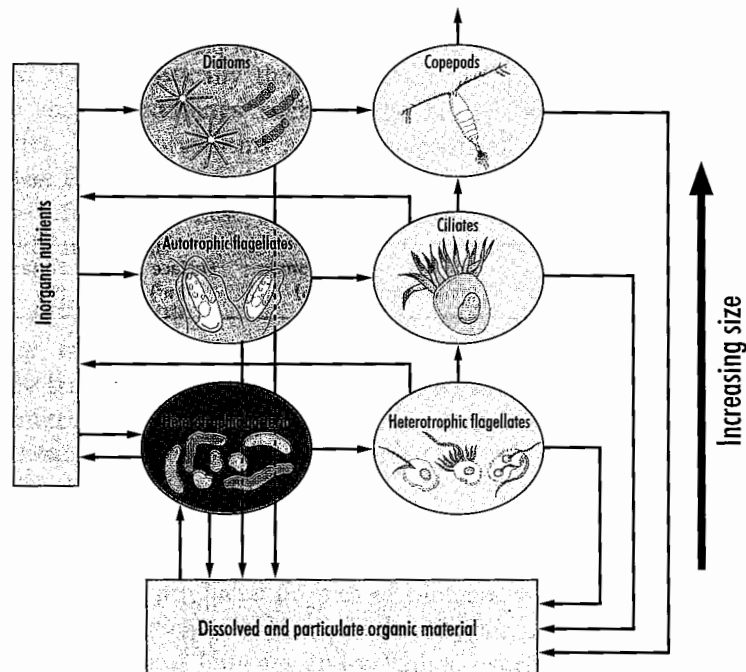


Fig. 3.14 The trophic connections within the microbial network.

Micro-organisms are almost certainly not homogeneously dispersed though the water. The simple dichotomy of organic material into dissolved and particulate used in chemical analysis is a poor representation of the reality in seawater, where there is a continuum of sizes of organic material. Micro-organisms can be found attached to living algae, where they are thought to play a key role by pruning mucus from the surface of the algal cell thereby reducing its stickiness, inhibiting aggregation and the consequent enhancement of settling of the algae out of the illuminated part of the ocean. Bacteria and other micro-organisms colonize all forms of detritus including fragments of body parts and faecal pellets, thereby facilitating their decomposition. Marine snow (3.4.2) would appear to provide a rich habitat for micro-organisms of all types, including a range of bacteria and autotrophic and heterotrophic protists. These types of associations have been discussed by Azam (1998) and are shown in cartoon fashion in Figure 3.15. The benefits and negative aspects of colonizing particles are complex. The particle may provide a source of organic material for microbial growth if the basic matrix is organic, but less so if it is primarily an inorganic matrix, for example a diatom test. The physical chemistry of adsorption leads us to expect that the availability of organic material will be lower in the vicinity of a surface than in the surrounding water (Box 3.2). The potential

● Bacteria and other micro-organisms colonize all forms of detritus including fragments of body parts and faecal pellets, thereby facilitating their decomposition.

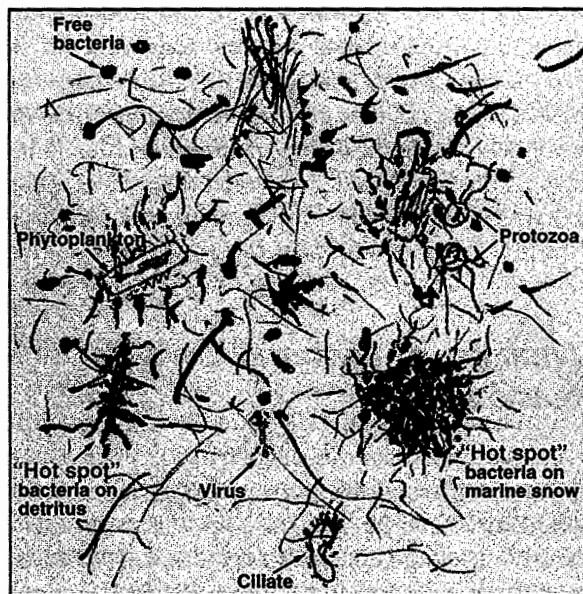


Fig. 3.15 Cartoon of the spatial distribution of micro-organisms within the various phases present in the oceans. The abundance of the organisms is exaggerated for presentational purposes. Reprinted with permission from Azam, F, 'Microbial Control of Oceanic Carbon Flux: the Plot Thickens', *Science*, 280: 694–6. Copyright 1998 AAAS.

Box 3.2 Adsorption and the concept of activity

A common misunderstanding is that as many surfaces adsorb organic material, they are areas that are favourable for the growth of micro-organisms. However, an understanding of the basis of adsorption indicates the opposite. The physical chemist defines a property 'activity', which is the fraction of the molecules present that are reactive. It is only the active molecules that can engage in chemical and biochemical reactions and set up diffusion gradients. Adsorption occurs because the adsorbing surface reduces the activity of the absorbed molecule below that in the bulk water. This sets up a diffusion gradient, which decreases towards the surface (in contrast to the concentration which increases). The consequence of this is that material diffuses towards the surface hence the elevated concentration at the surface (concentrations at surfaces however is a questionable concept). Thus, the availability of the compound for a micro-organism to assimilate is less at the surface, because its activity is lower than in the bulk medium. This notion was resisted for some considerable time but now it has been shown that bacteria grow more slowly on surfaces, which is consistent with these arguments.

disadvantages of being attached to particles are very real: the presence of the protist community will increase the threat due to grazing by these forms; further the large size and the rich microbial community on marine snowflakes make them choice food-items; these attached organisms are now available to metazoans, which would not have the capability to feed on individual microbial cells. Finally, hitching a ride on a rapidly sinking particle on its way to the cold organically sparse ocean depths would not seem a strategy that benefits the attached organisms. We should be wary of seeking for the benefits of attachment and be aware that the forces that give rise to attachment, van der Waal's forces, are extremely powerful on the microbial scale. Thus the micro-organisms simply may not be able to detach themselves – rather like the drunk on the barroom floor, who is there for no better reason than that he lacks the ability to remove himself.

- The benefits and negative aspects of colonizing particles are complex.

3.6 The Dynamics of Bacterial Growth and its Measurement

The 1/diameter rule (see 3.2.1) developed from the surface to volume relationship to account for the relationship between metabolism and size applies equally to microbial growth and the consequence is that bacteria can have very rapid growth rates. The record is a division every 10 min, the norm for cultures is 20 min to an hour, for natural populations it is nearer a day. Binary division gives rise to exponential growth: 1, 2, 4, 8, 16, etc., thus growth is literally explosive. Simply expressed, the change in cell numbers after 'n' divisions is 2^n . The consequence of this is impressive. An organism that divides at a rate of once every 10 min,

would result in $24 \times 60/10 = 144$ divisions after 24 h. From an initial single cell, this would give rise to $2^{144} = 2.2 \times 10^{43}$ cells. They would occupy a space of $1.5 \times 10^{15} \text{ km}^3$, 1000 times the volume of the earth! One has to be honest that the outcome of the calculation is highly dependent upon the growth rates assumed and the time scale considered; nonetheless exponential growth is clearly explosive. Even in the case of more slow-growing bacteria that occur in the sea, we would arrive at the same position after 4 months. This explosive nature of exponential growth is the problem that concerned the Victorian social scientist Malthus. He was concerned with the growth of the human population, but broadly the same rules apply. As with human populations, a variety of factors contrive to prevent the mathematical apocalypse (3.6.2).

● The explosive nature of exponential growth was the problem that concerned the Victorian social scientist Malthus.

3.6.1 The measurement of bacterial growth

In a natural population, where organisms are constantly being grazed or eaten by predators, one cannot, as in a culture, simply measure growth from an increase in numbers; much more subtle methods need to be employed. Two somewhat similar approaches are used to measure bacterial growth.

The first follows the incorporation into DNA of **tritium-labelled thymidine** added to seawater. Subsequent to the incubation, which can be as short as 30 min, the sample is filtered through a fine filter and the DNA extracted, purified and its radioactivity measured. This provides a rate of incorporation of thymidine into DNA. As thymidine represents close to $\frac{1}{4}$ of the bases in DNA, it is a very simple matter to calculate the quantity of DNA produced. Given the assumption over the total DNA content of a single bacterial cell and the mass of the cell, one can calculate the rate of formation of bacterial biomass. Nevertheless, it is important to note that the validity of the technique is intimately linked to the validity of the assumptions. The second approach follows the incorporation of **tritium-labelled leucine** into protein. The basic approach is much the same: the calculation in this case requires knowledge of the ratio between cell biomass and its leucine content (or the percentage leucine in proteins and the percentage protein in the cell). Again the uncertainties in these assumptions limit the accuracy of the techniques. The two techniques measure fundamentally different properties: the $[^3\text{H}]$ -thymidine technique is associated with the rate of cell production, the $[^3\text{H}]$ -leucine technique with the rate of biomass production. Any attempt to compare the two methods requires an accurate knowledge of the biomass of a single bacterial cell, which in a natural population is an extremely difficult property to determine (Ducklow 2000).

Table 3.4 Bacterial and Phytoplankton Production and Growth Rates in the Euphotic Zone of Various Oceanic Areas. (recalculated from Ducklow, 2000).

	Equatorial Zone	Subtropical Gyre	Temperate (N. Atlantic)	Polar (Ross Sea)
Euphotic zone depth (m)	120	140	50	45
<i>Average biomass (as mg C m⁻³)</i>				
Phytoplankton	11	2	20	5
Bacteria	9	4	90	254
<i>Average production rate (mg C m⁻³ d⁻¹)</i>				
Phytoplankton	2	1	6	0
Bacteria	11	3	22	28
<i>Average growth rate (d⁻¹)</i>				
Phytoplankton	0.1	0.1	0.3	0.3
Bacteria	0.7	0.8	0.3	0.1

Table 3.4 contains a summary of data for bacterial biomasses, production and growth rates in the euphotic zone of major zones of the oceans, along with comparable data for the phytoplankton. At low latitudes, bacterial and algal biomasses are comparable, but in cold waters, the bacterial mass may dominate. This may represent a community shift to compensate for reduced rates of bacterial metabolism at low temperatures. Consistent with this, in the warm water of low latitudes, bacteria grow much faster than the phytoplankton. The production rates draw attention to a major contemporary problem in biological oceanography: balancing the books. As a consequence of recycling (3.4.3) organic material can pass through the bacteria more than once, so in principle bacterial production can exceed primary production, this can only occur to a limited extent and the heterotrophic processes in the water column cannot exceed production by large amounts. However, when attempts are made to produce a budget for the oceans, most frequently we end up with a presently unexplained deficit of organic material (see also 3.8). This is currently a matter of active debate and without doubt there are issues of the errors due to temporal and spatial averaging as well as questions over the accuracy of the methods for measuring both photosynthetic and heterotrophic rates of production.

● A major contemporary problem in biological oceanography is balancing the books on autotrophic and heterotrophic processes.

3.6.2 The dynamics of micro-organisms

Given the potential for explosive growth, changes in bacterial numbers through the seasons are surprisingly muted (Fig. 3.16). In the case of

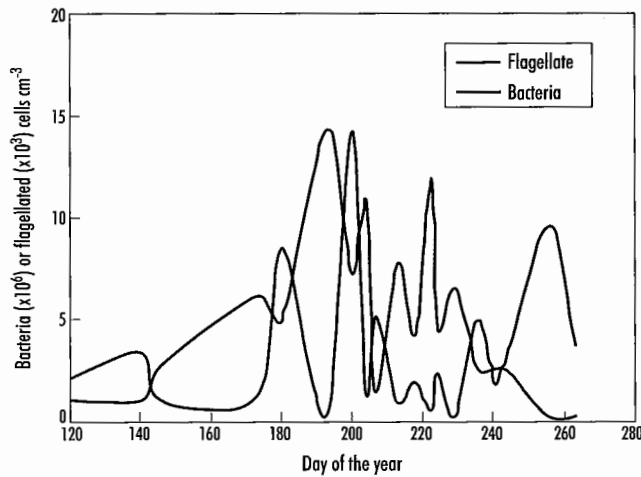


Fig. 3.16 Seasonal changes in the abundance of bacteria and heterotrophic nanoflagellates in a shallow marine fjord. Redrawn from Strom (2000), original material from Anderson and Sorensen (1986).

bacteria, probably three things constrain bacterial growth in the oceanic water column: (1) control by grazing, (2) resource limitation, and (3) mortality.

Grazing

Bacteria are grazed by small protozoa, in particular nanoflagellates. The dynamics between this predator–prey relationship and that of the phytoplankton–mesozooplankton coupling are different and a critical factor in the determination of the dynamics of the various plankton communities. In the latter case, the growth rates are very different; the zooplankton reproductive rate is about tenfold slower than that of phytoplankton. This mismatch allows the phytoplankton to bloom before their predators can increase in numbers or size sufficient to graze down the bloom. In the case of the bacteria–protozoan coupling, their growth rates are more comparable (approximately a day) so the bacteria have no opportunity to bloom, at least for any extended period, as their increase in abundance is quickly followed by an increase in the numbers of the protozoans. The latter graze down the bacteria again, giving rise to Lotka–Volterra limit cycle oscillations (Fig. 3.16). There is a secondary feature of the control by grazing that is related to prey-size selection. The protozoan predators tend to select the larger bacterial cells preferentially, so the size distribution of the bacterial population, when it is grazed, is shifted down from a modal diameter of $0.75\ \mu\text{m}$ to $0.5\ \mu\text{m}$, resulting in a threefold reduction in cell volume from $0.22\ \mu\text{m}^3$ to $0.065\ \mu\text{m}^3$.

Resource limitation

The seas are an organically dilute environment. Characteristically the concentration of individual molecules is in the region of 10^{-7} molar (10 grains of sugar per ton of seawater would give a similar concentration).

● Bacterial numbers through the season are controlled by grazing, resource limitation and mortality.

● Protozoan–bacterial predator–prey dynamics lead to Lotka–Volterra limit cycle oscillations.

- The seas are an organically dilute environment.

This dilute organic environment constrains both the rate and extent of bacterial growth.

Mortality due to viral attack

Marine viruses occur at abundances of about 10^7 cm^{-3} , i.e. about 10 viruses for every bacterial cell. They are known to infect and kill bacteria. We have a great deal to learn of the impact of viruses on marine biota: it is estimated that they may account for 5 to 40% of the mortality of bacteria (predation removes the remaining fraction).

- Virus infection may account for 5–40% of bacterial mortality.

3.7 Respiration and the Release of Nutrients

The ecological context and nutritional circumstances of respiration were dealt with in 3.3, but there was no consideration of rates. The measurement of respiration has proven a major challenge for the biological oceanographer, and there is no easy solution using radioisotopes as with photosynthesis. We are very much dependent upon very careful chemical measurements of *in vitro* oxygen consumption in the dark. The changes are commonly in the order of 0.25% per day, so to measure them with any precision is a daunting analytical task and one has to work at the limits of the analytical methods and often under difficult circumstances at sea. An alternative approach (Packard, 1985) is to extract the respiratory enzymes from bacteria caught on fine filters and assay them. This has a far greater sensitivity but as so often with the non-chemical methods, the price paid for the gain in sensitivity is uncertainty over interpretation. The uncertainty however is no worse than the methods for measuring bacterial growth.

3.7.1 The biochemical basis of respiration

Respiration is the last step in the decomposition process (3.4). At its most fundamental level this involves the transfer of a proton (a hydrogen ion, H^+) and an accompanying electron (e^-) from a proton donor to a proton acceptor. The proton gradient created gives rise to the formation of adenosine triphosphate (ATP), which is a primary energy currency in biology (Fig. 3.17). In most present-day circumstances, organic material is the principal proton donor and oxygen is the principal proton acceptor, water and carbon dioxide are the end products (Fig. 3.17).

- Respiration fundamentally involves the transfer of a proton and an accompanying electron from a proton donor (e.g. organic material) to a proton acceptor (e.g. oxygen).

Organic material and oxygen are not the only participants in this reaction. When oxygen is depleted a number of other proton acceptors may replace oxygen, the list of which is quite long with 14 compounds identified to date. Some of the proton acceptors are well-known, such as nitrate and sulphate, but others are more obscure and in many

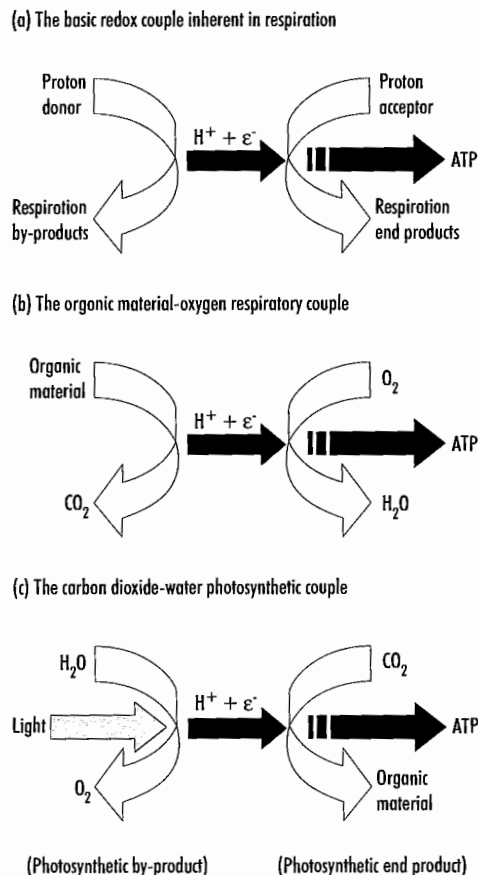


Fig. 3.17 A simple schematic of the flow of protons (H^+) and electrons (e^-) during respiration and photosynthesis. (A) the fundamental flow from a proton donor and a proton acceptor during respiration, (B) the specific example of the respiration of organic material by oxygen, (C) the flow during oxygenic photosynthesis.

respects surprising; for example, uranium (see Box 3.3), perchlorate, and arsenic can also be used by micro-organisms (see King 2005). There is a broad generalization that if a reaction is thermodynamically favourable some micro-organism will exploit it; it is a generalization more commonly respected than broken. As an environment depletes its oxygen then these alternative reactions become important. The proton acceptor and its reduced form (e.g. oxygen and water, nitrate and nitrite, sulphate and sulphide) are known as **redox couples**. There is a particular voltage (the **redox potential**) at which the two halves of the couple are in balance: +0.82 V in the case of the important O_2/H_2O couple, +0.43 V in the case of the nitrate/nitrite couple, -0.22 V in the case of the sulphate/sulphide couple. This determines the sequence in which a particular proton donor comes into play after the oxygen initially present is used

Box 3.3 Bacterial-run nuclear reactor

The utilization of uranium salts by bacteria as electron acceptors gave rise to a remarkable phenomenon; a bacterial run uranium reactor! This sounds the stuff of science fiction but here is an instance where fact is every bit as strange as fiction. About 1800 million years ago in the Precambrian, in the Oklo region of what is now the Gabon in West Africa, the fissile form of uranium U^{235} was concentrated to the extent that the deposits went critical. The likely explanation is that the metabolism of uranium by bacteria concentrated the element to the extent that the nuclear reaction went ahead, although at least one web site attributes this unhesitatingly to an early advanced civilization. Whatever the truth may be, Enrico Fermi and his Chicago team were forestalled by 1.8 billion years in producing a uranium reactor. One would prefer to believe that it was bacteria that beat them to it.

Table 3.5 The basic reactions of the some proton donors and acceptor reactions involved in respiration. $[CH_2O]$ as symbolism for organic material, for simplicity of presentation all compounds are shown in their non-ionized form.

Proton donor	Proton acceptor	Respiration end product(s)	Respiration by-product	Specific bacteria group responsible
Aerobic metabolism				
$[CH_2O]$	$+ O_2$	$\rightarrow CO_2 + H_2O$		No specific group
Anoxic metabolism – alternative proton acceptors to oxygen				
$[CH_2O]$	$+ 2HNO_3$	$\rightarrow CO_2 + H_2O$	$+ 2HNO_2$	Denitrifying bacteria
$[CH_2O]$	$+ HNO_2$	$\rightarrow CO_2$	$+ NH_3$	Denitrifying bacteria
$[CH_2O]$	$+ \frac{1}{2}H_2SO_4$	$\rightarrow CO_2 + H_2O$	$+ \frac{1}{2}H_2S$	Sulphate reducing bacteria
Chemoautotrophic metabolism – additional proton donors to organic material				
HNO_2	$+ \frac{1}{2}O_2$	\rightarrow	HNO_3	Nitrite oxidizing nitrifying bacteria
NH_3	$+ O_2$	$\rightarrow H_2O$	$+ HNO_2$	Ammonia oxidizing nitrifying bacteria
H_2S	$+ 2O_2$	\rightarrow	H_2SO_4	Sulphur bacteria

up and as the environment becomes more reduced, in other words when the redox potential of the environment becomes more negative. Thus, in order to attain maximum benefit, the couples present in the environment with the most positive redox potential are used first: thus we see a sequence in which oxygen is first used up, then nitrate, then nitrite, then later sulphide. The sequence, with the products and reactants is shown in the upper two parts of Table 3.5. The by-products of two of these reactions are toxic, ammonia and sulphide, and thus one of the fundamental aims in water management is to avoid the onset of anoxia, which promotes the production of these products. The proton and electron flow in oxygenic photosynthesis is depicted in Figure 3.17c, and it may be seen that in essence it is the pattern in Figure 3.17b, simply rotated round a diagonal axis.

- There are alternative proton acceptors to oxygen.

As there are alternative proton acceptors to oxygen, so there are alternative proton donors to organic material (see Chapter 2 and Table 3.5). The by-products of the reaction of the alternative proton acceptors are: nitrite in the case of nitrate, ammonia in the case of nitrite, sulphide in the case of sulphate, the list also includes the reduced forms of iron and manganese, methane, and also elemental sulphur; all are potential sources of energy in the presence of oxygen (bottom section of Table 3.5). There is an interesting common property of the micro-organisms carrying out these reactions: they are all **autotrophs**, in that they are unable to use external organic material for their energy and carbon for growth. As they gain their energy from the oxidation of inorganic compounds, they are commonly known as **chemoautotrophs** (although it is better to describe them as **lithoautotrophs**, as the heterotrophs use organic chemicals for their growth; the prefix 'litho' makes clear that inorganic substrates are utilized to provide the energy). This group of organisms is the basis of the food chain in the **deep-sea vents**. These chemoautotrophic bacteria were almost certainly among the earliest free-living forms that developed on our planet and their metabolism we believe reflects the then prevailing environment. Their ancient origins and phylogenetic similarities have resulted in them being classified in a group of their own, the **Archaea**, distinct from the second major group the **Bacteria**; the third group is the **Eukaryotes**, which contains all remaining living organisms: fungi, protozoa, plants, and animals. Among the chemoautotrophs is a group of organisms known as the **nitrifying bacteria** – the reactions they carry out are shown in the lower part of Table 3.5. It should be noted in passing that although the nitrifiers are autotrophs they are placed in the **Bacteria**, rather than the **Archaea**, thus an exception to the above generalization. They have been referred to already and the major role they play in the cycling of nitrogen in the terrestrial and marine environment. Indeed every molecule of nitrate used during photosynthesis on the planet will eventually pass through these organisms.

● There are alternative proton donors to organic material.

3.7.2 The ecology of respiration and photosynthesis

When we consider the ecology of respiration (the utilization and decomposition of organic material) it is logical to do this in conjunction with the companion process of photosynthesis, which is responsible for its production. The two processes represent the two halves of the massive cycle of nature, wholly dependent upon one another (Chapter 2). Photosynthesis provides the organic material for respiration, while for its part respiration provides the inorganic nutrients for photosynthesis. To a large extent they represent the yang and yin in the cycle of life, the **Tao**, the basis of much of Chinese philosophy. Interestingly, essential to

● Photosynthesis provides the organic material for respiration, while for its part respiration provides the inorganic nutrients for photosynthesis.

Box 3.4 Definition of Productivity Terms

There is a set of definitions used in ecology that derive basically from three physiological processes, namely:

- (1) Photosynthesis = P
- (2) Algal respiration = R_a
- (3) Whole community respiration = R_c

The primary photosynthetic event is termed **Gross Production** = P

The difference between production and respiration in the algal community is termed **Net Primary Production** (also **Net Photosynthesis**) = $P - R_a$

The difference between production and respiration within the whole community is termed **Net Community Production** (also **Net Ecosystem Production**) = $P - R_c$

Net Primary Production tells us how much energy and organic material is available to the heterotrophic community, whereas **Net Community Production** tells us about the balance within the community as a whole, i.e. whether the community is growing or contracting. It is important not to confuse these terms and the use of net production, which is commonly found in the literature and could refer to either is to be avoided.

this understanding is that both the yin and yang have the seeds of the other in itself (these are the dots in the yin–yang symbol), and we see the same in the biogeochemical cycle: photosynthesis produces organic material – the seed for respiration and respiration the inorganic nutrients – the seed for photosynthesis. For a number of reasons the two processes of photosynthesis (P) and respiration (R) are out of phase, so there will be places and times when and where $P > R$ and $R > P$. The difference between these two processes ($P - R$) is termed **net community production** (NCP) (see Box 3.4). Unlike photosynthesis and respiration, net community production is not a process in its own right: there is not a dedicated set of enzymes or a single metabolic pathway that gives rise to NCP; rather it is an arithmetic difference. Nevertheless it is arguably the most valuable planktonic rate measurement we can make, and is the best descriptor of the waxing and waning of the population. Net *community* production should be distinguished from the similar term **net primary production** (NPP – also referred to as net photosynthesis: see 2.8), which is photosynthesis minus autotrophic respiration. Arithmetically $NPP \geq NCP$.

Whereas the single structure for respiration shown in Figure 3.17 – with proton acceptors and donors and the transfer of protons and electrons between them – gives a largely satisfactory description of that occurring in most heterotrophic organisms, photosynthetic forms have a number of additional mechanisms of respiration; in all there are at least five distinct forms of respiration in algae (Raven and Beardall 2005). Algal respiration generally does not give rise to the release of inorganic nitrogen or phosphate from the cell (certainly not in large quantities)

- There are at least five distinct forms of respiration in algae.

presumably they are recycled and used for photosynthesis. Two forms of algal respiration occur (the Mehler reaction and the photorespiration pathway) only or mainly in the light. The Mehler reaction appears to serve to remove excess reductants and oxygen produced at high photosynthetic rates; the photorespiration pathway would appear to serve a similar function and it has been noted earlier (3.4.2) that by-products of this reaction, glycine, serine, and glyoxylic acid, may add to the dissolved organic pool.

3.8 The Seasonal Cycle of Production and Consumption

We now have all the pieces in place to look at the dynamics of the microbial network. In this and the following section we explore the changes that occur with time and in space. The seasonal cycle of temperate waters gives the best example to consider as it encompasses most of the characteristic situations seen elsewhere in the surface oceans.

The biology of the cycle of seasons, embedded in the overall biogeochemical cycle, introduced in Chapter 2 is shown again in Figure 3.18. The cycle involves a **throughput** of energy, entering as visible radiation and departing as heat in the form of long-wave radiation, and a

● The biogeochemical cycle involves a throughput of energy and a cycle of nutrients.

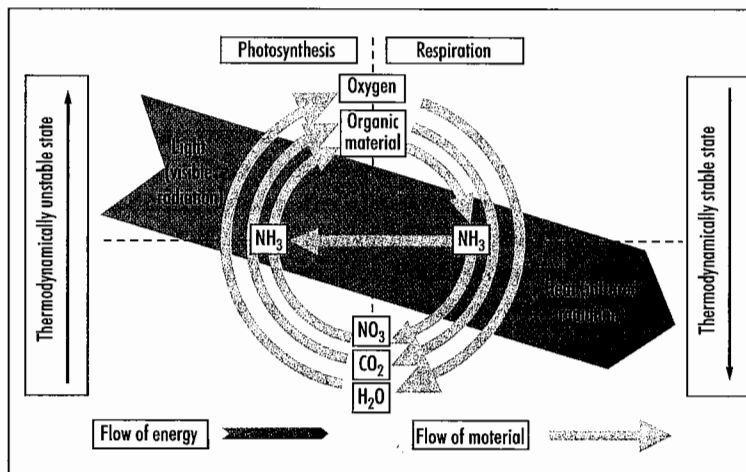


Fig. 3.18 A simple schematic of the principal reactants of the photosynthesis–respiration cycle. The broad, multicoloured arrow depicts the flow of energy through the system, entering as high grade, visible radiation, leaving as low grade energy – heat, i.e. long-wave infrared radiation. The cycle of nitrogen shows the intermediate production of ammonia and the short-circuiting of the nitrogen part of the cycle. The left-hand sector of the diagram represents the photosynthetic process, the right respiration. The food web interactions are not shown. (To simplify the diagram nitrate (NO_3) and ammonia are not shown in their charged form.)