

Chapter 1

Habitat Characteristics and Typical Functional Groups

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1.1 Particularities of the Aquatic Medium

In the aquatic environment, evolution has produced a number of life forms which are rare or missing in terrestrial ecosystems. These include sessile organisms, i.e. microbes, plants and animals living attached to hard substrata without trophically depending on these substrata. These life forms constitute the bulk of the hard bottom communities treated in this book. Consequently, hard bottom communities are typically aquatic, and reach their highest diversity and largest biomasses in the marine realm. Important examples are coral reefs and kelp forests.

The reason why many of the functional groups which compose marine hard bottom communities are missing on land lies in the fundamental differences between the media, air and salt water, with regard to a number of physicochemical properties with biological relevance. In the following, I will briefly review some of these and their ecological consequences (Fig. 1.1).

Water is denser and more viscous than air, and the ratios of these parameters (approx. 80:1 and 100:1 respectively) change with temperature, salinity and pressure. Additionally, the dipole nature of water molecules makes this fluid the ‘universal solvent’ for an extremely wide range of elements and molecules. As a further consequence of the dipole nature, water molecules interlinking by hydrogen bonds form clusters. The existence of such clusters is the basis for the high viscosity of water. Cluster forming also is the reason for the remarkable heat capacity of water as compared to other liquids: much solar energy is used to break up hydrogen bonds which link the molecules in a cluster, rather than raising water temperature. This stored energy is released during cooling when the clusters form. The released heat slows down the cooling. A further difference between the terrestrial and the aquatic environment concerns the availability of light for photosynthesis or optical orientation. Water molecules, and particulate or dissolved matter in the water, absorb light much more efficiently than does air, or the low concentration of molecules or particles in air. Absorption is strongest in the ultraviolet, yellow, red and infrared wavelengths. As a consequence, light changes with water depth both in quantity and quality. The role of solar radiation as a source of energy and information is virtually

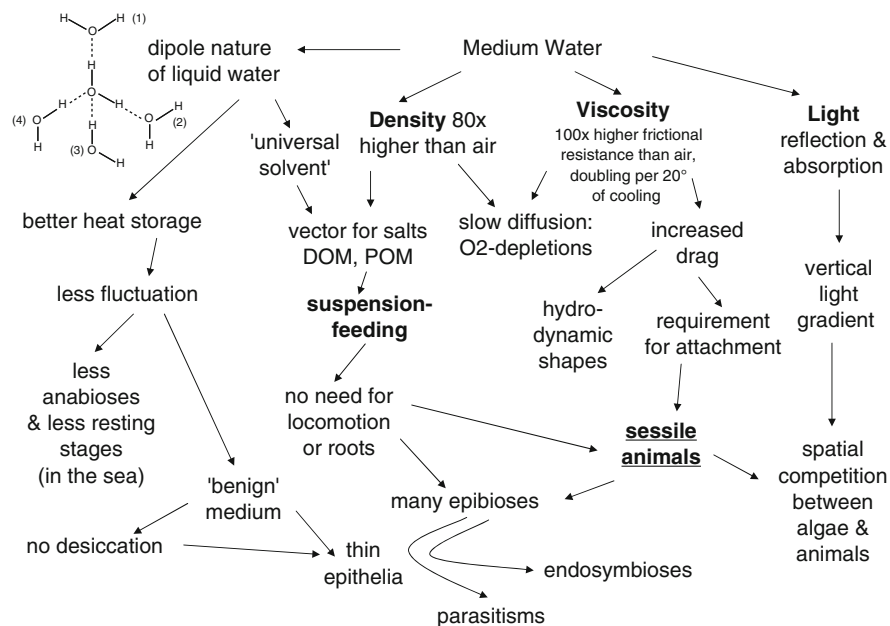


Fig. 1.1 Causal pathways illustrating how the high density, viscosity and solvent power of water enable the existence of the functional group of sessile suspension feeders, one of the most important components of hard bottom communities

nil below the first couple of hundred meters. On the other hand, the aquatic medium is better suited than air as a vector for acoustic, electric and chemical information.

These physicochemical properties, singly or in their interaction, have consequences which strongly affect marine life, enabling the evolution of life forms which have never made their way onto land. The high density of water reduces the relative weight of aquatic organisms. The proportions of heavy mineral skeletons, almost neutral organic tissue and buoyant gaseous or lipid inclusions determine the net weight of submerged organisms. This will always be lower than for a similarly built organism in air. One consequence of this is that floating in water consumes less energy, and aqueous nekton and plankton are incomparably richer in biomass and diversity than their aerial counterparts. The other side of the low-weight coin is a dramatic reduction in friction between bottom-dwelling organisms and the substratum. Reduced friction in conjunction with the elevated viscosity of the medium poses a challenge to 'staying put' in a water current. To avoid being entrained, aquatic organisms must swim or attach. Permanent attachment on land usually is possible only when the substratum also serves as a source for food, e.g. soil for plants, and hosts for parasites. Since water acts as a vector for a rich load of suspended organic material (seston, plankton, nekton), attached heterotrophic organisms may acquire all energy they need by filter feeding or by capturing deposited particles.

Animals usually require more food than is available within the immediate reach of their teeth or tentacles. They must exploit larger areas or volumes. The relative

movement between consumer and 'food space' is assured by locomotion of terrestrial and motile aquatic animals, and by currents around sessile animals in the sea. In addition, the by-flowing 'universal solvent' provides gases (O_2 , CO_2), nutrients used by algae, and organic compounds, and it eliminates excreted waste products. Many of these solutes may be taken up as additional energy sources (lipids, sugars, peptides), may enable intraspecific communication (various infochemicals), or may drive other interactions (interspecific cues, defence metabolites). Gametes and propagules may also be disseminated by the flowing medium. While the attached mode of living is energetically beneficial, one shortcoming is the inability to escape local biotic or abiotic stress. Consumption and overgrowth may be limited by the evolution of structural or chemical defences. Adverse abiotic conditions are more difficult to avoid. If the abiotic conditions in the sea were as variable as they are on land, then permanently attached animals would have to be extremely tolerant, capable of homeostasis, or able to pass stressful phases in a state of reduced activity (e.g. anabiosis). However, the underwater 'climate' in a given subtidal location varies much less in time than is the case for the terrestrial climate. Due to the high heat capacity, temperature is virtually constant below 1,000m, and at shallow depths of polar and tropical regions. Even in shallow (<20m) temperate seas, water temperatures typically vary by less than $1^\circ C$ on a diurnal scale and by less than $20^\circ C$ seasonally. Viscosity, inertia and internal friction buffer the temporal variability of currents, except at depths affected by surface waves and tidal currents. The chemical composition of salt water is extremely stable, with the exception of the compounds metabolized by organisms (e.g. nitrate, phosphate, silicate). One further notable exception to the general stability of abiotic variables in the oceans is oxygen. Because diffusion in water is much slower than in air, oxygen concentrations may range from anoxia to supersaturation, driven by local heterotrophic and autotrophic processes. This imbalance is enhanced when the relative movement between the water and organisms is reduced. Thus, anoxia is common in stagnant bottom waters, and hyperoxia may occur in plankton blooms.

Overall, aquatic habitats may be considered physicochemically more benign than terrestrial ones, because environmental variables vary less in the former. As a consequence, a menacing departure from the physiological optimum is less likely, and costly protective adaptations are less urgently required.

Across habitats, and particularly on a large spatial scale, however, the underwater climate exhibits notable gradients. Vertically, light decreases to biologically unusable levels within the upper tens or hundreds of meters, depending on the load of dissolved organic material and suspended particles; temperature outside the polar regions decreases to an almost constant $2-4^\circ C$ below 1,000m; pressure increases by 1bar per 10m depth, leading to a slight increase of density and a stronger increase of gas solubility with depth. In addition, temporal variability of all parameters generally decreases with depth. Horizontally, salinity increases towards regions of intense evaporation and little precipitation (e.g. the Red Sea), and decreases towards zones of high precipitation and low evaporation (e.g. the Baltic Sea). Nutrients tend to decrease from the sediment upwards, and from upwelling cells or estuaries outwards.

Despite strong large-scale gradients, at a given subtidal location conditions are usually relatively stable and predictable. A sessile organism experiences abrupt and strong changes only when water pockets of a different physicochemical nature drift by—a situation usually restricted to certain shallow coastal zones. For most sessile organisms, the challenge is to settle in a suitable (micro-) habitat.

In conclusion, the high density and viscosity of seawater, together with its solvent and heat capacity, have enabled the evolution of a typically aquatic functional group, the sessile suspension feeder, which is characteristic for and often dominant in marine hard bottom communities. In nutrient-rich and euphotic habitats, however, suspension feeding animals have to compete with macroalgae for substratum, a potentially limiting resource.

1.2 Life Forms in Hard Bottom Communities

Hard bottom communities around the world, also termed fouling communities (mostly used for assemblages on manmade substrata) and epibioses (on living substrata), harbour tens of thousands of species. In the following, I will concentrate on the sessile species, since many of the motile forms are not restricted to this substratum type. All major macroalgal groups are present in hard bottom communities, as long as sufficient light is available. Sessile forms of most animal classes and phyla share hard substratum with algae at light-exposed sites, and exclusively occupy these when light is low or absent: all sponges, most cnidarians, a few bivalves and sessile gastropods, most bryozoans and phoronids, a few boring urchins, many tube-building annelids, and all ascidians. Many sessile representatives of these phyla do not strictly differentiate between rocky, artificial or living substratum (Wahl and Mark 1999). Large groups with rare or no sessile representatives in hard bottom communities are the platyhelminths, nematodes, echinoderms and vertebrates. They do, however, contribute to the motile components of these communities.

In view of the enormous number of species and the apparent lack of phylogenetic predilection for hard substrata, we need an alternative method of classification of community components. One which is ecologically more meaningful than phylogenetics and which has seen a revival during the past 15 years is the concept of functional groups (e.g. Steneck and Dethier 1994; Bengtsson 1998; Petchey and Gaston 2002; Bremner et al. 2003; Micheli and Halpern 2005; Wright et al. 2006; Halpern and Floeter 2008). Functional groups are suites of species which play a similar ecological role (Petchey and Gaston 2002; Blondel 2003), i.e. have similar requirements with regard to one or more resources (e.g. light, food particles, prey, substratum) and/or provide similar services (e.g. oxygen production, denitrification, shelter). More traits may be added to characterize a functional group: e.g. degree of motility, adult body size, reproductive mode, larval feeding mode and dispersal, longevity and coloniality. The more dimensions are used to define a functional group, the more similar (in an ecological sense) are its members and the more intensively they may compete if one or more of the shared resources is or are limited.

By evolutionary convergence, phylogenetically very different species may share a functional group. Sponges and encrusting colonial ascidians, for instance, are all non-motile, require hard substratum for larval attachment, metamorphosis and colony growth, feed on similar size ranges of plankton, settle in similar habitats, may exploit still waters because they create their own filtering current, may grow at comparable rates, reach similar body sizes and live to similar ages. Such a degree of functional similarity should lead to pronounced competition where these forms co-occur. In contrast, different ontogenetic stages of the same species, like the meroplanktonic larva of barnacles and the sessile adult, belong to distinct functional groups and do not compete in the least.

The concept of functional groups is useful in two regards at least. When asking questions such as ‘which are typical components of hard bottom communities?’ or ‘what determines the stability of hard bottom communities?’, species identities are not informative at all. Species found on hard substrata vary from site to site for evolutionary and ecological reasons and do not provide a general pattern. In contrast, their functionality, i.e. their membership to a given functional group, or the degree to which species overlap with regard to a given functional trait, is highly relevant (Duffy et al. 2007). Functional diversity of a community, i.e. the number of different functional groups, is related to resource use and productivity (Naeem and Li 1997; Cardinale et al. 2002). Functional redundancy (Loreau 2004), i.e. the number of species in a community which play similar ecological roles, seems to be relevant for ecological and structural stability (Fonseca and Ganade 2001; Britton-Simmons 2006; Stachowicz et al. 2007).

Functional groups generally are defined as the suite of those species sharing a number of biological traits (but see Wright et al. 2006 for a critical review of classification schemes). Which and how many traits should be considered has been a matter of debate for some time (e.g. Petchey and Gaston 2006). The main issues of conflict have been (1) which life history traits are ecologically relevant, (2) how many traits are required to characterize the functionality of a species and (3) whether traits should be used in a categorical (either ‘suspension feeder’ or ‘deposit feeder’) or a continuous way (‘mostly suspension feeder, occasionally switching to deposit feeding’) (e.g. Bremner et al. 2003). Because certain traits are interrelated to some extent (e.g. longevity, size, trophic level), body size has been suggested to be the one most important trait, and suitable as a proxy or sum parameter for most ecologically relevant characteristics of a species (e.g. Woodward et al. 2005). A less extreme approach was taken in two studies on redundancy in functional diversity using the two traits motility and diet (Micheli and Halpern 2005), and on latitudinal diversity patterns emphasizing the traits diet and dispersal (the latter including larval dispersal and adult motility; Hillebrand 2004). Possibly the most sophisticated approach to functional group definition was suggested by Bremner et al. (2003), who used nine biological traits subdivided further into a total of 34 categories which again contained three levels each of applicability to a given species. However, the resolution of this system is so fine that it characterizes individual species ecologically, rather than grouping functionally similar species into guilds. Functional diversity concepts are treated in more detail by Crowe and Russell in Chapter 5 (5.2).

Marine Hard Bottom Communities

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