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Benthic suspension feeders: their paramount role in littoral marine food webs

Josep-Maria Gili and Rafel Coma

In recent years, particular attention has been paid to coupling and energy transfer between benthos and plankton. Because of their abundance, certain benthic suspension feeders have been shown to have a major impact in marine ecosystems. They capture large quantities of particles and might directly regulate primary production and indirectly regulate secondary production in littoral food chains. Suspension feeders develop dense, three-dimensional communities whose structural complexity depends on flow speed. It has been postulated that these communities can self-organize to enhance food capture and thus establish boundary systems capable of successfully exploiting a less structured system, namely, the plankton.

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The physical properties of seawater allow living creatures and particulate matter to remain in suspension, thereby creating a niche for suspension feeding – a trophic strategy that does not occur on land. Small cells (phytoplankton and microorganisms) predominate in such suspended (planktonic) communities. Suspension feeders have evolved mechanisms for capturing food that can be highly diluted within the water mass and, at the same time, be too small to be detected and captured individually. The possible mechanisms have been described by 'aerosol filtration' theory[1] (Box 1). The importance of this feeding strategy is particularly apparent in benthic marine communities, in which most animal groups have morphological structures capable of exploiting suspended particles as a potential food source.

For many species, suspension feeding involves food items that are either large enough to be individually seized or so small that they are only obtained in sufficient quantity by processing the surrounding water[2,3]. Therefore, many benthic sessile suspension feeders employ a variety of foraging behaviours to enable them to feed in the typically stochastic environments they live in. They have also adopted appropriate feeding strategies for a wide spectrum of prey, as has been observed in zooplankton organisms[4]. Recent field experiments investigating the natural diet of several species have provided new information suggesting that sessile suspension feeders feed on a wider spectrum of prey type and size than previous laboratory work pointed out[5,6] (Box 2).

Sessile organisms tend to capture food items in bulk rather than individually because they are adapted to moving fluid environments[7]. This adaptation, combined with the low cost of active filtering[8], means that benthic sessile suspension feeders could provide a prime example of optimal foraging in a marine context[9] (Box 2). The development of dense populations and multispecies communities, which are composed mainly of suspension feeders in shallow environments, has been explained by different theories, which corroborate the important contribution of suspension feeders to benthic communities. These theories are based on aspects reflecting statements such as 'the population density does not affect seston [i.e. the total particulate matter suspended in the water column] uptake or population growth' or 'sestonic food does not become limiting above a suspension feeding bed'[10]. They predict that the formation of colonies and clones (i.e. populations) is energetically more favourable than increasing the growth of an individual to its largest possible body size[11].

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Evidence for the exploitation of plankton in benthic communities

Recently[12], there have been attempts to assess the individual components of food webs within or between systems and thus achieve an overall understanding of marine ecosystems. Attention has focused on coupling between the benthos and the plankton and, in particular, on energy transfer between the pelagic and benthic ecosystems[13].

The level of exploitation of the plankton by suspension feeders can be measured by direct and indirect methods. Direct methods involve estimating capture rates, which can fluctuate greatly, depending upon food concentration, hydrodynamic conditions, temperature, and organism size and density[14,15]. These sources of variability have been studied by means of artificial diets and/or high prey concentrations[16], which limit their usefulness in analyzing natural communities. Therefore, capture rates have seldom been estimated for communities as a whole[6,17]. Indirect methods involve evaluating energy budgets by estimating the amount of energy needed by an organism for its basal metabolism and for growth and reproduction. These estimates also have to take into account any seasonal variations in these parameters[18].

The main components of the diets of different groups of suspension feeders are listed in Table 1. Although most groups are capable of capturing dissolved organic matter (DOM) bacteria and phytoplankton, the efficiency of the various taxa in capturing the plankton differs considerably and can be quite variable even within specific groups (e.g. soft corals[19]). Despite the paucity of studies on natural diets and particle concentrations, the results point to major resource partitioning within these communities.

Because of their abundance and filtration ability (up to $100\ m^3 d^{-1} m^{-2}$; Ref. 20), certain organisms, such as bivalves, have been intensely studied and shown to exert a major impact on the ecosystems in which they thrive. They capture large amounts of phytoplankton and might regulate primary production directly and secondary production indirectly[21]. Indirect estimates of the requirements of various species of tropical sponges[22] have revealed that some of them require quantities of particles at the same order of magnitude as some bivalves (Table 1). Recently, direct assessments have corroborated that both tropical and temperate sponges, as well as freshwater sponges[6], can inflict high capture rates on the picoplankton.

Studies of predation pressure on the plankton by cnidarians (hydrozoans, sea anenomes, jellyfish and corals) have revealed two main groups with distinct life strategies. Anthozoans, the first group, are characterized by slow growth rates, longevity and, often, associations with algal symbionts in tropical waters. Predation pressure on the planktonic population by individual colonies is negligible but because they are highly abundant, capture rates for the population as a whole are very high[17]. Hydroids, the second group, are characterized by rapid growth, ephemeral colonies and a lower frequency of associations with symbionts. Studies of energy transfer in Mediterranean rocky coralligenous communities provide examples of the quantitative importance of hydroids in exploiting plankton. It has been estimated that in such communities, a hydroid species contributing less than 0.5% of community biomass can capture approximately 10% of the algal production annually[23]. The role of the members of this group in energy transfer is thus much more important than would otherwise be expected on the basis of their size and abundance (Table 1).

Suspension feeders dominate sublittoral benthic communities that occur on hard substrata in zones with low light levels. Among them, sponges are one of the most abundant and widespread groups in marine ecosystems in tropical, temperate, polar and abyssal (i.e. <2000 m) regions. Cnidarians are the main components of coral reef ecosystems and are also crucial to sublittoral communities in temperate seas. In addition, recent work has highlighted the important trophic role of other groups of suspension feeders (i.e. polychaetes) as predators of nanoplankton[24]. The prevalence of these groups and the examples mentioned demonstrate that the effect of prey capture by macroinvertebrates on the planktonic community can no longer be overlooked and that benthic suspension feeders in littoral marine ecosystems are responsible for a large share of the energy flow from the pelagic to the benthic system.

Box 1. Aerosol filtration

Aerosol filtration theory[1] has suggested the following mechanisms by which suspension feeders capture food.

Sieving: items larger than the space between two adjacent food-catching structures (fibres) are trapped.

Direct interception: streamlined particles that are sufficiently close to the fibres are brought into contact with them.

Inertial impaction: the momentum of dense particles causes them to deviate from streamlines of ambient flow and to contact the fibres as water is deflected around them.

Motile-particle deposition: particles contact fibres through Brownian motion.

Gravitational deposition: particles that are denser than water settle on fibres at low rates of flow.

Box 2. Benthic sessile organisms as optimal foragers

Theories of optimal foraging indicate that species that expend low levels of energy in foraging for food are highly successful. Two aspects must be considered to postulate that benthic suspension feeders are among the optimal foragers in the marine context:
(1) The energetic cost for capturing prey is nil in passive sessile animals and very low in active filter feeders (the pump work in relation to the respiratory output is 0.8% in sponges[8,39]).
(2) Prey selection cannot be a common phenomenon among animals that depend on water flow to transport prey close to their feeding structures.

Information from field studies of natural diets supports the hypothesis that suspension feeders feed on a wide spectrum of prey type and size[5,32,40]. Many suspension feeders are capable of ingesting any type of food, limited only by morphological constraints[14]. The metabolic mechanisms that enable suspension feeders to assimilate many kinds of food (plant or animal), combined with various morphological (individual or colony) and ecological (spatial distribution and adaptation to different flow regimes) strategies, leaves no doubt that these animals include some of the most efficient optimal foragers, which allows them wide success in marine environments.

Communities of suspension feeders: life in patches

The colonies or individuals in a population act to slow current flow or increase the residence time of water in their vicinity, thereby increasing the residence time of particles. The substratum, on which the populations rest, also slows the flow and raises turbulence, again increasing the residence time of particles. In the case of closely spaced colonies,the operant hydrodynamic model is interactive flow, whereas in the case of more widely spaced colonies, flow is independent, generating small eddies around the colonies[25]. This gives rise to a spatial pattern determined by the optimum distance between colonies or individuals[26]. Where the current carries large quantities of highly diverse particles, species able to share a single resource or to partition that resource on the basis of particle size and mobility can form multispecific assemblages in a single location under the same hydrodynamic conditions[27].

For example, species in various zoological groups have been observed to capture particles of different sizes and to be more efficient for certain types of prey items, depending on their morphological structures and the flow rate of the surrounding water[8,28]. Species that trap smaller particles and thus require higher flow velocities can coexist in the same community with other species that feed on larger prey and hence require a smaller volume of water. Capture efficiencies vary according to whether the species are active suspension feeders (more effective on smaller particles) or passive ones (better at retaining larger, more energy-rich particles). Seston flux is an important factor affecting the organismal performance of passive suspension feeders, whereas the seston concentration is more relevant for active ones[27].

Levels of population heterogeneity span a continuum ranging from monospecific patches of colonial or individual suspension feeders to complex three-dimensional formations comprising communities with high species and functional diversity. At one extreme are the dense belts or aggregates of mussels (filter feeders that mainly feed on phytoplankton) and estuarine bivalve populations (such as oysters and clams) that have a direct role in sharply reducing primary production in the water column[21]. At the other extreme are the complex rocky 'coralligenous' communities in the Mediterranean Sea, the coral reefs and many other sublittoral communities[29–31], which are composed of a wide variety of organisms that prey on food sources ranging from the zooplankton to the picoplankton[32]. It would be a mistake to regard such communities as static simply because the efficiency of these suspension feeders fluctuates with prey density and water flow (which is constantly changing in intensity and direction)[14,33]. Overspecialization in a narrow range of flow rates and particle types might entail the risk that the species will be dislodged and replaced by another more efficient species with the same target range.

The rocky coralligenous community in the Mediterranean is an example of a highly diversified and yet highly structured community of suspension feeders (Fig. 1). This type of community consists of a large variety of species, including those with medium or long residence times (which range from erect colonies, such as gorgonians, to massive medium-sized species, such as sponges and ascidians) and many small colonies with short residence times (hydroids), as well as encrusting species, such as bryozoans. The habitats for this type of community are vertical walls and rocky blocks, which are continuously washed by strong currents and have little algal cover (owing to the increase in depth and decrease light). The biomass and diversity of suspension feeders decrease progressively as the current intensity and frequency decline[31], for instance, with increasing depth or towards the interior of caves (where depth gradients are condensed into short distances, Fig. 1). A decrease in erect forms, which require higher flow rates, is accompanied by a decrease in colony or zooid (individual within a colony) size. Overall change in the size, forms and strategies of suspension feeders along a hydrodynamic vector is commonplace and can also be observed in other communities[15].

Table 1. Main components of the diet of different taxa of suspension feeders and some values of their daily rates of ingestion (capture rates: in organic carbon units)[a]

Taxa	Diet	Capture rates	
		mgC polyp^{-1} d^{-1}	mgC m^{-2} d^{-1}
Porifera	DOM[b], bacteria and phytoplankton		
Mycale lingua			29.0
Baikalospongia bacillifera			1970.0
Several tropical species			80.0–1800.0
Cnidaria	DOM, bacteria, phytoplankton and zooplankton		
Anthozoa			
Hexacorallia			
Madreporaria		0.08–1.38	
Zoanthidea		0.02–0.09	
Octocorallia			
Alcyonacea		0.02–0.54	
Gorgonacea		0.01–0.46	1.0–85.0
Hydrozoa			
Hydroidea			
Silicularia rosea		4.10	79.8
Campanularia everta		0.48	11.1
Eudendrium racemosum		0.89	19.7
Tubularia larynx		12.01	150.2
Mollusca	Bacteria and phytoplankton		
Bivalvia			
Aulacomya ater			1787.0
Chlamys islandica			3621.0
Casostrea virginica			573.0
Geukensia demissa			30.0
Mercenaria mercenaria			351.0
Ostrea edulis			9.0–30.0
Anelida	DOM and phytoplankton		
Polichaeta			
Lanicea conchilega			2.7
Tunicata	DOM, bacteria and phytoplankton		
Ascidiacea			
Pyura stolonifera			3277.0
Halocynthia papillosa			21.0

[a]Compiled from Refs 6, 22, 23, 40, 46, 47 and Refs therein.
[b]Dissolved organic matter.

Suspension feeder communities: a successional approach

The structure (measured as complexity and diversity) and biomass of communities of suspension feeders can increase with food availability. This general pattern is linked to flow speed, with higher flow rates resulting in larger colony and individual sizes[27]. The effect of suspension feeder communities on planktonic ones is a sharp drop in the concentration and an increase in the retention time on the bottom of suspended particles of all kinds, depending on the density of suspension feeders and their different mechanisms for trapping particles[34]. Succession in suspension-feeder communities will depend upon the total energy input from particles made available by the water flow.

Margalef[35] has shown that physical energy is a vector for increasing system entropy while increasing information content. He has also pointed out that a gradual increase in energy from outside the community will increase community complexity because, although the energy entering a system is additive, the effect of new additions is to multiply the structural complexity of the system. Therefore, although the different exploitation strategies are an outcome of the ecological and morphological diversity of benthic invertebrates, a small increase in the available energy via an increase in the number and diversity of allochthonous particles (i.e. exogenous food particles transported into the system) will increase the opportunities for exploitation by communities of suspension feeders, causing the number of different strategies to rise. As a result, different communities of suspension feeders develop according to the available energy. The community starts with a variety of small and opportunistic species (e.g. hydroids, bryozoans and ascidians), which are similar to the fouling communities (i.e. assemblage of organisms growing on the surface of floating or submerged man-made objects) with a laminar flow above the suspension feeding bed. Step by step, while the size and the number of erect and massive species increase, the hydrodynamic regime becomes more heterogeneous, enhancing habitats that cause flow retention, which favour the development of rich and diverse communities. Consequently, a chain of succession can be drawn from estuarine bivalve communities to complex Mediterranean and coral reef communities.

As proposed by Margalef[35], succession and community development are bound together both spatially and temporally. It therefore follows that communities of suspension feeders have not only evolved towards highly complex, three-dimensional structures capable of processing and absorbing large quantities of energy, but have also become adept at economizing and maximizing the benefit derived from the energy captured from food particles. Mediterranean rocky coralligenous communities are a good example of this.

Suspension feeder communities as a boundary system: from the standpoint of succession and energy transfer

The sea shore is a clear example of a boundary between ecological systems (i.e. the terrestrial and marine). Communities of benthic suspension feeders also lie at a boundary between the substratum ('bottom') and the water column ('sea'). From the standpoint of water column structure and dynamics, the hard bottom benthos – that is, the living stratum immediately above the substratum – has usually been regarded as a sink where the remains of the water column production comes to rest. However, in littoral systems, the benthos, such as suspension feeder communities, is an extremely active part of the system, not only receiving food particles that settle out of the water column, but also actively exploiting and temporarily storing particles that are transported by current flows within the water column. Consequently, communities of suspension feeders make up a highly active boundary system. Given the Margalef proposal[35], this type of boundary system is more dynamic than those traditionally considered in ecology, that is, discontinuities and ecotones.

Among the main reasons that make this boundary system so active is that a system dominated by suspension feeders is highly structured and quite efficient at exploiting the less structured system of plankton. For example, the cost of capture is virtually nil in passive benthic suspension feeders, whereas in active suspension feeders, pumping may account for up to 4% of energy demand[8]. Furthermore, quantitative assessment of particle and prey capture by suspension feeders has shown them to be a key element in the economy of the littoral system. However, much more comparable information needs to be compiled on the amount of energy captured that is transferred to other marine ecosystems.

From a successional standpoint, the ability of suspension feeders to exploit the plankton links the benthic and planktonic systems together. Communities of benthic suspension feeders can be classified along a gradient of successional development, defined in terms of the energy they obtain from particulate matter. It has been suggested that

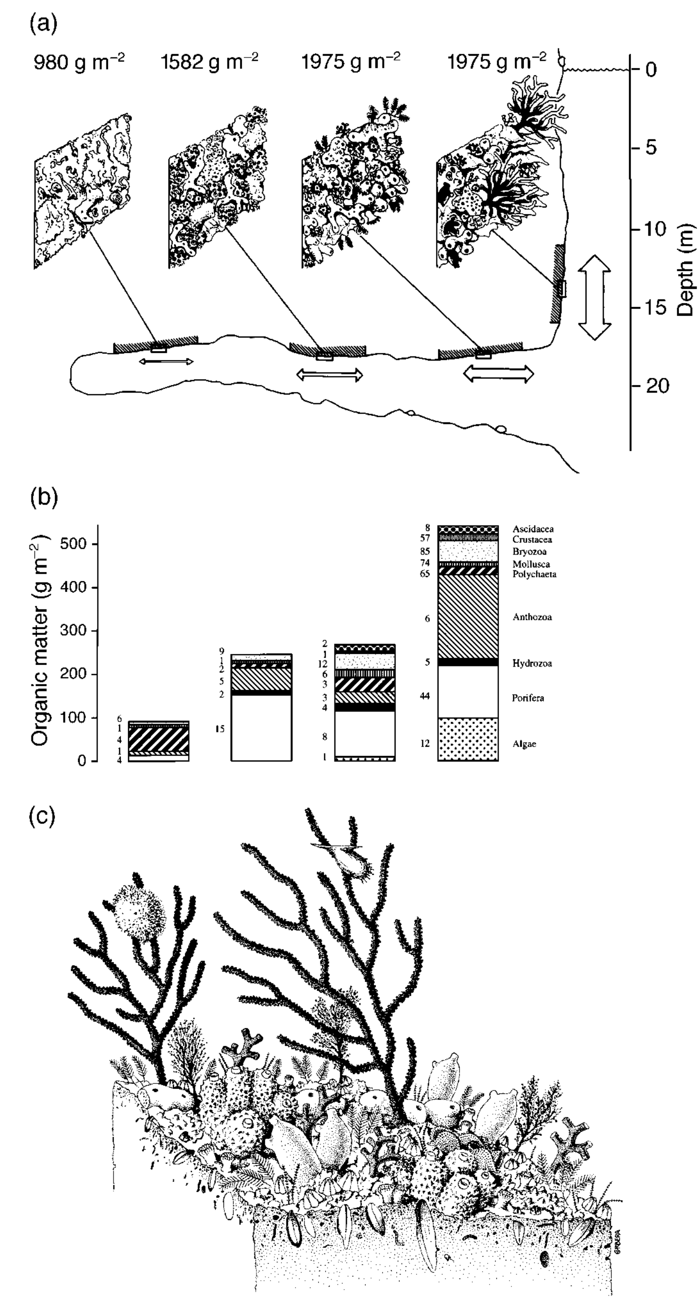

Fig. 1. (a) Diagrammatic localization and configuration of four Mediterranean sublittoral communities from a vertical wall outside a cave to a horizontal one inside the cave. The number at the top of each representation is the biomass in dry weight. The width and direction of arrows roughly indicate the direction and intensity of water flow in each community. (b) The stacked bars represent the biomass (ash free dry weight) of the main groups comprising each community. The numbers at the side of each bar indicate the number of species within each group. (c) Representation of the Mediterranean 'coralligenous' sublittoral community (approximately 1 m^2) as an example of a complex three-dimensional community dominated by suspension feeders.

Box 3. Are suspension feeder communities restricted to shallow waters?

The speed of water currents has been observed to increase near the top of the vertical walls of seamounts because of topographical effects. In such places, large aggregations of antipatharians (black corals) and other suspension feeders live on the food carried by the bottom currents, an effect analogous to upwelling[41]. Such communities have a number of general features similar to those of littoral ecosystems, namely the formation of dense patches of multispecific communities in which erect, massive, and encrusting species alternate[36].

Many of these communities depend not only on bottom currents, but also on resuspension processes. For the most part, when particles contributed from the water column are heavy, intense sedimentation of organic matter takes place, even when such contributions are not continual. This organic matter will later become available to suspension feeders when it is resuspended. Because of this, suspension feeders are able to form dense populations on the continental shelf and slope[42] and, in some cases, even on more deep bottoms, such as in the Antarctic. These deep-dwelling communities are dominated by species with long life spans[43], whose larvae have short planktonic stages (if any), and they make up one of the largest aggregations of biomass and density of benthic organisms yet known[44]. Their long life spans allow them to become highly structured, mature communities.

The patchwork of deep-water suspension-feeding communities observed today are the outcome of a very long and complex evolutionary history. These communities represent an extreme form of evolution, which cannot turn back the clock unless they are disrupted by an outside perturbation. From the point of view of succession, each community is the result of slow developmental processes that are difficult to quantify because long periods (possibly centuries) have had to go by for them to reach their present levels of diversity and structure. In addition, their evolution will have been affected by major disturbances, such as those caused by iceberg scouring[45].

the degree of complexity is linked both to the amount of energy available and to the efficiency of exploitation[35]. At one end of the spectrum, a community of suspension feeders, such as a mussel bed, exploits a planktonic system with a food web that contains few secondary consumers (e.g. estuarine planktonic systems). By comparison, sublittoral communities that exist by exploiting littoral planktonic systems with much more complex trophic structures are at the opposite end of the spectrum. In such systems, the presence of a thermocline increases the structure and diversity of the communities in the water column. The subsequent breakdown of the thermocline enhances production and furnishes the benthos with a diverse range of particles and organisms. Therefore, the structural and biological complexity of communities of suspension feeders is linked to the structure of the planktonic communities they exploit.

Suspension feeder communities in deep areas

Environments with strong, variable currents that are able to transport large concentrations of suspended particles can also be found at great depth on the continental shelf and slope. In fact, any topographical structure that breaks the smooth, even profile of the substratum will bring about a change in the direction and intensity of flow[36] (Box 3). Littoral communities of suspension feeders are usually composed of organisms with short larval development times that act to limit dispersal and enhance patch survival and development[37]. Sublittoral communities located at the edge of the continental shelf or on the upper portions of the walls of submarine canyons also tend to have a high proportion of these organisms. Here, aggregations of suspension feeders such as gorgonians, sponges and corals are very common and make up a transition zone between the shelf and deep-sea benthic communities. The three-dimensional structure of such communities is conducive to settlement by active suspension feeders, such as bivalves encrusting the substratum, building a sub-substratum resembling that of littoral suspension feeder communities (e.g. Mediterranean rocky coralligenous communities).

The self-organization of suspension feeder communities

Benthic suspension feeders form communities that can self-organize into patches by means of asexual reproduction or dispersal of larvae over short distances. However, the self-organizing concept is not only related to aggregated recruitment. After larval settlement, the number of colonies or individuals that survive decreases during their growth. Survival of suspension feeders is closely related to maximizing prey capture, which involves the spatial organization of all the members in each population and the partitioning of available food resources to avoid high levels of competition on similar prey items. An important advantage for such communities is that active and passive suspension feeders are able to share the same habitat and thereby make more efficient use of the energy available. The two feeding strategies are analogous – the canal system of an active suspension feeder (e.g. sponges), a highly efficacious structure that is inexpensive to operate[38], can be considered equivalent to the spatial distribution of the colonies or individuals of a passive suspension feeder (e.g. gorgonians), likewise highly effective and inexpensive to maintain.

Communities of suspension feeders are efficient at feeding because of their ability to self-organize to capture prey borne by currents and to develop concomitantly with the features of the planktonic system they exploit. As a result, suspension feeder communities could be responsible for a major share of the biomass and energy transport in marine ecosystems. However, confirmation of this hypothesis requires much more quantitative information on trophic ecology, in particular about different species within the same community, including how passive and active suspension feeders partition available food. The knowledge of natural diets from fieldwork in littoral areas, together with the study of life-history traits (quantification of energy budgets), the energy cost of pumping, and reproductive effort and growth are some of the topics that will significantly contribute to understanding the important ecological role of suspension feeding communities in marine ecosystems.

The complex communities of suspension feeders observable today (e.g. Mediterranean rocky coralligenous communities or Antarctic benthic communities), appear to be the end result of a lengthy developmental process during which the communities have removed large amounts of energy (in the form of organic particles) from the water column. The process has left behind the dead architecture of the coral reefs – for example, the skeletons of octocorals, sponges and bryozoans. In terms of boundary theory[35], as succession proceeds, the most highly structured part of the system (the benthic suspension feeders) draws ever larger amounts of energy from the less highly structured part (plankton and/or particles). Accordingly, communities of benthic suspension feeders can now be considered among the most efficient communities in the world ocean in extracting and processing energy from living marine ecosystems.

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