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MINI-REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Seasonal energetic constraints in Mediterranean benthic suspension feeders: effects at different levels of ecological organization

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The aim of this work is to examine the role of food as a constraining factor at different levels of ecological organization in benthic littoral ecosystems. In the search for patterns in ecological systems, it has recently been documented that seasonality in the dynamics of benthic suspension feeders (BSF) in the Mediterranean Sea is characterized by summer dormancy. We review recent studies on seston availability in the water column and feeding and respiration by BSF in the Mediterranean. The objective is to assess whether a pattern across particular studies exists that could provide evidence of food as a constraining factor. A pattern emerges from these organism-level studies, one which indicates the seasonal occurrence of an energy shortage in the taxa exhibiting summer dormancy. This energy shortage is closely related to low food availability and suggests that an energetic constraint underlie the summer dormancy phenomenon. The seasonal occurrence of summer energy shortage also appears to affect the dynamics of BSF at population and community level. In this sense, in late summer 1999, a mass mortality event of BSF affected several hundreds of kilometers in the Ligurian Sea (NW Mediterranean). The fact that the mass mortality event occurred in late summer and especially affected the taxa that exhibit energy shortage – such as anthozoans and sponges – suggests, that energetic constraints may contribute to the understanding of the mass mortality event. The energy shortage phenomenon may provide a mechanism to understand how the occurrence of anomalous climatic conditions may have induced the mass mortality of some BSF taxa. This review points out the existence of a common energy shortage phenomenon mainly related to low food availability as an important determinant of the dynamics of most BSF taxa at organism level in the Mediterranean. But this determinant also affects the dynamics of BSF at population and community level. Therefore, the extant data point up the crucial role of food as a constraining factor for benthic littoral ecosystems in oligotrophic areas like the Mediterranean, with important seasonal variations in seston abundance and composition.

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Early in the development of ecological theory, the need to manage the exploitation of ecosystems stimulated the study of food web interactions and the development of ecological energetics (Linderman 1942). Since then, the role of food as a constraining factor at the organism, population, and community level has been a pervasive issue in ecology (Hairston et al. 1960, Schoener 1974, Olson and Olson 1989). The aim of this work is to examine the role of food as a constraining factor at different levels of ecological organization in benthic littoral ecosystems.

Cold and temperate ecosystems exhibit a marked seasonal variation of environmental conditions that strongly affects the dynamics of benthic communities. However, the mechanisms by which the environmental variability affects the functioning of benthic communities are still unclear. In the search for patterns in ecological systems, it has been recently pointed out that seasonality in temperate ecosystems may differ between cold and warm regions of temperate ecosystems. Winter dormancy characterizes seasonality in cold temperate ecosystems (Hughes 1989) while summer dormancy characterizes seasonality in warm temperate ecosystems (Coma et al. 2000). Because seasonal patterns are strongly related to dominant environmental factors, this discrepancy provides a focus for research into the causes of seasonality.

The high levels of environmental variability exhibited by littoral ecosystems throughout the annual cycle, especially in cold and temperate areas, make the study of seasonal pattern a useful tool for examining factors that affect the functioning of benthic suspension feeders under natural conditions. Space competition, resource abundance, temperature and water movement are the main factors that have been suggested to explain seasonal patterns of growth, reproduction, and abundance in Mediterranean benthic suspension feeders (Boero et al. 1986, Boero and Fresi 1986). However, both temperature and food availability have been singled out as the most crucial environmental factors affecting the dynamics of benthic invertebrates (Clarke 1988, Coma et al. 2000). The relative simplicity of temperature measurement together with the correlation between seasonal patterns of most physiological processes and temperature variations has made temperature the most studied and most frequently invoked factor to explain seasonal patterns in marine invertebrates (Parry 1983).

The role of temporal variation in food quantity and quality has already been documented for opportunistic benthic deposit feeders (Tenore and Chesney 1985, Marsh and Tenore 1990, Hentschel and Jumars 1994, Gremare et al. 1997). In littoral areas, benthic suspension feeders such as sponges, cnidarians, ascidians, bryozoans, bivalves, and polychaetes are dominant on hard bottom under relatively low light conditions (Witman and Dayton 2000). However, there is little knowledge about the role of food as a constraining factor in organism, population and community ecology of long-lived benthic suspension feeders on hard bottoms. This lack of knowledge is mainly related to the scarcity of food availability studies.

There are two main reasons why food availability has been understudied. First, food data are difficult to obtain, manage and analyze because they are multivariate. Studying feeding requires consideration of the entire spectrum of potential food sources, including dissolved organic matter (DOM), detrital POM, and pico-, nano- and microplankton. Until recently, studies of natural diets were constrained by measurement problems such as the large volume required for sample analysis and the length of time required to evaluate potential food sources. Improvements in flow cytometry and related techniques have solved these measurement problems and facilitated examination of natural microbial populations (Reckermann and Colijn 2000). Second, the annual variations of temperature and food availability in cold and cold-temperate seas are positively correlated (Cushing 1975). This has made it difficult to separate both effects and has constrained the evaluation of the importance of food availability. In the Mediterranean, temperature and food availability are out of phase, with food being least available at the highest temperature. We focus the review on benthic suspension feeders in the Mediterranean Sea because of the characteristic attributes of this ecosystem that allows us to separate the effect of temperature from that of food availability (Coma et al. 2000).

Summer dormancy (aestivation) appears to be the predominant feature in the seasonal dynamics of benthic suspension feeders in Mediterranean littoral benthic ecosystems (Coma et al. 2000). In the Mediterranean, the main taxa contributing to the structure and biomass of sciaphillous hard bottom communities are long-lived organisms exhibiting low dynamics (Coma et al. 1998a, Garrabou 1999). Here, we examine the outcomes of recent studies on the seasonal variation of seston composition, natural feeding, and respiration rates from several benthic suspension feeders to assess whether a pattern across particular studies exists that could provide evidence of food as a constraining factor. The synthesized data on the temporal variations in seston abundance and composition and on the dynamics of these organisms allowed us to examine questions not explicitly asked in the original studies and also to search for the generality of outcomes across many studies. At the organism level, we addressed how seasonal episodes of low food contribute to understanding the seasonal dynamics of BSF in the Mediterranean. At population and community level, we addressed how seasonal episodes of low food may influence populations and communities by examining the potential role of energetics in mass mortality events.

An energetic approach to understanding organism level dynamics in BSF

Energy constraints may arise from a reduction in energy intake and/or an increase in energy output. A comparison of energy intake (ingesta) and energy output (respiration expenditure) throughout the annual cycle contributes to understanding how the seasonal dynamics are affected by energetic constraints. Specifically, we can determine whether energetic limitations may underlie the summer regression in activity of some BSF taxa (i.e. the energetic constraints hypothesis, Coma et al. 1998a).

The ingesta is determined by two main aspects: the availability of food throughout the year, and the natural diet and feeding rate of the species or taxa. Recent attention has been devoted to seasonality in dissolved organic carbon, particulate organic carbon (POC), pico-, nano-, and microplankton in littoral Mediterranean ecosystems (Vaque et al. 1997, Agawin et al. 1998, Ribes et al. 1999a), all of which are food resources for benthic suspension feeders. Three features distinguish the annual variation of water column food resources in littoral ecosystems. First, the importance of suspended detrital POC. This represents the main POC fraction and is about an order of magnitude higher than plankton in carbon units (Fig. 1a,b,c). Second, the relative dominance of pico- and nanoplankton among the plankton. These small organisms account for 43 and 33% of the biomass, respectively (Fig. 1d). Third, the differences in the pattern of variation of the different fractions throughout the year. Detrital POC and microplankton exhibit marked seasonal patterns with high values in winter and spring and low levels in summer (Fig. 1a,b). In contrast, pico- and nanoplankton communities exhibit little seasonal variation (Fig. 1c). Because BSF depend entirely on seston availability, a question arises from these patterns that distinguish the annual variation of the food resources in the water column: Does seasonality in resource abundance affect the dynamics of benthic suspension feeders?

Knowledge of the natural diet of benthic suspension feeding taxa is necessary to address this question. For the last five years, several studies have been conducted on natural diets, feeding rates and respiration rates of several groups of BSF in the Mediterranean, both those that exhibit summer dormancy and those that do not, such as hydrozoans, anthozoans, ascidians and sponges. The contrast of the natural diets between groups together with the comparison between feeding rates and respiration rates of these taxa may show how the environment affects the functioning of benthic suspension feeders. Do studies on diets, feeding rate and respiration rate support the hypothesis that an energetic constraint may underlie the summer dormancy phenomenon?

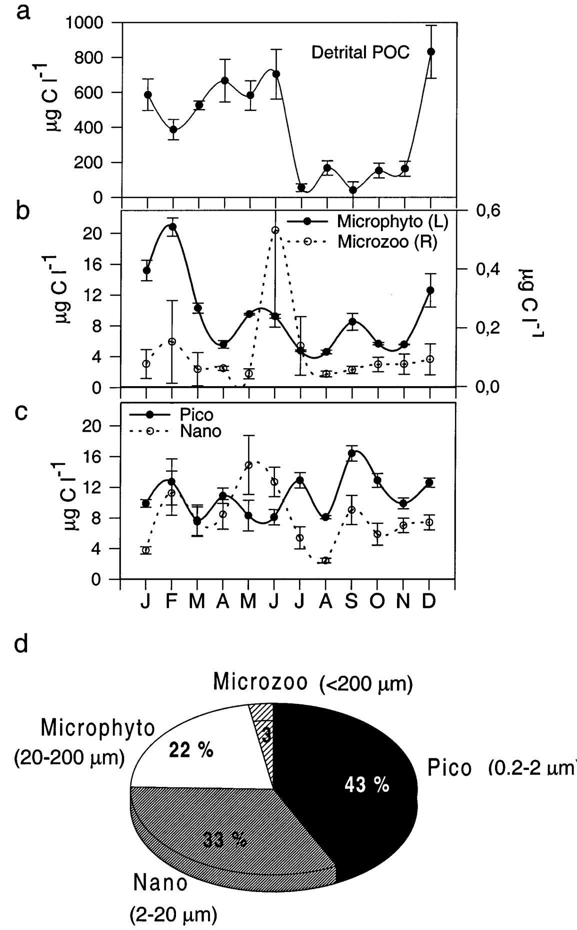

Fig. 1. Seston composition in littoral ecosystems and its seasonal variation in the water column: a) detrital particulate organic matter (POC), b) microplankton (20–200 µm), c) pico- (0.2–2 µm) and nanoplankton (2–20 µm), d) relative contribution of pico-, nano-, and microplankton to the overall live seston composition. Compiled from Coma et al. 1994 and Ribes et al. 1999a. L: left axis, R: right axis.

Hydrozoa and Anthozoa

Feeding studies of hydrozoans and anthozoans have shown that microplankton and detrital POC are the main components (Sebens and Koehl 1984, Fabricius et al. 1995, Coma et al. 1998a, Gili et al. 1998, Ribes et al. 1999b) of the diet, usually taken to account for over 90% of the ingestion (Fig. 2a,b). Few studies have examined prey capture variation throughout the year. The studies that do exist have been conducted in the Mediterranean and show that there is a marked seasonal pattern in prey capture which is characterized by low capture rates of prey during the summer period (Fig. 3a,b; Coma et al. 1994Coma et al. 1995bRibes et al. 1999b). This pattern matches that of the variation of their resources in the water column throughout the year (Fig. 1a,b). However, prey capture depends not only on prey abundance but also on flow speed (Fabricius et al.

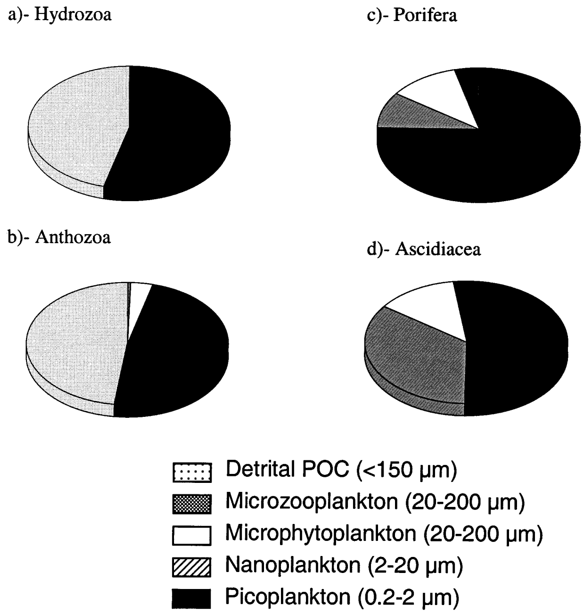

Fig. 2. Diet in several Mediterranean benthic suspension feeders taxa: a) Hydrozoa, b) Anthozoa, c) Porifera, and d) Ascidiacea. Compiled from Coma et al. 1994Coma et al. 1995bComa et al. 1998a, Ribes et al. 1998, 1999b, c.

1995, Sebens et al. 1998). Some of the seasonal studies have integrated the effect of both prey abundance and flow speed because they examined gut contents (Coma et al. 1998a), while others have examined the effect of prey abundance at a single flow speed (Ribes et al. 1999b). Flow speed has a clear seasonal pattern, higher during winter and spring and decreasing during the summer period (Font et al. 1995). Thus, the expected effect of increase in prey capture with flow speed (Dai and Lin 1993, Fabricius et al. 1995, Sebens et al. 1998) should accentuate the observed pattern of decrease in prey capture during the summer period.

The effects of low food availability in summer could be accentuated by an increase in basal metabolism because of high summer temperatures. This correlation has been clearly demonstrated in hydrozoans (Arillo et al. 1989, Gili and Hughes 1995). Increases in respiration rate with temperature accentuate the effects of low food availability by making energy requirements in summer greater than those provided by the ingesta (Fig. 3a, Coma et al. 1998a). However, this may not be the case in anthozoans. Respiration rates have been examined seasonally for only one species (the gorgonian *Paramuricea clavata*, Coma et al. 2002), and low respiration rates have been documented during the period of highest temperature (Fig. 3b). This was related to three main processes: the low synthesis of tissue during summer, the low Q_{10} value and the marked seasonal pattern of polyp expansion and contraction and the effect of polyp contraction on respiration (Coma et al. 1994, 1998a, 2002). The low Q_{10} value exhibited by the species (Q_{10}: 1.1, Coma et al. 2002) indicates that oxygen consumption in this species is not highly dependent on temperature. The species exhibits a marked seasonal pattern of polyp expansion and contraction, where polyps are expanded only about 20% of the time during summer versus about 80% of the time during the rest of the year (Coma et al. 1994). Polyp contraction reduces respiration expenditure by 50% (Coma et al. 2002), within the range of values (10–60%) reported in other cnidarian species (Sebens 1987, Fabricius and Klumpp 1995). The three processes explain why respiration rates are low during the period of highest temperature (Fig. 3b). The results suggest that

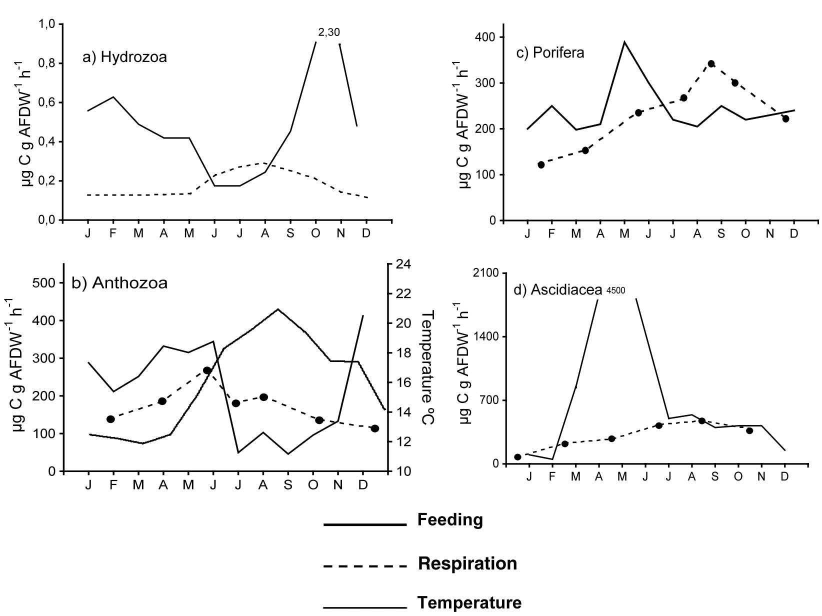

Fig. 3. Seasonal variation of total feeding and respiration rate in several Mediterranean benthic suspension feeders taxa: a) Hydrozoa, b) Anthozoa), c) Porifera, and d) Ascidiacea. Compiled from Coma et al. 1994Coma et al. 1995bComa et al. 1998a, 2002, Ribes et al. 1998, 1999b, c. All studies were conducted at the same location. The seasonal variation in temperature throughout the annual cycle is presented in b.

the gorgonian may have undergone an evolutionary adjustment of its physiology and ecology to the unfavorable Mediterranean summer conditions. A minor reduction in temperature dependence for oxygen consumption has important ecological significance for maintaining the energy budget under conditions of thermal and nutritive stress (Newell and Branch 1980). The responses of different cnidarian groups to summer adverse conditions range from polyp regression in hydrozoans to decreased feeding activity in gorgonians and temporal development of a glassy cuticle in alcyonaceans (Coma et al. 2000). A two-year monitoring of the pattern of polyp expansion and contraction of several benthic suspension feeders suggests that the patterns observed in *P. clavata* may be a common feature of gorgonacea, alcyonacea and zoanthidea species in the Mediterranean (Coma, unpubl.).

These results indicate that low food availability in summer is responsible or contributes to the summer dormancy phenomena exhibited by hydrozoan and anthozoan species in the Mediterranean, in agreement with the energetic constraints hypothesis (Coma et al. 1998a). Furthermore, it contributes to understanding why secondary production investment (i.e. growth and reproduction) exhibits its lowest rates during summer (Coma et al. 2000).

In the Mediterranean, bivalves cease growth and reproduction in summer (Ramón et al. 1995, Arnesi et al. 1998). This pattern of investment is consistent with the pattern of available resources for bivalves. Three facts suggest that bivalves may be subject to a similar energy shortage as exhibited by hydrozoan and anthozoan species. First, in bivalves, most of the energy intake comes from particles larger than 3 μm (Jørgensen 1990). Second, seston composition in summer is characterized by the low abundance of microplankton and detrital POC. Third, water processing in bivalves is adapted to the food concentrations of the environment that prevail during productive seasons (Jørgensen 1990) and they stop filtration by closing their valves at low food concentrations (Jørgensen 1996), such as those present during the summer period in the Mediterranean (0.2–0.3 μg chlorophyll a l^{-1}, Ribes 1998).

Ascidiacea

Field studies on diets and feeding studies of solitary ascidians (Ribes et al. 1998) agree with previous laboratory studies (Fiala-Medioni 1987, Petersen and Riisgård 1992) showing that they can feed indiscriminately on pico-, nano-, microplankton, and detrital POC, although the filtration efficiency is lower for particles < 1 μm such as bacteria (Jørgensen et al. 1984, Ribes et al. 1998). Although ingestion of detrital carbon is greater than that of live carbon, live particles are more significant to the dynamics of the species than particles from detrital origin because the seasonal variation of nitrogen uptake from live particles explains most of the variance in secondary production investment (Seiderer and Newell 1988, Ribes et al. 1998). In Fig. 2d, the representation of the ascidian diet does not include detrital POC in order to provide a clear picture of the composition of feeding on live carbon. Capture of pico- and nanoplankton accounts for most of the live carbon ingestion by ascidians (Seiderer and Newell 1988, Ribes et al. 1998) – on the order of 85% (Fig. 2d). In Mediterranean littoral ecosystems, annual fluctuations of seston primarily affect the abundance of detrital POC and microplankton but not that of pico- and nanoplankton (see above). Therefore, the seasonal pattern of investment in growth and reproduction of solitary ascidians appears to be little affected by food availability. In nature, clearance rate is positively correlated to temperature. Ascidian seasonal dynamics appear to be mainly determined by temperature because clearance rate, respiration rate, and somatic and reproductive investments increase in summer (Fig. 3d, Ribes et al. 1998, Coma et al. 2000, 2002). The positive correlation between clearance rate and temperature is consistent with the hypothesis that the ascidian pump operates in the absence of physiological mechanisms to regulate water pumping, suggesting that the clearance rate increase with temperature corresponds to a decrease in water viscosity (Petersen and Riisgård 1992, Jørgensen 1996).

The high filtration capacity of solitary ascidians (up to 261 g DW^{-1} h^{-1}, see Table 3 in Ribes et al. 1998) together with their feeding plasticity – some species can even consume invertebrate larvae and eggs (Bingham and Walters 1989) – are probably, the main features that allow solitary ascidians to overcome the unfavorable conditions of the Mediterranean summer period. This would explain why ascidians are able, during this period, to overlap the highest respiratory expenditure with somatic and reproductive investments.

Porifera

The main research effort in sponge feeding in nature has focused on the picoplankton fraction (Pile et al. 1996). However, while sponges have a higher efficiency in capturing picoplankton than in capturing microplankton, their natural diets are heterogeneous including pico-, nano- and microplankton (Fig. 2c, Ribes et al. 1999c). Under natural conditions, temperature appears to produce little effect on filtration rates (Ribes et al. 1999c), in contrast to the pattern of clearance rate rise with temperature observed in laboratory studies (Riisgård et al. 1993). Further in situ research is needed on this topic. Present knowledge about natural sponge feeding in the Mediterranean indicates that sponges obtain about 85% of ingesta from pico- and nanoplankton (Fig. 2c). The fact that these planktonic communities remain rather constant throughout the annual cycle (Fig. 1c), together with their heterogeneous diet, allows sponges to maintain a fairly constant food uptake throughout the year, although the contribution of the different groups to the total ingesta varies seasonally (Ribes et al. 1999a). This feeding plasticity represents an advantage for sponges and might distinguish the dynamics of sponges from that of other BSF because feeding plasticity attenuates the effects of seasonal fluctuations in planktonic communities. A fairly constant food uptake throughout the year is consistent with the observed phenomena of partitioning of the different productive processes, such as sexual and asexual reproduction, growth and production of chemical defenses throughout the year with little or no overlap (Corriero et al. 1996, 1998, Turon et al. 1996, 1998, Uriz et al. 1998). Different authors have suggested that the different productive processes follow each other throughout the year because these processes are constantly competing for resources (Corriero et al. 1996, Turon et al. 1998).

Seasonal variation in respiration rate was examined for the sponge *Dysidea avara*, where the highest respiratory expenditure occurs in summer (Fig. 3c). This appears to be related to the positive correlation between temperature and oxygen consumption and to the respiratory cost associated with the synthesis of new tissue, which has documented to be very high (139% of the biomass production, Thomassen and Riisgård 1995). In the case of the sponge, metabolic energy requirements may not be met during summer, due to an increase in respiration rate, and not due to a decrease in ingesta as previously observed in anthozoans (Fig. 3c). This evidence of a summer energy shortage contrasts with the observation that some investment in secondary production occurs during the summer period. Two hypotheses, not mutually exclusive, may contribute to understanding this paradox. First, although no relationship was observed between clearance rate of the sponge species and temperature, increasing clearance rate with temperature, as observed in laboratory studies (Frost 1980, Riisgård et al. 1993), cannot be completely ruled out because a size effect may have interfered with a potential temperature effect in the field experiments (Ribes et al. 1999c). Second, reserve substances could also be used in summer because there is evidence that sponge species can accumulate reserves (Barthel 1986). Therefore, other factors (such as larval survival, competition, predation, etc.) rather than food concentration may determine the seasonal dynamics of sponges.

Whether sponges are food limited or not, their dynamics throughout the year do not appear to be related to food availability. The relatively constant uptake of food throughout the year, together with the lack of temporal overlap in different productive processes suggests that food limitation occurs. Although some sponge species exhibit investment in secondary production during the summer period (Corriero et al. 1996, Turon et al. 1998), these species appear to be subjected to a seasonal energy shortage due to an increase in energy output (Fig. 3c). The dormant stages observed in between 5% and 20% of the population of some species in late summer and autumn (Turon et al. 1999) could be related to this energy shortage.

Do studies on diets, feeding rate and respiration rate support the hypothesis that an energetic constraint may underlie the summer dormancy phenomenon?

Ingesta instead of assimilation has been reported because the studies on natural diet examined ingesta but not assimilation efficiency. The values in the literature on assimilation efficiencies for the studied taxa range from 42–90% depending on the taxa and the nutritional content of the particles (Ivleva 1964, Paffenhöfer 1968, Simkina 1980, Klumpp 1984, Zamer 1986, Fiala-Medioni 1987). Therefore, the use of assimilation would accentuate the observed pattern of summer energy shortage. Furthermore, the error terms in the estimates of feeding and respiration rate are so small that they do not significantly affect the described patterns (Coma et al. 1998a, 2002, Ribes et al. 1998, 1999a, b).

These results indicate that animals from the different suspension feeding taxa can capture a wide variety of prey items ranging from picoplankton to microplankton and detrital POC. None of the taxa appears to ingest any significant amount of DOC. The capture of prey items is mainly restricted by morphological constraints of the capture structures (Coma et al. 2001). Feeding and respiration studies show that an energy shortage occurs in hydrozoa and anthozoa. This shortage is closely related to the seasonal availability of food, and may explain the occurrence of summer dormancy in these taxa. Studies of bivalves in the Mediterranean are also consistent with the occurrence of an energy shortage in summer. Therefore, the summer dormancy phenomena exhibited by some species and taxa appears to be related to low food availability. For those species and taxa that do not exhibit summer dormancy, feeding studies indicate that characteristics of their feeding strategies and of their response to environmental factors allow them to overcome the summer shortage in food availability (i.e. high filtration capacity and heterogeneous diet in solitary ascidians and diet heterogeneity in sponges). However, sponges appear to be subjected to a seasonal energy shortage due not to a reduction in energy intake but to an increase in energy output (i.e. respiration).

Overall, a pattern emerges from the studies of feeding and respiration of BSF which suggests that the seasonal environmental conditions in the Mediterranean may induce some taxa into a predictable pattern of summer dormancy. Physiological changes associated with dormancy help the organism survive adverse conditions such as low food and extreme weather. The great plasticity of invertebrates allows them to withstand net energy deficits by digesting themselves until additional food becomes available. A three-year monitoring of the protein-carbohydrate-lipid balance of some Mediterranean gorgonians (*Paramuricea clavata* among them) shows a periodic summer minimum in energy storage macromolecules such as lipids and proteins (Rossi 2002). These results agree with the expected physiological changes associated with a summer energy shortage, and with the annual pattern of investment in growth (Coma et al. 1998b) and reproduction (Coma et al. 1995a) of this and other Mediterranean gorgonians (Velimirov 1975, Weinberg and Weinberg 1979). The summer energy shortage may also be the possible cause of the formation of growth rings in Mediterranean gorgonians (e.g., Mistri and Ceccherelli 1993, 1994). Thus, the seasonal occurrence of an energy shortage appears to be an important determinant of the dynamics of BSF at organism level. All this evidence contributes to indicate that summer dormancy exhibited by some taxa in the Mediterranean (Coma et al. 2000) appear to be related to seasonal energetic constraints. Can the seasonal occurrence of an energy shortage influence the dynamics of BSF at population and community level?

An energetic approach to understanding population and community level dynamics in BSF

A recent mass mortality event of benthic suspension feeders that affected several hundreds of kilometers of coast line in the Ligurian sea (NW Mediterranean, Cerrano et al. 2000, Perez et al. 2000, Romano et al. 2000) may provide insights into the consequences of energetic constraints at population and community level. In general, anthozoans (gorgoniacea and zoanthidea) and sponges were the most affected taxa, with proportion of affected individuals ranging between 60 to 100% (Cerrano et al. 2000, Perez et al. 2000). We present the current state of knowledge about mass mortality events in Mediterranean benthic communities and address the contribution of the energetic constraint hypothesis to the understanding of these events.

Is mass mortality of benthic communities a new event?

Mass mortality events have occurred in the past in the Mediterranean. In September 1983, a mass mortality event affected soft bottom benthic communities in the Gulf of Trieste (North Adriatic Sea, Stachowitsch 1984). This event affected the complete spectrum of macroinfauna (sponges, brittle stars, holothurians, echinoids, polychaetes, sipunculids and bivalves) within an estimated area of several hundreds of square kilometers. Local scale (several tens of meters or kilometers) mass mortality events have been recorded in the Gulf of Trieste since the early 1970s (reported mass mortality events: 1974, 1976, 1980, 1983, Fedra et al. 1976, Stefanon and Boldrin 1982, Stachowitsch 1984). These events are related to the periodic occurrence of algal blooms (see below) which has been known for centuries (Molin et al. 1992). The regional scale (several hundreds of kilometers) event that affected soft bottom benthic communities in September 1983 coincided with the first report of a local mass mortality event in hard bottom communities in the Ligurian Sea (NW Mediterranean, Harmelin 1984). This mass mortality event on hard bottom communities affected red coral populations shallower than 20 m after the summer of 1983 at La Ciotat (Ligurian Sea; Harmelin 1984). Since then, several other local mass mortality events affecting cnidarian and sponge species in hard bottom communities have been reported in the NW Mediterranean (Coma and Zabala 1992, Gaino and Pronzato 1992, Bavestrello et al. 1994, Mistri and Ceccherelli 1996a, b, Rodolfo-Metalpa et al. 2000). A common feature of these previously reported mass mortality events in hard bottom communities is that they were all events affecting local scales of coast line. A mass mortality episode on a regional scale, such as the one that affected benthic communities in the Ligurian sea in summer-fall 1999, had not been previously reported in Mediterranean hard bottom communities. However, biological surveys of benthic communities capable of detecting an event of the characteristics of a mass mortality event were only initiated in the late 1950s in the Mediterranean (Tortonese 1958, Pérès and Picard 1964).

Causes of the mass mortality events of benthic communities

Oxygen depletion has been reported as the immediate cause of the mass mortality of soft bottom benthic communities in the North Adriatic Sea (Fedra et al. 1976, Stefanon and Boldrin 1982, Stachowitsch 1984). The high pelagic productivity of the North Adriatic Sea favors the development of filamentous algae (mainly Tribonemales and Ectocarpales) which produces large amounts of mucilage that sinks to the bottom and contributes to oxygen depletion (Štirn et al. 1974). The effect of mucilage and other factors interact to contribute to the anoxic conditions that caused the mass mortality events in the North Adriatic Sea (Stachowitsch 1984). These episodes are similar to the periodic phenomena that affect benthic communities in North Atlantic fjords, which are also attributed to oxygen depletion (Pearson and Rosenberg 1978, Jørgensen 1980).

Previous local scale mass mortality events in hard bottoms were characterized by coenenchymal necrosis in cnidarians (Harmelin 1984, Coma and Zabala 1992, Bavestrello et al. 1994, Mistri and Ceccherelli 1996a, b), and by a decay of spongine fibres in sponges (Gaino and Pronzato 1989, 1992, Gaino et al. 1992). The cause of the sponge mass mortality appears to be related to a bacterial infection (Gaino and Pronzato 1989, 1992). However, it is unclear whether the bacterial infection was the direct cause of the mortality or an indirect contributor (see below). Many possible causes have been suggested to explain local mass mortality events of gorgonian populations in the Mediterranean (Arnoux et al. 1992, Bavestrello et al. 1994, Mistri and Ceccherelli 1996a). Arnoux et al. (1992) related the mass mortality of deep gorgonians (>80 m) between Nice and Marselle (France) to sedimentation of particulate matter carried by the Ligurian current. Bavestrello et al. (1994) examined and rejected the hypothesis that a disease may have been involved in the mass mortality event observed in Portofino because microorganisms from healthy and damaged gorgonians were similar and did not differ in abundance. Mistri and Ceccherelli (1996a) attributed the coenenchymal necrosis of gorgonians that affected the demographic structure of the population in the strait of Messina (Tyrrhenian Sea, Mistri and Ceccherelli 1996b) to the large amount of mucilage produced by filamentous algae. The mucilage may have caused prolonged anoxic conditions when entangled in the branches of the colonies. In other locations, large accumulations of mucilage have been observed trapped in the branches of the gorgonians but without producing coenenchymal necrosis because the mucilage was rapidly removed by strong currents in a few days (Coma and Pola 2000). The involvement of microorganisms in the summer 1999 mass mortality event in the Eastern Ligurian Sea was disregarded by Cerrano et al. (2000) because only opportunistic pathogens were observed in damaged colonies. Furthermore, the mortality of gorgonians was not density dependent nor did it exhibit patchy distribution as would be expected if a disease had been involved (Cerrano et al. 2000). The effect of the same event on the gorgonian *Corallium rubrum* in the Marselle area exhibited a much patchier distribution (Garrabou et al. 2001). However, habitat related variations in temperature and chronic contamination (Arnoux et al. 1992) was suggested to explain patchy distribution of the event's effect (Garrabou et al. 2001) rather than microorganisms. Overall, no significant occurrence of disease or mucilage has been reported in relation to the 1999 regional scale mass mortality event that occurred in the Ligurian Sea (Cerrano et al. 2000, Perez et al. 2000). Biological surveys conducted after the mass mortality event suggest that the most probable cause was a climatic one. The elevated temperatures present during summer and early autumn have been invoked as the most likely cause of the 1999 mass mortality event (Cerrano et al. 2000, Perez et al. 2000).

Contribution of the energetic constraints hypothesis to the understanding of mass mortality events in Mediterranean benthic communities

The characteristic Mediterranean summer conditions of high water column stability and high temperature are conducive to stratification of the water column, particle sinking, and nutrient exhaustion, thus resulting in a severe depletion of suspended resources (Estrada 1996) that primarily affects microplankton and detrital POC (Fig. 1). These climatic conditions are the basis of the low food supply that subjects many BSF taxa to starvation in the summer. The fact that the mass mortality event specially affected the taxa that exhibit energy shortage, such as anthozoans and sponges, suggests that energetic constraints may contribute to the understanding of the mass mortality event.

Biological surveys suggested high temperature values as the cause of the mass mortality event (Cerrano et al. 2000, Perez et al. 2000). However, the systematic observations of the thermal structure in the Gulf of Marseilles (NW Mediterranean) indicate that the surface temperature did not show exceptionally high values ($24.1°C \pm 0.5$ in September, Romano et al. 2000). The persistence of both the water column stability and the high temperature values (Cerrano et al. 2000, Romano et al. 2000) were the most distinctive climatic anomaly. This stability was due to the scarcity of NW winds during this time period (Romano et al. 2000).

Climatic conditions of high water column stability and high summer temperature are common features of both soft bottom and hard bottom mass mortality events (Stachowitsch 1984, Romano et al. 2000). These climatic conditions appear to trigger the interaction of other factors leading to mass mortality events of benthic communities. The fact that all these events, both in soft and hard bottom communities, always occur in early autumn supports this reasoning.

The climatic and hydrographic conditions that occurred during the summer of 1999 in the Ligurian Sea represented a prolongation of the characteristic Mediterranean summer conditions (i.e. reduced resources, high water column stability, and high temperature) at a temperature 2–3°C above average (Cerrano et al. 2000, Romano et al. 2000). Organisms may be able to withstand the normal duration of adverse conditions that the summer period represents (Coma et al. 2000). However, the anomalous environmental conditions that occurred in the summer of 1999 may have led to a prolongation of the period of reduced resources which, together with the temperature increase, may have driven taxa to an acute energy shortage. Prolonged starvation has been shown to decrease defense systems against pathogens (Newell and Branch 1980). Therefore, despite the observed presence of antimicrobial compounds in many healthy invertebrate taxa (Jensen et al. 1996), prolonged starvation together with the increase in respiration rate related to temperature increase may lead to an acute energy shortage, the lost of defensive capacity, and death of the organisms. In this sense, the pathogen would not be the direct cause of the mortality but an indirect contributor (Harvell et al. 1999). Our interpretation is that organisms may have failed to withstand an anomalous prolongation of the summer conditions, which was accentuated by an increase in temperature. The energy shortage phenomenon may provide a mechanism to understand how the anomalous climatic conditions may have induced the mass mortality of some BSF taxa.

Conclusions

We have examined the outcomes of recent studies on the seasonal variation of seston composition, natural feeding and respiration rates of BSF in the Mediterranean Sea to assess whether a pattern across particular studies exists that could provide evidence of food as a constraining factor. This has contributed to understanding why summer conditions are unfavorable to some taxa and why the response of different taxa to the same conditions vary. The present review stresses the existence of a common energy shortage phenomenon mainly related to low food availability as an important determinant of the dynamics of most BSF taxa at organism level. Furthermore, the seasonal occurrence of an energy shortage has been seen to contribute to the understanding of the mechanism that triggers mass mortality events in the Mediterranean, thus indicating that seasonal energetic constraints also affect the dynamics of BSF at population and community level. Therefore, the extant data points up the crucial role of food as a constraining factor for benthic littoral ecosystems in oligotrophic areas like the Mediterranean, with important variations in seston abundance and composition.

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