On the ecophysiology of the sponge *Halichondria panicea* in Kiel Bight. II. Biomass, production, energy budget and integration in environmental processes

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ABSTRACT: The role of the sponge *Halichondria panicea* was analyzed in the red algal zone of the Western Baltic. Data on biomass changes in a field population of *H. panicea* at Boknis Eck at the entrance of Eckernförde Bight agree well with observations from cage growth experiments (Barthel 1986); this indicates that the population suffers only negligible mortality through predators. Biomass data are combined with results on respiration rates (Barthel & Theede 1986) to yield information on energy demand of this species. Using field data on water temperature and sediment structure in Kiel Bight estimates are made of total biomass and nutrient release by *H. panicea* in Kiel Bight. Field observations on the life cycle and relations to other animal species are discussed.

INTRODUCTION

The sponge *Halichondria panicea* Pallas occurs in sometimes enormous numbers in the red algal zone in the Western Baltic Sea. Despite its ubiquity, virtually nothing is known about its biomass, production and the role it plays in the red algal community.

The genera *Phyllophora* and *Phycodrys* form the preferred substrata for *Halichondria panicea* (Barthel 1986), implying that the majority of the sponges occur within the euphotic zone. Whereas studies have been made in this area on the role of some benthic infauna in energy and matter cycles (Graf et al. 1984) and on the importance of mobile epibenthos (Asmus et al. 1980), the role of sessile epibenthos such as sponges or tunicates has been more or less neglected up to now.

Considering the high biomass values these sponges can attain (Theede 1981), their population dynamics, energy demand and interactions with other community members certainly merit attention.

MATERIALS AND METHODS

Biomass data were collected at the 'Hausgarten' station at Boknis Eck near the entrance of Eckernförde Bight, Western Baltic Sea. Between December 1983 and April 1985 the sponge population was sampled by divers at about monthly intervals. A $0.25 \, \text{m}^2$ metal frame was deployed and all algal material within the frame was removed from the substratum and collected in net bags. Two parallel samples were taken at 6, 8 and 10 m water depth at each sampling date. In the laboratory, general characteristics of the sample, e.g. mass occurrence or absence of single macrobenthos species, appearance and colour of sponges were recorded. The sponges were then removed from their substratum and the drained wet weight (WW) was determined. Subsamples were taken for the determination of dry weight (DW) and organic substance expressed as ash-free dry weight (AFDW). Biomass values are expressed as mean AFDW m^{-2}.

Respiration rate measurements were carried out with a flow-through respirometer as described by Dries et al. (1978) and were published in an earlier paper (Barthel & Theede 1986).

Temperature data for the sampled station were supplied by M. Weigelt & P. Seifert and were published by Barthel (1986).

RESULTS

Biomass and production

Biomass of *Halichondria panicea* at Boknis Eck varied considerably with season at all 3 depths investi-

gated (Fig. 1). Starting from a low biomass in winter, sponges began to grow in early spring, when ambient water temperature rose. At first, growth was slow, but accelerated towards summer. In August, highest biomass values were reached simultaneously at all depths, but while the biomasses found at 8 and 10 m depth were quite similar (about 24 g AFDW m^{-2}), a much higher biomass of 40 g AFDW m^{-2} was found at 6 m water-depth. At 6 m, the vivid green colour of many sponges indicated the presence of high numbers of algae in the sponge tissue.
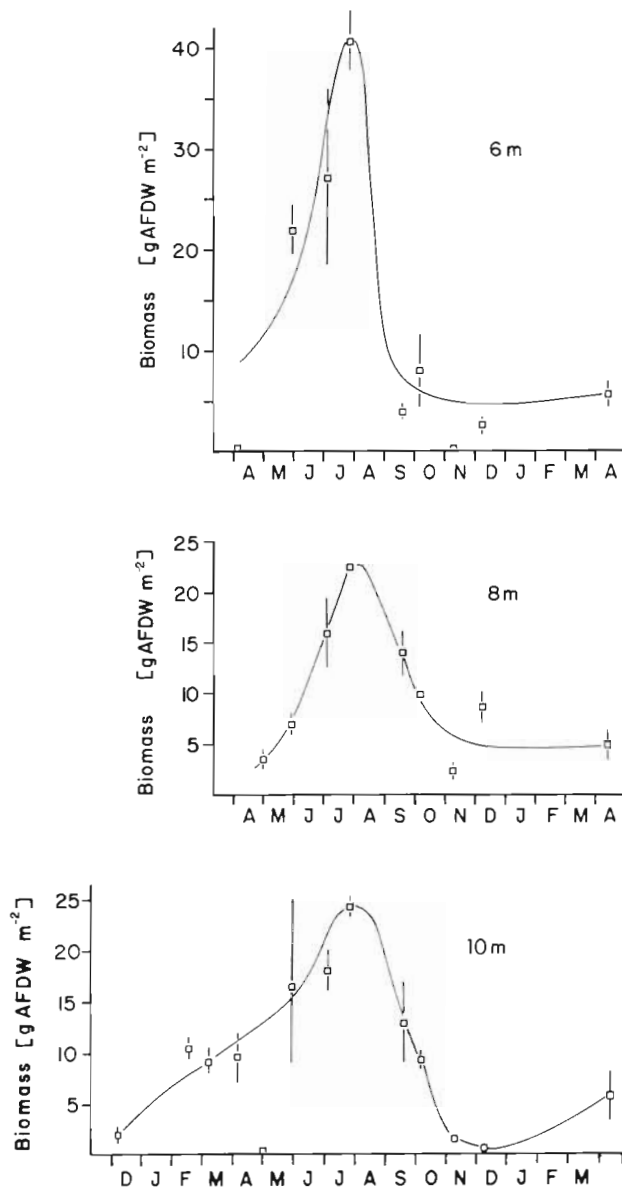

Fig. 1 *Halichondria panicea*. Development of biomass in the natural population at Boknis Eck, Western Baltic Sea at 6, 8 and 10 m water depth. Curves are hand-fitted. Biomass development follows a similar time course at all depths with strong growth in early summer and decrease in fall. Note the high peak value in 6 m water-depth compared to 8 and 10 m

After August, sponge biomass decreased at all depths; this process was accompanied by weight and size decrease of individual sponges and also by an alteration in sponge shape, which changed from lumpy/compact to a thin and stringy form. The same process has been recorded in cage experiments conducted at this station and was attributed mostly to degeneration of adult sponges after reproduction (Barthel 1986). During the time of most intense biomass loss in the field, the only ascertained predator of *Halichondria panicea* in the Western Baltic, the small dorid nudibranch *Lamellidoris muricata* O. F. Müller, occurred in very large numbers in the samples. Higher numbers were noted first in August and September and highest numbers of about 25 to 35 ind. 0.25 m^{-2} were recorded in October. In contrast, *L. muricata* was hardly detected at other times of the year.

From the data presented in Fig. 1, it is possible to calculate the minimum production of *Halichondria panicea* at the Boknis Eck station as the difference between the lowest and highest observed biomass (Arntz 1971): At 10 and 8 m depth, the lowest biomass value (December) was about 2 g AFDW m^{-2}, at 6 m, the lowest value (April) was about 8 g AFDW m^{-2}; the highest (August) was 24 g AFDW m^{-2} at 8 and 10 m and 40 g AFDW m^{-2} at 6 m water-depth. Thus, minimum production amounts to 22 (8 and 10 m) and 32 g AFDW m^{-2} (6 m). The mean biomass would be 10.5 (8 and 10 m) and 21 g AFDW m^{-2} (6 m). This would mean rather low P/B ratios of 2.1 (8 and 10 m) and 1.8 (6 m), but it has to be borne in mind that this minimum production is certainly an underestimate as it neglects that part of production lost to predation etc. (Arntz 1971).

Energy demand

In combination with previous laboratory respiration experiments (Barthel & Theede 1986) it is possible to calculate a minimum energy demand C for this species ($C = G + R + U + F$, where C = consumption, G = growth and reproduction, U = excretion, F = faeces, according to the formulation suggested by the International Biological Program [Crisp 1971]). An example for 10 m water depth was obtained by performing the following steps: (1) Temperature data for the Boknis Eck station at different times during the year were taken and the respiration rate of *Halichondria panicea* at these temperatures was calculated or extrapolated from previous respiration measurements (Barthel & Theede 1986, Fig. 2). (2) Respiration rates (ml O_2 [g AFDW]$^{-1}$ h^{-1}) were multiplied by sponge biomass (data from Fig. 1, 10 m depth). Multiplied in turn by 24, this yielded the respiration in ml O_2 m^{-2} d^{-1}, neglecting possible circadian rhythms which might occur in the

field. In the laboratory experiments, no such rhythms were observed during 24 h measurements. (3) By using the relation 1 ml O_2 consumption $\triangleq$ 19.62 J, the respiration data were converted into energy demand. (4) Energy loss via respiration was assumed to account for 50 % of the total food energy requirement C, which in turn was calculated by multiplying the Joule values by a factor 2.

Table 1 gives a summary of the calculations done and the data used as a basis. Results in terms of energy requirements of *Halichondria panicea* over the year are illustrated in Fig. 3. The combined effects of high biomass values in summer and higher temperatures requiring more energy for total energy expenditure cause a pronounced peak of estimated energy demand in August. After August, quickly decreasing biomass values, even more than lower temperatures, cause food energy demand to fall again.

The main questions arising from these calculations are: (1) How is the estimated energy demand met during various times of the year? (2) How high a biomass does *Halichondria panicea* constitute in Kiel Bight and (3) How is this biomass built up by sponges in spring and early summer utilized in the Kiel Bight food web?

DISCUSSION

The results on biomass development of *Halichondria panicea* at Boknis Eck in the Western Baltic Sea are in excellent agreement with those drawn from cage growth experiments at the same location (Barthel 1986; Fig. 4). In spring, growth seems to be primarily dependent on ambient water temperature and even a good supply of food during spring phytoplankton bloom in March when water temperatures are low does not trigger growth. Comparison with cage growth experiments shows that growth of *H. panicea* in the field really lasts until the middle of August, which could not be documented with the cages due to sampling difficulties (Barthel 1986). Furthermore, as mean individual size investigated with the cages and population biomass observed in the field show exactly the same qualitative and quantitative development (cages: increase from 100 to 240 % mean individual organic body mass between March and August; field biomass: increase from 10 to about 24 g AFDW m^{-2} during the same time span), it can be argued that loss of whole sponges, e.g. by predation or mortality, is negligible in this biotope. If destruction of whole sponges was occurring, biomass reached in the field would – on the basis of identical growth rates in cages and in the field – be visibly lower. This conclusion confirms the view of Burton (1948), who argued that death of whole *H. panicea* occurred comparatively seldom, but that older sponge parts disappeared with time.
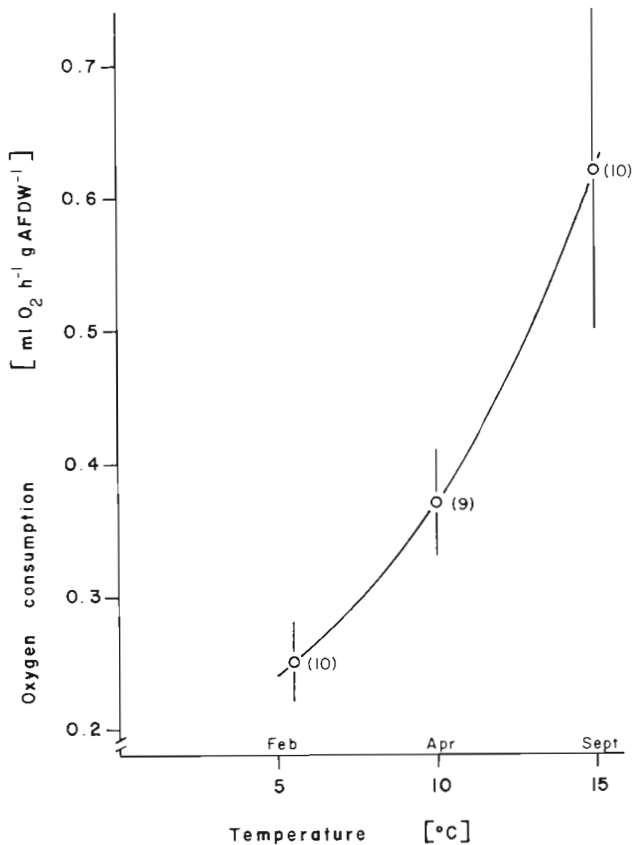
Fig. 2. *Halichondria panicea*. Dependence of oxygen consumption on temperature. Acclimation time in the lab at least 3 wk. Duration of each measurement about 24 h. Values in brackets: number of parallel experiments. From Barthel & Theede (1986)
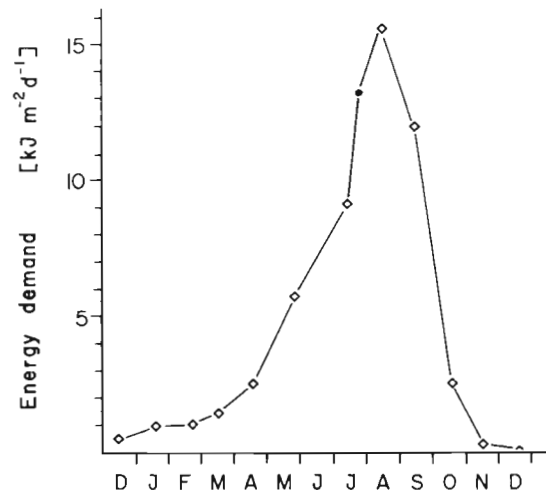
Fig. 3. *Halichondria panicea*. Food energy demand at the Boknis Eck station, 10 m water-depth, 1984. Data from Table 1
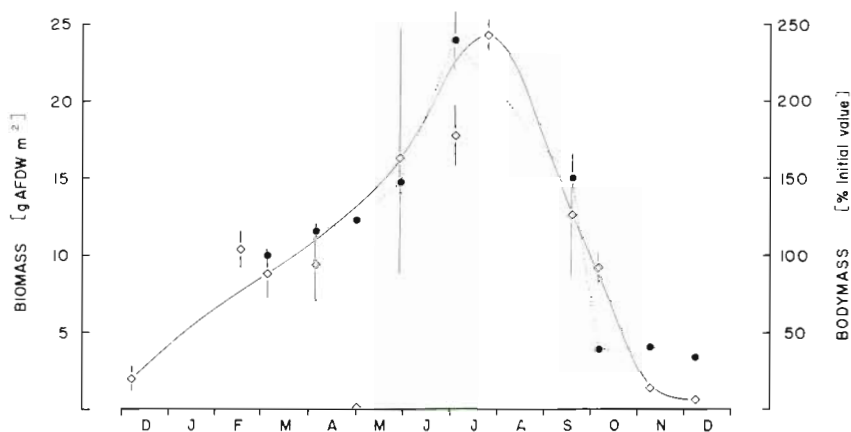
Fig. 4. *Halichondria panicea*. Comparison of results from field growth experiments (●·····●) and monitoring of biomass development (◇——◇) atr the Boknis Eck station, 10 m water-depth. Means and standard deviation of means. Curves are almost parallel and respective units show that the development matches qualitatively as well as quantitatively

In other marine areas predation on sponges can be quite important and often serves to control population development (Bakus 1964, 1969, Carefoot 1967, Randall & Hartman 1968, Elvin 1976, Guida 1976, Dayton 1979). The relative absence of predators in Kiel Bight is probably partly caused by low salinities (10 to 25 ‰) inhibiting the invasion of osmotically less resistant species. Up to now we lack data concerning the grazing potential of the common sponge-eating dorid nudibranch *Lamellidoris muricata,* so it is very difficult to assess its impact on the sponge population.

Low salinities and ensuing osmotic stress may also be a reason for the rather low P/B ratio found for *Halichondria panicea.* Observations (Barthel 1986) indicate that the life of a *H. panicea* starts with release of larvae about August and ends with the sponge's degeneration after reproduction the following year about December, when the sponges usually almost totally disappear.

This implies a mean life span of about 1.5 yr in the Baltic Sea red algal zone (life spans are higher in the North Sea; Barthel 1985). According to an equation by Robertson (1979) the P/B ratio for a species with this life span should be 3.55, not 2.1 at 8 and 10 m and 1.8 at 6 m respectively, found for *H. panicea.* Waters (1977) gives a P/B ratio of 5 for univoltine species, and of 2 for hemivoltine species. If we assume the life span of *H. panicea* to range somewhere between these extremes, a mean P/B ratio of 3.5 would result. On the other hand, it is also possible that P/B ratios calculated for metazoans do not hold for the more simply organized sponges. As data of sponge P/B ratios are lacking, and my calculations are based on minimum production, this hypothesis requires further investigation.

Biomass measurements of *Halichondria panicea* have never been performed in a larger area of Kiel Bight; the only other data available also derives from

Table 1. *Halichondria panicea*. Calculation of energy demand at the Boknis Eck station in 10 m water depth, 1984. Dates are those of the temperature measurements, except *, which is the date of highest sponge biomass in the field; respiration rate at this temperature calculated from laboratory experiments (Barthel & Theede 1986); biomass calculated from biomass curve (Fig. 1); oxygen consumption calculated by multiplying respiration rate × biomass × 24 h; energy requirement for respiration alone based on the conversion factor 1 ml oxygen consumption $\triangleq$ 19.62 kJ; total food energy demand C based on the assumption that respiration accounts for 50 % of total energy consumption

Date	Water temperature (°C)	Respiration rate ml O_2 g AFDW^{-1} h^{-1}	Biomass (g AFDW m^{-2})	Oxygen consumption (ml O_2 m^{-2} d^{-1})	Energy requirement of resp. (kJ m^{-2} d^{-1})	Total energy demand (kJ m^{-2} d^{-1})
14 Dec 83	4.6	0.21	2.5	12.6	0.25	0.50
18 Jan 84	3.0	0.18	6.0	25.2	0.50	1.00
22 Feb 84	1.4	0.15	7.5	26.1	0.51	1.02
16 Mar 84	1.9	0.16	9.5	36.5	0.72	1.44
17 Apr 84	4.7	0.22	12.0	63.4	1.24	2.48
25 May 84	10.7	0.40	15.0	144.0	2.83	5.66
13 Jul 84	13.4	0.55	17.5	231.0	4.53	9.06
25 Jul 84 *	14.0	0.58	24.0	331.0	6.50	13.00
15 Aug 84	16.1	0.70	23.5	394.8	7.75	15.50
14 Sep 84	14.7	0.61	14.0	203.3	3.99	7.98
18 Oct 84	12.6	0.49	5.5	64.0	1.26	2.52
15 Nov 84	9.5	0.35	1.0	8.3	0.16	0.32
18 Dec 84	4.6	0.21	0.5	2.5	0.05	0.10

Boknis Eck station (Theede 1981). Hence, in calculating a total for the Bight, we must rely on data from this site alone. However, since previous workers have assumed the ecological situation at Boknis Eck to be fairly typical for the Western Baltic Sea (e.g. Martens 1975), we may assume the sponge biomass found in the red algal zone between 2 and 10 m at Boknis Eck to be typical for the area considered.

Macroalgae, which form the most important substrate for *Halichondria*, need substrata like bedrock or glacial lag sediment (stones up to boulder size). While bedrock is not exposed in Kiel Bight, Babenerd & Gerlach (1987), report that 530 km² or 21 % of Kiel Bight is covered with lag sediment. With few exceptions (Black 1978), *H. panicea* only occurs from 2 to about 10 m water depth in the Baltic, leaving 203 km² or 8 % as an area suitable for the settlement of macroalgae forming the most important substrate for *Halichondria*. Thus the total sponge biomass in Kiel Bight in 1984 amounts to between 400 t AFDW in winter and 4900 t in summer.

Biomass development in *Halichondria panicea* through the year closely resembles that of other macrobenthos (e.g. Anders & Möller 1984, Brey 1984). But different species of macrofauna with similar seasonal development can have quite different impacts on the ecosystem, depending on their location and metabolic strategy. Many quantitatively important benthic invertebrates in the Baltic Sea store energy during sedimentation of the spring phytoplankton bloom and later utilize e.g. stored glycogen to meet their energy requirements for growth, metabolism and reproduction (Graf et al. 1984). *H. panicea* does not store large amounts of glycogen or fat during the spring bloom (Barthel 1986), nor have high amounts of glycogen been found in other sponge species (Stone 1970, Elvin 1979). This and the fact that low ambient temperatures prevent *H. panicea* from taking advantage of the high food concentrations during the spring phytoplankton bloom imply that the sponge probably has to rely mostly on phytoplankton production in summer, as does herbivorous zooplankton. The role of dissolved organic matter, known to be important for other species (e.g. Reiswig 1974, Ferguson 1982) cannot be assessed as yet for *H. panicea*. According to Reiswig (1974), dissolved organic matter is probably not taken up by the sponge cells themselves in the first place, but by symbiotic bacteria (for a detailed discussion of this problem see Vacelet 1979). Electron microscope studies have not revealed such symbiotic bacteria in *H. panicea* (Barthel 1985, Langenbruch pers. comm.). Hence, *H. panicea* seems to occupy a similar nutritional niche to herbivorous zooplankton and is less comparable to those macrobenthos species possessing energy stores, such as bivalves.

In the calculations leading to Table 1 and Fig. 3, suspended particulate matter is thus considered to be the prime energy source sustaining the observed growth. Energy loss via respiration is assumed to account for 50 % of the total food energy requirement $C = G + R + U + F$. This estimate is mainly derived from results obtained by Reiswig (1971, 1974) on *Mycale* sp. The resulting food energy demand (Fig. 3) of *Halichondria panicea* peaks during summer, and a corresponding part of the shallow water phytoplankton, detritus and bacteria, which also serve as food, is removed from the water column by the sponges.

This means that the food energy taken up by this organism is quite considerable and the corresponding excretion of plant nutrients coupled to this energy flux should be intense. We have as yet no direct measurements of sponge phosphorus and nitrogen excretion, but on the basis of the respiration measurements and the Redfield ratio of $C:N:P$ of $106:16:1$ (Redfield 1934 in Parsons et al. 1984) we can calculate that during the time of highest oxygen consumption (Fig. 3) *H. panicea* takes up about 0.36 g C m^{-2} d^{-1}, of which 50 % are lost by respiration. According to the Redfield ratio this would correspond to 0.023 g m^{-2} d^{-1} excreted inorganic nitrogen and 0.0007 g m^{-2} d^{-1} excreted phosphate-phosphorus or 4.7 tons inorganic nitrogen and 0.4 tons phosphate-phosphorus per day in Kiel Bight. These amounts are much lower than those calculated for example for *Mytilus edulis* in the Eastern Baltic by Kautsky & Wallentinus (1980), but a much greater amount of nutrients will be released during the time of degeneration of the adults within the euphotic zone. If we assume that practically all sponge biomass produced during spring and summer is remineralized, and again apply the Redfield ratio, this yields a release of about 2350 t carbon, 303 t nitrogen and 9 t phosphate in the second half of the year which certainly contributes to the sustenance of the summer and fall phytoplankton production.

The calculations presented so far bear uncertainties in the respiration rates: firstly respiration rates vary individually to a large extent, and secondly it is problematic to use uncorrected field AFDWs as a biomass basis for these calculations in an organism where a large part of the organic substance is metabolically inactive skeletal protein, and moreover recent investigations (Barthel unpubl.) have shown that the amount of skeletal material and thus activity of *Halichondria panicea* varies with season. Also the presence of varying numbers of probably photosynthetically active algae in the sponge tissue might affect respiration and nutrient release and perhaps growth of *H. panicea* (for a discussion of sponge/algae symbioses see Sará & Liaci 1964a, b, Sará 1966, 1971, Eimhjellen 1967, Muscatine et al. 1967, Gilbert & Allen 1973, Wilkinson &

Vacelet 1979, Frost & Williamson 1980, Christensen 1985).

Halichondria probably also influences sedimentation. Of the materials *Halichondria* filters through its aquiferous system, a certain part will leave again as either feces or pseudofeces, i.e. material taken up and exocytosed by the sponge undigested as larger membrane-covered units. These particles will sink to the bottom more quickly than the original small particles ingested. So while the absolute amount of sedimentable material in summer is reduced by the activity of the sponge, the part passing through it will sink more quickly, resulting in an even flow of food to the bottom community in the sedimentation-poor period of summer.

The question of the fate of the sponge biomass, i.e. how much will enter the sedimentation process and detrital food chain, how much will be reconverted into dissolved plant nutrients and dissolved organic matter, and how much will be either washed ashore or transported as bed load into the deeper muddy parts of Kiel Bight remains to be investigated.

Besides influencing primary production and sedimentation, *Halichondria panicea* also has a structuring effect by being obligatory or additional host for a number of other organisms in the Kiel Bight area. The hydrozoan *Dipurena spongicola* spends its entire life cycle in *H. panicea* (Anger 1972) and the polychaete *Polydora ciliata* which normally bores in clam shells and similar substrata settles on the sponge surface (Hempel 1957, author's obs.) as do a number of ciliates, nematodes and ostracods (Anger 1972). Hence, *H. panicea* contributes to the diversity in the red algal community.

CONCLUSIONS

In terms of both biomass and energetics, the sponge *Halichondria panicea* comprises an interesting compartment of the Kiel Bight ecosystem. Its most notable interaction with the ecosystem is withdrawal of shallow-water phytoplankters from the euphotic zone in summer, when the sponge's energy demand is greatest, and in turn supplying plant nutrients and dissolved organic substance to the system. In the absence of noteworthy predation, only a minor share of sponge biomass in the Western Baltic Sea seems to be transported directly to higher trophic levels. Most seems to be recycled immediately within the euphotic zone, or to enter the detrital food chain. Hence, sponges can be considered as a trophic loop, converting phytoplankton into animal biomass in the euphotic zone, thus diminishing the amount of sedimenting organic substance in summer; on the other hand, sponges also enhance sedimentation speed for particles passing through

them undigested. This again influences the flux of energy and matter from water to sediment. Year-to-year variations in total sponge biomass are likely to divert the flow of primary production either more to the detritus food chain, or, when sponge biomass is low, more to the grazing food chain.

Nutrient excretion by sponges stabilizes primary production in summer; in late summer, when nutrients in the water column are depleted, degeneration and disintegration of sponges again provide a nutrient pulse to primary producers. Nutrients appear never to be really depleted in the immediate vicinity of sponge- and other macrobenthos-bearing algae (Schramm pers. comm.), but to be continuously and quickly recycled along the short pathways between substrate algae and epibiont. Thus, measurements of nutrient release by both metabolically active and degenerating sponges are desirable. *Halichondria panicea* also adds to the diversity of the red algal community, by supplying substrate for other macrobenthos. Sponges and other epibenthic animals, such as tunicates, deserve more attention in energy budgets calculated for the Kiel Bight area.

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