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In situ determination of PCB biodeposition by *Mytilus edulis* in a Baltic coastal ecosystem

Mikael Björk[1,*], Michael Gilek[1], Nils Kautsky[1], Carina Näf[2]

[1]Department of Systems Ecology, Stockholm University, 106 91 Stockholm, Sweden
[2]Institute of Applied Environmental Research (ITM), Laboratory for Aquatic Ecotoxicology, Stockholm University, 106 91 Stockholm, Sweden

ABSTRACT: Biodeposits of the blue mussel *Mytilus edulis* and pelagic and near-bed settling particulate matter were collected *in situ* over a 1 yr period in a coastal area of the Northern Baltic proper. The amounts of carbon and PCBs (polychlorinated biphenyls) in the collected biodeposits were compared to those in pelagic and near-bed settling material and rates of carbon and PCB biodeposition by mussels were estimated. The filter-feeding activity and subsequent release of faecal matter by the mussels increased gross sedimentation of carbon to benthos by 45% if compared to areas with no mussels. By selectively feeding on particles rich in organic carbon the mussels also concentrated associated contaminants and thereby increased gross sedimentation of PCBs by 50%. This suggests that mussel biodeposition will enhance the availability of PCBs to benthic deposit feeders living in or in the vicinity of mussel beds. Extrapolation of the experimental results to the total Swedish coastal zone of the Baltic proper indicates that mussel biodeposition is responsible for a significant part of PCB net sedimentation, i.e. 17% or 96 kg yr^{-1} Consequently, even when seen from a large geographical scale, mussels are important modifiers of PCB cycling by directing considerable amounts of PCBs towards the benthic food web and thereby influencing the retention time of these and probably many other contaminants in the coastal zone. It is also likely that changes in mussel biomass, for example owing to shifts in primary production or salinity, will markedly affect the transport and fate of contaminants in the Baltic Sea.

KEY WORDS: *Mytilus edulis* · Biodeposition · Contaminant fate · Sedimentation · Organic carbon · Suspension feeding

INTRODUCTION

Today the magnitude of carbon flows are usually rather well understood and quantified in coastal areas, whereas comparatively little information is available on how pollutants are circulated through the ecosystem. Since dense beds of filter-feeding mussels may significantly affect carbon flows and nutrient cycling, and thus have a large influence on ecosystem processes in shallow coastal waters (Kautsky & Wallentinus 1980, Cloern 1982, Officer et al. 1982, Dame 1993, Kautsky 1995), it is of interest to also assess their role in the circulation of pollutants, especially those that can be assumed to be linked to the carbon flows. In the Baltic Sea, the blue mussel *Mytilus edulis* totally dominates benthic animal biomass in coastal areas (Kautsky 1981, Kautsky & Kautsky 1996). These mussels function as a connection between pelagic production and the benthos through biodeposition of faecal matter (Kautsky & Evans 1987). Biodeposition has been shown to significantly increase the downward transport of particulate matter from the water column to the bottom (Smaal et al. 1986, Kautsky & Evans 1987, Dame 1993, Graf & Rosenberg 1997) and may also increase the vertical flux of hydrophobic organic contaminants (HOCs) associated with this particulate matter (Gilek et al. 1997). This will increase not only the net sedimentation of HOCs to mussel beds, but also the exposure of HOCs to other benthic organisms. Mussels may even on a large geographical scale influence the transport and fate of contaminants. In a budget model of HOC cycling by blue mussels, Gilek et al. (1997) estimated from literature data that mussel biodeposition is responsible for a sig-

*E-mail: mikaelb@kemi.se

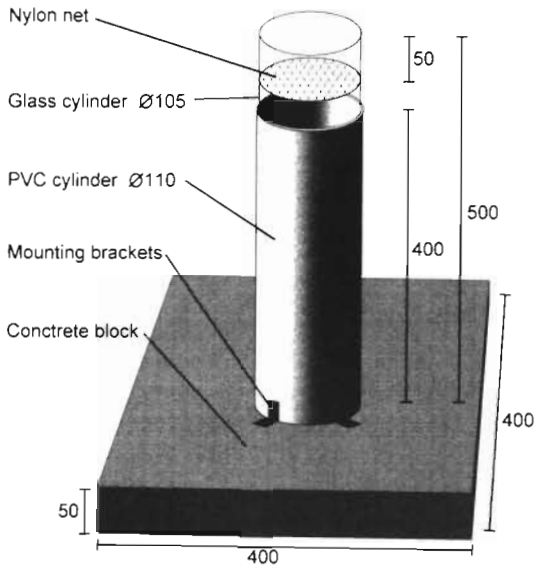

Fig. 1. Design of the bottom sediment traps used to collect settling particulate matter (SPM) or *Mytilus edulis* biodeposits. Settling material was collected in glass cylinders (height 500 mm, diameter 105 mm). The tops of all used cylinders were covered by a nylon net (3 mm mesh, 50 mm from the top). A group of 30 mussels (15 to 20 mm in shell length) was placed on the nylon net of each cylinder used to collect biodeposits (not shown in the figure), whereas cylinders used to collect SPM did not receive any mussels. All distances are given in mm

nificant part of PCB net sedimentation in the Swedish coastal zone of the Baltic proper, i.e. 17 %. However, the authors concluded that this model had a low numerical precision due to a lack of data on near-bed PCB exposure and insufficient knowledge of several processes in the field. The objectives of the present study were to generate more information on the PCB content of near-bed particulate matter, which is utilised as food by the mussels, and to quantify the *in situ* rates of PCB biodeposition by Baltic blue mussels.

MATERIALS AND METHODS

Experimental methods and design. Mussel biodeposits and settling particulate matter (SPM) were collected during 2 periods, from October 21, 1996, to March 24, 1997, and from May 15, 1997, to September 22, 1997, referred to as the winter and the summer period, respectively. To collect biodeposits and near-bed SPM, sedimentation traps (Fig. 1) were deployed directly on a mussel bed at 2 depths (7 and 15 m) off the wave-exposed shore of the island of Vrångskär in the vicinity of the Askö Laboratory (Southern Stockholm archipelago, Baltic proper, Sweden) (Fig. 2). Within each depth the sedimentation traps were placed approximately 7 m apart. In addition, self-buoyant pelagic sedimentation traps (Broman et al. 1990) were used to collect pelagic SPM only. These pelagic traps were anchored at a depth of 15 m (approximately 10 m apart), with the top of the sampling device floating approximately 7 m below the water surface (Fig. 2).

In the sedimentation traps settling material was collected in glass cylinders (height 500 mm, diameter 105 mm). The tops of all used cylinders were covered by a nylon net (3 mm mesh, 50 mm from the top, Fig. 1). At the beginning of each sampling period the glass cylinders were filled with seawater, and 10 ml of chloroform was added at the bottom of each cylinder as a preservative. The mussel *Mytilus edulis* was collected at a depth of 5 m at the site of the traps and sorted to a shell length of between 15 and 20 mm, which is typical of the slow-growing *Mytilus edulis* in the Baltic Sea. A group of 30 mussels was placed on the net floor of each cylinder used to collect biodeposits, whereas cylinders used to collect SPM did not receive any mussels. Mussel biomass within the biodeposition cylinders ranged between 66 and 103 g tissue dry weight (dry wt) m^{-2} during the experiments, which can be compared with an average mussel biomass in the surrounding mussel bed of 85 g tissue dry wt m^{-2} (Littorin & Gilek 1999). The glass cylinders were temporarily covered with aluminium foil before being placed in, or retrieved from, the traps with the help of SCUBA divers.

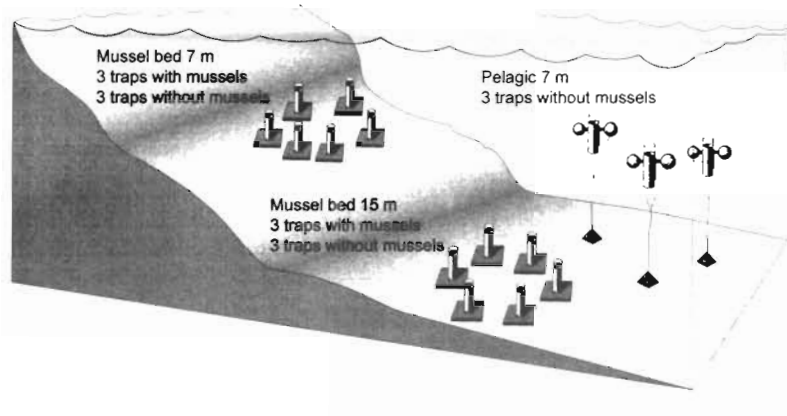

Fig. 2. Experimental design of the *in situ* determination of PCB biodeposition by *Mytilus edulis*. The experiment was performed on a natural mussel bed (Southern Stockholm archipelago, Baltic proper, Sweden) during both a winter (October 1996 to March 1997) and a summer period (May to September 1997). Note that the actual distances between sediment traps in the experiment were larger (approximately 7 to 10 m apart within each depth) than illustrated in this simplified picture (as described in the 'Materials and methods' section)

Table 1. *Mytilus edulis* shell length and shell-free tissue dry weight (mean ± SE) at the start (n = 30 mussels) and at the end (n = 15 mussels) of the winter and summer biodeposits sampling periods. Mussel density is the geometric mean ± SE of the mussel biomass at the start and end of each sampling period. Extractable organics and organic carbon content as % of dry wt (mean ± SE, n = 3 and n = 15, respectively), and organic carbon-normalised sum PCB_7 concentrations in shell-free tissue (geomean, [95% CI], n = 3). NA = not analysed

Sampling period (mo/yr)	Depth (m)	Mussel length (mm)	Mussel dry wt (mg)	Mussel loss & mortality (%)	Mussel density on traps (g C m^{-2})	Organics (%)	Carbon (%)	Mussel sum PCB_7 (ng g^{-1} C)
Winter start (10/96)		17.3 ± 0.3	15.8 ± 0.9	–	28 ± 1.6	12.9 ± 0.5	47.0 ± 0.0	48 [46–51]
Winter end (03/97)	7	20.2 ± 0.4	30.1 ± 2.2	3.3	39 ± 1.3	13.5 ± 0.8	47.0 ± 0.5	68 [60–78]
Winter end (03/97)	15	19.3 ± 0.5	21.4 ± 2.2	3.3	31 ± 1.8	10.7 ± 0.7	44.9 ± 0.2	86 [52–143]
Summer start (05/97)		17.9 ± 0.2	27.0 ± 1.4	–	48 ± 2.5	NA	NA	NA
Summer end (09/97)	7	22.4 ± 0.4	56.3 ± 4.4	43.3	46 ± 0.5	13.5 ± 0.1	46.8 ± 0.3	45 [39–53]
Summer end (09/97)	15	21.5 ± 0.5	37.5 ± 2.8	19.2	45 ± 2.6	13.5 ± 0.4	46.4 ± 0.5	69 [50–96]

The experimental design consisted of 3 treatments: season (winter and summer), depth (7 and 15 m) and biodeposits (traps with added mussels and traps without mussels to measure SPM) and 3 replicate traps (n = 3) of each treatment combination. Thus, during each collection period (winter and summer) 2 groups of triplicate traps (n = 3) were placed at each depth (7 and 15 m) directly on the mussel bed, 1 group of traps with mussels to collect biodeposits and 1 group without mussels to collect SPM (Fig. 2). At the start of each sampling period traps within each depth were randomly allocated to collect either biodeposits or SPM. An additional sampling of pelagic SPM (as described above) was also included to allow comparison of near-bed and pelagic SPM (n = 3 traps during each season).

Sampling. At the start and end of each sampling period the following measurements were made on mussels: shell length, tissue dry weight, carbon content, extractable organics and PCB content (Table 1). At the start of each sampling period measurements and analyses were performed on mussels taken from a stock of newly collected and sorted (15 to 20 mm) mussels. Mussels were then taken from the same stock and placed in the glass cylinders used in the biodeposition traps. Shell length and tissue dry weight were measured on n = 30 mussels, carbon content on n = 15 mussels, PCB content and extractable organics were measured on n = 3 pooled samples each consisting of 30 mussels. At the end of each sampling period the number of living and dead (shells) mussels remaining in each trap was recorded. Furthermore, the length of all remaining mussels and shells was measured, tissue dry weight and carbon content were analysed on a subsample of 5 mussels from each trap and the tissues from the remaining mussels in each trap (between 10 and 25) were pooled (n = 3) and used to analyse PCB content, total tissue dry weight and extractable organics. The trap material was collected at the end of each sampling period. A sub-sample of approximately 0.5 g dry wt was taken for carbon analysis from each trap. The rest of the SPM or biodeposits in each trap was used to determine total dry weight, and PCB concentrations (Tables 2 & 3).

Sample analysis. Mussel tissue dry weight was determined by drying shell-free mussels to constant weight at 60°C. Prior to carbon analysis all samples were dried at 60°C to constant weight and homogenised by grinding in an agate mortar. The carbon content of the samples was determined with a Carlo Erba elemental analyser (E1108 CHNS-O). Samples for PCB analysis were Soxhlet ex-

Table 2. Gross sedimentation and biodeposition (mean ± SE, n = 3), as well as organic carbon content in settling particulate matter (SPM) and biodeposits (BD) as % of dry wt (mean ± SE, n = 3) at the end of the winter and summer sampling periods. Biodeposition at 7 and 15 m (mean ± SE, n = 3) was calculated using site-specific data on mussel biomass from Littorin & Gilek (1999) of 54 and 24 g C m^{-2} from 5 and 10 m, respectively

Sampling period	Depth (m)	Gross sedimentation (mg C m^{-2} d^{-1})	Carbon in SPM (%)	Biodeposition (mg C m^{-2} d^{-1})	Carbon in BD (%)	Biodeposition as % of gross sedimentation
Winter	7 pelagic	500 ± 120	5.5 ± 0.0	–	–	–
	7 near-bed	720 ± 90	5.6 ± 0.0	460 ± 20	5.5 ± 0.0	63
	15 near-bed	880 ± 30	5.4 ± 0.0	180 ± 10	5.3 ± 0.0	21
Summer	7 pelagic	680 ± 230	13.6 ± 0.1	–	–	–
	7 near-bed	530 ± 80	11.7 ± 0.3	210 ± 170	12.1 ± 0.3	40
	15 near-bed	370 ± 50	9.1 ± 0.3	220 ± 70	10.0 ± 0.4	61

Table 3. Organic carbon-normalised sum PCB_7 concentration (geomean, [95% CI], n = 3) in settling particulate matter (SPM) and biodeposits (BD) of *Mytilus edulis*. Sum PCB_7 biodeposition at 7 and 15 m (mean ± SE, n = 3) was calculated using site-specific data on mussel biomass from Littorin & Gilek (1999) of 54 and 24 g C m^{-2} from 5 and 10 m, respectively

Sampling period	Depth (m)	PCB conc. in SPM (ng g^{-1} C)	PCB conc. in BD (ng g^{-1} C)	PCB gross sedimentation (ng m^{-2} d^{-1})	PCB biodeposition (ng m^{-2} d^{-1})	PCB biodeposition as % of gross sedimentation
Winter	7 pelagic	36 [24–53]	–	18 ± 3	–	–
	7 near-bed	82 [51–131]	65 [48–88]	62 ± 16	30 ± 5	48
	15 near-bed	57 [51–63]	84 [73–98]	50 ± 4	17 ± 0	34
Summer	7 pelagic	105 [63–174]	–	68 ± 20	–	–
	7 near-bed	63 [37–106]	63 [34–118]	38 ± 16	23 ± 20	61
	15 near-bed	50 [40–62]	70 [62–79]	19 ± 4	16 ± 6	84

tracted with toluene for 24 h. The amount of extractable organic material in the samples was determined by weighing the extract residues after evaporating the toluene. The extract residues were then cleaned up on a silica open column and analysed by GC/MS (Hewlett-Packard GC 5890 Ser. II/MD 5971A) as described by Gilek et al. (1996). The following congeners (denoted by their IUPAC numbers) were added as ^{13}C-labelled internal standards and subsequently quantified in the samples: 52, 101, 105, 118, 138, 153 and 180. To ensure high accuracy of the PCB analysis, the quantification was limited to the above-listed 7 congeners added as ^{13}C-labelled internal standards. PCB concentrations were expressed as the sum of these congeners (sum PCB_7). These 7 analysed PCB congeners represent approximately 40% of all analysable PCBs (tri- to octachlorinated) present in SPM and sediments from the area of the present study (Näf unpubl. data).

Biodeposition calculations and statistical methods. Biodeposition was calculated using the conservative method described by Kautsky & Evans (1987) with slight modifications. The amount of SPM in the traps without mussels was subtracted from the amount of biodeposits in the mussel traps (which represented both faeces and pseudofaeces from the mussels, and SPM). To correct for differences in mussel biomass and to compensate for mussel growth or loss during the sampling period, all values were divided by the geometric mean of the tissue dry weight in each trap at the start and the end of the sampling period. Biodeposition was then related to mussel density data from natural mussel beds in the sampling area (Littorin & Gilek 1999), i.e. biodeposition at 7 and 15 m was estimated using site-specific data of mussel biomass of 54 and 24 g C m^{-2} reported for 5 and 10 m, respectively.

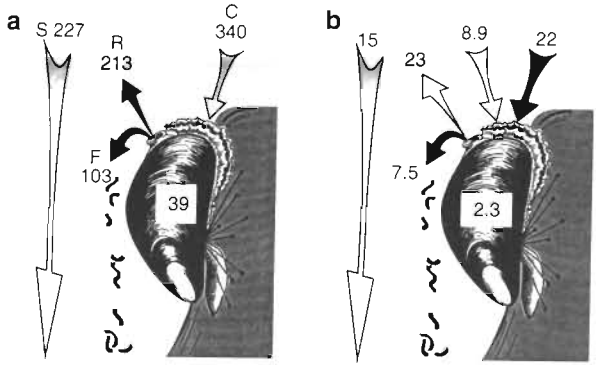

Fig. 3. Carbon and sum PCB_7 budgets for the studied mussel bed (Southern Stockholm archipelago, Baltic proper, Sweden). (a) Mussel shell-free biomass (g C m^{-2}) and annual carbon flows (g C m^{-2} yr^{-1}). S = gross sedimentation, C = consumption, R = respiration and F = faecal deposition. (b) Sum PCB_7 in mussels (µg m^{-2}) and annual flows (µg m^{-2} yr^{-1}). Black arrows indicate exposure and elimination of carbon-associated PCBs, white arrows indicate exposure and elimination of freely dissolved PCBs. Budget assumptions are given in Table 4

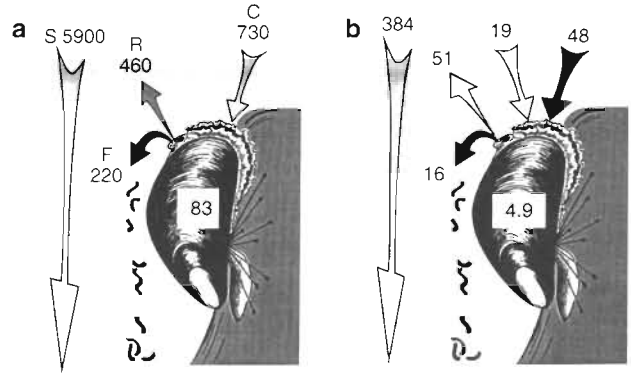

Fig. 4. Carbon and sum PCB_7 budgets for the entire Swedish coastal zone of the Baltic proper. (a) Mussel shell-free biomass (kg C 10^6) and annual carbon flows (kg C 10^6 yr^{-1}). S = gross sedimentation, C = consumption, R = respiration and F = faecal deposition. (b) Sum PCB_7 in mussels (kg) and annual flows (kg yr^{-1}). Black arrows indicate exposure and elimination of carbon associated PCBs, white arrows indicate exposure and elimination of freely dissolved PCBs. Budget assumptions are given in Table 4

Table 4. Budget assumptions for the calculated annual fluxes of carbon and PCB in the studied mussel bed (Fig. 3) and in the entire Swedish coastal zone of the Baltic proper (Fig. 4). C = consumption, A = assimilation, F = faecal production (biodeposition), R = respiration, P = production and E = excretion

Mussel density: studied mussel bed (near the Askö Laboratory)	39 g C m^{-2}	Average mussel biomass in the studied mussel bed (Littorin & Gilek 1999)
Mussel density: Swedish coastal zone of the Baltic proper	3.2 g C m^{-2}	Gilek et al. (1997)
Swedish coastal zone of the Baltic proper (area with water depth ≤ 20 m)	2.6 10^4 km^2	Gilek et al. (1997)
Biodeposition rate	0.0072 d^{-1}	Measured
Gross sedimentation rate	0.62 g C m^{-2} d^{-1}	Measured
Bioenergetics	C = A + F; where A = R + P + E, and C = 3.3 × F	Based on the assumptions of A = 0.7 × C and R = 0.9 × A (Gilek et al. 1997)
Clearance rate	4 l g^{-1} C h^{-1}	Gilek et al. (1997)
Sum PCB_7 in mussel tissue	59 ± 3 ng g^{-1} C	Measured grand geometric mean values ± SE, n = 12
Sum PCB_7 in near-bed SPM	65 ± 7 ng g^{-1} C	Measured grand geometric mean values ± SE, n = 12
Sum PCB_7 in biodeposits	73 ± 6 ng g^{-1} C	Measured grand geometric mean values ± SE, n = 12
Sum PCB_7 freely dissolved in the water	6.5 pg l^{-1}	Estimated based on a carbon normalised PCB partition coefficient (K_{oc}) between SPM and water of 10^7 (Axelman et al. 1997)
PCB assimilation efficiency from food and water	0.6	High end of PCB AE estimated in (Björk & Gilek 1999)

All data were carbon normalised and PCB concentrations were log-transformed before statistical analysis to decrease heterogeneity of variance. To test for differences in carbon deposition, PCB deposition and PCB concentration between sample periods, depths and types, 2- or 3-way analysis of variance (ANOVA) and *a posteriori* Student-Newman-Keuls (SNK) tests were used.

Budget calculations. Obtained biodeposition and sedimentation data were used to calculate 2 annual budgets of carbon and PCB fluxes, one estimating fluxes per square meter and year in the studied mussel bed (Fig. 3) and one estimating the total annual fluxes for the Swedish coastal zone of the Baltic proper (Fig. 4). Budget assumptions are given in Table 4. Details of the bioenergetic assumptions underlying the budgets, and mussel density estimates for the Baltic proper are given elsewhere (Gilek et al. 1997). In short, the budgets are based on estimates of average mussel biomass in the 2 areas (Gilek et al. 1997, Littorin & Gilek 1999) as well as the data on sedimentation, biodeposition and PCB concentrations obtained in this study (Table 4). In the carbon budgets food consumption and respiration by the mussels were calculated using simple bioenergetics based on the measured biodeposition rate in this study (Table 4). In the PCB budgets most sum PCB_7 fluxes and storages (i.e. gross sedimentation, biodeposition, consumption and amount PCB_7 in mussels) were calculated by multiplying measured PCB_7 concentrations from the present study with estimates of carbon fluxes from the corresponding carbon budget. This is basically the same as assuming equilibrium partitioning and is a common and well-motivated assumption when modelling the transport and fate of hydrophobic organic contaminants in aquatic environments (e.g. Mackay et al. 1992). The water uptake of PCB by mussels was calculated using a conservative estimate of water pumping (4 l g^{-1} C h^{-1}, Gilek et al. 1997), an assimilation efficiency from water of 0.6 (Björk & Gilek 1999) and an estimated freely dissolved PCB_7 concentration of 6.5 pg l^{-1} (Axelman et al. 1997). Furthermore, we have assumed that PCB concentrations in the mussel tissues are at steady state. This implies that the annual PCB loss from mussels was assumed to be equal to the total annual uptake. Thus, the annual elimination of PCBs (which also may include metabolism) was estimated by the equation: elimination = consumption + water uptake – faeces. At present no better estimates of elimination can be achieved, because empirical determinations of the rates of elimination and metabolism of the studied PCBs by Baltic Sea blue mussels are almost completely lacking (Gilek et al. 1997).

RESULTS

The mussels on the sampling traps increased their shell length and tissue dry weight during the sampling periods. Mussel growth, i.e. increase in tissue dry weight, was generally higher during the summer period and at the shallow site (7 m). The average daily increase in tissue dry weight during the summer period was 0.8 and 0.3%, and during the winter period, 0.6 and 0.2%, at 7 and 15 m depth, respectively. The overall loss and mortality of mussels from the

traps were markedly higher during the summer period, 31% compared with 3% during the winter (Table 1). Mussel growth and/or loss was corrected for by calculating geometric mean densities of mussel from biomass data at the start and end of each sampling period (Table 1).

The carbon concentration of the trap material (Table 2) was generally twice as high during the summer period compared with the winter period (ANOVA, $F_{1,24} = 3.2$, $p < 0.01$). A trend of decreasing carbon concentration from the pelagic SPM to 7 m and 15 m near-bed SPM was observed for SPM collected during the summer, but not during the winter. The average carbon-normalised gross sedimentation rate was significantly different between types of traps (ANOVA, $F_{1,20} = 10.6$, $p < 0.01$), with the amount of material being significantly higher in traps with mussels than in traps without mussels (SNK, $p < 0.05$). The gross sedimentation rate was also significantly higher during the winter period (ANOVA, $F_{1,20} = 7.38$, $p < 0.05$) than during the summer period. No significant difference in sedimentation rate was found between near-bed traps at different depths. Carbon biodeposition by the mussels at the sampling site was estimated to be in the range of 180 to 460 mg C m^{-2} d^{-1} (Table 2), corresponding to an average annual increase in gross sedimentation of 45% if compared to areas with no mussels (Fig 3a)

The carbon-normalised sum PCB_7 concentration in the mussels (Table 1) was significantly higher after the winter than after the summer period (ANOVA, $F_{1,8} = 10.5$, $p < 0.05$), but no significant effect of depth was observed. The higher observed PCB tissue concentration after the winter period could not be explained by differences in the extractable organics (mainly lipids) or the organic carbon content of the mussels (Table 1). The pelagic trap material tended to have lower PCB concentrations during the winter and higher PCB concentrations during the summer period compared to near-bed material. However, no statistically significant differences in the PCB concentration in the trap material between sample periods, depths or types of material were found. The average sum PCB_7 concentration in the SPM and biodeposits is shown in Table 3. Sum PCB_7 gross sedimentation in the near-bed traps was significantly higher during the winter season (ANOVA, $F_{1,8} = 5.5$, $p < 0.05$), though no significant effects of depth was found. Gross sedimentation and biodeposition of PCBs are presented in Table 3. Sum PCB_7 biodeposition was not significantly affected by sampling period or depth, and the filter-feeding activity of the mussels was estimated to increase annual gross sedimentation of PCBs through biodeposition by 50% if compared to areas with no mussels (Fig. 3b).

DISCUSSION

Sedimentation and biodeposition of carbon

The SPM collected in the traps represents gross sedimentation, which includes primary settling matter as well as resuspended sediments, benthic microalgae, faecal pellets, bacteria and macrophyte detritus. The portion of resuspended material in these types of traps commonly exceeds 50% in the coastal area where this study was performed (Askö archipelago, Northern Baltic proper) and shows a high variability both within and between years owing to, for example, storm events and seasonal differences in primary production (Blomqvist & Larsson 1994). Spatial differences in resuspension may also occur. Shallow areas such as mussel beds are, for example, more likely to be influenced by wave- and current-induced resuspension (e.g. de Jonge & van Beusekom 1995). However, despite this high variability, the average annual net sedimentation rate in the Askö archipelago can roughly be estimated to be 50 to 60 g C m^{-2} yr^{-1} from data given in Blomqvist & Larsson (1994). This corresponds to about 50% of the annual pelagic primary production in this area, which averaged 132 g C m^{-2} yr^{-1} during the years 1977 to 1988 (Johansson 1992).

Thus, the annual average gross sedimentation rate, 227 g C m^{-2} yr^{-1} (Fig. 3a), recorded over the studied mussel bed is approximately 4 times higher than the estimated average net sedimentation rate in the Askö area, but is similar to the gross sedimentation rate measured over the same mussel bed during the years 1980 to 1981 (246 g C m^{-2} yr^{-1}) reported by Kautsky & Evans (1987). This observed high rate of gross sedimentation may, as mentioned above, be explained by the location of the traps at relatively shallow sites (i.e. 7 and 15 m water depth), where wave-induced resuspension and water movement are likely to influence concentrations of particles in the water mass. Prins et al. (1996), for example, found in an *in situ* study carried out on an intertidal mussel bed that high water concentrations of particulate organic carbon coincided with high wind speeds. Not surprisingly, the gross sedimentation rate observed in the present study was significantly higher during the winter period with its higher incidence of windy weather. A clear seasonality was also observed in the carbon composition of the SPM material, with an approximately doubled carbon concentration during the summer period. This can be assumed to reflect a higher portion of primary produced material and a lower portion of resuspended material during the summer.

The energy demand of the dense mussels beds in the study area even exceeds the high sedimentation rate recorded. The estimated biodeposition corresponds to

a consumption rate of 340 g C m^{-2} yr^{-1} (Fig. 3a), which is approximately 1.5 times the gross sedimentation, or more than double the annual pelagic primary production. A model of the energy demand of *Mytilus edulis* in the Baltic proper (Kautsky 1995) indicated that, on an annual average, mussels have to assimilate approximately 7 times their own biomass of carbon to meet energy demands. This corresponds to a consumption rate of 390 g C m^{-2} yr^{-1} for mussel beds in the Askö area (given a density of 39 g C m^{-2} and a carbon assimilation efficiency of 70%), which is somewhat higher than the consumption rate calculated from estimated biodeposition in the present study.

When viewed on a local geographical scale (e.g. when comparing mussel beds to areas with low abundance of mussels) blue mussels increase the downward flux of carbon by filtering off small particles that otherwise would have stayed in suspension (Kautsky & Evans 1987). Our estimated biodeposition, 103 g C m^{-2} yr^{-1}, corresponds to an increase in the annual gross sedimentation rate of at least 45% if compared with areas with no mussels (Fig. 3a), and is fairly close to the biodeposition of 81 g C m^{-2} yr^{-1} reported by Kautsky & Evans (1987). However, these biodeposition estimates are thought to be conservative. The reason for this is that the sedimentation in the traps with mussels is likely to have been lower than in the traps without mussels (used to correct for sedimentation), since mussels can be assumed to have consumed some of the settling material. This is supported by the fact that the observed growth of mussels in the traps (69 g C m^{-2} yr^{-1}, based on the difference in grand mean dry weight over time) was much higher than the growth potential (approximately 24 g C m^{-2} yr^{-1}) indicated in the budget calculation based on estimated biodeposition. This could also explain why the food consumption of the mussels was lower when calculated on estimated biodeposition compared with the consumption rate calculated on the basis of energy demand estimated by Kautsky (1995).

Mussel growth and mortality

The average mussel biomass on the traps ranged between 31 and 48 g C m^{-2} over the sampling periods. These values are consistent with reported mussel densities in the study area (Littorin & Gilek 1999), corresponding to approximately 54 and 24 g C m^{-2} at 5 and 10 m depth, respectively. The mussel growth on the traps, i.e. increase in tissue dry weight over time, at the deep sampling site (15 m) was only 30 to 40% of the growth at the shallow site (7 m). This difference in growth is believed to be caused by a lower food availability at the deeper site, as a result of a combination of water movement and food quantity and quality, and is consistent with the estimated decline in somatic growth with depth reported by Littorin & Gilek (1999) and Kautsky (1982). The overall loss of mussels from the traps was high during the summer period (average 31%) and more pronounced at the shallow site than at the deep site. Similar outbreaks of enhanced summer mortality have been described in natural mussel beds in the Askö archipelago during 1994 and 1997 (the year of this study) (Kautsky 1998) and there were no indications that the observed mortality was an experimental artefact. Since most of the lost mussels were recovered as empty shells and all potential predators in the Baltic Sea would remove the shells (Kautsky 1981), predation can be excluded as a significant mortality factor. One plausible explanation for the observed mortality is starvation due to low food availability in combination with unusually high water temperature during the summer of 1997 (Kautsky 1998), which leads to increased energy demand. However, since several other factors such as disease and parasitism can also be important causes of mortality (Bower 1992) the exact mechanisms for the observed summer mortality are unclear.

PCB biodeposition and fate

The sum PCB_7 concentration in the mussels was significantly lower after the summer period than after the winter period, a difference that cannot be explained by differences in lipids or carbon content of the mussels. However, there might be several other causes for this observation. Spawning in the early summer is known to be related to decreases in tissue burdens of PCBs in mussels (Hummel et al. 1990). To some extent, the summer decline can also be explained by growth dilution. Even though periods with possible starvation might have occurred, the growth during the summer was still approximately 30% higher than during the winter. Lower PCB concentrations were also found in mussel tissue from the shallow site with faster growth, even though the effect of depth on PCB concentration was not statistically significant.

However, water depth related differences in PCB tissue concentration may also indicate that the particulate matter consumed by the mussels was not the same as the material collected in the sedimentation traps, i.e. the mussels may consume small particles rich in organic carbon that otherwise would have stayed in suspension, and thereby also increase their dietary exposure to PCBs. An interaction between depth and PCB concentration in SPM and faeces, though not significant, gives some support to this theory. As shown in Table 3, PCB concentrations in the SPM decreased

with depth whereas PCB concentrations in the faecal material increased with depth. This indicates that mussels at the deep site with lower food availability concentrate PCBs more, probably by feeding on particulate matter with a higher PCB content compared with the SPM, which is reflected in the slightly higher sum PCB_7 concentrations in the mussel faeces compared with the SPM. Food selection has earlier been suggested to increase contaminant exposure to deposit-feeding bivalves (Lee et al. 1990) and sediment-feeding oligochaetes (Klump et al. 1987). This feeding behaviour of the mussels will also increase the biodeposition rate of PCBs relative to the gross sedimentation rate. If the ratios of carbon biodeposition to carbon sedimentation are compared with the ratios of PCB biodeposition to PCB sedimentation, we see that the mussels increase PCB biodeposition to a larger extent than can be explained by carbon deposition, with 1 exception, which is the shallow site during the winter period. Hence, on an annual average the mussels increased gross sedimentation of carbon by 45% and gross sedimentation of PCBs by 50% if compared with areas with no mussels (see Fig. 3).

The objective of this study was also to generate more information on the PCB content of near-bed particulate matter eventually utilised as food by the mussels. No significant differences in carbon-normalised sum PCB_7 concentration were found between the pelagic and near-bed SPM; however, some trends were observed. On a seasonal scale, the PCB concentration in the pelagic SPM appeared to be lower during the winter and higher during the summer compared with the near-bed SPM, a discrepancy that was levelled out on an annual basis. Further, there was a tendency for PCB concentrations to decrease in the SPM with depth. The reason for this pattern is not known but it might reflect differences in the source and/or the quality of the carbon with which the PCBs were associated. The geometric mean sum PCB_7 concentrations of the analysed material were 75 and 65 ng g^{-1} C for the pelagic and the near-bed SPM, respectively. This is somewhat higher than previously reported estimates of PCB concentrations for the Baltic Sea (see compilation in Gilek et al. 1997).

To be able to compare the present *in situ* estimates with previous budgets established from the literature data (Gilek et al. 1997), the carbon-normalised sedimentation and biodeposition rates together with PCB concentrations were used to calculate annual budgets for the entire Swedish coastal zone of the Baltic proper (Fig. 4). The carbon budget based on biodeposition (Fig. 4a) is, for reasons discussed above, thought to be a conservative estimate and is approximately 15% lower than the carbon budget previously published by Gilek et al. (1997). However, since the measured PCB concentration in SPM and faeces was higher than previously reported, the estimated PCB biodeposition by the mussels in the present study was a factor of 4 higher than in the previous budget. If the PCB gross sedimentation rate given in Fig. 4b is corrected for an estimated resuspension of 4 times the net sedimentation (estimated from Blomqvist & Larsson 1994), we arrive at a PCB net sedimentation of 96 kg yr^{-1}, which indicates that mussel biodeposition is responsible for a significant part of PCB net sedimentation, i.e. 17% This is the same estimated role of mussel biodeposition in net deposition of PCBs as previously estimated by Gilek et al. (1997). Hence, both budgets indicate the same contribution of biodeposition to the vertical flux of PCBs in the Baltic proper, but the rate estimates for PCB net sedimentation and biodeposition in the present study were approximately 4 times higher than in the previous budget, mainly as a consequence of higher PCB concentrations in the collected SPM and faecal material.

Ecological implications

The *in situ* PCB biodeposition data presented in this study indicate that even when seen from the large geographical scale of the Baltic coastal zone, blue mussels are important modifiers of PCB cycling by directing considerable amounts of PCBs towards the coastal benthic food web. In this respect the abundant mussel population acts as a filter increasing the retention time of contaminants in the coastal zone by delaying export to the open sea and subsequent burial in deeper largely anoxic sediments devoid of higher life. Consequently, aside from direct transfer of contaminants from mussels to predators (Gilek et al. 1997), mussel biodeposition of faecal pellets rich in PCBs (and presumably many other contaminants) is probably a substantial source of contaminant exposure to the benthic organisms in coastal areas of the Baltic proper. This may be especially important for deposit-feeding and omnivorous benthic animals such as the bivalve *Macoma balthica*, gastropods *Hydrobia ulvae* and *H. ventrosa*, amphipods *Gammarus* sp., the polychaete *Nereis diversicolor*, as well as benthic meiofauna.

It is also likely that changes in mussel biomass, for example owing to shifts in primary production or salinity, will markedly affect the transport and fate of contaminants in the coastal zone of the Baltic Sea. As a matter of fact, the biomass of *Mytilus edulis* in the Swedish coastal zone of the Baltic proper has increased by about 50% since 1975 (Kautsky et al. 1992). This biomass increase is probably a consequence of a simultaneous increase in primary production in the area owing to eutrophication (Elmgren 1989), which has led to enhanced availability of food for the food-limited blue mussel beds (Kautsky 1982).

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