

# Varying nutritional dependence of the thyasirid bivalves *Thyasira sarsi* and *T. equalis* on chemoautotrophic symbiotic bacteria, demonstrated by isotope ratios of tissue carbon and shell carbonate

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**ABSTRACT:** The bivalves *Thyasira sarsi* and *T. equalis*, with symbiotic sulphur-oxidising bacteria in their gill tissue, were collected from various sites in N. Europe, including the 115 m deep basin in Gullmar fjord, Sweden, between 1986 and 1990. The tissues of most specimens were more depleted in <sup>13</sup>C than bivalve species without bacteria, indicating the importance of carbon fixed by the autotrophic endosymbionts to the nutrition of these bivalves. In contrast, thyasirids collected in 1988 in the Gullmar fjord showed a  $\delta^{13}\text{C}$  composition indistinguishable from those of heterotrophic bivalves, suggesting that in that year there was little input of carbon from the bacteria. Shell carbonate  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  determinations on thyasirids from different sites suggest that the observed isotopic disequilibrium was proportional to growth rate, as for carbonates deposited by corals, foraminifera and algae. The carbon isotope ratios indicated that the thyasirids from the Gullmar fjord collected in 1988 had a slower growth rate than those collected in 1986. Between 1986 and 1988, in the upper 15 cm of sediment in the Gullmar fjord, the elemental sulphur concentration decreased from 0.5–8.0 to only 0.003–0.04 mg-at. S dm<sup>-3</sup> and total sulphide decreased from 1.0–18.0 to 0.1–3.6 mg-at. S dm<sup>-3</sup>. Below 20 cm depth, the limit to which *T. sarsi* forms tunnels in the sediment, the reduced sulphur concentrations were still high in 1988, >12 mg-at. dm<sup>-3</sup>. It is proposed that the utilisation and oxidation of reduced sulphur in the sediment, following the population explosion of *T. sarsi* post-1980, was greater than the sulphate reduction rate, with the result that the symbiotic bacteria were eventually starved of substrate, and that most of the bivalves died. High sediment sulphide levels had been restored by 1990, following the death of most of the infauna after de-oxygenation of the deep-water.

## INTRODUCTION

Thyasirids are small burrowing bivalve molluscs which live in fine-grained sediments and are predominantly found in boreal coastal seas (Kauffman 1967). Different species show a range of nutritional dependence on symbiotic bacteria from no bacterial associations and complete dependence on heterotrophic nutrition to almost complete dependence on chemoautotrophic bacteria in their gills (Dando & Southward 1986, Southward 1986, Spiro et al. 1986). The palps are reduced and the gut is short and simplified (Allen 1958).

*Thyasira sarsi* (Philippi) is a species of up to 20 mm shell length which is known to favour organic-rich muds. This species has enlarged gills which weigh 39 % of the total body fresh weight in good habitats (Dando & Southward 1986). Typically these gills are pinkish-white due to the elemental sulphur stored in the bacterial cells. The anatomy and fine structure of the epithelia of the gills, with their specialised bacteriocytes containing symbiotic Gram-negative bacteria, has been described by Southward (1986). The bacteria are sulphur-oxidising chemoautotrophs, as indicated by the presence of ribulosebiphosphate carboxylase and adenylylsulphate reductase (Dando

& Southward 1986). The carbon isotope composition of the tissues was unusually depleted in  $^{13}\text{C}$ , ranging from  $-28.2$  to  $-39.5\%$   $\delta^{13}\text{C}$ , in individuals collected from a Norwegian fjord (Spiro et al. 1986), and from sediments in the vicinity of methane seeps in the North Sea (Dando et al. 1991) and the Skagerrak (Schmaljohann et al. 1990). It has been estimated that between 50 and 100 % of the tissue carbon in *T. sarsi* is derived from carbon fixed by the bacteria (Spiro et al. 1986, Schmaljohann et al. 1990).

*Thyasira equalis* (Verrill & Bush) is a smaller species than *T. sarsi*, up to 7 mm shell length, which has been less studied. It is the most common thyasirid species on the North European continental shelf and survives in less organic-rich sediments than *T. sarsi*, apparently disliking hydrogen sulphide rich sediments (Dando & Southward 1986). The gills are thin and transparent with short filaments which contain only a few bacteriocytes (Southward 1986). The bacteria associated with *T. equalis* are also autotrophic, containing ribulose-bisphosphate carboxylase (Dando & Southward 1986). Both *Thyasira* species have an approximate lifespan of 2.5 yr (Josefson 1987a).

Gullmar fjord is a 27 km long fjord on the west coast of Sweden. It has a sill at 42 m water depth which restricts water flow to the deep basin of 115 m water depth. *Thyasira sarsi* and *T. equalis* co-exist in the deep basin, from which the related species *T. flexuosa* is absent, although it is present at shallower depths in the fjord. Periodically the water in the bottom of the basin has low oxygen levels. During the 1979/1980 winter the bottom of the basin became azoic, due to oxygen deficiency (Josefson & Widbom 1988). Following subsequent re-colonisation of the sediment *T. sarsi* again became a dominant species with later re-colonisation by *T. equalis*. (Fig. 1). This study relates changes in the isotopic composition of the tissue carbon,  $\delta^{13}\text{C}$ , from these bivalves to changes in the sediment chemistry during the period 1986 to 1988, with additional observations in 1990 following another population crash due to oxygen deficiency of the bottom water. The tissue  $\delta^{13}\text{C}$  indicates the nutritional source of the carbon, since from an identical  $\text{CO}_2$  source the carbon fixed by sulphur-oxidising bacteria is more  $^{13}\text{C}$ -depleted than that fixed by phytoplankton (Spiro et al. 1986, Ruby et al. 1987). An indication of the source of bicarbonate for the bivalve, whether from the overlying water or from the breakdown of organic matter in the sediment, is provided by the carbon and oxygen isotope composition of the shell carbonate,  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ . The kinetic isotope effects during carbonate deposition in shell growth are indicative of the growth rate of the animals. In conjunction the isotope markers record the microenvironment and nutrition of the thyasirids.

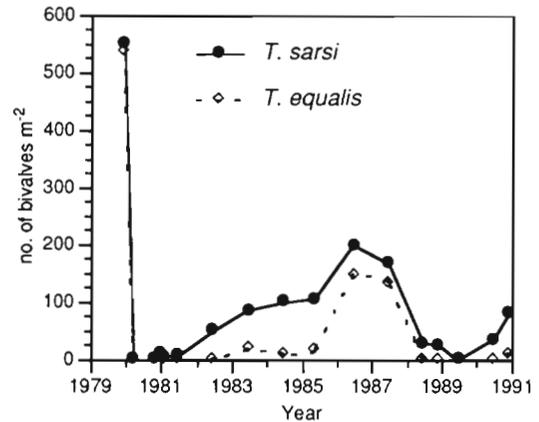


Fig. 1. *Thyasira* spp. Changes in thyasirid density in the 115 m deep basin in Gullmar fjord from 1979 to 1990. Data from Josefson (1986b, 1987a, b, 1988, 1989), Tunberg (1990) and this study

## MATERIALS AND METHODS

The deep basin in Gullmar fjord was sampled at 115 m depth at Alsbäck ( $58^{\circ} 19.06' \text{ N}$ ,  $11^{\circ} 32.93' \text{ E}$ ) in October 1986, September–October 1988 and May 1990. In October 1986 the sediment temperature was  $5.3^{\circ}\text{C}$  and in September 1988 it was  $6.0^{\circ}\text{C}$ ; the annual mean is  $5.2^{\circ}\text{C}$  (Odd Lindahl pers. comm.). Sediment samples and animals were collected with a box corer (Jonasson & Olausson 1966) sampling  $0.085 \text{ m}^2$ . Samples for chemical analysis were taken from sub-cores from the central part of the box. The remaining sediment was washed through a sieve of 1 mm mesh to collect the animals.

Additional specimens of *Thyasira sarsi* were collected from the following sites: Grimstadfjorden, Norway, during October 1987, at Knappen ( $60^{\circ} 19.50' \text{ N}$ ,  $05^{\circ} 15.18' \text{ E}$ ) in 65 m water depth and in October 1986 in the outer fjord in 90 m depth ( $60^{\circ} 19.48' \text{ N}$ ,  $5^{\circ} 14.40' \text{ E}$ ); in Oslofjord, Norway, during October 1986, at Slemmestad ( $59^{\circ} 47.01' \text{ N}$ ,  $10^{\circ} 30.87' \text{ E}$ ) in 39 m water depth and Moss ( $59^{\circ} 23.50' \text{ N}$ ,  $10^{\circ} 34.40' \text{ E}$ ) in 268 m water depth; in the Skagerrak at 340 m water depth ( $58^{\circ} 2.85' \text{ N}$ ,  $9^{\circ} 40.04' \text{ E}$ ) in October 1987. The Grimstadfjord stations were those used in a previous study on thyasirids (Dando & Southward 1986). The annual mean bottom temperature in the Skagerrak is  $6^{\circ}\text{C}$  (Josefson 1986a), at Knappen it is  $8.5^{\circ}\text{C}$  (Johannessen 1984), at Slemmestad it is  $6.5^{\circ}\text{C}$  (Jan Magnusson pers. comm.) and the temperature measured at Moss was  $5.0^{\circ}\text{C}$ . Soft tissues for carbon isotope analysis were dissected free of shell and soaked in 2M HCl to remove any residual carbonate. The tissues were then well rinsed with de-ionised water and dried at  $55^{\circ}\text{C}$ . Carbon dioxide formation from dried tissues

and shells and mass-spectrometry were by methods described previously (Spiro et al. 1986). The results were corrected according to Craig (1957) and Deines (1970) and reported as permil (‰) deviation from the PDB standard:

$$\delta^{13}\text{C} (\text{‰}) = \left[ \frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}}}{(^{13}\text{C}/^{12}\text{C})_{\text{standard}}} - 1 \right] \times 1000$$

$$\delta^{18}\text{O} (\text{‰}) = \left[ \frac{(^{18}\text{O}/^{16}\text{O})_{\text{sample}}}{(^{18}\text{O}/^{16}\text{O})_{\text{standard}}} - 1 \right] \times 1000$$

The overall analytical reproducibility was 0.1 ‰ for both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ .

Analysis of elemental sulphur, acid-labile sulphide, chromous reducible sulphide, ammonia and ferrous iron and measurements of the sulphate reduction rate were carried out according to previously described methods (Dando et al. 1991). Total sediment carbon was determined using a Carlo Erba CHN analyser, organic carbon was measured after first treating aliquots of the sediment with HCl to remove carbonate, and inorganic carbon was estimated as the difference between these values.

## RESULTS

The change in the numbers of *Thyasira sarsi* and *T. equalis* following the de-oxygenation of the bottom water in the deep basin of Gullmar fjord in 1979–80 is shown in Fig. 1. Low oxygen levels in 1987–88 and 1988–89 caused another loss of thyasirids from the deep basin. Sediment samples were collected from the 115 m deep site at Alsback in 1986 at the post-1980 thyasirid population peak, in October 1988 during subsequent low-oxygen conditions and in May 1990 during re-colonisation by thyasirids.

The depth profile of elemental sulphur and of total reduced sulphur species in sediment taken in 1986, 1988 and 1990 from the deep basin in Gullmar fjord is shown in Fig. 2. The total reduced sulphur is the total sulphide measured after chromous chloride reduction of the sediment and includes FeS, FeS<sub>2</sub> and S<sup>0</sup>. In no core sample could a smell of hydrogen sulphide be detected in freshly-exposed sediment, down to at least 40 cm depth. This indicated that any free sulphide must have been below 0.1 μM (Dando et al. 1985), an observation supported by the high dissolved ferrous iron concentrations, 2 to 28 μg-at. Fe l<sup>-1</sup>, in 1986. Interstitial ammonia concentrations were measured in 1986 and found to be fairly constant at 70 to 100 μM over the upper 20 cm of sediment (Fig. 3a). The sediment has an organic carbon content of between 2.2 and 3.8 % of the dry weight. In May 1990 the mean sulphate reduction rates, measured at a temperature of 6 °C over the upper 30 cm of the sediment, were in the range 1.5 to 19 μmol of sulphate reduced dm<sup>-3</sup> d<sup>-1</sup> (Fig. 3b).

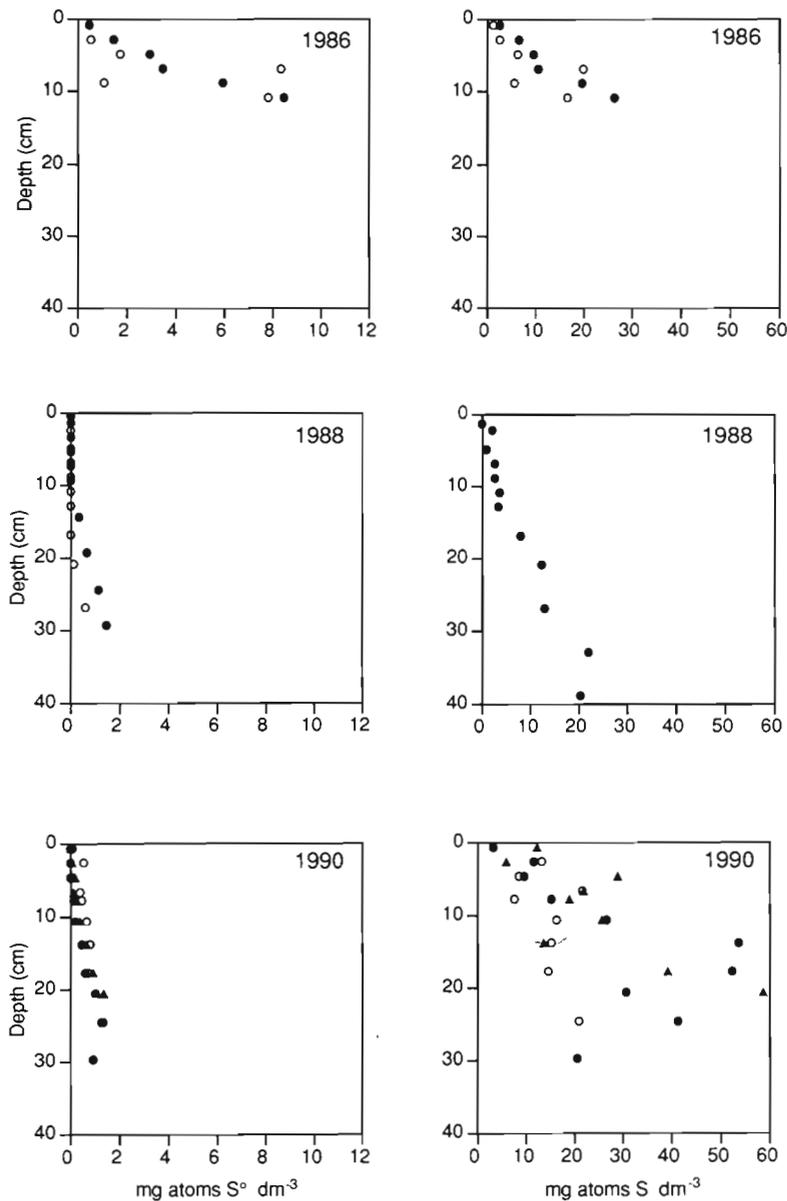


Fig. 2. Elemental sulphur (left) and total reduced sulphur (right) concentrations in the 115 m deep Gullmar fjord basin in October 1986, October 1988 and May 1990. Different symbols represent different core samples

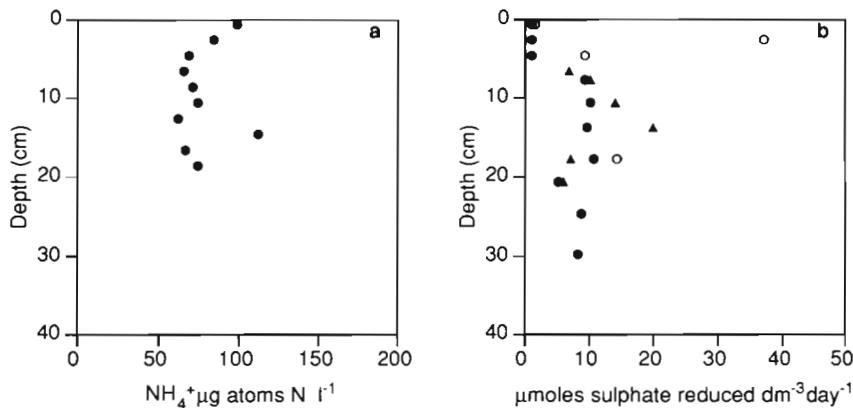


Fig. 3. Sediment cores from the 115 m deep basin in Gullmar fjord. Different symbols represent different core samples. (a) Ammonia concentrations in October 1986. (b) Sulphate reduction rates in May 1990

The  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for shell carbonate and the  $\delta^{13}\text{C}$  determinations for organic carbon from soft tissues of *Thyasira sarsi* are listed in Table 1. Values for *T. equalis* are given in Table 2. Data for *T. sarsi* and *T. equalis* from Oslofjord, Grimstadfjord, the North Sea and the Skagerrak are listed in these tables for comparison. There were insufficient specimens of other bivalves in the Alsbäck sediment for isotope analysis. Two specimens of heterotrophic bivalves were analysed from Slemmestad in Oslofjord; *Nucula tenuis* had  $\delta^{13}\text{C}$  values of  $-16.44\text{‰}$  for gill and  $-16.08\text{‰}$  for other tissues and *Tellina gracilis* had a value of  $-16.45\text{‰}$  for its soft tissues.

The specimens of *Thyasira sarsi* examined from Alsbäck in 1986 had typically plump creamy-white

gills indicative of a high concentration of elemental sulphur in the symbiotic bacteria. The  $^{13}\text{C}$  content of the gills and the other tissues was within the range of that found for this species at other sites. In contrast, in 1988, the bivalves were less abundant, had thinner and more pallid gills and were exceptional in that they had a  $^{13}\text{C}$  content typical of that found in heterotrophic bivalves. The *T. equalis* tissue  $^{13}\text{C}$  values from the Alsbäck specimens showed less differences between the 2 years, probably because of the smaller input from the symbiotic bacteria, but the values for the 2 specimens collected in 1988 from Gullmar fjord were among the lowest found.

The shell  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  data for the 2 thyasirid species from all sites are plotted in Fig. 4. With the

Table 1. *Thyasira sarsi*. Tissue and shell isotope ratios

Area	Shell length (cm)	Mean tissue organic C $\delta^{13}\text{C}$	Gill organic C $\delta^{13}\text{C}$	Shell carbonate $\delta^{13}\text{C}$	Shell carbonate $\delta^{18}\text{O}$	Month & year
Alsbäck	9.75	-21.52	-22.22			Oct 1986
Alsbäck	3.0	-25.40				Oct 1986
Alsbäck	5.0	-29.20	-31.7			Oct 1986
Alsbäck	6.0			-3.62	2.20	Oct 1986
Alsbäck	5.90			-4.57	2.20	Oct 1986
Alsbäck	7.25–7.30	-17.13		-3.03	2.12	Sep 1988
Alsbäck	6.4	-17.41	-17.78	-2.41	2.07	Sep 1988
Knappen	5.5–5.95	-31.36		-2.72	2.31	Oct 1987
Knappen	6.25	-33.59		-1.71	2.46	Oct 1987
Knappen	7.25	-33.75		-1.94	2.58	Oct 1987
Knappen	9.5	-34.07		-1.95	2.52	Oct 1987
Knappen	10.15	-31.36		-3.03	2.12	Oct 1987
Skagerrak		-39.50	-41.56	-12.000	3.17	Oct 1987
Slemmestad	2.7–3.1		-17.84			Oct 1986
Slemmestad	5.6–6.7	-23.70	-24.98	-4.02	0.51	Oct 1986
Slemmestad	6.4–7.3	-24.00	-25.25	-3.43	0.96	Oct 1986
Slemmestad	8.55	-22.40	-22.57			Oct 1986
North Sea		-34.00	-34.30	-5.00		Jul 1989 <sup>a</sup>
North Sea		-31.40		-4.80		Jul 1989 <sup>a</sup>

<sup>a</sup>Data from Dando et al. (1991)

Table 2. *Thyasira equalis*. Tissue and shell isotope ratios

Area	Shell length (cm)	Mean tissue organic C $\delta^{13}\text{C}$	Gill organic C $\delta^{13}\text{C}$	Shell carbonate $\delta^{13}\text{C}$	Shell carbonate $\delta^{18}\text{O}$	Month & year
Alsback	4.5–5.3	-19.30	-19.86	-6.16	0.15	Oct 1986
Alsback	5.2		-20.70			Oct 1986
Alsback	2.9, 3.0	-21.70				Oct 1986
Alsback	4.7–5.4	-17.85				Oct 1986
Alsback	6.6			-5.81	1.64	Oct 1986
Alsback	4.1–5.0	-21.10				Oct 1986
Alsback	3.70–4.05	-22.00	-21.70			Oct 1986
Alsback	6.85	-19.02	-18.65	-5.69	1.47	Sep 1988
Alsback	3.85–4.55	-17.43		-5.70	1.35	Sep 1988
Moss	2.9–3.0	-21.70				Oct 1986
Slemmestad	3.0–3.6	-18.80				Oct 1986
Slemmestad	3.65, 3.90		-20.70			Oct 1986
Slemmestad	4.52, 4.12	-21.90				Oct 1986
Slemmestad	4.1–5.0	-20.30				Oct 1986
Grimstadjord	2.9, 3.0	-21.70				Oct 1986

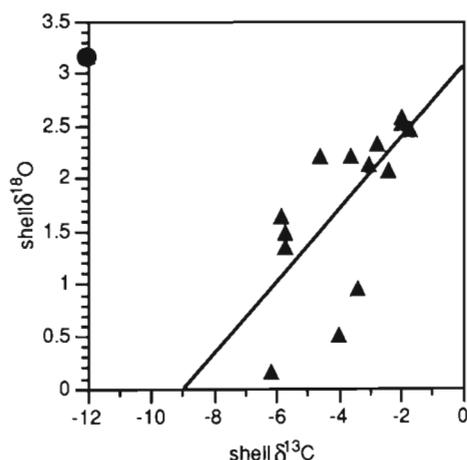


Fig. 4. *Thyasira sarsi* and *T. equalis*. Relationship of shell carbonate  $\delta^{13}\text{C}$  to  $\delta^{18}\text{O}$  from the sites studied; data from Tables 1 & 2. (●) *T. sarsi* from methane seeps in the Skagerrak

exception of the value from the Skagerrak methane seep these values fall close to the regression line  $\delta^{18}\text{O} = 0.33 \delta^{13}\text{C} + 3.0$ , indicating that the bicarbonate sources used for shell deposition at the other sites were isotopically similar to each other.

## DISCUSSION

*Thyasira sarsi* burrows in the sediment to a depth of up to approximately 9 times the length of its shell and constructs a 3-dimensional network of tunnels with its vermiform foot to a similar depth below the shell (Dando & Southward 1986). Thus this bivalve, which grows to a length of 12 mm at Alsback, can form

tunnels in the sediment to a depth of approximately 20 cm, giving it access to any pockets of dissolved sulphide in this part of the sedimentary column. In addition, seawater from the sediment surface pumped through the permeable inhalant tube causes oxidation of the insoluble sulphides, and the partial oxidation products, notably thiosulphate, diffuse back into the tunnel systems and are further oxidised by the symbiotic bacteria.

Sulphur-oxidising chemoautotrophic bacteria in culture at 22 °C produce cell carbon with a  $\delta^{13}\text{C}$  approximately 25 ‰ lower than their carbon source due to discrimination against  $^{13}\text{C}$  by the enzyme ribulose-bisphosphate carboxylase (Ruby et al. 1987). This fractionation is likely to be greater at lower temperatures and slower growth rates, as shown for phytoplankton (Sackett et al. 1965). The gills of other bivalves with symbiotic sulphur-oxidising bacteria from shallow waters often have  $\delta^{13}\text{C}$  values as low as -34 ‰ (Spiro et al. 1986). This compares with  $\delta^{13}\text{C}$  values of -16.2 to -20.1 ‰ for tissues of heterotrophic bivalves examined from *Thyasira* habitats (Spiro et al. 1986, Dando et al. 1991, this study). Most of the specimens analysed from the 5 sites were more depleted than this, indicating a significant carbon input from the autotrophic endosymbiotic bacteria.

The 2 specimens of *Thyasira sarsi* collected in September 1988 from Alsback, with  $\delta^{13}\text{C}$  values of -17.1 to -17.8 ‰, would thus have been feeding heterotrophically, with little or none of their carbon derived from fixation by symbiotic bacteria. They have similar isotope ratios to the smallest specimens of the species examined from Slemmestad in Oslofjord, 2.7 to 3.1 mm shell length, a stage at which the symbiotic association with bacteria may not be developed. In

contrast, the specimens of *T. sarsi* collected from Alsbäck in 1986 were all significantly depleted in  $^{13}\text{C}$  compared to heterotrophically feeding bivalves and lay within the range of values of similarly-sized specimens from other sites.

The site at Knappen, in Grimstadfjorden, is the most sulphide-rich of the fjord sites studied (Dando & Southward 1986) and it is probable that the *Thyasira sarsi* there obtain virtually all their carbon from their symbiotic bacteria. The mean  $\delta^{13}\text{C}$  of the soft tissues of *T. sarsi* at Knappen is  $-32.8\text{‰}$ . This is similar to the depletion found in purified fractions of symbiotic bacteria isolated from the gills of 2 other bivalves, *Solemya velum*,  $-31.7$  to  $-33.6\text{‰}$  (Conway et al. 1989), and *Lucinoma aequizonata*,  $-34 \pm 0.8\text{‰}$  (Cary et al. 1989). If we assume that a specimen with no carbon contribution from bacteria has a mean soft tissue  $\delta^{13}\text{C}$  of  $-17.5\text{‰}$  then we may estimate that the 3 specimens examined from Gullmar fjord in 1986 obtained between 26 and 76 % of their tissue carbon from their bacterial symbionts. The very low  $\delta^{13}\text{C}$  values of  $-39.5$  and  $-41.56\text{‰}$  from the Skagerrak specimen are attributable to the very depleted, partly methane-derived, bicarbonate source (Schmaljohann et al. 1990).

*Thyasira equalis* has fewer symbiotic bacteria (Southward 1986) and the gills show approximately 10 % of the ribulosebiphosphate carboxylase activity present in *T. sarsi* (Dando & Southward 1986). The nutritional importance of carbon fixed by the bacteria should therefore be less than in the larger species. The  $\delta^{13}\text{C}$  ratios support this, *T. equalis* tissues being, in general, less depleted in  $^{13}\text{C}$  than those of *T. sarsi* (Table 2). Most of the *T. equalis* specimens were, however, more depleted in  $^{13}\text{C}$  than heterotrophic bivalves, indicating that the bacteria do contribute significantly to the nutrition of this species. As for *T. sarsi*, the indication is that the dependence of *T. equalis* on carbon input from symbiotic bacteria at Alsbäck was reduced between 1986 and 1988. The 2 specimens analysed from 1988 had  $\delta^{13}\text{C}$  values for their tissues between  $-17.4$  and  $-19.0\text{‰}$ , within the range of those found for heterotrophically feeding bivalves. These specimens were among the least depleted in  $^{13}\text{C}$  of all those examined in this study.

The  $\delta^{13}\text{C}$  of shell carbonate will primarily reflect that of the bicarbonate in the water passed through the mantle cavity. It will also be affected by the kinetic isotope effect, observed in biological carbonates from corals, foraminifera, cidaroid urchins and calcareous algae (McConnaughey 1989a, b): faster shell growth will lead to a greater depletion of both  $^{13}\text{C}$  and  $^{18}\text{O}$  in the deposited carbonate. The data plotted in Fig. 4 present a similar pattern to those reported for these other biological carbonates and indicate that this kinetic isotopic disequilibrium also applies to thyasirid shell deposition. Certainly the relatively small temperature

differences between the sites cannot account for the observed  $^{18}\text{O}$  differences. The close fit of most of the thyasirid shell data to the regression line suggests that the bicarbonate sources are of similar isotopic composition and are probably mainly derived from seawater bicarbonate. The one exception was the specimen from the Skagerrak; this was from a sediment in which the interstitial  $\text{CO}_2$  had a  $\delta^{13}\text{C}$  of  $-19.4\text{‰}$ , probably due to a contribution from the oxidation of methane. The interstitial bicarbonate was estimated to contribute 62 % towards the shell carbonate (Schmaljohann et al. 1990). Interstitial bicarbonate from the 2 fjord samples,  $-2.09$  and  $-4.07\text{‰}$   $\delta^{13}\text{C}$ , was much closer to seawater bicarbonate,  $\sim 0\text{‰}$ .

More rapid growth will lead to faster carbonate deposition and a greater depletion in the  $^{13}\text{C}$  and  $^{18}\text{O}$  isotopes in the shell carbonate. Examination of the Gullmar fjord data (Tables 1 & 2) indicates that for both thyasirid species there was less  $^{13}\text{C}$  depletion in shell carbonate in 1988 than in 1986, indicative of slower growth in the later period when the symbiotic bacteria appear to be contributing little towards the nutrition of these bivalves. The  $^{18}\text{O}$  values are more variable and did not show a consistent trend.

An explanation for the marked change in the nutritional dependence of thyasirids from Alsbäck on their bacteria comes from a study of the sediment chemistry at the site. Death of the infauna in 1979–80 due to deoxygenation would have led to high sulphate reduction rates and high iron sulphide levels in the sediment. In 1986 the sediment in the deep basin of Gullmar fjord was unusual in having high concentrations of elemental sulphur, 0.5 to 10.4 mg-at. S  $\text{dm}^{-3}$ , throughout the upper 20 cm of sediment. This indicated deep penetration of oxygen into the sediment by bioturbation with consequent oxidation of the iron sulphides. It is possible that dead polychaete tubes, such as those formed by *Melinna cristata*, also form channels permitting diffusion of oxygen deep into the sediment. Large specimens of *Thyasira sarsi*, up to 11 mm shell length, were present, giving a potential bioturbation depth with this species alone of 20 cm. Another indicator of bioturbation to at least this depth was the absence of an obvious gradient in ammonia concentrations over this depth range (Fig. 3a).

The total reduced sulphur in the sediment had fallen from a range, over the upper 10 cm of the sediment, of between 1.6 and 20.3 mg-at. S  $\text{dm}^{-3}$  in 1986 to a range of 0.2 to 2.8 mg-at. S  $\text{dm}^{-3}$  in 1988. The decrease in total sulphide was also apparent over the 10 to 20 cm depth range. Elemental sulphur had decreased to a mean concentration of 18  $\mu\text{g}$ -at. S  $\text{dm}^{-3}$  over the upper 10 cm of the sediment column in 1988, indicating the lack of easily oxidisable sulphides. The 2 core samples analysed were collected on different days and are

therefore unlikely to have come from exactly the same position. The numbers of *Thyasira sarsi* were greatly reduced and *T. equalis* were rare. Following the 1988–89 deoxygenation and fauna kill sulphate reduction rates would have been initially high, regenerating the sulphide necessary for the thyasirids. The May 1990 core sample demonstrates that total sulphide levels had increased in 2 yr to the 1986 levels. The observed sulphate reduction rates in 1990 (Fig. 3b) were not sufficient to account for this increase over 2 yr. However the low oxygen levels in the bottom water, together with a large input of organic matter from the dead macrofauna, would have created conditions for very high sulphate reduction rates during the de-oxygenation.

It is proposed that the utilisation and oxidation of reduced sulphur in the sediment in the deep basin at Alsåkk in Gullmar fjord, following the population explosion of thyasirids post-1980, exceeded the sulphate reduction rate. Oxidation would have resulted from bioturbation due to burrowing echinoids and annelids as well as from the activities of the thyasirid bivalves. The result of this was that by 1988 the upper sediment contained little reduced sulphur and the symbiotic bacteria in the gills of *Thyasira sarsi* were starved of substrate so that the few young bivalves which survived had to exist by feeding heterotrophically on plankton-derived organic matter. A population collapse of *Thyasira* spp., coinciding with a steady decline in sediment sulphides, has been observed over the same period at Knappen, Grimstadfjorden, west Norway (P. R. Dando & P. Johannessen unpubl.).

The observations reported in this paper were part of a series on thyasirid habitats and were not designed to follow changes in the growth of a thyasirid population following extinction of the bottom infauna. It is apparent that the 115 m deep basin in Gullmar fjord is subject to periodic anoxia, resulting in the death of the bottom fauna, and would be a good area for systematic studies on thyasirid recolonization, nutrition and growth rates.

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