

# Topical and trophic relationships in a boring polychaete–scallop association: fatty acid biomarker approach

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**ABSTRACT:** The association between the Japanese scallop *Patinopecten yessoensis* and the scallop-shell-boring polychaete worm *Polydora brevipalpa* was investigated in the natural environment. Fatty acid analyses were performed on the scallop, polychaete, and potential food materials available in the environment, with the aim of determining the main food sources of these animals and the trophic relationships between species. The scallop and the polychaete showed a similarity in their fatty acid compositions. High concentrations of 20:5n-3 and 14:0, substantial concentrations of 16:2n-4, 16:3n-4, and 16:4n-1, and ratios of 16:1n-7 to 16:0 close to 1 indicated significant contributions of diatoms in the diets of both mollusk and polychaete. Detectable levels of 18:4n-3 suggest that dinoflagellates also contributed to the diet of the animals. The fatty acid markers showed that the scallop and polychaete feed extensively on a mixed, but probably diatom-dominated phytoplankton diet. Additionally, the elevated level of bacterially derived fatty acids and saturated (mainly 18:0) acids in polychaete lipids point to an additional dietary source, detritus and bacteria. Elevated amounts of 22:6n-3 and 18:1n-9 in the scallop digestive gland are indicative of zooplankton consumption. The similarity of the diets is a major determinant of the feeding competition between these species in the community. The decrease in the scallop internal volume concurrent with an increase in the degree of shell occupation by polychaetes suggests a reduction in water-filtering potential by the scallop. Linear regressions of the degree of polychaete occupation against scallop weight and shell height revealed negative relations in both cases. With high levels of shell occupation by polychaetes, the commensal relationship between scallop and polychaete acquires some elements of parasitism.

**KEY WORDS:** Community · Inter-specific relationships · Trophic biology · Fatty acids · Mollusks · Polychaetes

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## INTRODUCTION

The study of a total complex of inter-specific relationships in a community consisting of many species is a task so great as to be practically unmanageable. Associations of marine invertebrates with their epibenthic organisms generally include a small number of species and provide a convenient model for understanding the features of the inter-specific relationships in communities in the natural environment. Animals with hard shells give shelter to both epibenthic organ-

isms (e.g. sponges, barnacles, mollusks, bryozoans, hydroids, algae), which inhabit the outer shell surface, as well as to shell-boring organisms (polychaete worms, sponges, pearlworks, prey gastropods, algae) (Ward & Thorpe 1991, Lescinsky 1993, Martin & Britayev 1998, Chan & Chan 2005). Specific composition of the epibiosis, as well as the number of species of epibionts, greatly varies among species of shellfish-hosts. Sometimes, many species occur together on the shellfish, and in some cases, a few species dominate the epibiosis. In certain habitats, only 1–2 species are

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dominant among such organisms. For instance, in muddy bottom areas of Peter the Great Bay of the Sea of Japan, the shell surface of the benthic mobile Japanese scallop *Patinopecten* (= *Mizuhopecten*) *yessoensis* (Jay) is free of epibionts (Silina 2002), and generally only one species (the boring polychaete *Polydora brevipalpa* Zachs) occurs in association with the scallop shell (Silina 2003, 2006).

The effect of boring worms on oysters, abalones, scallops, clams and mussels have mainly been studied in mariculture conditions. Some researchers have shown that boring worms affect the health and growth of mollusks (Lleonart et al. 2003), whereas others did not find such an effect (Caceres-Martinez & Tinoco-Orta 2001, Calvo et al. 2001, Handley & Bergquist 1997). We investigated the association of the Japanese scallop *Patinopecten yessoensis* and the polychaete worm *Polydora brevipalpa* that inhabit muddy bottom sites.

Japanese scallop is widespread in the northwestern Sea of Japan and often dominates the coastal benthic zone. *Polydora brevipalpa* excavates a U-shaped borehole into scallop shell. The burrows stretch outside the shell as short mud or sand tubes up to 10 mm high. This species can form dense aggregations of several tens of individuals in one scallop shell (Radashevsky 1993). Sometimes, boreholes of this polychaete can cover the whole of the upper valve of the scallop (Silina 2003, 2006). This simple association of scallops and polychaete worms provides a convenient model for the study of the inter-specific relationships in communities in the natural environment.

The main interactions that determine the functioning of communities are trophic and topical relationships between the component species (Turpaeva 1987). Direct trophic relationships occur only between predator and prey. Indirect trophic relationships involve e.g. food competition, decrease or increase in the quantity of prey, diminishment or enhancement of foraging rates, and facilitation or impediment of access to food. Topical relationships include the creation of substrate, the modification of its quality and the alteration of the environment. These relationships are common among organisms of different species living in close association. Thus, organisms of some species use other species as a refuge or substrate, as a means of defence from competitors or predators, to help alter the light intensity or water turbidity to which they are exposed or for their ability to alter the surrounding chemical environment which may be useful or harmful to organisms of other species; they can also affect the host in such ways as influencing growth rates, or retarding or enhancing their motion. Such relationships are especially relevant when certain organisms (hosts) provide a substrate for others (epi- and endobionts). The range of such relationships is incredibly broad, from beneficial to pathogenic (Turpaeva 1987).

The scallop *Patinopecten yessoensis* is believed to be an active filter-feeder. Microscopic analysis of the scallop gut content showed that algae (chiefly diatoms), zooplankton (mainly invertebrate larvae) and especially detritus are the most common food sources of this mollusk. Detritus was found to constitute 30 to 70% of the bolus (Mikulich & Tsikhon-Lukanina 1981). The polychaete *Polydora brevipalpa* collects food particles from water actively pumped by the mollusk-host. The food spectrum of this species of polychaete is not well known. However, Fauchald & Jumars found that *P. brevipalpa* consumes particles of <30 to 50  $\mu\text{m}$  (Fauchald & Jumars 1979).

Recent studies have shown the effectiveness of the use of fatty acids to trace invertebrate feeding (Falk-Petersen et al. 2001, Phleger et al. 2005). Fatty acids have been extensively used to investigate the trophic interactions between marine consumers and their food supply (Budge et al. 2007, Stevens et al. 2008), as well as marine food web structure (Sargent et al. 1987, Kharlamenko et al. 1995). Most species of invertebrates are not selective in their choice of prey. It is difficult and sometimes impossible to determine diet by analyzing stomach content. Primary producers principally differ in their fatty acid composition, and a close relationship exists between fatty acids of food and consumers. Most of the different food types available to filter-feeders have many fatty acids in common; however, some specific fatty acids, groups of fatty acids and fatty acid ratios serve as biomarkers of certain food sources (Sargent et al. 1987). In brief, high concentrations of 20:5n-3 and 16:1n-7, a ratio of 16:1n-7 to 16:0 that is >1, and the presence of C16 PUFA (mainly 16:4n-1) are diatom markers (Volkman et al. 1989). The branched (*iso*- and *anteiso*-) chain and odd fatty acids, as well as 18:1n-7, are typical for bacteria (Perry et al. 1979). The principal indicators of dinoflagellates are 18:4n-3 and 22:6n-3 (Mansour et al. 1999). 18:2n-6 and 20:4n-6 together with 22:6n-3 are produced by heterotrophic flagellates and ciliates, which are components of the microbial food web (Zhukova & Kharlamenko 1999). Lipids of zooplankters have high concentrations of 22:6n-3 coupled with 18:1n-9, providing an indicator of carnivorous organisms (Graeve et al. 1997). By examining the fatty acid compositions of particulate organic matter (POM) in water, and of bottom sediments and benthic invertebrates within these environments, the trophic interactions between these components can be followed. Fatty acid marker analysis is, therefore, a useful tool in identifying food resources utilized by scallops and polychaetes and in determining trophic relationships between them.

The aim of this study was to investigate the ecology of the scallop and boring polychaete association. We performed the fatty acid analysis of the Japanese scal-

lop *Patinopecten yessoensis*, polychaete *Polydora brevipalpa*, and potential food materials available in the environment with the aim of determining the principal food sources of the animals and the trophic relationships between the two species. In addition, scallop morphometric parameters at different abundances of polychaete were compared to clarify the topical and trophic relationships in the investigated community.

## MATERIALS AND METHODS

**Study sites and sampling.** To simplify the study of the scallop–epibiont community, we selected a site with muddy bottom sediments, where shell-boring polychaetes are the only scallop epibionts. Scallop samples ( $n = 164$ ) were taken using SCUBA from a muddy bottom in Amurskii Bay (Peter the Great Bay, northwestern Sea of Japan).

For biochemical analysis, 5 specimens of adult 5 yr old scallops (at the same ontogenetic stage) were selected. Six polychaete worm samples, each comprising 5 specimens, were removed from the scallop shells. For lipid analysis, 3 samples of plankton, near-bottom POM, and bottom sediments were taken. Samples of the top layer of bottom sediments were collected in the same area and kept frozen under  $-20^{\circ}\text{C}$  until analysis. Plankton samples were collected from the water column and from near-bottom water (0 to 6 m and the 5 cm layer adjacent to the bottom, respectively) with a net (mesh size 20  $\mu\text{m}$ ) directly above the scallop collecting sites. Samples of POM from near-bottom water were collected using a pump. Samples of plankton from the water column and near-bottom water were filtered through 37 mm Whatman GF/A glass-fiber filters to obtain plankton POM and near-bottom POM. The filters were placed in flasks with chloroform/methanol (1:2, v/v).

**Analysis.** Light microscopic examination (magnification  $\times 160$ ) on the plankton samples was performed to determine the structure and abundance of micro-organism assemblages.

Lipid analyses were performed on scallop digestive glands, whole polychaetes, water-column plankton samples, near-bottom water POM and bottom sediments. Lipids were extracted by the modified method of Bligh & Dyer (1959). Separation of phospholipids (PL) and triacylglycerols (TAG) from the lipids of the polychaetes was performed by thin-layer chromatography (TLC) on silica gel using a solvent system, which consisted of hexane/diethyl ether/acetic acid (80:20:1, v/v). The extracted lipids of sediments were fractionated into neutral lipids, glycolipids, and PL, by column chromatography on silica gel by using chloroform, acetone, and methanol, respectively. The PL fractions of

sediments, the PL and TAG fractions of the polychaetes, and the total lipids of other samples were analyzed for fatty acids using gas-liquid chromatography (GLC). The fatty acids were converted to their respective methyl esters (FAMES) and analyzed by capillary GLC. FAMES were prepared by transesterification of lipids according to the method of Carreau & Dubacq (1978), and purified by TLC using benzene as a solvent. The FAMES were analyzed on a GC-14A gas chromatograph equipped with a flame ionization detector (Shimadzu), using a fused silica capillary column (30 m  $\times$  0.25 mm inner diameter, i.d., Supelcowax-10) at  $210^{\circ}\text{C}$ . Helium was used as a carrier gas. Fatty acids were identified using standard mixtures and equivalent chain length values. Identification was confirmed by GC-MS using a model GCMS-QP5050A (Shimadzu) fitted with a MDN-5S capillary column (30 m  $\times$  0.25 mm i.d.). The column temperature was programmed as follows: a 1 min hold at  $170^{\circ}\text{C}$ , followed by an increase to  $240^{\circ}\text{C}$  at  $2^{\circ}\text{C min}^{-1}$  and a hold at  $240^{\circ}\text{C}$  for 20 min. The temperature of the injector and detector was  $250^{\circ}\text{C}$ .

Dark brown coloration on the inside of the scallop shell is an indication of polychaete occupation, and boreholes on the outer surface correspond to these colored areas. The degree of polychaete occupation (percentage of total scallop valve area) was estimated by measuring the extent of such dark brown coloration on the the inner side of the valve using a light and a transparent palette with a 1  $\times$  1 mm grid. The internal volume of each scallop was determined by measurement of the volume of water that is contained within the scallop valves. For this purpose, a gap between tightly closed valves was covered by plastic material, leaving open an aperture (hole) at the scallop apex. Water was poured into the empty internal cavity of the scallop up to the hole edges. Then the water was emptied into a vessel and weighed on a GC-17A balance (Shimadzu). Measurements of internal volume were carried out 3 times for each scallop.

For each scallop, shell height, total wet weight, and weights of soft tissues and adductor muscle were measured. Also, thickness of the upper valve of each scallop was measured with a slide gauge near the valve edge at the central radial rib.

The age of each scallop during its lifetime was determined retrospectively from the growth layers revealed in the microsculpture of the external surface of the upper valve according to the method suggested by Silina (1996). Winter and summer growth layers differ in their appearance and width. The Japanese scallop forms one broad elementary growth layer weekly from November to April (when water temperature is  $< -5^{\circ}\text{C}$ ), and one narrow elementary growth layer daily during the rest of the year. Growth layers are narrowest every

year around late July / early August (when water temperatures are  $>16^{\circ}\text{C}$ ) and merge into a visible annual ring. Thus we were able to determine the age of each scallop by counting the number of annual shell rings.

**Data analysis.** The relationships between the portion of the scallop valve occupied by polychaete worms (degree of occupation) and shell height, weights, and valve thickness were studied only for the scallop upper valves, as the lower valves were eroded insignificantly. Linear regressions for the degree of occupation on various scallop morphometric parameters were calculated for 5 yr old scallops (the most numerous age group in the scallop sample). A 1-way ANOVA test was used to verify the significance of the relationships between the degree of occupation and scallop morphometric parameters.

Tree clustering methods based on the Euclidean distances between clusters and *K*-means clustering (Statistica 5.0) were used to determine groups of environments and individuals that differed significantly in fatty acid content. ANOVA was applied to reveal the fatty acid components that were the main cause of group difference. The concentrations of the marker fatty acids in the animals and potential food sources were analyzed with principal components analysis (factor analysis).

## RESULTS

### Distribution of polychaete aggregations on the shell of scallop-host

Only one species of polychaete worm, *Polydora brevipalpa*, inhabited the scallop shell in the study site. The portion of the upper scallop valve occupied by polychaetes considerably increased with the host age (Table 1). The ANOVA revealed that this relationship

Table 1. *Polydora brevipalpa* on *Patinopecten yessonsis*. Changes in proportions of upper and lower scallop valves occupied by polychaete worm (mean  $\pm$  SE). Some age classes were absent in scallop samples

Age (years)	N	Portion of the valve area occupied by polychaetes (%)	
		Upper valve	Lower valve
1	12	0 $\pm$ 0	0 $\pm$ 0
2	16	1 $\pm$ 0	0 $\pm$ 0
3	22	8 $\pm$ 2	0 $\pm$ 0
4	20	38 $\pm$ 3	1 $\pm$ 0
5	72	56 $\pm$ 2	2 $\pm$ 0
6	18	63 $\pm$ 4	3 $\pm$ 1
7	2	66 $\pm$ 5	4 $\pm$ 2
10–11	2	89 $\pm$ 5	6 $\pm$ 4

was statistically significant (age was an independent variable,  $df = 1$ ,  $n = 164$ ,  $F = 228.4$ ,  $p < 0.0001$ ). The equation representing this dependence was  $y = 13.197x - 14.538$  ( $r = 0.765$ ,  $n = 164$ ), where  $x$  is scallop age (yr), and  $y$  is degree of occupation by polychaetes (%).

The highest polychaete expansion rates were found for 3 to 6 yr old scallops. Shells of young (0 to 3 yr old) scallops were practically free of boring polychaetes (Table 1).

### Comparison of fatty acid compositions of potential food sources and consumers

Tree clustering analysis of the fatty acid contents in organic matter of bottom sediments, near-bottom water POM, plankton in the water column, polychaetes, and scallops revealed 2 main clusters. The first cluster contained samples of potential food sources, and the second included scallop and polychaete samples. The clusters were separated at a very high level (14.2) of Euclidean distance between them (Fig. 1).

*K*-means clustering of the fatty acid compositions of potential food sources, polychaetes, and scallops defined after one iteration 2 groups that differed significantly. First group contained samples of food sources; the second group was represented by polychaetes and scallops. The ANOVA revealed that fatty acid components 16:0, 18:0, 18:1n-7, 18:1n-9, 18:2n-6, 20:1n-11, 20:2 non-methylene interrupted (NMI), 20:5n-3, and 22:6n-3 and the sum of odd and branched fatty acids were the main origins of the differences between the groups ( $df = 18$ ,  $F = 8.98$  to 183.67,  $p < 0.001$ ).

Factor analysis of the contents of marker fatty acids of diatoms, bacteria, flagellates, and zooplankton in the potential food sources and the animals extracted 2 factors and revealed significant differences between the animals and bottom sediments, near-bottom water POM, and plankton (Fig. 2). Food sources separated into 3 homogenous groups: (1) bottom sediments, (2) near-bottom water POM, and (3) plankton. Scallop samples and polychaete samples separated into 2 partially overlapping groups, indicating the similarity of distribution of marker fatty acids in the animals.

### Fatty acid composition of potential food sources

At the studied site, the fatty acids 14:0, 16:0, 16:1n-7, 18:0, 18:1n-9, 18:2n-6, 20:5n-3, and 22:6n-3 made up the major components in the samples of potential food sources (plankton, near-bottom water POM, and bot-

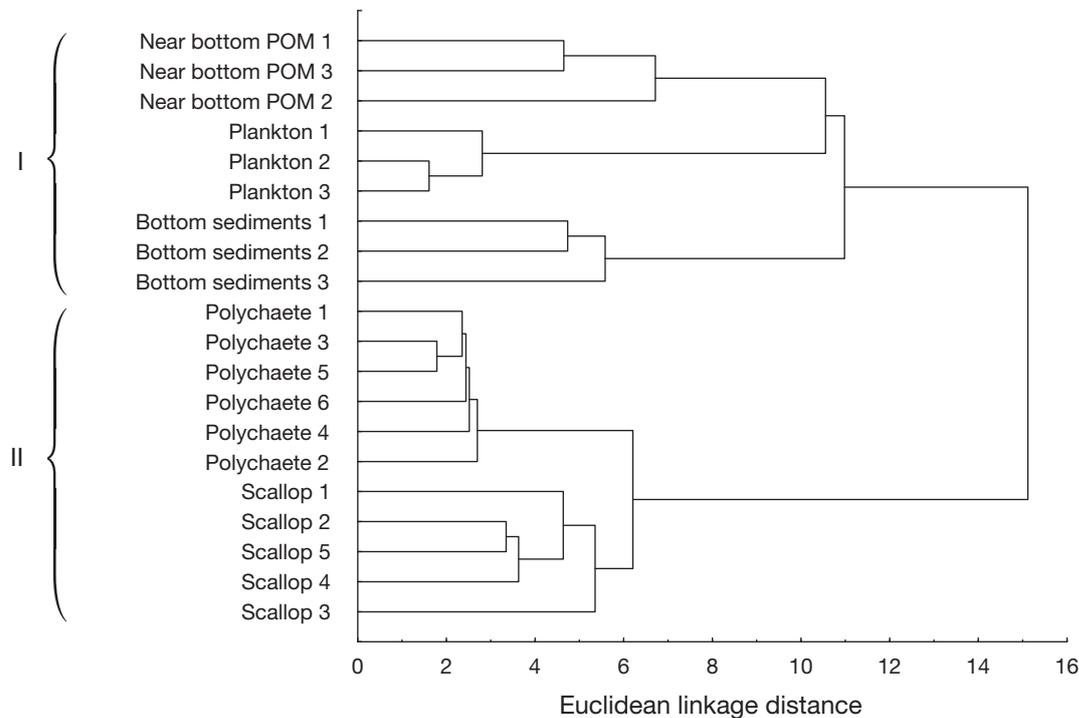


Fig. 1. *Polydora brevivalpa* and *Patinopecten yessoensis*. Tree diagram of cluster analysis of organic-matter fatty acid content in bottom sediments, near-bottom water particulate organic matter (POM), water-column plankton, polychaete and scallop

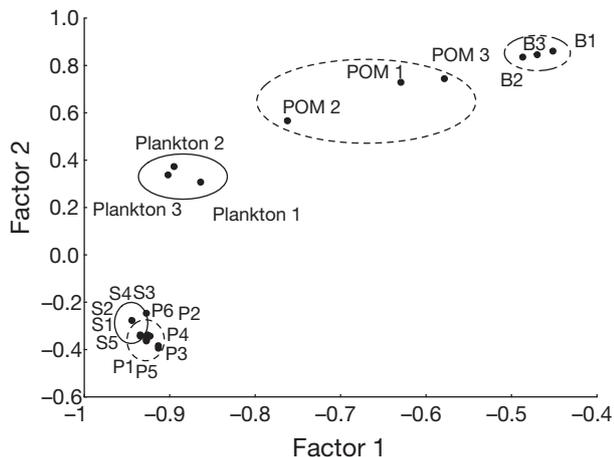


Fig. 2. Factor analysis of the content of the marker fatty acids of diatoms, bacteria, flagellates and zooplankton in the potential food sources and the animals. B1, B2 and B3 are samples of bottom sediments. POM1, POM2 and POM3 are samples of near bottom layer particulate organic matter (POM). Plankton 1, Plankton 2 and Plankton 3 are samples of plankton from water column. S1, S2, S3, S4 and S5 are samples of scallop. P1, P2, P3, P4, P5 and P6 are samples of polychaete worms

tom sediments) (Table 2). Significant differences were found in the fatty acid composition of these sources of organic carbon (food sources). The tree clustering method revealed 3 clusters amongst environmental

samples that had similar fatty acid components. The first cluster included bottom sediment samples, the second consisted of samples of near-bottom water POM, and the third one contained plankton samples. These clusters were separated at a level of 10.4 to 12.2 Euclidian distances between the clusters. *K*-means clustering of fatty acid contents in organic matter of bottom sediments, POM of near-bottom water, and plankton of the water column revealed, after one iteration, 2 groups that significantly differed in their fatty acids. The first group contained samples of near-bottom water POM and bottom sediments; the second group was represented by plankton samples. ANOVA revealed that fatty acid components 14:0, 15:0-i, 15:0-ai, 15:0, 16:0, 17:0-i, 16:4n-1, 18:4n-3, 20:5n-3, and 22:6n-3 mainly accounted for differences between the groups ( $df = 7$ ,  $F = 12.65$  to 176.59,  $p < 0.001$ ).

The plankton samples were rich in the PUFAs 20:5n-3, 22:6n-3, 18:4n-3, and 18:2n-6, with 20:5n-3 being dominant among them (45.4%). In addition, substantial amounts (6.9%) of C16 PUFA (16:2n-4, 16:3n-4, 16:4n-3, and 16:4n-1), and high levels of 22:6n-3 and 18:1n-9, were found in these samples. Considerable amounts of 20:5n-3 (6.8%) and C16 PUFA (6.7%) indicate the presence of diatoms in the plankton. Microscopic analysis of plankton samples showed that the diatoms *Rhizosolenia setigera*, *Pseudo-nitzschia* sp., *Chaetoceros* sp., and *Skeleto-*

Table 2. Fatty acid composition (wt %) of potential food sources: plankton, near-bottom water particulate organic matter (POM) and bottom sediments. Mean  $\pm$  SD, n = 3

Fatty acid	Total lipids		Phospholipids Bottom sediments
	Plankton	Near-bottom water POM	
12:0	0.5 $\pm$ 0.1	0.7 $\pm$ 0.1	0 $\pm$ 0
iso-14:0	0 $\pm$ 0	0.3 $\pm$ 0.1	0 $\pm$ 0
14:0	6.7 $\pm$ 0.2	4.8 $\pm$ 0.1	3.2 $\pm$ 0.3
14:1	0.2 $\pm$ 0.1	0.4 $\pm$ 0.1	1.1 $\pm$ 0.2
iso-15:0	0.4 $\pm$ 0.1	1.0 $\pm$ 0.1	0.8 $\pm$ 0.1
aiso-15:0	0.3 $\pm$ 0.1	1.2 $\pm$ 0.1	1.5 $\pm$ 0.4
15:0	0.7 $\pm$ 0.1	1.2 $\pm$ 0.1	1.7 $\pm$ 0.2
15:1	0 $\pm$ 0	0.2 $\pm$ 0.2	0 $\pm$ 0
iso-16:0	0.2 $\pm$ 0.0	0.3 $\pm$ 0.1	0.6 $\pm$ 0.2
aiso-16:0	0.2 $\pm$ 0.0	0.1 $\pm$ 0.2	0 $\pm$ 0
16:0	18.8 $\pm$ 0.8	23.4 $\pm$ 3.0	23.0 $\pm$ 0.8
16:1n-11	0 $\pm$ 0	0.1 $\pm$ 0.2	0.9 $\pm$ 0.1
16:1n-9	0.7 $\pm$ 0.1	1.6 $\pm$ 0.2	3.0 $\pm$ 1.0
16:1n-7	5.8 $\pm$ 0.5	9.8 $\pm$ 1.0	4.7 $\pm$ 0.8
iso-17:0	0.8 $\pm$ 0.1	0.5 $\pm$ 0.1	1.8 $\pm$ 0.8
16:2n-6	0.4 $\pm$ 0.1	0.5 $\pm$ 0.1	0.3 $\pm$ 0.1
16:2n-4	1.2 $\pm$ 0.1	0.6 $\pm$ 0.2	0.6 $\pm$ 0.3
17:0	0.6 $\pm$ 0.1	0.8 $\pm$ 0.1	1.5 $\pm$ 0.2
16:3n-4	0.8 $\pm$ 0.1	1.4 $\pm$ 0.2	0.7 $\pm$ 0.3
16:3n-3	0 $\pm$ 0	0.3 $\pm$ 0.1	0.2 $\pm$ 0.1
iso-18:0	0.5 $\pm$ 0.1	0.6 $\pm$ 0.2	4.9 $\pm$ 1.1
16:4n-3	2.1 $\pm$ 0.5	3.2 $\pm$ 0.9	0.8 $\pm$ 0.1
16:4n-1	2.4 $\pm$ 0.3	0.7 $\pm$ 0.2	0 $\pm$ 0
18:0	6.7 $\pm$ 0.3	10.0 $\pm$ 2.5	9.1 $\pm$ 0.3
18:1n-9	8.1 $\pm$ 0.5	8.9 $\pm$ 1.3	12.4 $\pm$ 0.9
18:1n-7	2.5 $\pm$ 0.2	4.9 $\pm$ 0.4	3.0 $\pm$ 0.2
18:2n-6	6.5 $\pm$ 0.2	6.0 $\pm$ 1.1	10.8 $\pm$ 0.6
18:3n-6	0 $\pm$ 0	0 $\pm$ 0	1.0 $\pm$ 0.2
18:3n-3	1.2 $\pm$ 0.2	0.8 $\pm$ 0.3	0.7 $\pm$ 0.2
18:4n-3	4.7 $\pm$ 0.4	0.8 $\pm$ 0.3	0.6 $\pm$ 0.2
20:0	0.5 $\pm$ 0.1	0.3 $\pm$ 0.5	1.2 $\pm$ 0.2
20:1n-11	0.2 $\pm$ 0.0	0.3 $\pm$ 0.3	0 $\pm$ 0
20:1n-9	0.3 $\pm$ 0.0	0.2 $\pm$ 0.2	0 $\pm$ 0
20:4n-6	0.4 $\pm$ 0.1	0.8 $\pm$ 0.2	1.0 $\pm$ 0.4
20:5n-3	13.3 $\pm$ 0.2	6.8 $\pm$ 2.0	3.9 $\pm$ 0.2
22:4n-3	0.2 $\pm$ 0.0	0.2 $\pm$ 0.3	0 $\pm$ 0
22:5n-3	1.1 $\pm$ 0.2	0.4 $\pm$ 0.4	0.9 $\pm$ 0.3
24:0	0.3 $\pm$ 0.0	0.6 $\pm$ 0.6	0 $\pm$ 0
22:6n-3	10.2 $\pm$ 1.4	4.2 $\pm$ 0.6	4.4 $\pm$ 1.0
16:1/16:0	0.3	0.4	0.2
$\Sigma$ C16 PUFA	6.9 $\pm$ 1.1	6.7 $\pm$ 1.6	4.4 $\pm$ 1.6
$\Sigma$ odd, branched	3.6 $\pm$ 0.3	6.6 $\pm$ 1.3	11.1 $\pm$ 2.3
$\Sigma$ PUFA	44.0 $\pm$ 3.6	26.2 $\pm$ 6.6	25.9 $\pm$ 3.9

*nema costatum* were dominant. Their concentrations were one or 2 orders of magnitude higher than those of minor species.

Near-bottom water POM had low levels of PUFA (26.2%), high concentrations of saturated, 16:0 and 18:0, and elevated contents of odd and branched fatty acids, mainly 15:0-i, 15:0-ai, 15:0, 17:0-i, and 17:0 (6.6% in sum). The high concentration of odd and branched fatty acids in suspended matter suggests bacterial contribution. High abundances of saturated and odd- and branched fatty acids were reported in detritus by Mayzaud et al. 1989. Along with the high

content of saturated fatty acids, near-bottom water POM had high levels of 16:3n-4 and 16:4n-3, as well as 20:5n-3. This suggests the presence of benthic diatoms in substantial amounts. Microscopic analysis showed the predominance of vegetative cells of *Thalassiosira* sp., resting cells of *Skeletonema costatum*, and resting spores of *Chaetoceros* sp. in near-bottom water samples. Furthermore, cysts and resting cells of dinoflagellates (with *Prorocentrum micale* as main species), as well as tintinnids and ciliates, were found.

Bottom sediments were rich in saturated fatty acids and also contained high level of odd and branched (iso- and anteiso-) fatty acids (11.1% of the total fatty acids), compared to both plankton and near-bottom water POM (3.6 and 6.6%, respectively). PUFA accounted for 25.9% of the total fatty acids, and among them C16 PUFA comprised 4.4% in bottom sediments.

#### Fatty acid composition of scallops and polychaetes

For the polychaete, fatty acids were analyzed separately from TAG and PL (Table 3). Fatty acids of the scallop digestive gland were analyzed to identify the food supply (Table 3). Fatty acid profiles of scallops and polychaetes were different but showed some general similarities. The principal fatty acids of these animals were 14:0, 16:0, 16:1n-7, 18:1n-9, 18:1n-7, 18:4n-3, 20:5n-3, and 22:6n-3 (Fig. 3). High abundance of 20:5n-3 and 14:0, the ratio of 16:1n-7 to 16:0 close to 1, and substantial amounts of 16:2n-4,

16:3n-4, and 16:4n-1 were characteristic for both species. However unlike the scallop, the polychaete was characterized by the detectable contribution of odd and branched fatty acids in the total fatty acids (5.0% versus 2.0%), as well as 22:2 NMI fatty acids (up to 3% in TAG of polychaetes). The concentrations of the bacterial markers and 22:2 NMI fatty acids significantly differed among the species studied ( $p < 0.01$ ). Furthermore, the fatty acid profile of the scallop digestive gland showed significantly higher percentages of 22:6n-3 and 18:1n-9 in comparison with that of TAG of polychaetes ( $p < 0.01$ ).

Table 3. Fatty acid compositions (wt %) of the total lipids of the digestive gland of the scallop *Patinopecten yessoensis* and triacylglycerols (TAG) and phospholipids (PL) of the polychaete *Polydora brevipalpa*. Mean  $\pm$  SD

Fatty acids	<i>P. yessoensis</i> (n = 5)	<i>P. brevipalpa</i> (n = 6)	
	Total lipids	TAG	PL
14:0	5.0 $\pm$ 0.6	8.4 $\pm$ 0.3	2.3 $\pm$ 0.3
iso-15:0	0 $\pm$ 0	0.8 $\pm$ 0.2	0.3 $\pm$ 0.1
aiso-15:0	0 $\pm$ 0	0.5 $\pm$ 0.1	0.1 $\pm$ 0.0
15:0	0.4 $\pm$ 0.1	0.8 $\pm$ 0.1	0.3 $\pm$ 0.1
16:0	13.2 $\pm$ 1.2	12.7 $\pm$ 1.8	12.6 $\pm$ 1.2
16:1n-11	0 $\pm$ 0	0.3 $\pm$ 0.1	1.4 $\pm$ 0.3
16:1n-9	0.4 $\pm$ 0.1	0.5 $\pm$ 0.2	0.3 $\pm$ 0.1
16:1n-7	12.2 $\pm$ 1.8	11.4 $\pm$ 0.5	3.5 $\pm$ 0.2
iso-17:0	0.3 $\pm$ 0.0	0.6 $\pm$ 0.2	0.3 $\pm$ 0.1
aiso-17:0	0.5 $\pm$ 0.1	0.9 $\pm$ 0.3	0.4 $\pm$ 0.1
16:2n-6	0.2 $\pm$ 0.0	0.2 $\pm$ 0.1	0 $\pm$ 0
16:2n-4	1.2 $\pm$ 0.2	2.3 $\pm$ 0.4	0 $\pm$ 0
17:0	0.4 $\pm$ 0.1	0.5 $\pm$ 0.1	0.6 $\pm$ 0.1
16:3n-4	1.1 $\pm$ 0.2	2.0 $\pm$ 0.1	0.5 $\pm$ 0.1
16:3n-3	0.1 $\pm$ 0.0	0.5 $\pm$ 0.2	0.6 $\pm$ 0.2
16:4n-3	0.3 $\pm$ 0.1	0.6 $\pm$ 0.3	0.6 $\pm$ 0.1
16:4n-1	1.2 $\pm$ 0.4	4.9 $\pm$ 0.0	0 $\pm$ 0
18:0	2.7 $\pm$ 0.1	2.3 $\pm$ 0.3	5.1 $\pm$ 0.7
18:1n-11	0.2 $\pm$ 0.0	0.8 $\pm$ 0.0	1.5 $\pm$ 0.3
18:1n-9	5.6 $\pm$ 0.6	3.2 $\pm$ 0.3	1.8 $\pm$ 0.2
18:1n-7	5.0 $\pm$ 0.6	2.5 $\pm$ 0.2	3.1 $\pm$ 0.3
18:2n-6	2.9 $\pm$ 0.2	1.9 $\pm$ 0.0	1.2 $\pm$ 0.1
18:2n-4	0 $\pm$ 0	0.7 $\pm$ 0.2	0.4 $\pm$ 0.1
18:3n-6	0 $\pm$ 0	0.4 $\pm$ 0.0	0 $\pm$ 0
18:3n-3	1.1 $\pm$ 0.1	0 $\pm$ 0	0 $\pm$ 0
18:4n-3	5.1 $\pm$ 0.6	6.1 $\pm$ 0.3	0.3 $\pm$ 0.1
20:1n-11	0.8 $\pm$ 0.2	1.1 $\pm$ 0.1	4.1 $\pm$ 0.3
20:1n-9	0.5 $\pm$ 0.1	0.4 $\pm$ 0.0	1.4 $\pm$ 0.1
20:1n-7	1.0 $\pm$ 0.2	0.7 $\pm$ 0.1	2.9 $\pm$ 0.2
20:2 NMI	0.2 $\pm$ 0.1	0.2 $\pm$ 0.0	0.7 $\pm$ 0.1
20:3n-6	0.3 $\pm$ 0.1	0 $\pm$ 0	0 $\pm$ 0
20:4n-6	1.4 $\pm$ 0.5	0.5 $\pm$ 0.1	1.1 $\pm$ 0.2
20:4n-3	0.6 $\pm$ 0.2	0 $\pm$ 0	0.3 $\pm$ 0.1
20:5n-3	25.0 $\pm$ 1.6	26.1 $\pm$ 1.6	33.0 $\pm$ 2.1
22:1n-11	0.2 $\pm$ 0.0	0 $\pm$ 0	0.4 $\pm$ 0.1
22:2 NMI	0.1 $\pm$ 0.0	0 $\pm$ 0	2.2 $\pm$ 0.3
22:2 NMI	0.1 $\pm$ 0.0	0.2 $\pm$ 0.0	3.0 $\pm$ 0.2
22:4n-6	0.3 $\pm$ 0.1	0 $\pm$ 0	0.5 $\pm$ 0.1
22:5n-3	0.4 $\pm$ 0.1	0.4 $\pm$ 0.1	2.3 $\pm$ 0.2
22:6n-3	8.7 $\pm$ 1.7	4.2 $\pm$ 0.3	10.1 $\pm$ 1.2
16:1/16:0	0.9	0.9	0.3
$\Sigma$ C16 PUFA	4.1 $\pm$ 0.9	10.3 $\pm$ 0.8	1.7 $\pm$ 0.5
$\Sigma$ odd, branched	2.0 $\pm$ 0.2	5.0 $\pm$ 0.3	2.5 $\pm$ 0.2

Tree clustering methods revealed 2 clusters among animal samples having similar fatty acid components. The first cluster included polychaete samples, the second one consisted of scallop samples. The clusters were separated at the level of 6.8 Euclidian distances between them. *K*-means clustering of fatty acid contents in animals revealed, after one iteration, 2 significantly different groups. The first group contained polychaete samples, and the second was represented by scallop samples. ANOVA showed that 18:1n-9, 18:1n-7, 18:2n-6, 18:3n-6, 18:3n-3, 20:4n-6, 22:2 NMI,

22:5n-6, 22:6n-3 and the total odd and branched fatty acids were the main origins of the differences between the groups (df = 9,  $F$  = 1.36 to 478.15,  $p$  < 0.001).

### Effect of polychaete on scallop

Polychaete worms negatively affected the morphometric parameters of scallop. The scallop shell height decreased with increase in degree of occupation by polychaete worms (Fig. 4). The ANOVA test clearly recognized the significance of this relationship (the upper valve portion occupied by polychaetes was an independent variable, df = 1, n = 72,  $F$  = 55.3,  $p$  < 0.0001, 5 yr old scallops). Wet total weight and weight of soft tissues and adductor muscle of the scallop also decreased with increase in degree of polychaete occupation (Fig. 5). These relationships were statistically significant (ANOVA,  $F$  = 10.3, 121.5 and 136.2,  $p$  < 0.007, 0.0001 and 0.0001, for the respective weight parameters). Polychaete worms especially influenced the weight of soft tissues and adductor muscle of the scallop. For instance, for 5 yr old scallops, a 10% increase in polychaete occupation of the upper valves led to a 5.2% decrease in total wet weight, and soft tissue and adductor muscle wet weight decreased by 7.1 and 7.7%, respectively.

The thickness of the scallop upper valve significantly increased (ANOVA,  $F$  = 10.325,  $p$  < 0.001), but the internal volume of scallop decreased (ANOVA,  $F$  = 8.453,  $p$  < 0.001) with expansion of the valve by polychaete worms (Fig. 6).

## DISCUSSION

### Topical relationships

Japanese scallop provide shelter for polychaetes. However, *Polydora brevipalpa* settles in a nonrandom and uneven fashion on the scallop shell. Different topical conditions occur on scallop shells, and polychaete larvae prefer the upper valve which is situated above bottom sediments.

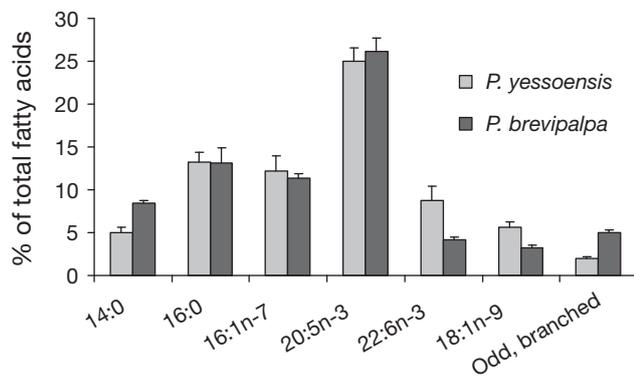


Fig. 3. Content of marker fatty acids in digestive gland of the scallop *Patinopecten yessoensis* and polychaete *Polydora brevipalpa*. Results are means  $\pm$  SD,  $n = 5$  for scallop and  $n = 6$  for polychaete

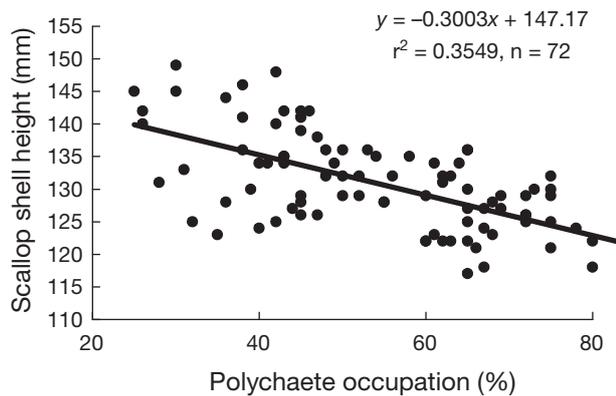


Fig. 4. *Patinopecten yessoensis*. Linear regressions for the degree of polychaete occupation of the upper valves on shell height of 5 yr old scallops

This is not the only topical relationship in the community. Because scallops are mobile active suspension feeders, their epibionts experience changes in environmental conditions. Increased water flow produced by scallop movements and respiratory activity leads to the resuspension of bottom sediments and, thereby, improves the oxygen conditions and food supply of endobionts, including spionid polychaetes (Grant et al. 1990, Hentschel 2004). Wisshak & Neumann (2006) also found that the boring *Polydora complex* similarly takes advantage of organic matter resuspended by echinoid *Echinocorys ovata* locomotion and feeding activity. Thus polychaetes benefit from the topical occupation of Japanese scallop shells, while this endobiont may impair conditions for scallops, since competition for oxygen may be occurring between the animals (Ropert & Gouletquer 2000). Sato-Okoshi & Okoshi (1993) argued that the scallop soft body may be directly affected by the polychaete because of e.g. substances secreted for dissolution of scallop shell, or constant mechanical stimulation of the soft body of the host.

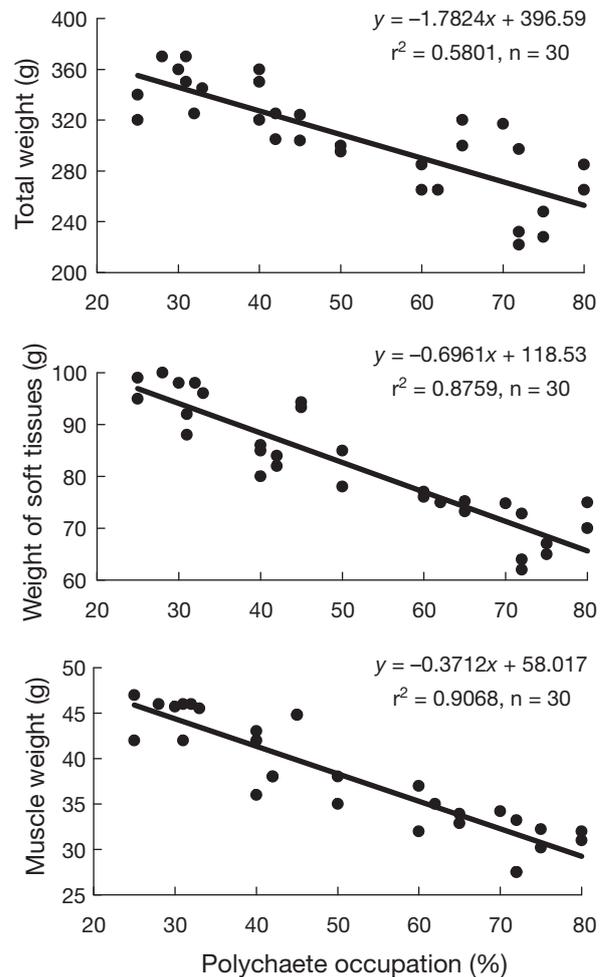


Fig. 5. *Patinopecten yessoensis*. Linear regressions for the degree of polychaete occupation of the upper valves on total wet weight, weight of soft tissues and adductor muscle wet weight of 5 yr old scallops

### Trophic relationships

The study of fatty acid composition of potential prey items is very important in defining food chain relationships (Nelson et al. 2001). The fatty acid profiles of plankton, near-bottom water POM, and bottom sediments allowed us to determine the links between these sources of organic matter and consumers and to clarify the importance of individual components (e.g. diatoms, bacteria) as food sources.

In the study area, the phytoplankton is dominated by diatoms throughout the summer season (Stonik & Orlova 1998). As expected, fatty acid composition of the samples of plankton exhibited features specific to diatoms, namely, a high content of 20:5n-3, C16 PUFA, 14:0 and 16:1n-7 (Table 2), i.e. similar to those described for phytoplankton populations dominated by diatoms (Mayzaud et al. 1989). Moderate amounts of

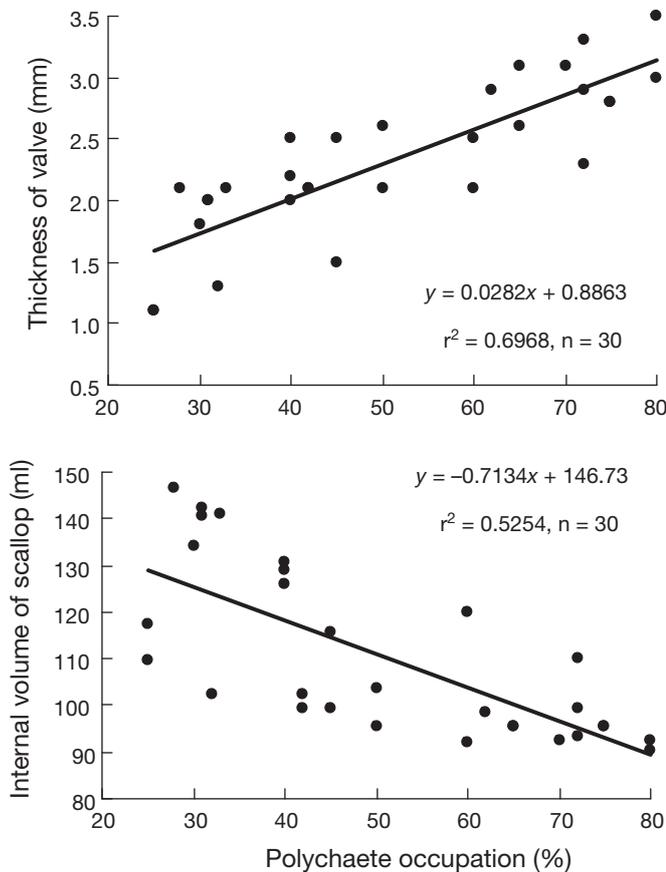


Fig. 6. *Patinopecten yessoensis*. Linear regressions for the degree of polychaete occupation of the upper valves on thickness of the upper valve and internal volume of 5 yr old scallops

18:4n-3 found in plankton were most likely derived from planktonic dinoflagellates, though some species of diatoms may also contain this fatty acid (Dunstan et al. 1994). Additionally, 18:1n-9 and 22:6n-3, which are indicators of zooplankton (Graeve et al. 1997, Auel et al. 2002), were detected in appreciable amounts. Species composition of the plankton samples was further evidence for greater importance of diatoms and a lesser role of dinoflagellates in the nutrition of the investigated species. Microscopic analysis of plankton indicated the dominance of the diatoms *Rhizosolenia setigera*, *Pseudo-nitzschia* sp., *Chaetoceros* sp. and *Skeletonema costatum*. Results obtained are in accordance with our previous work concerning the fatty acid composition of plankton at neighboring coastal locations (Silina & Zhukova 2007): plankton samples exhibited high levels of fatty acids characteristic of diatoms, with an elevated input of components specific to dinoflagellates.

Phytoplankton was mainly associated with PUFA, while near-bottom POM was associated with signifi-

cant levels of saturated fatty acids (mainly 16:0, monounsaturated fatty acids, and *iso*- and *anteiso*-branched fatty acids derived from bacteria and detritus), as well as with PUFA. The high abundance of saturated, odd and branched fatty acids has been reported earlier in detritus and related to the bloom decay (Mayzaud et al. 1989). The variability of the fatty acid composition is related to the type of particles (plankton, microzooplankton, and detritus) and to their state. At the study site the high level of C16 PUFA and moderate content of 20:5n-3 in near-bottom water POM implies that benthic diatoms, mainly as resting forms, were present in substantial quantities. Indeed, vegetative cells of *Thalassiosira* sp., resting cells of *Skeletonema costatum*, and spores of *Chaetoceros* sp. were dominant in near-bottom water. In addition, cysts and resting cells of dinoflagellates with *Prorocentrum micale* as a main species, as well as tintinids and ciliates were found. Benthic microalgae are reported to be the main food sources for many benthic invertebrates (Pellizzari et al. 2005). In addition to typical bacterial fatty acids, bottom sediments contained quite high levels of PUFA (Table 2), which suggests the presence of benthic microalgae as well as fresh phytodetritus on the sea floor.

The changes in fatty acid compositions of neutral lipids of some marine invertebrates are considered to be largely attributable to their diets (Falk-Petersen et al. 2001, Gannefors et al. 2005). Therefore, we estimated the TAG fatty acid profile of polychaetes, which reflects feeding activity and, hence, may reveal more about food supplied than PL and total lipid profiles. For the scallop, the occurrence of dietary fatty acids is more clearly reflected in the total fatty acid composition of the digestive gland of this mollusk (Napolitano & Ackman 1993). The scallop digestive gland contains large lipid deposits in the form of intracellular drops of oil (Chang et al. 1989). Accordingly, the fatty acids of scallop digestive glands are shown to mirror the major changes in the quality of the food supply (Napolitano & Ackman 1993). The bivalve digestive gland incorporates a large number of food particles by the process of phagocytosis (Chang et al. 1989), and it is suspected that food items including membrane lipids of plankton cells contribute substantially to the fatty acids of this organ. Therefore, the use of total lipids of the digestive gland, rather than TAG, is the most efficient means to trace scallop feeding (Napolitano & Ackman 1993, Silina & Zhukova 2007).

In the present study, scallops and polychaetes had similar fatty acid compositions (Fig. 3). High abundance of 20:5n-3 and 14:0, the ratio of 16:1n-7 to 16:0 close to 1, and substantial amounts of 16:2n-4, 16:3n-4, and 16:4n-1 typical for diatoms (Volkman et al. 1989, Dunstan et al. 1994) indicated significant contributions

of diatoms in the diets of both mollusk and polychaete. Elevated levels of 18:4n-3—a major fatty acid in dinoflagellates—were detected in the species of the investigated community. This suggests that dinoflagellates from near-bottom water also contributed to the diet of the animals studied. Thus, on the basis of the fatty acid markers, we can conclude that both scallops and polychaetes feed extensively on a mixed, but probably diatom-dominated phytoplankton diet.

However, 2 distinct differences between the investigated species were apparent in the relative proportions of components, indicating variations in the importance of several inputs (Fig. 3). (1) The amount of odd and branched fatty acids constituted 4.4% of the total fatty acids in polychaetes versus 2% in scallops. The presence of only minor amounts of odd and branched fatty acids in the digestive gland of scallops reflected insignificant consumption of bacteria by the mollusk. Even on muddy substrates rich in bacterial fatty acids, the bacterial contribution to the scallop diet was insignificant (Silina & Zhukova 2007). The substantial quantities of fatty acids specific to bacteria in the polychaete suggest that the polychaete ingests decayed material of planktonic origin (abundant in near-bottom water) or free-living bacteria. It is known that free-living bacteria can reach high biomass levels (Wright et al. 1982); in addition, a significant portion of bacteria is associated with particles (Dijkman & Kromkamp 2006). Detritus and bloom decay contribute substantial amounts of saturated 16:0 and 18:0 fatty acids (Perry et al. 1979, Mayzaud et al. 1989). The elevated levels of odd and branched fatty acids and saturated (mainly 18:0) acids in polychaete lipids point to detritus as an additional dietary source. Higher levels of 22:2 NMI fatty acids in *Polydora brevipalpa* than in *Patinopecten yessoensis* may indicate that fatty acids originating from bacteria are important in polychaete lipid biochemistry. The presence of NMI unsaturated fatty acids derived from 18:1n-7 had been suggested as an indicator of bacterial contribution (McKenzie et al. 2000, Pond et al. 2002, Phleger et al. 2005).

(2) Elevated levels of 22:6n-3 and 18:1n-9 found in the scallop digestive gland are indicative of zooplankton consumption (Graeve et al. 1997, Auel et al. 2002). This agrees with the data of gut content analysis of this species (Mikulich & Tsikhon-Lukanina 1981) and our previous results based on the analysis of fatty acid markers (Silina & Zhukova 2007).

The differences in the distribution of fatty acid markers of zooplankton and bacteria are undoubtedly reflected in differences in the diets of the investigated species, which, in turn, are readily accounted for by their feeding habits (Martin & Britaev 1998). Scallops are active filter feeders and, by means of water filtration, can capture zooplankton, swimming larvae of

arthropods and mollusks. The structure of the mouth apparatus of the polychaete *Polydora brevipalpa* facilitates the capture and retention of bacteria on the microvilli of the palps. Hence, the polychaete can consume bacteria, while Japanese scallop is only capable of catching particles in the size range from 9 to 950  $\mu\text{m}$  (Mikulich & Tsikhon-Lukanina 1981).

Based on fatty acid marker distributions and literature data, we can conclude that species from the scallop–polychaete community extensively feed on mixed, but probably diatom-dominated phytoplankton diets. The similarity of the diets is a major determinant of the feeding competition between species in this community.

There are other trophic relationships in the community studied. Mikulich & Tsikhon-Lukanina (1981) showed that the gut of Japanese scallop contains detritus (up to 70% of bolus), whereas biomarker analysis revealed that scallops do not consume detritus which is instead expelled into the surrounding environment with pseudofeces. However, detritus is part of the *Polydora brevipalpa* diet. Thus, in the process of feeding, the scallop increases the concentration of food for *P. brevipalpa*.

*Polydora brevipalpa* may indirectly influence the quantity of food consumed by the scallop–host. The scallop internal volume decreases with an increase in the degree of occupation by the polychaete. This reduces the potential volume available for the scallop to filter water, and accordingly for respiration and feeding. It has been found that biodeposit production by Japanese scallop with shells that are heavily eroded by polychaetes is lower than that in healthy scallops (Makoto 1981). This is further evidence that scallop feeding is inhibited by dense infestations of polychaete worms. The decrease in scallop morphometric parameters with an increase in the degree of occupation by polychaete worms also indicated a reduction in the potential for growth of scallop as a result of the expansion of scallop shell occupation by polychaetes. Thus, in terms of feeding activity, the scallop–polychaete association is harmful to scallops. Moreover, it is evident that the higher the polychaete occupation of scallop shell, the greater the energy required for regeneration of scallop shell and the lower the efficiency of scallop growth. Day et al. (2000) estimated that the cost of shell erosion for limpets is about 8 to 12% of the total energy devoted to somatic growth, shell production and gonadal output.

This study revealed a number of aspects of the scallop–polychaete association. It is generally accepted that the interactions between the organisms in this association can be defined as ‘commensalism’, with the assumption that the polychaete benefits from the mollusk but does not cause damage to its host (Wisshak &

Neumann 2006). However, the study of the trophic and topical relationships in the scallop and polychaete association showed that with abundant polychaete occupation these relationships acquire some elements of parasitism.

Close associations of boring organisms (e.g. many species of polychaetes belonging to the families Spionidae, Sabellidae, and Cirratulidae, as well as sponges of the genus *Cliona*) and species bearing a calcareous skeleton (including mollusks, corals, barnacles, encrusting coralline algae, bryozoans, and echinoids) are widespread (Martin & Britayev 1998, Royer et al. 2006, Wisshak & Neumann 2006). Our comprehensive investigations on the scallop and polychaete worm association may be useful as a model for the study of other 2-species marine-invertebrate communities that are common in the animal world.

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