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### Diet analyses of the scale-worms *Lepidonotus squamatus* and *Harmothoe imbricata* (Polychaeta, Polynoidae) in the White Sea

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## ORIGINAL ARTICLE

# Diet analyses of the scale-worms *Lepidonotus squamatus* and *Harmothoe imbricata* (Polychaeta, Polynoidae) in the White Sea

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## Abstract

Under the harsh environmental conditions of the White Sea, the polynoid polychaetes *Lepidonotus squamatus* and *Harmothoe imbricata* coexist in the same habitats, often showing recurrent alternations in dominance. The present study focused on their diet and food preferences based on the analyses of gut contents (after dissection of preserved specimens) and faecal pellets (released by selected living specimens). Our results pointed out that the dietary regimes were significantly dependent on the collection site (and the respective dominant prey species) and not on the scale-worm species, suggesting that *L. squamatus* and *H. imbricata* are non-selective at the species level. There was also a significant overlap of their dietary regimes and our data support the existence of intra- and inter-specific aggressive behaviour, with *H. imbricata* being more aggressive than *L. squamatus*. These findings, combined with their life cycle strategies and other biological and environmental constraints, arose as significant driving forces explaining the population dynamics of the two studied scale-worms in the White Sea.

**Key words:** Diet, gut contents, faecal pellets, population dynamics, scale-worms, White Sea

## Introduction

The observation of organization and structuring processes of trophic chains is still one of the main challenges for marine ecosystem theory (Fauchald & Jumars 1979). Many papers suggest that macrofaunal trophic guilds may be a useful tool in the study of ecosystem functioning (Pinedo et al. 1997), particularly among polychaetes (Paiva 1993; Porras et al. 1996; Carrasco & Carbajal 1998; Martin et al. 2000). However, most of these are based on assumptions inferred from general works, such as the classic study of polychaete feeding and behaviour (Fauchald & Jumars 1979) and some later adaptations (Dauvin & Ibanez 1986) and revisions (Pagliosa 2005). A few more recent studies warned against broad generalizations and recommended direct experimental observations of food preferences, based on examination of faecal pellets and gut contents as a means of obtaining more precise information (Giangrande et al. 2000). Such infor-

mation is a small but valuable step towards the overall goal of ecosystem understanding. Trophic web relations in remote marine ecosystems such as the White Sea have only been studied for the most obvious energy-transfer organisms, such as plankton, benthic bivalves, fishes and marine birds (Loginova & Perzova 1967; Peruva 1984; Pavlov & Novikov 1993; Soloviev & Kosobokova 2003). The diet and trophic role of other members of the community, especially marine benthic carnivorous invertebrates, is still largely unknown and, therefore their contribution to ecosystem functioning also remains speculative (Sokolova 1986; Haytov & Gornih 2002). Among invertebrate carnivores, polychaete worms play an important role in energy transfer and cycling, generally occupying an intermediate trophic position within marine ecosystems. Three decades ago, Fauchald and Jumars (1979) recognized a substantial lack of information on the diet of about 90% of the described polychaete species.

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At the time, nothing was known of the feeding behaviour of almost 30% of the families identified at that time; there was some information inferred from taxonomic and anatomic studies for another 14%, and for the remaining 56%, diet was unknown except for a very small number of species. Unfortunately, this situation persists to the present day, although with some outstanding exceptions (Dauer et al. 1981; Dauer 1983, 1984, 1985, 1991, 1994, 1997, 2000; Dauer & Hutchings 1984; Petch 1986; Dauer & Ewing 1991; Magnino & Gaino 1998; Giangrande et al. 2000).

Polynoid polychaetes (scale-worms) are a highly diversified group including more than 700 species (Martin & Britayev 1998). They are usually considered as free-living carnivorous-polyphagous (Sarvala 1971; Fauchald & Jumars 1979) based on the shared structure of feeding and digestive organs: two pairs of chitinous jaws, a strong muscular proboscis, and a straight intestine with paired metameric diverticula (Fauchald & Rouse 1997). However, the life strategies and known dietary regimes within the family appear to be highly diverse, including more than 20% of symbiotic species, ranging from parasites such as *Thormora jonstoni* (Hauenschild et al., 1968), *Gastrolepidia clavigera* (Britayev & Lyskin, 2002) and *Branchipolynoe seepensis* (Britayev et al., 2007), to commensal and mutualistic species such as *Acholoe astericola* (Freeman et al. 1998) and *Arctonoe vittata* (Britayev & Smurov 1985; Britayev 1991), respectively.

*Harmothoe imbricata* (Linnaeus, 1767) and *Lepidonotus squamatus* (Linnaeus, 1758) are two very common and widely distributed scale-worms in shallow-water marine benthic assemblages, particularly on hard substrata around the northern hemisphere (Tebble & Chambers 1982). In the White Sea, both species coexist in the same habitats, showing markedly different life strategies and recurrent alternations in dominance (Plyusheva et al. 2004). Although it has been postulated that the respective strategies may drive a differential response of the populations of *H. imbricata* and *L. squamatus* to the harsh environmental constraints of the White Sea, it was not possible to demonstrate any direct causal relationships (Plyusheva et al. 2004). Therefore, in the present paper, we explored the trophic preferences based on direct observations of both gut contents and faecal pellets, as possible variables which may explain the population dynamics of these two scale-worms in the White Sea.

## Material and methods

The specimens of *Lepidonotus squamatus* and *Harmothoe imbricata* analysed in this paper were collected

in the vicinity of the White Sea Biological Station of the Moscow State University at Kandalaksha Bay (WSBS MSU) (Figure 1), from an abandoned mussel farm built in 1989 and never exploited commercially, and from two sponge communities, one at the Biostation Bay and the other facing Velikiy Island (Figure 1B).

The remaining rows of hanging ropes for larval settlement at the abandoned mussel farm today represent a naturalized, stable and limited environment, highly suitable for the purposes of the present study. Fauna associated with these ropes are hereafter referred to as the Mussel Community (Table I).

The Biostation Bay and Velikiy Island locations supported an invertebrate fauna similar to that of the Mussel Community (Table I). However, the less intense currents and deeper waters in the former caused *Corophium bonnellii* and *Amphithoe rubricata* to be the dominant species, while the shallower waters subjected to strong tidal currents caused *Caprella septentrionalis* to dominate in the latter (Plyusheva 2005).

At the Mussel Community, mussel druses of approximately 3 m in length were separated into single shells and all polychaetes were picked out. The shells were then washed through a 500- $\mu$ m sieve to extract any remaining polychaetes. The target scale-worms were fixed with 4% formaldehyde, then washed with fresh water and preserved in 70% alcohol. In the laboratory, 145 specimens of *Lepidonotus squamatus* and 143 of *Harmothoe imbricata* were dissected from their ventral sides, then gut contents were extracted with the help of a pipette, mounted on a slide in a glycerol/alcohol mixture, and analysed under a Zeiss Axioplan stereomicroscope equipped with a digital camera.

At the Biostation Bay and Velikiy Island locations, 40 specimens of each target scale-worm species were collected from 18 to 20 m depth and from 12 to 15 m depth by SCUBA diving, respectively. The specimens were sorted immediately and stored in single jars with filtered seawater for 48 h, until the gut became empty. All released faecal pellets were collected, mounted on a slide in a glycerol/alcohol mixture, and analysed under a stereomicroscope.

The differences in prey composition in the analysed guts were assessed by means of the Multi-Dimensional Scaling (MDS) and ANOSIM routines of the Primer 6.0 software, based on normalized data and a Bray-Curtis similarity matrix and using the scale-worm species and tree locations as factors (Clarke & Warwick 2001). The differences in the presence of remnants of the two scale-worm species (i.e. chaetae and elytra) inside their respective guts were analysed by means of a Student *t*-test (Zar 1984).

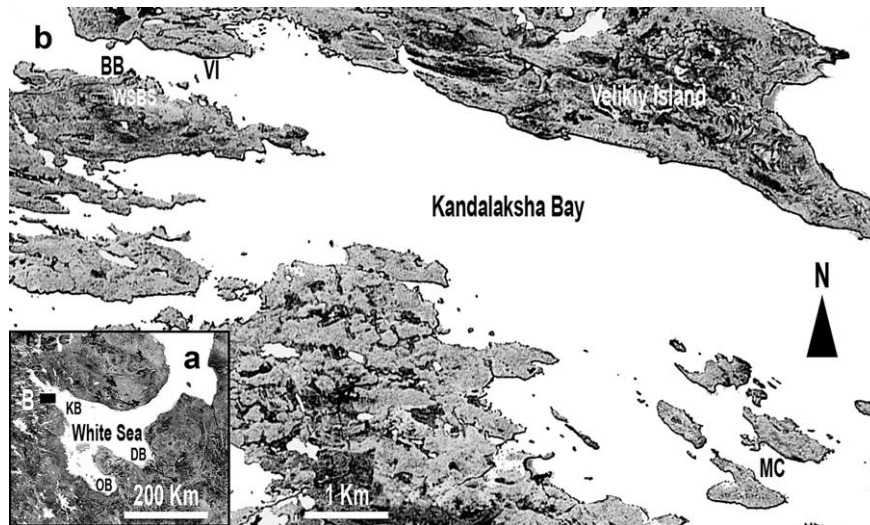


Figure 1. Location map. (a) Scheme of the White Sea subdivision with location of the White Sea Biological Station of Moscow State University. KB, Kandalaksha Bay; OB, Onega Bay; DB, Dvina Bay. (b) Vicinities of the White Sea Biological Station of Moscow State University. WSBS, White Sea Biological Station; BB, location of Biostation Bay community; VI, location of Velikiy Island community; MC, location of Mussel Community.

## Results

### *Lepidonotus squamatus*

Food fragments were found in 68.6% of the *Lepidonotus squamatus* individuals collected from the Mussel Community (Figure 2 and 5A). Their gut contents were dominated by diatomean and hydroid thecae, algal filaments, tintinoid loricae, bryozoan skeletons and sponge spicules (Table II). Other important components of the gut contents were small crustacean exoskeletons (e.g. caprellid and gammarid amphipods, and ostracods), shells of juvenile bivalves (*Mytilus* sp.), gastropods radulae and polychaete chaetae and elytra (Table II). Polychaete remnants were mainly from nereidids, phyllodocids and polynoids, among which the chaetae and elytra of *L. squamatus* were particularly abundant, although those of *Harmothoe imbricata* were also found (Table II).

Among the living *Lepidonotus squamatus* 87% of the specimens excreted all food remnants after 24 h, with a maximal gut transit time of 30 h. Worms with empty guts still ejected faecal pellets, which did not contain food remnants, but granular formations identical to the 'sphaerulae' found in the gut diverticula of *Aphrodita aculeata* Linnaeus, 1761 (Fordham 1926).

Among the *Lepidonotus squamatus* individuals collected from the Biostation Bay, 100% had food remnants in their guts. The faecal pellets most frequently contained skeletons of small amphipods (i.e. *Corophium bonnellii*, *Amphithoe rubricata* and *Caprella septentrionalis*) and sponge spicules, followed by shells of bivalve juveniles, polychaete remnants (i.e. polynoids, nereidids and phyllodocids) and algal filaments. Diatomean and hydroid thecae, as well as

bryozoan skeletons, were present with lower frequencies (Table II).

Among the *Lepidonotus squamatus* individuals from Velikiy Island, 87.5% contained food remnants in their guts, and analysis of the pellets revealed a more restricted diet, the most frequent food remnants being amphipod exoskeletons (i.e. *C. septentrionalis*), sponge spicules, diatomean and hydroids thecae, bryozoan skeletons and pantopod exoskeletons (Table II).

It must be pointed out that chaetae and elytra of *Lepidonotus squamatus* were only found inside the guts of conspecific worms at the Biostation Bay, whereas chaetae of *Harmothoe imbricata* were not found at this site, nor at Velikiy Island (Table II).

### *Harmothoe imbricata*

Food remnants were found in 62.5% of the individuals of *Harmothoe imbricata* sampled from the Mussel Community (Figure 3 and 5B), the most frequent being diatomean thecae, algal filaments, exoskeletons of small crustaceans (i.e. gammarid amphipods, ostracods, and calanoid and laophontid harpacticoid copepods), hydroid thecae, gastropod radulas and tintinnid loricae (Table II). Polychaete chaetae were also present (mainly from nereidids). Chaetae and elytra of *H. imbricata* and *Lepidonotus squamatus* also occurred, but with very low frequencies. Among the large variety of different remnants contained their guts, the absence of *Caprella septentrionalis* was remarkable in the comparison with other locations.

Among the living *Harmothoe imbricata*, 91% of the specimens excreted all gut contents after 24 h, with a maximal gut transit time of 30 h. As was the case for

Table I. Description of the communities from studied localities.

	Mussel community	Biostation Bay	Velikiy Island
Bivalvia	<i>Hiatella arctica</i> (Linnaeus, 1767) <i>Mytilus edulis</i> (Linnaeus, 1758)	<i>Hiatella arctica</i> (Linnaeus, 1767) <i>Modiolus modiolus</i> (Linnaeus, 1758)	<i>Hiatella arctica</i> (Linnaeus, 1767) <i>Modiolus modiolus</i> (Linnaeus, 1758)
Polychaeta	<i>Amphitrite cirrata</i> (O. F. Müller, 1771 in 1776) <i>Amphitrite figulus</i> (Dalyell, 1853) <i>Eulalia viridis</i> (Johnston, 1829) <i>Harmothoe imbricata</i> (Linnaeus, 1767) <i>Lepidonotus squamatus</i> (Linnaeus, 1758) <i>Nereimyra punctata</i> (Müller, 1788) <i>Nereis pelagica</i> (Linnaeus, 1758) <i>Nereis virens</i> (M. Sars, 1835)	<i>Eulalia viridis</i> (Johnston, 1829) <i>Harmothoe imbricata</i> (Linnaeus, 1767) <i>Lepidonotus squamatus</i> (Linnaeus, 1758) <i>Nereimyra punctata</i> (Müller, 1788) <i>Nereis pelagica</i> (Linnaeus, 1758) <i>Nereis virens</i> (M. Sars, 1835)	<i>Eulalia viridis</i> (Johnston, 1829) <i>Lepidonotus squamatus</i> (Linnaeus, 1758) <i>Nereimyra punctata</i> (Müller, 1788) <i>Nereis pelagica</i> (Linnaeus, 1758) <i>Nereis virens</i> (M. Sars, 1835)
Crustacea	<i>Amphithoe rubricata</i> (Montagu, 1808) <i>Caprella septentrionalis</i> (Kröyer, 1838) <i>Corophium bonellii</i> (Milne-Edwards, 1830) <i>Metopa</i> sp. <i>Pseudopallene</i> sp.	<i>Amphithoe rubricata</i> (Montagu, 1808) <i>Balanus balanus</i> (Linnaeus, 1758) <i>Corophium bonellii</i> (Milne-Edwards, 1830)	<i>Balanus balanus</i> (Linnaeus, 1758) <i>Corophium bonellii</i> (Milne-Edwards, 1830)
Cnidaria	<i>Coryne tubulosa</i> (M. Sars, 1835) <i>Obelia longissima</i> (Pallas, 1766) <i>Metridium senile</i> (Linnaeus, 1767)	<i>Abietinaria pulchra</i> (Nutting, 1904) <i>Thuiaria articulata</i> (Pallas, 1766)	<i>Abietinaria pulchra</i> (Nutting, 1904) <i>Thuiaria articulata</i> (Pallas, 1766)
Echinodermata	<i>Asterias rubens</i> (Linnaeus, 1758) <i>Ophiopholis aculeata</i> (Linnaeus, 1767)	<i>Asterias rubens</i> (Linnaeus, 1758) <i>Ophiopholis aculeata</i> (Linnaeus, 1767) <i>Ophiura robusta</i> (Ayres, 1851) <i>Stegophiura nodosa</i> (Lütken, 1855)	<i>Asterias rubens</i> (Linnaeus, 1758) <i>Ophiopholis aculeata</i> (Linnaeus, 1767) <i>Ophiura robusta</i> (Ayres, 1851) <i>Stegophiura nodosa</i> (Lütken, 1855)
Porifera	<i>Halichondria panicea</i> (Pallas, 1766)	<i>Dysidea fragilis</i> (Montagu, 1818) <i>Halichondria panicea</i> (Pallas, 1766) <i>Mycale stolonifera</i> (Merejkowski, 1878) <i>Polymastia arctica</i> (Merejkowski, 1878)	<i>Dysidea fragilis</i> (Montagu, 1818) <i>Halichondria panicea</i> (Pallas, 1766) <i>Mycale stolonifera</i> (Merejkowski, 1878) <i>Polymastia arctica</i> (Merejkowski, 1878)
Tunicata	<i>Molgula retortiformis</i> (Verrill, 1871)	<i>Molgula retortiformis</i> (Verrill, 1871)	<i>Molgula retortiformis</i> (Verrill, 1871)
Bryozoa	<i>Electra pilosa</i> (Linnaeus, 1767)	<i>Electra pilosa</i> (Linnaeus, 1767)	<i>Electra pilosa</i> (Linnaeus, 1767)

*Lepidonotus squamatus*, worms with empty guts still ejected faecal pellets, which contained similar granular formations or 'spaerulae'.

Among the *Harmothoe imbricata* from the Biostation Bay, 100% of the collected specimens had full guts. The most frequent remnants in the pellets were sponge spicules, exoskeletons of small crustaceans and polychaete chaetae and elytra (i.e. polynoids, nereidids and phyllodocids; Table II). As for the Mussel Community, remnants of *Caprella septentrionalis* were absent from the guts.

Among the *Harmothoe imbricata* specimens from Velikiy Island, 66.7% had full guts. The most frequent remnants in the pellets were exoskeletons of small crustaceans (with the notable presence of *Caprella septentrionalis*) and polychaete chaetae and elytrae, followed by sponge spicules, hydroid thecae and undefined organic fragments (Table II).

At the Biostation Bay, chaetae and elytra of *Harmothoe imbricata* were very frequent, whereas those of *Lepidonotus squamatus* were never found; at Velikiy Island, remnants of both scale-worms were found with lower but similar proportions (Table II).

#### Comparative analyses of prey composition in the gut contents

The MDS analysis of prey composition contained in the guts of *Lepidonotus squamatus* and *Harmothoe imbricata* (Figure 4a) indicated that the differences between the sampling sites were more marked (ANOSIM, Global  $R=1$ ,  $P=6.6\%$ ) than between the target scale-worm species (ANOSIM, Global  $R=-0.37$ ,  $P=90.0\%$ ), suggesting that prey availability is an important factor driving food selection.

The food remnants significantly contributing to the intra-site similarity of the gut contents were

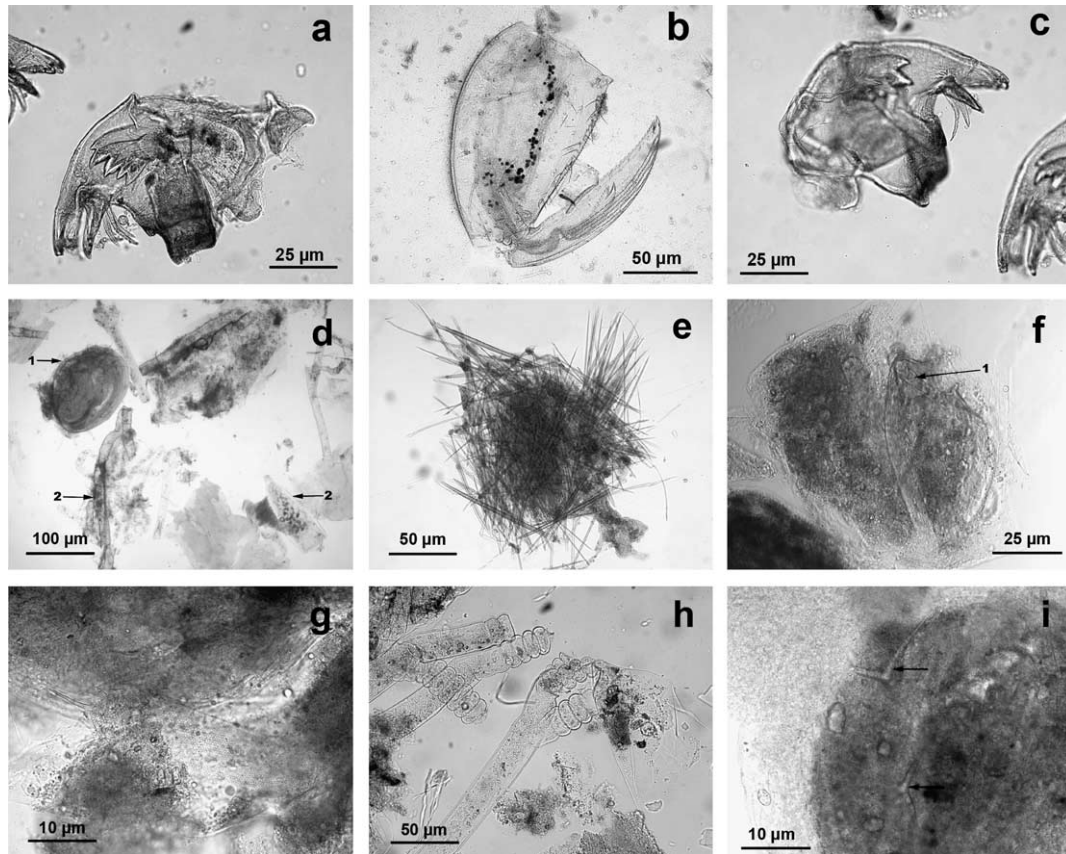


Figure 2. Gut contents of *Lepidonotus squamatus*. (a–c) Fragments of caprellid amphipods. (d) Bivalve juvenile (1) and fragments of hydroid thecae (2). (e) Bunch of nereidid chaetae. (f) Gastropod radula (1). (g) Tintinnid loricae. (h) Fragments of hydroid zooids. (i) Sponge remnants, spicules indicated by the arrow.

Table II. Dietary regime of *Lepidonotus squamatus* and *Harmothoe imbricata*: Frequency of occurrence (%) of food remnants in the respective guts at three studied locations. MC, Mussel Community; BB, Biostation Bay; VI, Velikiy Island.

Food particles	<i>Lepidonotus squamatus</i>			<i>Harmothoe imbricata</i>		
	MC	BB	VI	MC	BB	VI
Tintinnids	6.9	0	0	10	0	0
Radiolarians	0	0	0	2	0	0
Algae	9.7	13.3	0	18	12.5	0
Diatoms	94.4	6.7	50	90	25	0
Hydroids	15.3	6.7	33.3	14	0	16.7
Sponges	4.2	40	66.7	4	75	16.7
<i>H. imbricata</i>	1.4	0	0	2	37.5	16.7
<i>L. squamatus</i>	6.9	13.3	0	2	0	16.7
Other polychaetes	1.4	6.7	0	4	25	0
Bivalves	5.6	20	0	6	0	0
Gastropods	2.8	0	16.7	14	25	0
Caprellid amphipods	1.4	26.7	83.3	0	0	50
Other amphipods	6.9	33.3	0	18	62.5	0
Ostracods	4.2	0	0	4	0	0
Harpacticoid copepods	0	0	0	4	0	0
Other copepods	0	0	0	2	0	0
Pantopods	0	0	16.7	0	12.5	0
Halacarid mites	0	6.7	0	0	0	0
Bryozoans	5.6	6.7	16.7	2	0	0
Organic remains	0	0	0	0	0	33.3

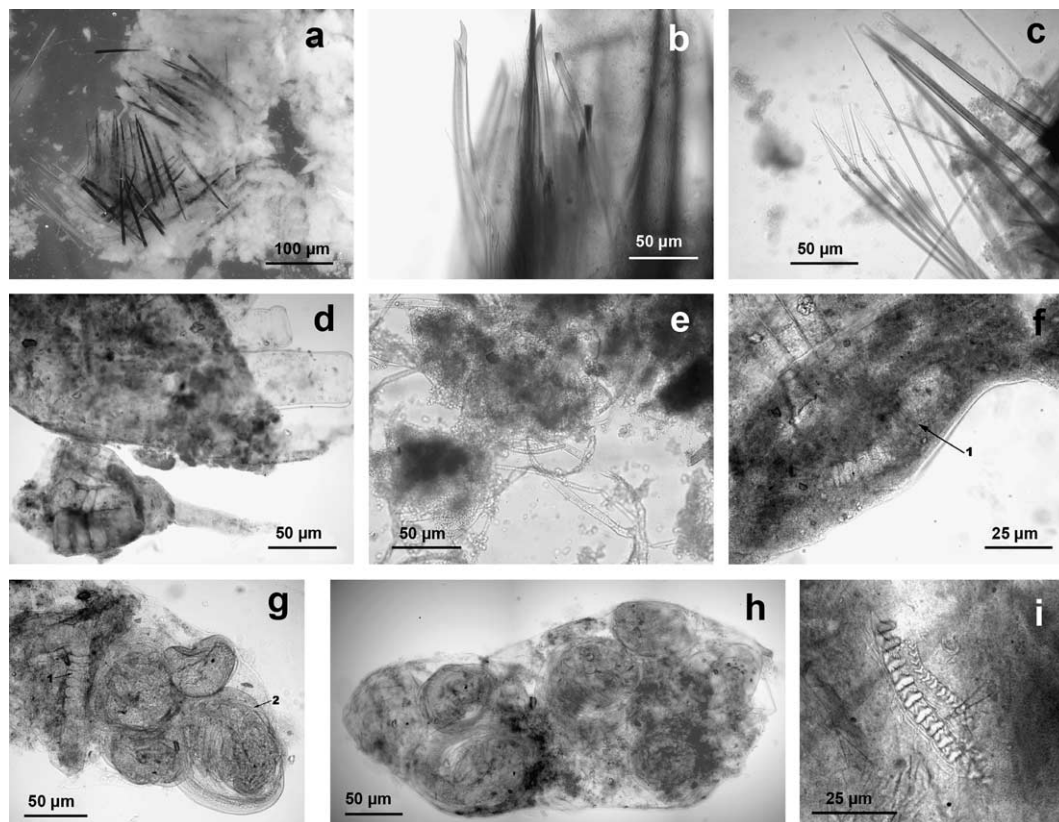


Figure 3. Gut content of *Harmothoe imbricata*. (a–c) Nereidid chaetae. (d) Fragment of a hydroid from a faecal pellet. (e) Algal filament. (f) Laophontid harpacticoid from a faecal pellet (1). (g) Hydroid fragments (1) and bivalve juvenile (2) from a faecal pellet. (h) Bivalve juvenile from a faecal pellet. (i) Part of a gastropod radula.

diatomean thecae, caprellid amphipods and sponge spicules, respectively, at the Mussel community, Biostation Bay and Velikiy Island (Table III), whereas the major contributions to the inter-site differences corresponded to diatomean thecae and caprellid amphipods (Mussel Community vs. Biostation Bay), diatomean thecae, sponge spicules and other crustaceans (Mussel Community vs. Velikiy Island), and caprellid amphipods and other crustacea (Biostation Bay vs. Velikiy Island) (Table IV). It is noteworthy that the chaetae and elytra of *Lepidonotus squamatus* and *Harmothoe imbricata* did not contribute to the intra-site similarity and their contribution to the inter-site dissimilarities was always <5% (Table III and IV).

The food remnants more significantly contributing to the intra-specific gut content similarity for each target scale-worm were sponge spicules and diatomean thecae, which also gave the most significant contribution to the inter-specific differences, together with caprellid amphipods (Table V). In this comparison, however, there was a notable difference in the contribution of the chaetae and elytra of *Lepidonotus squamatus* and *Harmothoe imbricata*. The former contributed slightly to the inter-specific differences, whereas the latter showed a significant

contribution to the intra-specific similarity and a relatively high contribution to the inter-specific differences (Table V).

Chaetae and elytra of *Harmothoe imbricata* were always present inside the gut contents of conspecifics (Table II), and were significantly more frequent (Student *t*-test = -3.42,  $p < 0.04$ ) within conspecifics (18.7% on average) than within *Lepidonotus squamatus* specimens (0.5% on average) (Figure 4b).

The chaetae and elytra of *Lepidonotus squamatus* were present in the gut of conspecifics from the Mussel Community and the Biostation Bay, and absent in the case of conspecifics from Velikiy Island (Table II). In the gut of *Harmothoe imbricata*, they were present at the Mussel Community and the Biostation Bay, but absent at Velikiy Island (Table II). Furthermore, there were no differences in their frequency in the guts of the two target scale-worms (about 6% on average in both species) (Figure 4c).

## Discussion

The studies on gut contents are most often carried out to analyse the prey consumption by a given species as an approach to assess dietary preferences, and this was among the main objectives of our study.

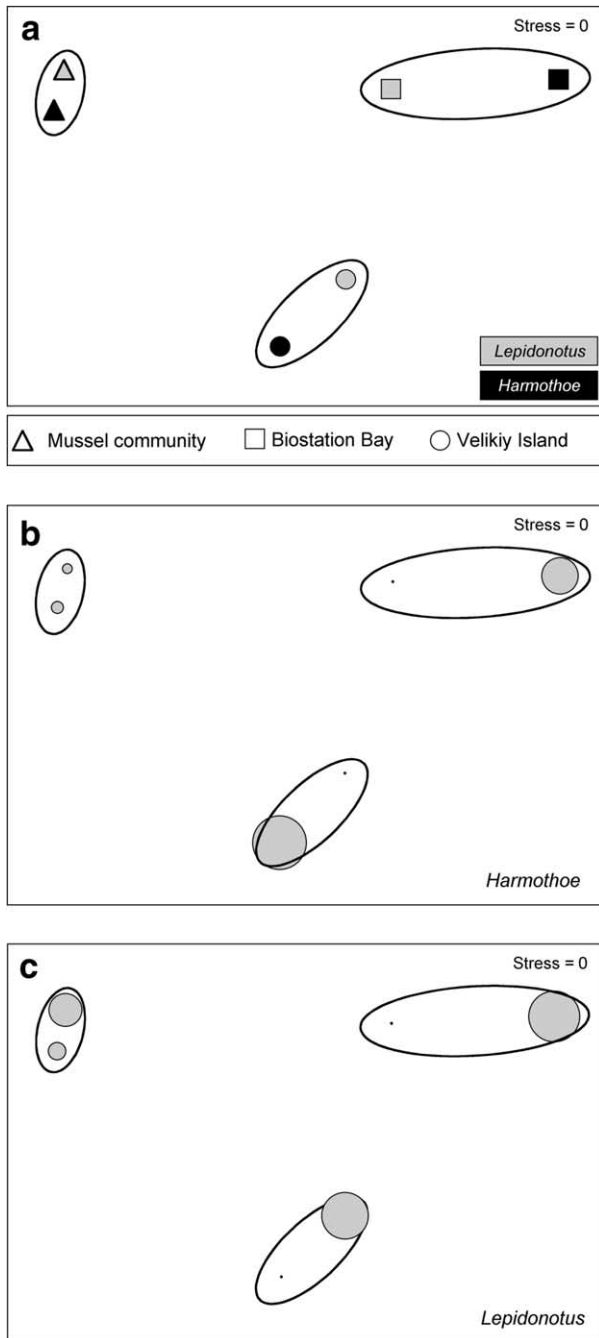


Figure 4. (a) MDS analysis of the gut contents of *Harmothoe imbricata* and *Lepidonotus squamatus* from the studied locations. Relative frequencies of chaetae and elytra (with the diameter of the circles proportional to the frequency): (b) *Harmothoe imbricata*; (c) *Lepidonotus squamatus*.

However, it is evident that guts may contain various other items in addition to prey, and our study also points out that, in the case of the two target scale-worms, some objects (e.g. algal filaments, sponge remnants) were most likely taken together with prey, while some others (e.g. elytra and bristles from conspecifics) were most likely ingested as a result of territorial combats.

Table III. Results of the SIMPER analysis comparing the studied locations: Percentages of average similarity and species contribution.

	Mussel community	Biostation Bay	Velikiy Island
Average similarity	79.7	51.64	52.69
Sponge spicules	—	21.54	42.16
Diatoms	57.61	—	—
Caprellid amphipods	—	56.91	—
Other amphipods	5.19	—	35.09
Hydroids	8.96	21.54	—
Algal filaments	7.3	—	8.63
Other polychaetes	—	—	7.06
Tintinnids	5.19	—	—
Bivalve juveniles	3.84	—	—
Ostracods	2.56	—	—

In the case of *Harmothoe imbricata*, the gut analyses of specimens from Danish waters proved its diet to consist mainly of small crustaceans (such as gammarids or cumaceans), small brittle-stars, polynoid and flabelligerid (i.e. *Pherusa*) polychaetes, gastropods, sponges and hydroids (Blegvad 1915). In the Barents Sea, the diet was similar but slightly more varied, also including foraminiferans, nematods, oligochaetes, bryozoans, other crustaceans (mainly harpacticoid copepods and ostracods), pan-topodes, halacarid mites, chironomid larvae and bivalves (Strel'tsov 1966). However, the gammarid amphipods *Amphithoe rubricata* and *Gammarus* sp. were consistently among the main prey items.

Our data from the White Sea also confirmed the major role of small crustaceans (more specifically amphipods) in the *Harmothoe imbricata* and *Lepidonotus squamatus* diet, particularly in the former (Table II, Figure 5a, b). The main prey species were *Amphithoe rubricata* and *Caprella septentrionalis* (Mussel Community), *A. rubricata* and *Corophium*

Table IV. Results of the SIMPER analysis comparing the studied locations: Percentages of average dissimilarity and species contribution.

	MC/BB	MC/VI	BB/VI
Average dissimilarity	75.57	68.91	62.36
Diatoms	28.09	32.56	7.07
Caprellid amphipods	20.46	5.38	19.2
Sponge spicules	9.96	16.3	6.47
Other amphipods	4.41	10.12	16.52
Organic remains	7.34	—	8.89
Hydroids	2.17	4.57	7.68
<i>H. imbricata</i>	3.68	4.95	5.47
<i>L. squamatus</i>	3.68	2.68	4.46
Algal filaments	4.96	—	4.78
Other polychaetes	—	3.6	5.14
Bivalve juveniles	—	4.03	4.45
Tintinnids	3.06	3.35	—
Gastropod radulas	2.36	3.3	—



Table V. Results of the SIMPER analysis comparing *Lepidonotus squamatus* and *Harmothoe imbricata*. Species contribution to the similarity (S) and dissimilarity (D). The average percentages are indicated between brackets.

	<i>Lepidonotus</i> S (38.62)	<i>Harmothoe</i> S (22.85)	<i>Lepidonotus</i> vs. <i>Harmothoe</i> D (58.64)
Diatoms	21.65	13.26	20.9
Caprellid amphipods	14.24	—	13.74
Sponge spicules	23.52	22.19	10.21
Other amphipods	3.57	13.4	8.69
<i>H. imbricata</i>	—	19.21	7.09
Organic remains	—	—	6.31
Hydroids	14.34	10.42	4.23
<i>L. squamatus</i>	—	—	4.16
Gastropod radulas	—	10.42	3.9
Bivalve juveniles	—	—	3.82
Algal filaments	5.02	6.63	3.43
Bryozoans	9.01	—	3.4
Other polychaetes	—	—	3.05

*bonnellii* (Biostation Bay), and *C. septentrionalis* (Velikiy Island). This fully agrees with the pattern of species dominance characterizing the macrofauna at the three study sites (Plyuscheva 2005).

Polychaetes were the next more relevant prey items, particularly for *Harmothoe imbricata* (Table II, Figure 5a, b), as revealed by the presence of

nereidid and phyllodocid chaetae (most likely from the dominant species *Nereis virens*, *N. pelagica* and *Eulalia viridis*). However, molluscs, usually juvenile bivalves and gastropods, also seemed to play a very important role. Gastropod radulas could be more important for *H. imbricata*, whereas this group and the bivalves apparently share a similar role for *Lepidonotus squamatus* (Figure 5a, b). Besides the fact that bivalves were obviously highly abundant in the Mussel Community, the predation effort on this group was not particularly higher there. In fact, the frequency of shells of bivalve juveniles was higher in the *H. imbricata* from Velikiy Island and in the *L. squamatus* from Biostation Bay. Accordingly, we suggest that the two scale-worms mainly prey upon recently settled juveniles, whose presence in a given habitat was independent of the previous presence of adults, but dependent on the general pool of progenitors of the region. Like molluscs, pantopods could also be a targeted prey. However, their presence was scarce and, due to their large size, they were only found in the gut of the largest specimens, with a similar frequency in both scale-worm species (Figure 5a, b).

Algal fragments have been previously reported as important components of the gut contents for *Harmothoe imbricata* and *Lepidonotus squamatus* (Strel'tsov 1966; Schafer 1972; Rauschenplat 1991). According to Strel'tsov (1966), a major nutritional importance could be attributed to these algal fragments, which seemed to be almost as frequent (83%) as amphipods (87%) in the guts of *H. imbricata*. However, they have also been considered to be an artefact related to encrusting or tubicolous animals taken in as food (e.g. in Fauchald & Jumars 1979). In addition to algal fragments, sponge remnants, as well as those of some common epibiotic organisms (e.g. tintinnids, hydroids, halacarids, ostracods, bryozoans) may be accidentally

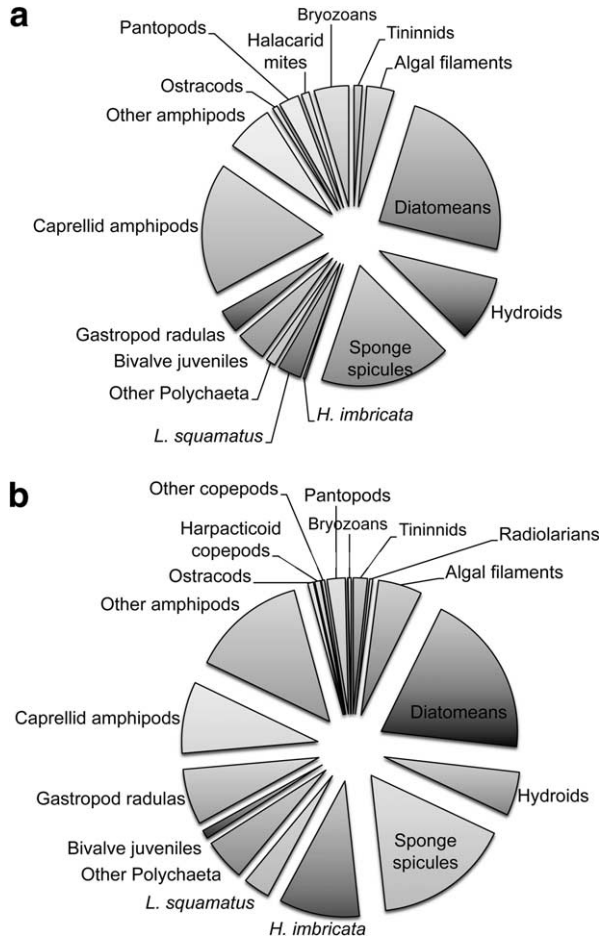


Figure 5. Average relative frequency of prey in gut contents. (a) *Harmothoe imbricata*. (b) *Lepidonotus squamatus*.

grazed when the scale-worms capture their prey. This may likely explain the rather high frequency of some of these particular components in both the gut contents and faecal pellets of the studied species. In the White Sea, for instance, members of *Amphithoe rubricata* build their tubes using small algal fragments and filaments, whereas individuals of *Corophium bonnellii* excavate burrows in sponges, building their tubes from debris (A. Tzetlin, personal communication). Therefore, most of the above-mentioned remnants found inside the guts could be collateral captures (i.e. associated with the predation on targeted prey), so that their contribution as food for the two scale-worms still remains unclear.

Traditionally, *H. imbricata* and *L. squamatus* have been considered as carnivorous–polyphagous polychaetes with a highly diversified range of food items and an active capture of single targeted animal prey individuals (Fauchald & Jumars 1979). Our results clearly support this trophic behaviour. However, by demonstrating that the entire gut contents of both species changed significantly depending on the collection site, we strongly support the non-selectivity of the two scale-worms at the species level.

Selecting animal prey items of high caloric value seems to be a typical strategy for carnivorous invertebrates living in cold waters. In fact, many of them consume small single-shot portions of food, usually representing from 5 to 10% of their body mass (Sokolova 1986). The duration of the intervals between food intakes may vary according to physiological and ecological factors, but tends to be relatively long, leading to frequent findings of animals with empty guts (Blegvad 1915; Hunt 1925; Sokolova 1986). In our samples, however, guts were mostly full (67–100% of the specimens), except at the Mussel Community (where the extent of sample sorting may likely allow the worms to discharge their guts). In cold deep-sea waters, polynoids such as *Eunoe nodosa* (M. Sars 1861), *Harmothoe rarisipina* (M. Sars 1861), *H. derjugini* (Annenkova 1937) or *Laetmonice wyvillei* McIntosh 1885 seemed to feed on sessile or slow-moving preys, and the frequency of full guts among them was two to four times higher than among active hunters (Sokolova 1986). Accordingly, we may also suggest that in the extreme thermal conditions of the White Sea, *H. imbricata* and *L. squamatus* also prefer sessile (e.g. tubicolous or burrowing amphipods such as *Amphithoe rubricata* or *Corophium bonnellii*) or slow-moving prey (e.g. *Caprella* species). This will certainly require a lower energy expenditure for capture, thus representing an energy-saving strategy benefit.

Apart from the assessment of prey composition inside the guts, and the corresponding inferences on

trophic behaviour, particular attention should be given to the presence of conspecific chaetae and elytral fragments in the guts of the studied *Harmothoe imbricata* and *Lepidonotus squamatus* individuals from the White Sea. This presence was considered as a demonstration of cannibalism in the case of *H. imbricata*, although the worms only attacked similarly sized specimens, but never juveniles (Strel'tsov 1966). Our analyses revealed the presence of both chaetae and elytral remnants, while adult jaws were never found. In turn, intraspecific territorial interactions are common among polychaetes, and are particularly well-known for scale-worms, where the existence of traumas (i.e. bites in elytra or in parapodia) have recently been reported as an excellent tool to infer such interactions, as well as the type of association in which they may be involved (Britayev 1991; Britayev & Zamyshliak 1996; Britayev et al. 2007). This leads us to suggest that the 'cannibalistic' interpretation for the presence of conspecific remnants inside the guts of *H. imbricata* and *Lepidonotus squamatus* may be discarded. At the same time, we postulate that this phenomenon could more likely be the result of the aggressive behaviour characterizing the territorial interactions in polychaetes.

In summary, two aspects may be highlighted from our study on gut contents analyses: the significant overlap in the dietary regimes of *Harmothoe imbricata* and *Lepidonotus squamatus* (i.e. the location influences gut contents more than species) and the evidence of an aggressive territorial behaviour. The first aspect may be considered as an indication of inter-specific competition for food, with the most active or abundant species consuming the resources required by the second one to maintain its presence in a given location. The second aspect may also drive the intra-specific interactions, as either an already established species may prevent the settlement of recruits of a newly arrived species (e.g. by attacking the juveniles; see Strel'tsov 1966) or the most aggressive species may displace the other from a given location (this resulting in attacks to adults, as revealed by the bites to parapodia or elytra resulting in the presence of remnants of these structures inside their guts).

These two mechanisms may certainly contribute to explain the recurrent alternation in dominance of the coexisting populations of *Harmothoe imbricata* and *Lepidonotus squamatus*, previously reported under the harsh environmental conditions of the White Sea (Plyuscheva et al. 2004). One of the species may be dominant for several months (i.e.  $>300$  ind.  $m^{-2}$  vs.  $<20$  ind.  $m^{-2}$  from June to August for *L. squamatus* and *H. imbricata*, respectively), then show similar densities (i.e.  $<200$  ind.  $m^{-2}$  for

both species in August), invert the former pattern (i.e.  $<200$  ind.  $\text{m}^{-2}$  vs.  $>550$  ind.  $\text{m}^{-2}$  up to next June for *L. squamatus* and *H. imbricata*, respectively) and show again similar densities (i.e. around 150 ind.  $\text{m}^{-2}$  vs. 200 ind.  $\text{m}^{-2}$  up to next August for *L. squamatus* and *H. imbricata*, respectively). This alternation was partly explained as the expression of the different life strategies of the two scale-worms: the former being a short-living, quick-growing species with a complex reproductive behaviour, whereas the latter was a long-living, slow-growing broadcast spawner (Plyusheva et al. 2004).

Nevertheless, neither dietary overlapping, nor aggressive behaviour, are exclusive mechanisms. They may interact in different ways, either within them with respect to the respective life cycle strategies, or with other biological and environmental ecosystem constraints to drive the population dynamics. Certainly, these combined influences may lead to changes in the structure of the benthic assemblages (often recurrent), such as those previously reported in the White Sea (Plyusheva et al. 2004). However, this could only be fully understood by means of adequate long-term (i.e. multi-annual) surveys, which may be a very interesting topic for future research.

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