

Population ecology of two sympatric polychaetes, *Lepidonotus squamatus* and *Harmothoe imbricata* (Polychaeta, Polynoidae), in the White Sea

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ABSTRACT: Under the critical environmental conditions of the White Sea, *Lepidonotus squamatus* and *Harmothoe imbricata* coexist in the same habitat, often showing recurrent alternations in dominance. *L. squamatus* is a long-living, slow growing broadcast spawner, while *H. imbricata* is a short-living and quick growing species, with complex reproductive behaviour. These different life strategies may allow them to respond in a different way to the environmental limitations of the study site, this likely being the most appropriate explanation to the observed alternation in dominance.

KEYWORDS: Population dynamics; growth; scale-worms; the White Sea.

Экология популяций двух симпатрических видов полихет *Lepidonotus squamatus* и *Harmothoe imbricata* (Polychaeta, Polynoidae) в Белом море

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РЕЗЮМЕ: В экстремальных условиях Белого моря, *Lepidonotus squamatus* и *Harmothoe imbricata* занимают сходные экологические ниши, демонстрируя периодическое чередование в доминировании. В условиях Белого моря *L. squamatus* является сравнительно долгоживущим медленно растущим видом с внешним оплодотворением, в то время как *H. imbricata* является относительно короткоживущим и быстро растущим видом со сложным репродуктивным поведением. Судя по всему, именно эти различия жизненных стратегий позволяют по-разному реагировать на изменения условий среды обитания, что и объясняет наблюдаемое периодическое чередование в доминировании.

КЛЮЧЕВЫЕ СЛОВА: Динамика популяции; рост; чешуйчатые черви; Белое море.

Introduction

The scale-worms *Lepidonotus squamatus* and *Harmothoe imbricata* (Polynoidae) are among the most abundant carnivorous polychaetes. Both species are very common and widespread in shallow-water marine benthic communities all around the northern hemisphere, being particularly abundant on hard substrata and in the macrophyte rhizoids community (Tebble, Chambers, 1982). Accordingly, both species likely play an important role in hard bottom assemblages, although their contribution has been poorly studied up to date.

Few studies provided data on their biology, particularly for *H. imbricata*. Its reproductive biology has been studied in the North Sea (Daly, 1972; Daly et al., 1972) and its larval development at the coast of Danmark (Thorson, 1946; Rasmussen, 1956), the English Channel (Cazaux, 1968), and the Black (Kiseleva, 1957), White (Sveshnikov, 1959), Japanese (Sveshnikov, 1967) and Mediterranean (Bhaud, 1987) seas. The age structure of its populations is only known for the Barents (Streltsov, 1966) and Black (Britayev & Belov, 1992) Seas.

The information on *L. squamatus* is restricted to its reproductive period at the coasts of Scotland (McIntosh, 1900), Danmark (Rasmussen, 1973), north-eastern USA (Bumpus, 1898) and eastern Canada (Lacalli, 1980), as well as to the description of several stages of its larval development (Nolte, 1936; Thorson, 1946; Rasmussen, 1973), while the size and age structures of their populations are completely unknown.

The life cycle and population ecology of *L. squamatus* and *H. imbricata* in the White Sea are currently unknown. Under the critical environmental conditions of these coasts, both species coexist in the same habitat, often showing recurrent alternations in dominance. Particularly, they may dominate the motile fauna in mussel (*Mytilus edulis*) community. The present study focused on the analysis of size and age structure and growth rate of the two target polynoid species, providing new and relevant information for the respective White Sea populations.

Material and methods

All samples were collected in the vicinity of the White Sea Biological Station of the Moscow State University (White Sea, Kandalaksha Bay) from the fouling community of cultivated mussels. The seasonal monitoring of the population dynamics of both species was carried out from June 1998 to August 1999 (over 10 sampling dates).

All worms were collected from sections of mussel cultures of about 3 m long. Mussel druses were knocked down to single shells and all polychaetes were picked out. Then, the sampled mussel druses were griddled out and worms were picked out again from the rest of the sample. The polynoids were fixed with 4% formaldehyde. Then, all worms were washed with fresh water and preserved in 70% alcohol.

Size of worms was measured not as the length, but as the width at the 10th–15th-segment level, to avoid the frequent cases where worms lost their posterior end, in order to increase the number of measured worms per sample. Width of worms was measured under a binocular microscope with a calibrated micrometric ocular and was used to estimate growth, to identify cohorts or generations and to reveal the size structure of the populations. Size-frequency histograms were plotted using size-class intervals of 0.2 mm, estimated with the Sterdges formula. The age-class segregation was based on the probability paper method (Cassie, 1954) and the cohort analysis was done using the Bhattacharya (1967) method. Growth rates for each size class were estimated on the basis of the changes in mean modal size from summer 1998 to summer 1999. Mortality rate for both species was revealed by comparison of number of specimens in each age class.

The age structure was analysed by counting the growth lines on the jaws under light microscope. The worms were dissected from ventral side and their proboscises were taken out. Each proboscis was then embedded in Tripsin to macerate the tissues and to reveal jaws.

Results

During the first period of study (June to August 1998) *L. squamatus* was dominant, while

during the second part, the abundance of *H. imbricata* highly increased so that it became dominant from October 1998 to August 1999 (with the exception of June 1999, when the abundance of *L. squamatus* rise up and dominated punctually) (Fig. 1).

Lepidonotus squamatus

The adult specimens measured from 0.45 to 6.2 mm in width. The size histograms are poly-modal, with asymmetry towards the smallest size classes (Fig. 2). According to the probability paper, the population can be subdivided into

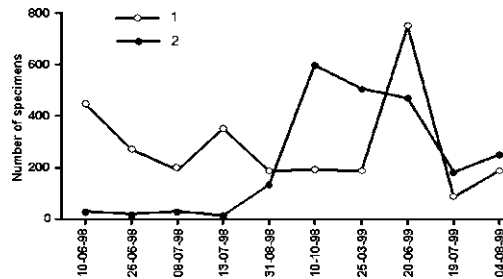


Fig. 1. Number of *Lepidonotus squamatus* (1) and *Harmothoe imbricata* (2) specimens in samples.
Рис. 1. Количество особей *Lepidonotus squamatus* (1) и *Harmothoe imbricata* (2) в пробах.

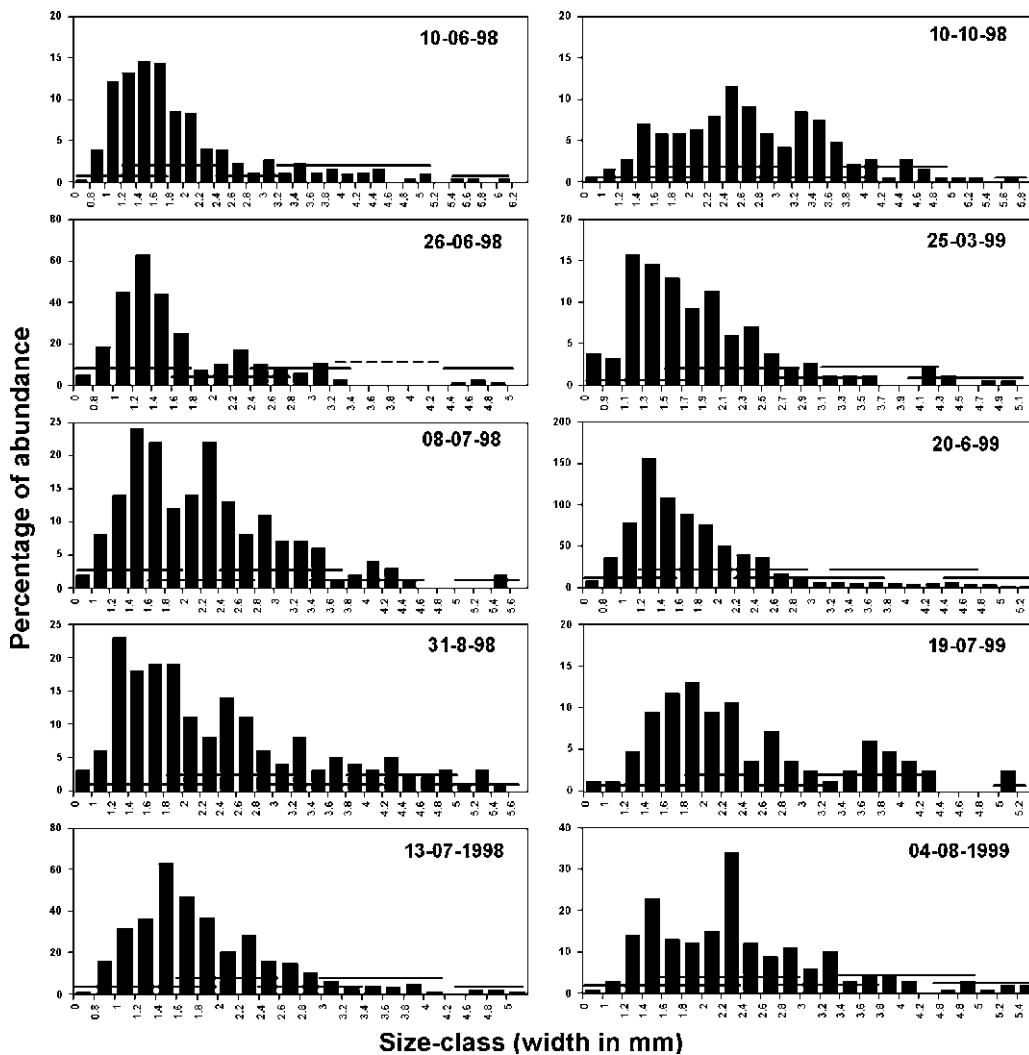


Fig. 2. Size-frequency histograms, *Lepidonotus squamatus*.
Рис. 2. Гистограммы размер-численность, *Lepidonotus squamatus*.

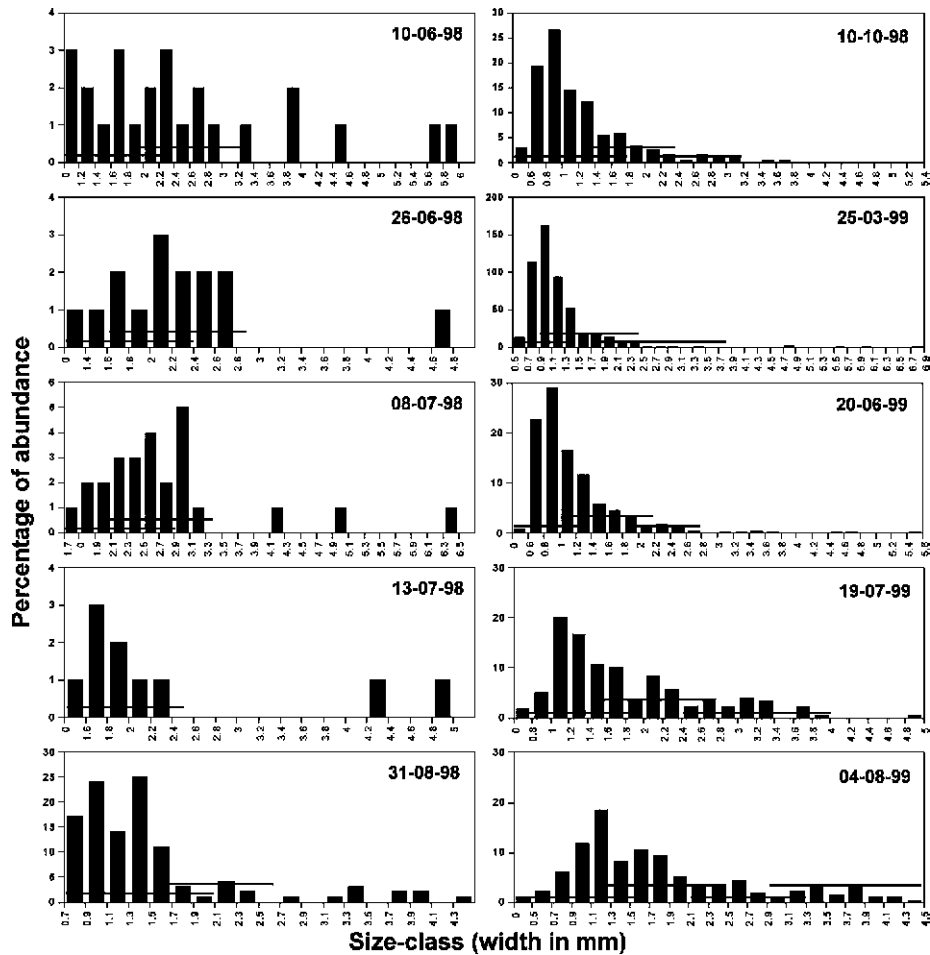


Fig. 3. Size-frequency histograms, *Harmothoe imbricata*.

Рис. 3. Гистограммы размер-численность, *Harmothoe imbricata*.

five size classes (i.e. age groups). The amount of growth lines on jaws ranged from 0 (smallest specimens) to 5 (largest specimens) (Fig. 4, 6A), with the first growth line more likely appearing during the second year of life (Britayev et al., 2002). The comparison of these two methods allowed estimating the maximal worm's age as 6+ years.

Both the modal range and the growth rate increased progressively from the first to the third age class during summer (table 1), while they cannot be stated for the fourth and the fifth age classes (worms growth is not synchronized so that size class limits are not clear). In October, growth was apparently stopped and the

respective modal parts are the same as in August. During winter, the modal means of the first three size classes decrease.

The growth rate varied from 0.30 to 0.44 mm month⁻¹ within the different age classes during summer and became negative during autumn–winter. The highest mortality rate occurred during the third age classes (Fig. 7A).

Harmothoe imbricata

The adult specimens measured 0.5 to 6.5 mm in width. The size distribution histograms are polymodal with asymmetry towards the smallest size classes. According to the probability

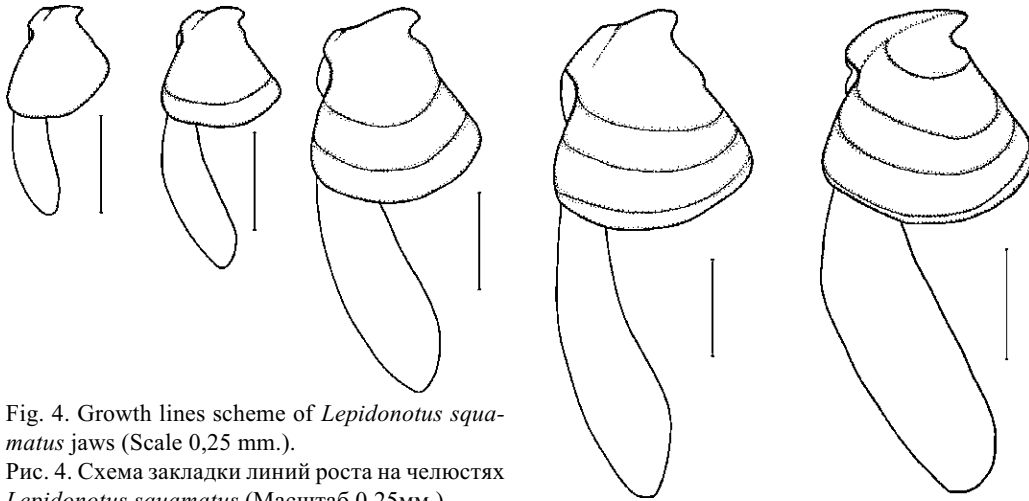


Fig. 4. Growth lines scheme of *Lepidonotus squamatus* jaws (Scale 0,25 mm.).

Рис. 4. Схема закладки линий роста на челюстях *Lepidonotus squamatus* (Масштаб 0,25мм.).

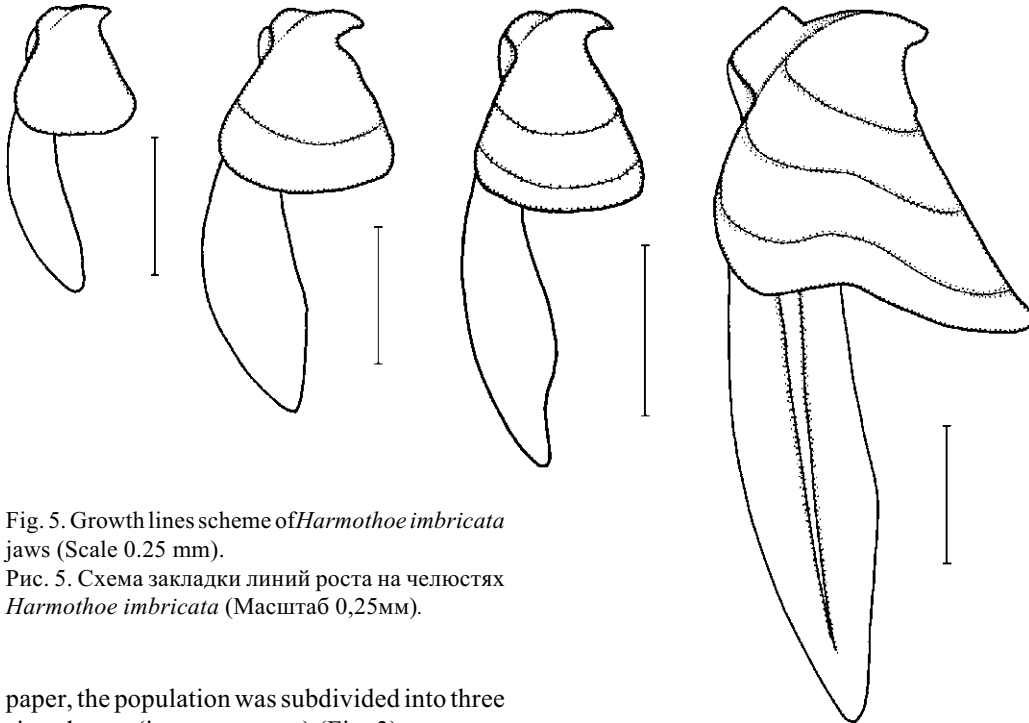


Fig. 5. Growth lines scheme of *Harmothoe imbricata* jaws (Scale 0.25 mm).

Рис. 5. Схема закладки линий роста на челюстях *Harmothoe imbricata* (Масштаб 0,25мм.).

paper, the population was subdivided into three size classes (i.e. age groups) (Fig. 3).

The number of growth lines on jaws ranged from 0 (smallest specimens) to 3 (largest specimens) (Fig. 5, 6B), with the first growth line more likely appearing during the first year of life (Britayev et al., 2002). The comparison of these two methods allowed estimating the maximal worm's age as 3+ years. Both the modal range and the growth rate increased progres-

sively from the first to the third age class (table 1). The growth rate varied from 0.59 to 0.85 mm month⁻¹ within the different age classes during summer and became negative during autumn-winter. The highest mortality rate occurred during the second age class (Fig. 7B).

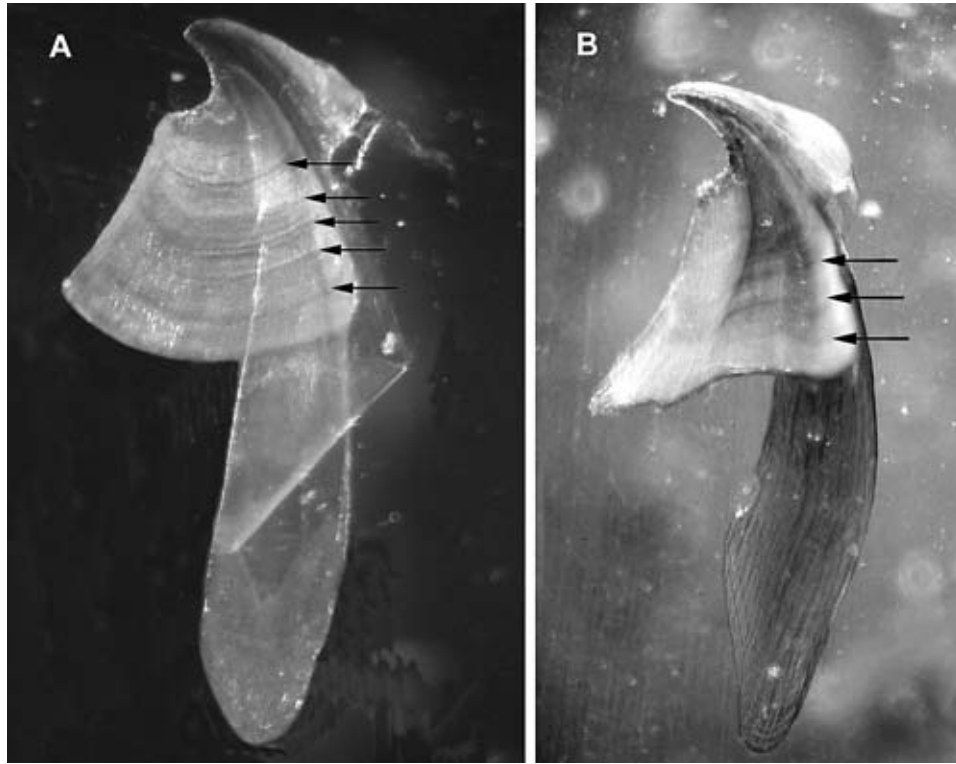


Fig. 6. Growth lines on the jaws. A — *Lepidonotus squamatus*, B — *Harmothoe imbricata*.
Рис. 6. Линии роста на челюстях. А — *Lepidonotus squamatus*, В — *Harmothoe imbricata*.

Discussion

Size and age structure of *Lepidonotus squamatus* and *Harmothoe imbricata* populations have been poorly studied. For instance there are only scarce data on the sizes of *L. squamatus* from the Isefjord (Rasmussen, 1973) which were about 50 mm long, while in the White Sea maximum length was about 40 mm. The Japanese populations measured 2.3–2.6 mm wide, while in the White Sea they are about three times wider (i.e., 6.4 mm). As for *Harmothoe imbricata*,

the Black Sea specimens varied from 0.6 to 2.4 mm wide (Britayev, Belov, 1993), while in the White Sea this species raises up to 7 mm wide.

Increases in size in a whole population in conditions of decreasing temperatures are usually correlated with slowing down (moderation) of metabolism and growth, this resulting in a delayed pubescence and an elongated life span (Kinne, 1963). Accordingly, the life span of *Harmothoe imbricata* in the White Sea was twice longer (up to four years) than in the Black

Table 1. The growth rate of first 3 size classes of *L. squamatus* and *H. imbricata* during summer period.
Таблица 1. Скорость группового роста первых 3 размерных классов *L. squamatus* и *H. imbricata* в летний период.

Size classes	<i>Lepidonotus squamatus</i>		<i>Harmothoe imbricata</i>	
	Modal range (mm)	Growth rate (mm per month)	Modal range (mm)	Growth rate (mm per month)
I	1.2–2	0.296	1–2.1	0.59
II	2–3	0.37	1.4–2.9	0.65
III	2.8–4	0.44	2.2–3.3	0.85

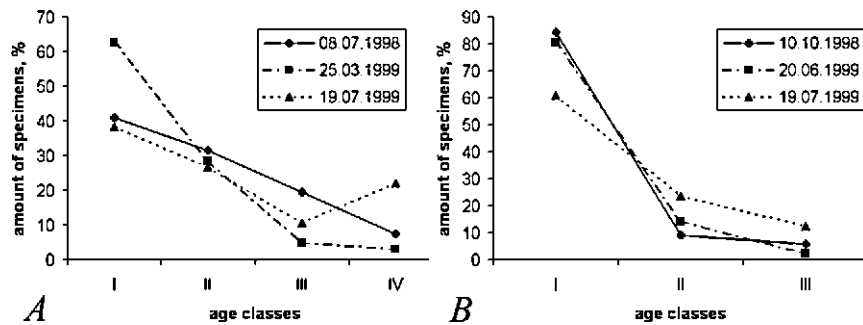


Fig. 7. Number of specimens in different age classes. A — *Lepidonotus squamatus*, B — *Harmothoe imbricata*.

Рис. 7. Количество особей в разных возрастных классах. A — *Lepidonotus squamatus*, B — *Harmothoe imbricata*.

Sea, where this species had a two-year life span (Britayev, Belov, 1993). In the White Sea, *H. imbricata* demonstrated to be a polytelic species (authors, unpublished data), while in the Black Sea it was apparently monotelic, with most of the worms dying after breeding (Britayev, Belov, 1993) as it happened in the North Sea (Daly et al., 1972) and Baltic Sea populations of *Harmothoe sarsii* (Sarvala, 1971). In the case of *Lepidonotus squamatus*, the maximum life span in the White Sea (estimated by means of the growth lines on the jaws) was seven years (Britayev et al., 2002), while in the Sea of Japan the species only reached five years (Britayev, Belov, 1993). In all cases, however, this species was polytelic.

The reduction in size during late autumn and winter, occurring both in *Harmothoe imbricata* and *Lepidonotus squamatus*, is a relatively common phenomenon among polychaetes (Newell, 1948; Dales, 1951), as their growth usually decreases or stops during the gonad development (Clark, 1965). In the case of *H. imbricata* and *L. squamatus*, growth stops in Autumn while gonad development starts in September–October (Sveshnikov, 1978; Plyuscheva, unpublished data). From August to October the size did not change and the body width decreased among all size classes in March, likely as a consequence of the low temperatures and/or the scarcity of food.

Data on growth rates for scale-worm polychaetes are also rather scarce. The growth of

Harmothoe sarsii was first slow but progressively increased with age, whereas the initially rapid segment proliferation became slow with age (Sarvala, 1971). The grow rate of *Harmothoe imbricata* increased during the second year of life in comparison with the first one (Strelzov, 1966; our data) while, in *Lepidonotus squamatus* the rapid increase of the third and fourth years was followed by a slow decrease and a further restart of growth.

The highest mortality among polychaete populations usually occurs just after recruitment, during the first few months in the bottom (Sarvala, 1971; Garwood, 1982), due to intra-specific competition for a limiting resource or predators impact. The next mortality peak is frequently connected with the first participation in the reproduction (Olive, 1984). The highest mortality rate in the studied *Lepidonotus squamatus* and *Harmothoe imbricata* populations occurred in the third and second age classes, respectively. In both cases, these are the first classes participating in reproductive activities. Previous mortality peaks were not observed, which may be explained by the absence of intra-specific competition due to the absence of limiting resources. In both cases, the adult populations can be considered as stable. There is little mortality of sexually mature age classes until senescence, and the highest mortality takes place in relation to the first reproductive event (Olive, 1984).

The dynamics of both scale-worm populations may depend on different biotic and abiotic

factors and it is not possible to discern these influences in light of our data. However, both species inhabit the same biotope and have very similar food requirements (Plyuscheva & Britayev, in prep.). Thus, we may suppose the existence of competitive interactions between both species. In comparison with *Harmothoe imbricata*, *Lepidonotus squamatus* has low growth rate and higher life span and is a free spawner. Thus, it appears that, in stable conditions, *L. squamatus* behaved as a K-strategist. Conversely, *H. imbricata* has comparatively short life span, higher growth rate and brooding embryos, which certainly pointed towards a r-strategy behaviour. In a situation without limiting factors, K-strategists have selective advantages, while the existence of any type of restrictions often tends to favour r-strategists. We may assume that a situation with changes of some limit factors (e.g. food, space) occurred during study period, this favouring the observed alternation population dynamics.

In conclusion, the White Sea population of *Lepidonotus squamatus* has long-living, slow growing broadcast spawning individuals, while *H. imbricata* is a short-living and quick growing species, with complex reproductive behaviour. Although our data do not allow us to demonstrate causal relationships between these two different life strategies and the dynamics observed at the study site, it seems evident that the respective strategies of *L. squamatus* and *H. imbricata* may allow their populations to respond to the critical environmental constraints of the White Sea in a different way, this being likely the most appropriate explanation to the alternation in dominance.

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