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Long-term variations in the diet composition of Atlantic wolffish, *Anarhichas lupus marisalbi* (Zoarcoidei: Anarhichadidae), in Kandalaksha Bay, White Sea

P.N. Yershov[1]* and V.M. Khaitov[2, 3]

[1] *Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia; e-mails: Peter.Yershov@zin.ru; peteryershov@yandex.ru*

[2] *Department of Invertebrate Zoology, Saint Petersburg State University, Universitetskaya Emb. 7/9, 199034 Saint Petersburg, Russia; e-mail: polydora@rambler.ru*

[3] *Kandalaksha State Nature Reserve, Lineynaya 35, 184042 Kandalaksha, Murmansk Region, Russia.*

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ABSTRACT

Understanding the diet variability of the White Sea wolffish, *Anarhichas lupus marisalbi* Barsukov, 1956, is essential for explaining its population dynamics and variations in its life cycle. This study examined the food spectrum of wolffish from the coastal waters of Chupa Inlet (Kandalaksha Bay, White Sea) and analyzed interannual and seasonal changes in the species composition of its diet. During the summer period, wolffish feeds on a variety of macrobenthic organisms in its feeding grounds, particularly molluscs, echinoderms, crustaceans, and ascidians. The diet was predominantly composed of bivalves and gastropods, with *Buccinum undatum* Linnaeus, 1758 and *Serripes groenlandicus* (Mohr, 1786) being the most important prey species. Statistical analysis of multi-year diet data from 2001 to 2023 revealed interannual variations in the frequency of occurrence of key food organisms in wolffish stomachs. The results showed that in the early 2000s, the role of epibenthic crustaceans *Hyas araneus* (Linnaeus, 1758) and *Pagurus pubescens* Krøyer, 1838 in the wolffish diet was significantly greater compared to other years of the study. The dietary importance of the bivalve *S. groenlandicus* increased gradually and statistically significantly during the observation period, while *Buccinum undatum* dominated the wolffish diet throughout the entire study period. Overall, three species (*B. undatum, S. groenlandicus,* and *Mytilus edulis* Linnaeus, 1758) accounted for a significant portion of the wolffish diet during 2001–2023. In some years, other mollusc species, as well as crustaceans and the ascidian *Styela rustica* Linnaeus, 1767, were also included in the group of important prey items. The feeding intensity of wolffish in Chupa Inlet showed interannual variability. Throughout the observation period, certain years were identified as having the greatest frequency of fish with empty stomachs. Female wolffish showed a seasonal pattern in the frequency of occurrence of individuals with empty stomachs: the highest occurrence of such fish was observed during the spawning period of wolffish, in late July to early August. No significant seasonal changes in the frequency of occurrence of individuals with empty stomachs were found in males.

Key words: diet, ecology, long-term changes, White Sea, wolffish

Многолетние изменения в составе питания полосатой зубатки *Anarhichas lupus marisalbi* (Zoarcoidei: Anarhichadidae) в Кандалакшском заливе Белого моря

П.Н. Ершов[1]* и В.М. Хайтов[2, 3]

[1] *Зоологический институт Российской академии наук, Университетская наб. 1, 199034 Санкт-Петербург, Россия; e-mails: Peter.Yershov@zin.ru; peteryershov@yandex.ru*

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* *Автор-корреспондент / Corresponding author*

[2] *Санкт-Петербургский государственный университет, кафедра зоологии беспозвоночных, Университетская наб. 7/9, 199034 Санкт-Петербург, Россия; e-mail: polydora@rambler.ru*

[3] *Кандалакшский государственный заповедник, Линейная ул. 35, 184042 Кандалакша, Мурманская область, Россия.*

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РЕЗЮМЕ

Важным компонентом для понимания изменчивости жизненного цикла и динамики популяций беломорской полосатой зубатки *Anarhichas lupus marisalbi* Barsukov, 1956 является знание изменчивости состава ее питания. В работе изучены пищевой спектр, межгодовые и сезонные изменения видового состава пищи зубатки из прибрежных вод губы Чупа (Кандалакшский залив Белого моря). В летний период зубатка на нагульных участках питается различными организмами макробентоса, а именно моллюсками, иглокожими, ракообразными и асцидиями. Доминирующим компонентом в ее пище являются двустворчатые и брюхоногие моллюски, причем наибольшее значение в рационе рыб имели два вида – *Buccinum undatum* Linnaeus, 1758 и *Serripes groenlandicus* (Mohr, 1786). Статистический анализ многолетних данных (2001–2023 гг.) по составу пищи зубатки выявил межгодовые изменения частот встречаемости наиболее важных пищевых организмов в ее желудках. Показано, что в начале 2000-х гг. роль эпибентических ракообразных *Hyas araneus* (Linnaeus, 1758) и *Pagurus pubescens* Krøyer, 1838 в ее питании была значительно выше по сравнению с остальными годами исследований. Значение двустворчатого моллюска *S. groenlandicus* в пище зубатки постепенно и значимо увеличилось в период наблюдений. *Buccinum undatum* доминировал в рационе зубатки на протяжении всего периода мониторинга. В целом, три вида (*B. undatum*, *S. groenlandicus* и *Mytilus edulis* Linnaeus, 1758) обеспечили значительную часть рациона зубатки в период 2001–2023 гг. В отдельные годы в группу важных пищевых объектов входили и некоторые другие виды моллюсков, а также ракообразные и асцидия *Styela rustica* Linnaeus, 1767. Обнаружена межгодовая изменчивость интенсивности откорма зубатки в губе Чупа. На протяжении периода наблюдений выявлены годы, когда встречаемость рыб с пустыми желудками была наибольшей. У самок зубатки обнаружена сезонная динамика частоты встречаемости особей с пустыми желудками. Наибольшая встречаемость таких рыб была отмечена в период нереста зубатки, в конце июля – начале августа. У самцов значимых сезонных изменений в частоте встречаемости особей с пустыми желудками не наблюдалось.

Ключевые слова: питание, экология, многолетние изменения, Белое море, зубатка

INTRODUCTION

The structure and dynamics of trophic relationships between fish and benthic organisms in marine coastal communities are complex phenomena influenced by multiple factors and mechanisms. The diet composition and the importance of forage species for predatory fish are largely determined by the availability and abundance of prey items in feeding grounds (Johannesen et al. 2012; Sell and Kröncke 2013; Townhill et al. 2021). In local coastal habitats, the biomass and species richness of benthic assemblages show constant small-scale variability over different time intervals. Long-term studies exploring the dynamics of this variability in the structure of benthic macrofauna in coastal ecosystems and the driving factors of this dynamics are among the most important areas of research in marine ecology (Petersen 1978; Golikov et al. 1986; Fromentin et al. 1997; Beukema et al. 2001; Schückel et al. 2010; Sukhotin and Berger 2013; Varfolomeeva and Naumov 2013). Fluctuations in the abundance of dominant species in communities are primarily related to the impact of local or regional drivers, as well as internal processes – population dynamics of species abundance, intraspecific competition, hydrological regime, and others. The dynamic processes occurring in benthic biocenoses under the influence of these factors affect the structure of marine communities and impact the trophic relationships of invertebrate organisms and several common species of benthivorous fish that inhabit or spend certain periods of their life in shallow coastal marine habitats. One such species that can serve as an indicator of long-term variation in the structure of coastal benthic biocenoses is the Atlantic wolffish, *Anarhichas lupus* Linnaeus, 1758.

The Atlantic wolffish is a demersal species widely distributed in the boreal waters of the North Atlantic (off the coasts of the USA, Canada, Greenland, and Iceland), from the British Isles and further north to the Arctic and the White Sea in northern Russia (Barsukov 1986). A number of authors have shown that this predator is a major consumer of various macrobenthic organisms (Barsukov and Nizovtsev 1960; Kudersky and Rusanova 1963; Jónsson 1982; Albikovskaya 1983; Templeman 1985) and can affect the abundance of its prey species in biocenoses. For instance, in the Northwest Atlantic, wolffish is considered a key predator of echinoids and has the capacity to influence green sea urchin populations (Keats et al. 1986; Hagen and Mann 1992). The understanding of how the population of wolffish relates to their habitats through trophic webs over space and time is crucial for analyzing the impact of multi-scale processes on its population dynamics and life-history variations. It is clear that such biocenotic relationships are best studied in areas where local wolffish populations and their habitats are not subjected to intensive fishing-induced impact or other external influences.

Anarhichas lupus marisalbi Barsukov, 1956, a subspecies of the Atlantic wolffish, primarily inhabits the coastal waters of Kandalaksha Bay in the White Sea (Altukhov et al. 1958). The White Sea wolffish is most abundant along the Karelian coast of the bay (Nikolaev 1951; Barsukov 1956; Mukhomediyarov 1963), an area characterized by long stretches of rocky coastlines and a relatively deep coastal zone with a rocky seabed. Wolffish is generally not commercially harvested in the White Sea region, but is caught as by-catch, and local residents use the existing stocks for personal consumption. The literature contains some information on the morphology and biological traits of the species (Barsukov 1959; Mukhomediyarov 1963; Pavlov and Novikov 1993; Yershov 2010a) and detailed studies have been conducted under experimental conditions on its early ontogeny, sexual maturation, and reproduction (Pavlov and Radzikhovskaya 1991; Pavlov et al. 1992; Pavlov 1994; Pavlov and Moksness 1994). By contrast, published data on the feeding characteristics of the White Sea wolffish are scarce. Some publications provide only a brief description of the food spectrum and diet composition. It has been shown that the White Sea wolffish is a typical benthic predator that does not make long feeding migrations and consumes a fairly broad range of prey organisms (Barsukov 1956; Kudersky and Rusanova 1963; Yershov 2010a). The bulk of the adult wolffish diet in the studied areas of the sea (Gridina and Chupa inlets; Velikaya Salma Strait) consists of bivalve and gastropod molluscs. To a lesser extent, wolffish consumes other representatives of the macrofauna – crustaceans, polychaetes, ascidians, and echinoderms. Molluscs are known to dominate the structure of coastal biocenoses and form fairly dense aggregations and large biomasses in the intertidal and subtidal zones in different regions of the White Sea (Kudersky 1966; Lukanin and Oshurkov 1981; Naumov 2006). Populations of some bivalve mollusc species that form dense settlements and are part of wolffish's main prey items (*Mytilus edulis*, *Serripes groenlandicus*, and *Arctica islandica*) often show cyclical fluctuations in abundance and structural characteristics (Lukanin et al. 1986; Gerasimova and Maximovich 1988, 2000, 2001, 2013). These fluctuations in the biomass of these molluscs, in turn, lead to changes in the species richness of benthic assemblages (Golikov et al. 1978; Büttger et al. 2008; Khaitov 2013). In this regard, long-term data on fish diet in specific habitats of wolffish are of particular interest for analyzing variation in its trophic relationships with hydrobionts in coastal communities. It should be emphasized that variability in the feeding habits of the White Sea wolffish at different temporal scales remains unexplored.

The aim of this study was to examine long-term variation in the qualitative composition of the diet of the Atlantic wolffish during the summer period (June–August) in Chupa Inlet of Kandalaksha Bay of the White Sea.

MATERIAL AND METHODS

Collection and processing

The material for the study was collected from June to August 2001–2023 in the mouth of Chupa Inlet of Kandalaksha Bay (White Sea), at two stations (Kruglaya Inlet and Kartesh Cape) located approximately 0.5 km apart (Fig. 1).

Fish were caught during the observation period at these fishing sites using 30-m long nets with a mesh size of 30–40 mm. Control fishing data showed that the wolffish feeding grounds included both relatively deep (15–20 m) and shallow (up to 3 m) areas of the coastal zone; therefore, the material from these two closely located stations was combined. The largest

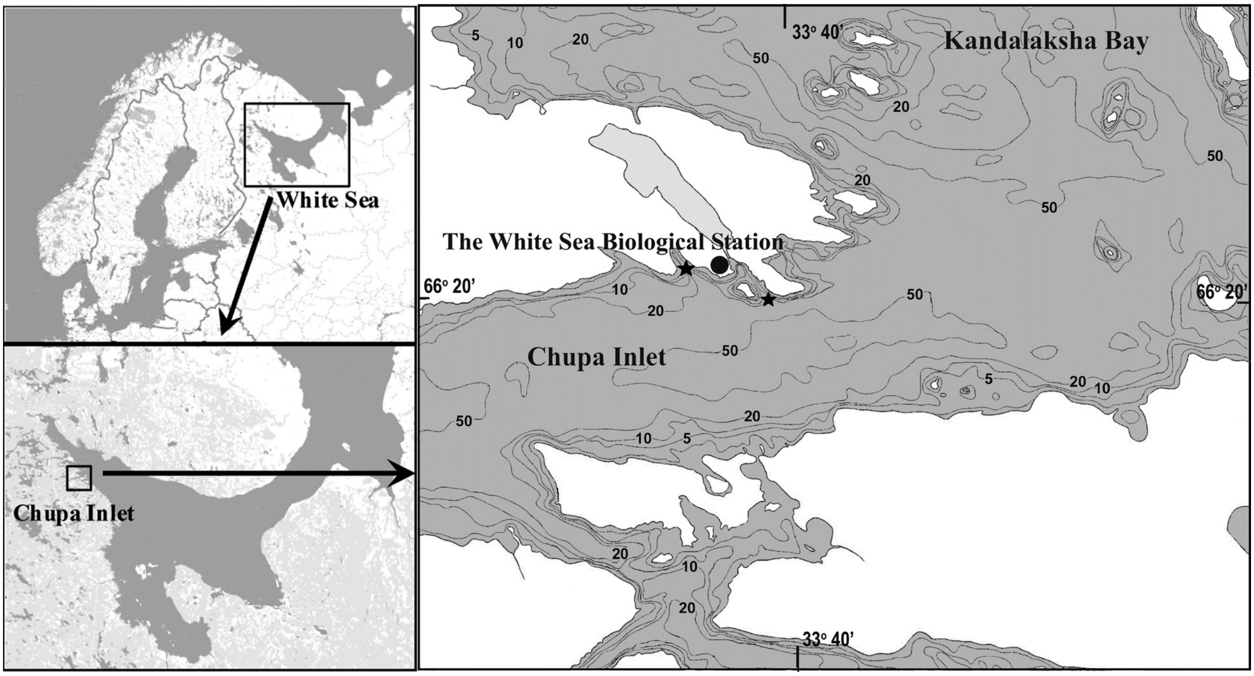

Fig. 1. Map of the study area. Asterisks indicate the sampling locations. Numbers show depths in meters.

number of biological samples during the field seasons was taken in July, which is explained by the active pre-spawning and feeding migrations of wolffish in the coastal zone of Chupa Inlet occurring during this period. The total length (*TL*) of the caught fish (830 individuals) was measured to the nearest 0.1 cm and their sex and gonad maturity stages were determined after dissection.

The qualitative composition of the stomach contents of wolffish was studied in 438 individuals (*TL* 27.4–64.2 cm). All prey items extracted from the fish stomachs were identified to the species level. The species list was checked for validity and made consistent with World Registry of Marine Species database (WoRMS 2024). The importance of each prey item was evaluated using the frequency of occurrence (%) only for those fish that had food in their gastrointestinal tract (Borutskiy 1974). Feeding intensity was assessed by the proportion of empty and full stomachs.

Statistical Analysis

All analyses and visualizations were performed using packages from the statistical programming language R 4.2.3 (R Core Team 2023). To analyze the dynamics of the sex ratio in catches depending on the season and year, a generalized additive model (*GAM 1*) was constructed, where the dependent variable was the probability of encountering a female. In this and the following analyses, additive model parameters were assessed using functions from the "mgcv" package (Wood 2017). In all cases, cubic splines were used as the basis for fitting additive models. The predictors in *GAM 1* were the day of the year (*DOY*, characterizing the dynamics during the summer season) and the year (*Year*, describing the multi-year dynamics).

$$GAM\ 1: Outcome = b_0 + s_1(DOY) + s_2(Year) + \varepsilon,$$

where:

b_0 is the intercept;

s_1 is a non-parametric smoothing function with 6 knots describing the change in the frequency of encountering females depending on *DOY*;

s_2 is a non-parametric smoothing function with 6 knots characterizing the change in the frequency of encountering females depending on *Year*;

ε are the residuals.

Only those individuals that had food in their stomachs were selected for further statistical analysis. For each prey item, the frequency of occurrence was calculated as the ratio of the number of fish in which the species was found to the total number of fish caught in that year. The Shannon index was used to estimate the diversity of the dietary spectrum in different years, which in this case was described using the following formula:

$$H = -\Sigma \frac{n_i}{\Sigma n_i} \cdot log_2(\frac{n_i}{\Sigma n_i})$$

where n_i is the number of occurrences of the i-th species in a given year and Σn_i is the total number of occurrences of all species in that year.

A non-parametric smoothing curve constructed using the LOESS method (Cleveland and Loader 1996) was fitted to describe the multi-year trend of this value.

To analyze the dynamics of occurrence of individual species in the wolffish diet, 11 species were selected whose frequency of occurrence in the aggregated data exceeded 5%. Based on the data for these species, the following logistic additive model (*GAM 2*) was constructed:

$GAM2$: $Outcome = s_k(Year_i|Species_k) + b_0 + \sum b_k Species_k + \varepsilon_{i,k}$,
where:

b_k is the coefficient for each individual species;

s_k are non-parametric smoothing functions fitted for each individual species that describe the change in the probability of encountering each species over the observation period (Year).

If a given species was found in the fish stomachs, the response variable was coded as 1; if it was absent, the variable was coded as 0.

To analyze the seasonal and multi-year dynamics of the frequency of wolffish with empty stomachs, a logistic additive model (*GAM 3*) was constructed. The model described the relationship between the probability of encountering the fish with empty stomachs and three predictors: *Sex*, *DOY*, and *Year*. The dependent variable for this model was coded as 1 if the fish had an empty stomach, or 0 if its stomach contained food. The model is described by the following formula:

$GAM\ 3$: $Outcome = b_0 + b_1 Sex_\text{Male} + s_1(DOY|Sex) + s_2(Year) + \varepsilon$,
where:

b_1 is the parametric coefficient for the "Male" level of the "Sex" factor (the "Female" level was set as the baseline);

s_1 is a non-parametric smoothing function with 6 knots that describes the variation in the frequency of occurrence of individuals with empty stomachs depending on *DOY,* for each sex separately;

s_2 is a non-parametric smoothing function with 6 knots that describes the variation in the frequency of occurrence of individuals with empty stomachs depending on *Year*, regardless of sex.

RESULTS

Species composition of prey items and its long-term changes

Most of the captured wolffish were mature individuals, with 85% of the catch measuring 30–50 cm in total length. No statistically significant differences were found in the feeding habits between smaller and larger individuals.

The male-to-female ratio in the combined sample was 1:1 across all years. The constructed model (*GAM 1*) showed no significant seasonal or multi-year variations in this parameter within the wolffish population from Chupa Inlet ($p > 0.05$) (Table 1).

Stomach content analysis of the caught fish revealed that wolffish in Chupa Inlet have a broad diet consisting of benthic invertebrates (Table 2). Over the entire observation period (2001–2023), their diet was found to include 36 species of the Mollusca, Crustacea, Ascidiacea, Ophiuroidea, and Echinoidea. Aggregated data from all observation years showed that the most common species found in the wolffish gastrointestinal tract were the molluscs *Buccinum undatum* (50.2%) and *S. groenlandicus* (32.4%) (Table 2). Secondary in importance were some species of bivalves: *M. edulis*, *Ciliatocardium ciliatum*, and *A. islandica* (12.3–16.4% by frequency of occurrence). The molluscs *Musculus discors*, *Littorina littorea*, and *Tonicella marmorea*, two epibenthic crustaceans (*Hyas araneus* and *Pagurus pubescens*), and the ascidian *Styela rustica* accounted for a small proportion of the wolffish diet (5–10% by frequency of occurrence). Other foods were of incidental occurrence in stomach contents and contributed very little to the overall diet. The exoskeletons of benthic organisms were almost always found crushed.

Table 1. Parameters of smoothing functions for the *GAM 1* model that describes changes in the frequency of occurrence of female wolffish during the summer months and throughout the entire observation period in Chupa Inlet.

Model Term	edf	Chi.Sq	p.value
s(DOY)	1.00	0.77	0.381
s(Year)	1.00	1.48	0.223

Table 2. Species composition of the food components of wolffish in Chupa Inlet from 2001 to 2023.

Species	Taxon details	Frequency of occurrence, %
Buccinum undatum Linnaeus, 1758	Mollusca: Gastropoda	50.2
Serripes groenlandicus (Mohr, 1786)	Mollusca: Bivalvia	32.4
Mytilus edulis Linnaeus, 1758	Mollusca: Bivalvia	16.4
Arctica islandica (Linnaeus, 1767)	Mollusca: Bivalvia	12.8
Ciliatocardium ciliatum (O. Fabricius, 1780)	Mollusca: Bivalvia	12.3
Styela rustica Linnaeus, 1767	Chordata: Ascidiacea	10.7
Pagurus pubescens Krøyer, 1838	Arthropoda: Malacostraca	9.4
Musculus discors (Linnaeus, 1767)	Mollusca: Bivalvia	6.8
Hyas araneus (Linnaeus, 1758)	Arthropoda: Malacostraca	6.6
Littorina littorea (Linnaeus, 1758)	Mollusca: Gastropoda	5.9
Tonicella marmorea (O. Fabricius, 1780)	Mollusca: Polyplacophora	5.9
Cryptonatica affinis (Gmelin 1791)	Mollusca: Gastropoda	3.2
Modiolus modiolus (Linnaeus, 1758)	Mollusca: Bivalvia	2.5
Tridonta elliptica (T. Brown, 1827)	Mollusca: Bivalvia	2.1
Tridonta borealis Schumacher, 1817	Mollusca: Bivalvia	2.1
Littorina obtusata (Linnaeus, 1758)	Mollusca: Gastropoda	2.1
Margarites groenlandicus (Gmelin, 1791)	Mollusca: Gastropoda	1.8
Stongylocentrotus pallidus (Sars G.O., 1872)	Echinodermata: Echinoidea	1.6
Tridonta montagui (Dillwyn, 1817)	Mollusca: Bivalvia	0.9
Littorina saxatilis (Olivi, 1792)	Mollusca: Gastropoda	0.9
Sclerocrangon boreas (Phipps, 1774)	Arthropoda: Malacostraca	0.9
Ophiopholis aculeata (Linnaeus, 1767)	Echinodermata: Ophiuroidea	0.9
Testudinalia testudinalis (O.F. Müller, 1776)	Mollusca: Gastropoda	0.7
Lacuna vincta (Montagu, 1803)	Mollusca: Gastropoda	0.7
Crenella decussata (Montagu, 1808)	Mollusca: Bivalvia	0.5
Hiatella arctica (Linnaeus, 1767)	Mollusca: Bivalvia	0.5
Lyonsia arenosa (Møller, 1842)	Mollusca: Bivalvia	0.5
Musculus niger (J.E. Gray, 1824)	Mollusca: Bivalvia	0.2
Chlamys islandica (O.F. Müller, 1776)	Mollusca: Bivalvia	0.2
Ariadnaria borealis (Broderip et G.B. Sowerby I, 1829)	Mollusca: Gastropoda	0.2
Boreotrophon truncatus (Strøm, 1768)	Mollusca: Gastropoda	0.2
Margarites olivaceus (T. Brown, 1827)	Mollusca: Gastropoda	0.2
Velutina velutina (O.F. Müller, 1776)	Mollusca: Gastropoda	0.2
Margarites helicinus (Phipps, 1774)	Mollusca: Gastropoda	0.2
Stenosemus albus (Linnaeus, 1767)	Mollusca: Polyplacophora	0.2
Boltenia echinata (Linnaeus, 1767)	Chordata: Ascidiacea	0.2

The number of species in the wolffish food spectrum varied little over the years (Table 3) and did not differ between males and females. The highest number of prey species in the wolffish diet was observed in 2001 (19 species) and the smallest number (9 species) in 2012. No significant multi-year trend was found in the number of benthic organisms consumed by wolffish. The diet diversity index was highest for the catches of 2001 (Fig. 2). In 2004, it dropped significantly and in the subsequent years stayed within a narrow range without a clearly expressed trend.

Dynamics of the frequency of occurrence of individual species in the wolffish diet

Table 4 shows the results of modelling the dynamics of the frequency of occurrence of prey organisms that played a dominant or secondary role in the wolffish diet during the summer. Significant interannual variations in occurrence were noted for the following species: *S. groenlandicus*, *M. discors*, *L. littorea*, *T. marmorea*, *H. araneus*, *P. pubescens*, and *S. rustica*.

Table 3. Sex composition of wolffish catches and a brief description of the feeding habits of wolffish in different years in Chupa Inlet.

Year	Number of males	Number of females	Number of specimens with empty stomachs	Number of prey species
2001	19	26	18	19
2004	22	31	21	12
2007	24	23	16	15
2010	28	24	31	17
2012	34	30	40	9
2013	39	47	60	11
2014	50	32	44	14
2015	24	37	22	15
2017	24	27	16	18
2018	29	26	29	12
2019	23	16	17	14
2021	40	31	38	14
2022	25	35	29	18
2023	36	28	11	12

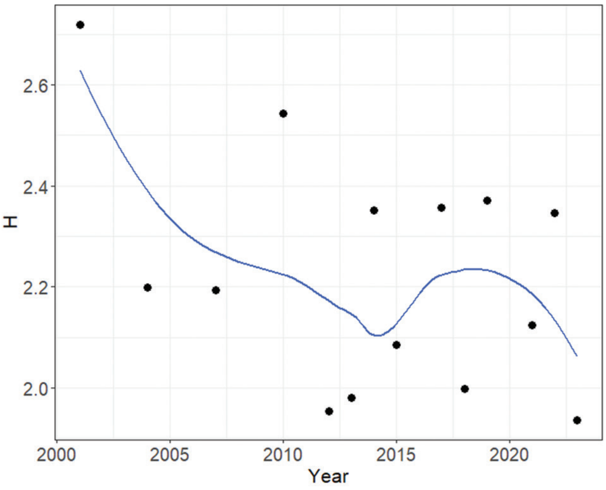

Fig. 2. Long-term changes in the diversity index (H – according to Shannon) of the food spectrum of wolffish in Chupa Inlet. The curve is a trend line fitted by the LOESS method.

Table 4. Parameters of smoothing functions for the *GAM 2* model.

Model Term	edf	Chi.Sq	p.value
s(Year):*Mytilus edulis*	3.23	7.16	0.125
s(Year):*Arctica islandica*	1.00	0.29	0.589
s(Year):*Ciliatocardium ciliatum*	1.00	3.68	0.055
s(Year):*Serripes groenlandicus*	2.27	8.91	0.022
s(Year):*Musculus discors*	2.79	8.80	0.043
s(Year):*Buccinum undatum*	1.00	3.28	0.070
s(Year):*Littorina littorea*	1.50	9.42	0.006
s(Year):*Tonicella marmorea*	1.54	8.91	0.020
s(Year):*Hyas araneus*	1.52	49.61	<0.001
s(Year):*Pagurus pubescens*	1.00	9.81	0.002
s(Year):*Styela rustica*	3.42	18.82	0.001

The visualization of the model describing the multi-year dynamics of occurrence frequencies for individual species is shown in Fig. 3. The resulting curves showing the frequency of occurrence of prey items over the years can be divided into three provisional groups: 1) relatively stable occurrence of the species across different years, 2) downward trend, and 3) upward trend. The first group included four abundant mollusc species (*M. edulis*, *A. islandica*, *C. ciliatum*, and *B. undatum*). The second group was represented by two mollusc species (*L. littorea* and *T. marmorea*) and two species of epibenthic crustaceans (*H. araneus* and *P. pubescens*). The frequency of occurrence of these species in the wolffish diet consistently decreased over the course of our multi-year observation period. In the third group, the frequency of occurrence of prey species in the wolffish diet demonstrated a gradual and statistically significant increase, either throughout the entire study period from 2001 to 2023 (*S. groenlandicus*) or over a shorter period from 2012 to 2019 (*S. rustica* and *M. discors*).

The species composition of prey items, whose occurrence frequency in wolffish stomachs exceeded 20% in each individual year of observation, is shown in Fig. 4. It can be seen that the number of species most commonly found in the wolffish diet varied over the years within a narrow range. In

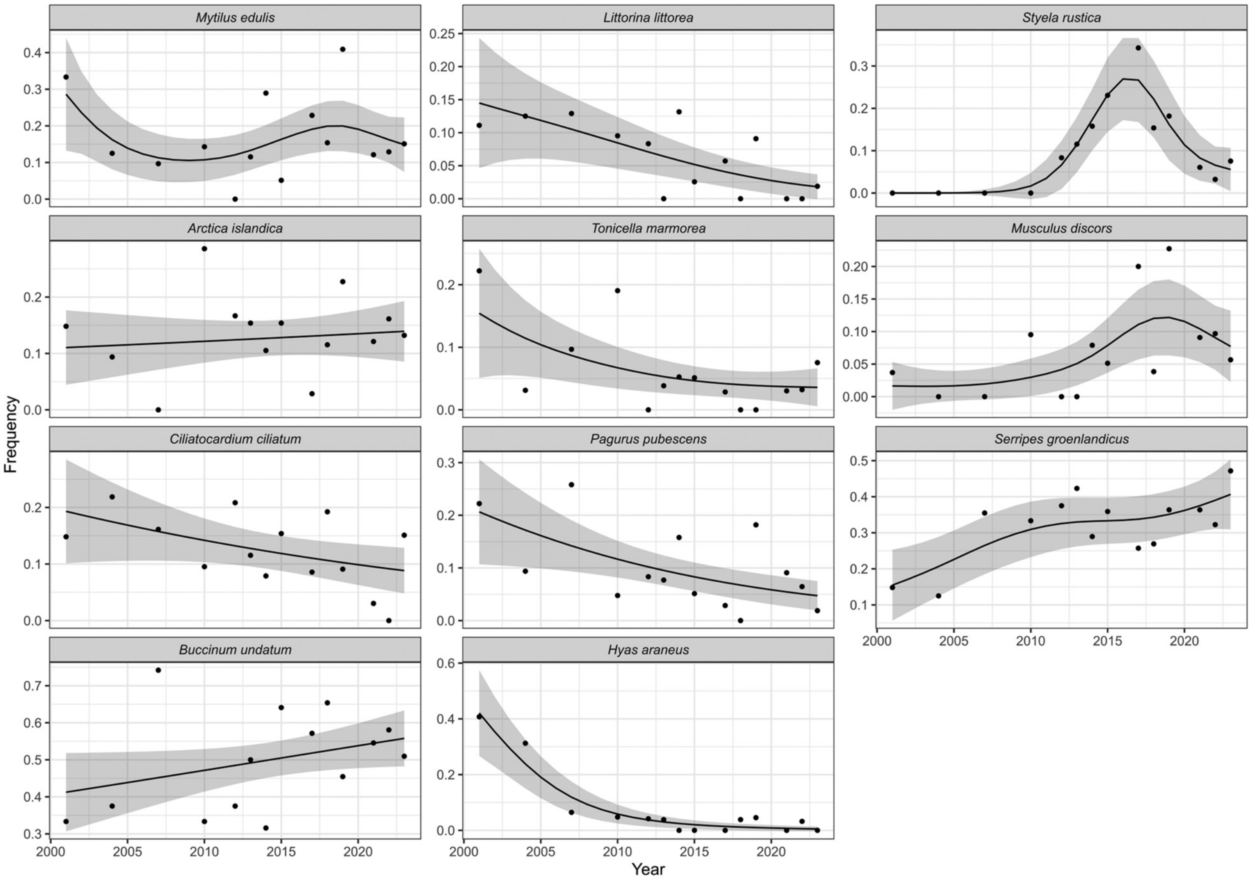

Fig. 3. Long-term changes in the occurrence of the most significant prey items in wolffish stomachs. The curves are trend lines fitted using the *GAM 2* model.

2001, there were five such species, while in subsequent years there were mostly three (rarely two or four), and in the last three years only two species dominated the diet. *Buccinum undatum* was a frequently occurring species every year over the 14 years of observations. *Serripes groenlandicus* was among the dominant species slightly less often, in 12 years. The blue mussel *M. edulis*, with a frequency of occurrence greater than 20%, was noted in the diet only four times. Each of the remaining 8 species was included in the group of significant prey items only 1–2 times over the entire observation period. The bulk of the overall wolffish diet from 2001 to 2023 was therefore represented by three species: *B. undatum*, *S. groenlandicus*, and *M. edulis*. It should be noted that in certain years (2001–2007), the role of crustaceans was also relatively important. The rare occurrence of other prey species is likely due to their small size and low abundance in the study area of Chupa Inlet.

Seasonal and long-term dynamics of the frequency of occurrence of wolffish with empty stomachs

In addition to fish with food in their stomachs, catches each year also included wolffish with empty stomachs (Table 3). The percentage of such individuals varied widely from year to year, ranging from 17.2% to 69.8%, with an average of nearly half (47.2%) of all examined fish. The analysis of the constructed *GAM 3* model revealed a clear seasonal pattern in the proportion of females with empty stomachs (Table 5, Fig. 5A). The lowest occurrence of such females was in the first half of the summer, i.e., during the pre-spawning period. The highest probability of encountering a female with an empty stomach was

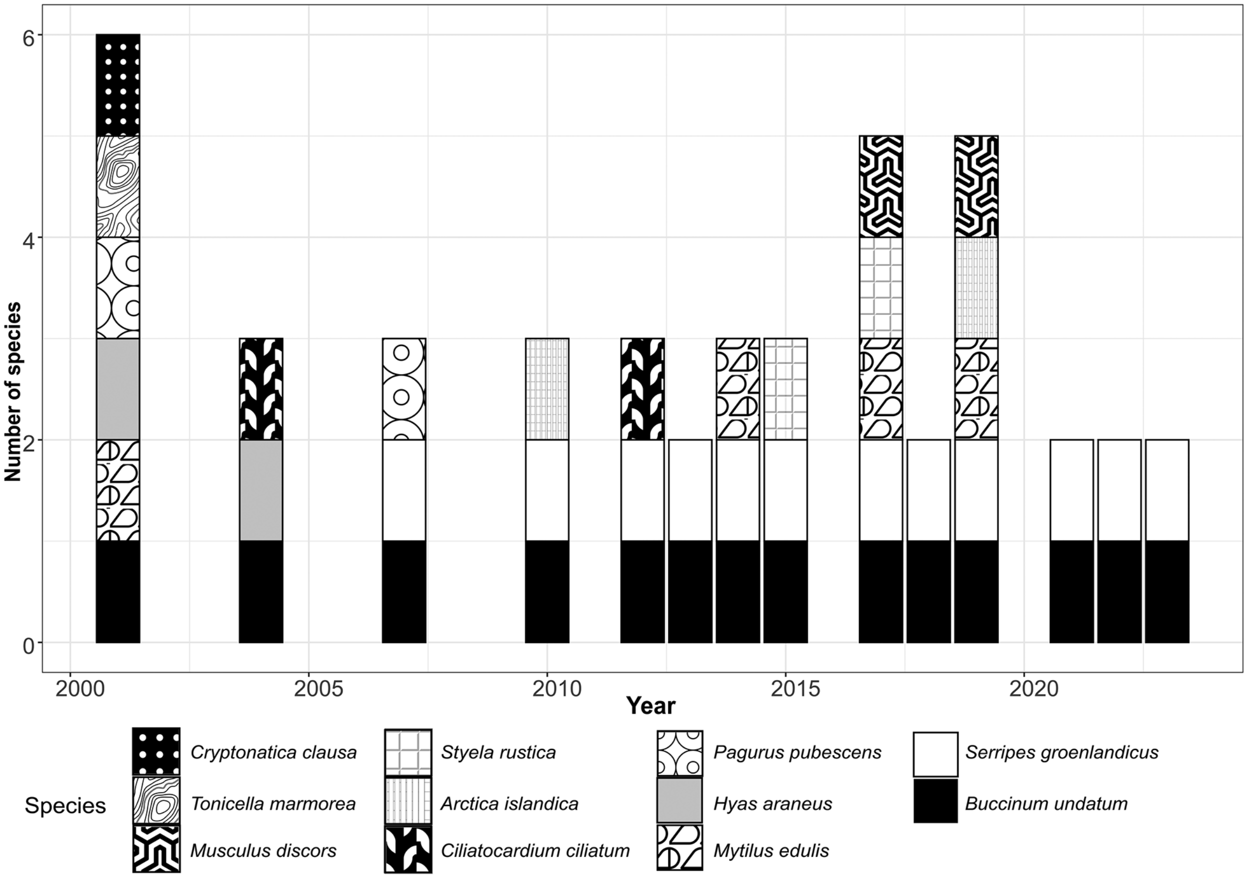

Fig. 4. Long-term variation in the diet composition of wolffish, listing prey items with a frequency of occurrence in the stomachs exceeding 20%.

in late July to early August, during peak spawning ($p < 0.01$; Table 5, Fig. 5A). A different pattern of encountering fish with varying stomach contents was observed in males. Throughout the observation period (June to August), no statistically significant changes were found in the frequency of males without food in their stomachs (Table 5, Fig. 5B). On average, among females individuals with empty stomachs were encountered more frequently than among males (Table 5).

The frequency of wolffish with empty stomachs in Chupa Inlet showed statistically significant multi-year variation (Table 5, Fig. 6). Since no interannual differences in sex ratio were found in the samples (Table 1), data for both sexes were combined for the analysis of the model. The resulting curve (Fig. 6) shows two distinct peaks, indicating years when the probability of encountering individuals with emp-

Table 5. Parameters of the additive model *GAM 3* that describes seasonal and long-term changes in the frequency of occurrence of wolffish individuals with empty stomachs in Chupa Inlet.

Smoothers			
Model term	edf	Chi.Sq	p.value
s(DOY):Sex$_{\text{Female}}$	1.00	7.18	0.007
s(DOY):Sex$_{\text{Male}}$	1.00	2.32	0.128
s(Year)	4.96	60.36	<0.001
Parametric terms			
Model term	estimate	z-statistic	p.value
(Intercept)	0.18	1.73	0.084
Sex$_{\text{Male}}$	−0.61	−4.15	<0.001

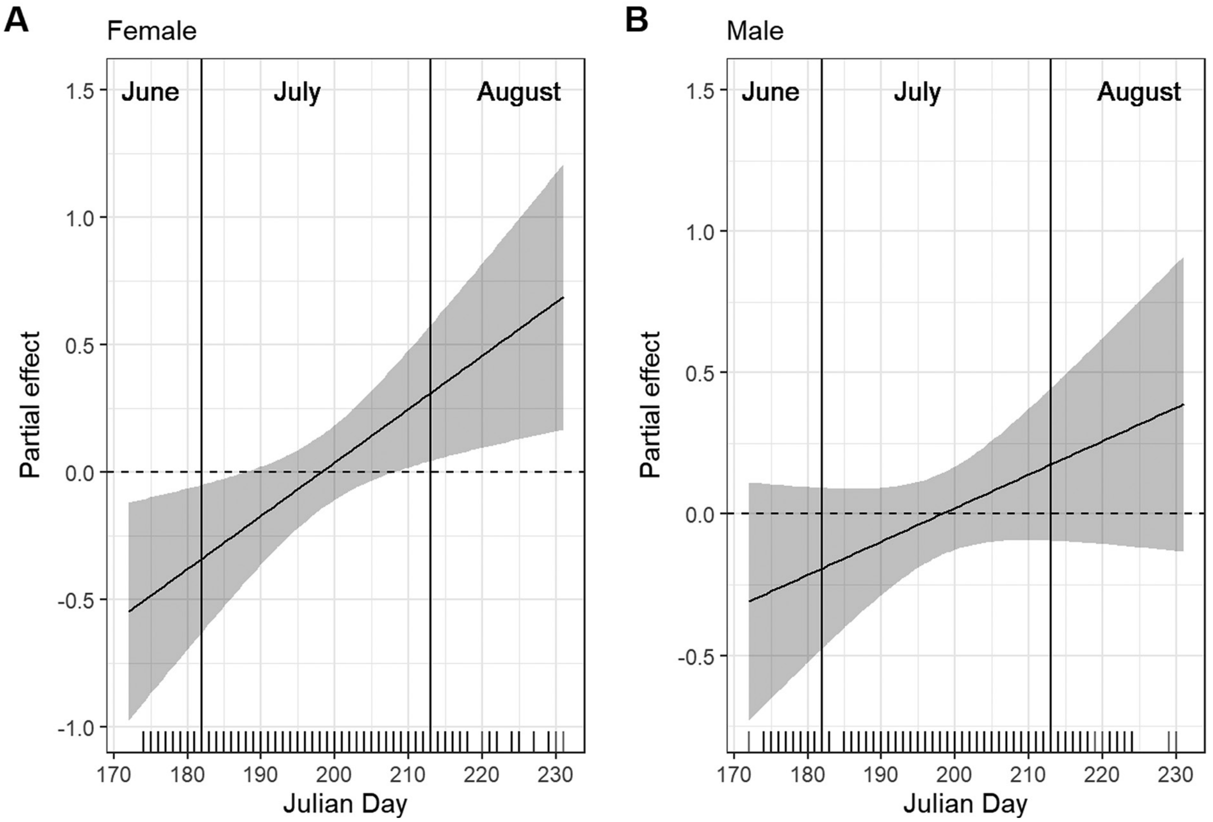

Fig. 5. Seasonal changes in the frequency of occurrence of individuals with empty stomachs among female (A) and male (B) wolffish, according to the *GAM 3* model.

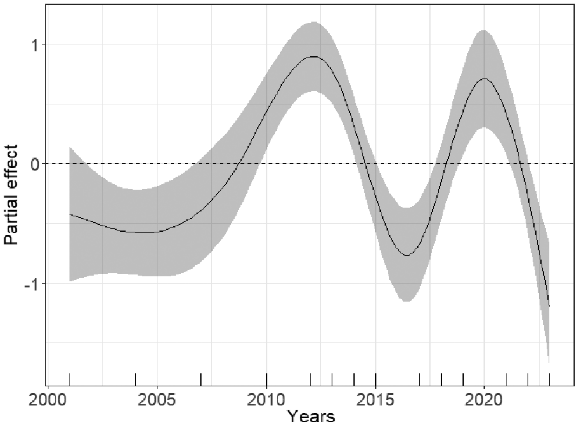

Fig. 6. Long-term dynamics of the frequency of occurrence of wolffish individuals with empty stomachs in Chupa Inlet, according to the *GAM 3* model

ty stomachs was significantly higher than in other years. The “lean” years for wolffish, when the proportion of individuals with empty stomachs in the catches was highest, occurred during the periods of 2010–2014 and 2019–2021.

DISCUSSION

Feeding of wolffish

Our study has shown that wolffish in Chupa Inlet feed on benthic organisms from various taxonomic groups, with only a few mollusc species being the primary components of their diet. A high and similar diversity of benthic macrofauna consumed by wolffish has also been previously noted in other areas along the Karelian coast of the White Sea (Letneretskaya Inlet, Gridina Inlet, and Velikaya Salma Strait). In these locations, the primary prey items for wolffish were also gastropods and bivalves (Barsukov 1956; Kudersky and Rusanova 1963), and the range of encountered species was nearly identical to that in Chupa Inlet. In addition to molluscs, a significant role in the diet of wolffish from Letneretskaya Inlet was also played by crabs *H. araneus* (Barsukov 1956).

A comparison of our data with published results showed that the dominant prey items of wolffish in all the aforementioned areas included similar mollusc species: *B. undatum*, *S. groenlandicus*, and *M. edulis*. Wolffish preferred these prey species in different years of observations. It is noteworthy that these molluscs typically have much higher biomass in the structure of sublittoral benthic biocenoses along the coasts of Kandalaksha Bay (Brotskaya et al. 1963; Golikov et al. 1982, 1985a, b, 1988; Oshurkov and Lukanin 1982; Lukanin et al. 1983; Naumov et al. 1986) compared to most other species of bivalves and gastropods found in wolffish stomachs. It is clear that the abundance of these molluscs in wolffish habitats, their relatively large sizes, and their exposed position on the seabed contributed to the wolffish's preference for these prey species.

Jónsson (1982) previously demonstrated that the diet of wolffish depends on the availability of prey organisms. According to his observations, in areas along the Icelandic coast where sea urchins were abundant, their proportion in the wolffish diet was high. By contrast, in other marine areas where horse mussels (*Modiolus modiolus*) were common, the stomachs of wolffish were filled exclusively with these invertebrates.

Wolffish are visual predators and exhibit a high degree of size selectivity towards larger prey items, as this is more energetically advantageous (Keats et al. 1986). After choosing a large individual as prey, wolffish crushes it before swallowing. Overall, the role of large-sized molluscs (*B. undatum*, *S. groenlandicus*, etc.) and other benthic macrofauna organisms in the diet of wolffish increases with the age and size of the fish (Barsukov 1956; our observations). The predation rate of wolffish on such individuals remains high, even when smaller prey species are abundant and available.

Relationship of feeding with reproduction

Barsukov (1953) noted that both male and female wolffish in Letneretskaya Inlet of the White Sea fed intensively during the summer period (from June 18 to August 30). Our multi-year observations on the seasonal dynamics of wolffish predation in Chupa Inlet revealed differences between males and females in the occurrence of individuals with empty stomachs during the summer season. Both sexes fed actively prior to breeding, in June and the first half of July. However, in late July and early August, i.e. during the spawning period, the occurrence of females with empty stomachs in the catches was significantly higher than that of males. This indicates that female wolffish, unlike males, show significantly reduced feeding intensity during the breeding season.

Similar results were previously obtained by Keats et al. (1985) when studying the influence of reproduction on feeding of wolffish in the coastal waters of Newfoundland (Northwest Atlantic). According to these authors, both males and females reduce or stop feeding at spawning time, but males do so to a lesser extent. Females resume feeding shortly following egg laying, while males remain at the nesting sites and "feed little or not at all while they are guarding eggs" (Keats et al. 1985: 2567). The seasonal variability in feeding intensity of wolffish in the North Sea was also demonstrated by Liao and Lucas (2000). The authors noted a high proportion of individuals with empty stomachs and the lowest food intake by wolffish during the autumn-winter period, which is the spawning season of these fish.

Barsukov (1956) observed a shortage of males in the catches during the spawning period of wolffish in Letneretskaya Inlet (Karelian coast) and suggested that they were guarding the eggs laid by females. Several subsequent studies have confirmed this characteristic trait of male behavior during the spawning period (Keats et al. 1985; Pavlov and Novikov 1986), but the exact duration that a male can stay near an egg cluster remains unknown. According to our data, males do not cease feeding during the spawning period and no change in sex ratio is observed in coastal wolffish catches during this time. It is possible that males can remain near the spawning site for a brief period (several days) to guard the eggs but soon leave in search of food. This assumption is supported by the fact that molluscs are typically digested in the wolffish gastrointestinal tract within 3–4 days (Keats et al. 1986; Orlova et al. 1989). If males stayed near the egg cluster for an extended period, it would have affected the sex ratio of wolffish caught in coastal waters in late July–August. The egg-guarding behavior of males after spawning requires further study.

Long-term diet variations

The spectrum of prey items consumed by wolffish has not changed significantly over 20 years of observation. The greatest diversity of prey species in the wolffish stomachs was observed in 2001. Our results indicate that wolffish feed on a variety of macrobenthic organisms, which can be found in their feeding grounds. When certain preferred foraging species are scarce or absent, wolffish switch to predominantly consuming other available prey. This allows wolffish to exploit the food resources available in coastal biotopes in the most efficient manner. Since the feeding period of wolffish in the coastal areas of the White Sea is relatively short (about 3 months), a broad food spectrum allows this species to quickly meet its energy needs for growth and generative metabolism. The size of prey also appears to play an important role in predation, as adult individuals prefer larger representatives of various taxonomic groups.

The species composition and production parameters of animal macrobenthos in the sublittoral bottom biocenoses of Chupa Inlet have been much less studied compared to littoral communities (Naumov 2006). It is known that the species most frequently found in wolffish stomachs – *M. edulis*, *S. groenlandicus*, and *B. undatum,* are typical inhabitants of various sublittoral biocenoses in the study area. These species were found at depths of 3 to 15 meters, where wolffish forage during the summer, and in Chupa Inlet they can reach relatively high densities in various biocoenoses (Rusanova 1963; Oshurkov and Lukanin 1982; Golikov et al. 1985a, b; Gerasimova and Maximovich 2001; Maximovich and Gerasimova 2007). *Mytilus edulis* and *S. groenlandicus* dominate in abundance in the structure of benthic communities on rocky or gravel bottoms mixed with sand and dense silt. *Buccinum undatum* reaches its highest density and biomass on silted bottoms containing pebbles and scattered stones and is often noted in biocoenoses of *M. edulis* (Rusanova 1963; Golikov et al. 1985b). It should be noted that the total biomass of macrobenthos in our study area was highest at the sublittoral zone at depths of up to 15 meters (Golikov et al. 1985a).

The frequencies of occurrence of individual species that play a dominant or secondary role in the diet of wolffish varied significantly over the observation period, and the trends in these interannual changes differed among prey species. The importance of some key prey items in the wolffish diet, especially crustaceans, decreased over the study period. Crabs *H. araneus*, which together with blue mussels were major food components for wolffish in the early 2000s, have now almost completely disappeared from its diet. The occurrence of *P. pubescens* in wolffish stomachs in 2023 was almost half that observed at the beginning of the study. It should be noted that in parallel with wolffish the frequency of occurrence of crabs in the diet of another coastal predator, the shorthorn sculpin, *Myoxocephalus scorpius* (Linnaeus, 1758), decreased significantly (from 73% to 11%) between 1998 and 2008 (Yershov 2010b). Based on this information, it can be concluded that the abundance of *H. araneus* in the mouth of Chupa Inlet significantly declined in the first decade of the 21st century. Against the backdrop of the decreasing occurrence of crustaceans in the wolffish diet, a significant gradual increase, from 15% in 2001 to 47% in 2023, was observed in the role of the bivalve mollusc *S. groenlandicus*. One large and abundant prey species has therefore been replaced in the wolffish diet by another. The continued dominance of *B. undatum* in the wolffish diet throughout the observation period is also noteworthy, indicating relative stability of population of this mollusc as well as the ease of detection of molluscs on the seafloor and, consequently, its availability as prey. *M. edulis* also remained a constant, albeit secondary, prey item for wolffish in Chupa Inlet. Interestingly, during the period from 2014 to 2019, there was an increase in the occurrence of the ascidian *S. rustica* and the mollusc *M. discors* in wolffish stomachs, although previously these species were rarely observed in its diet.

The observed alternation between "typical" and "lean" years for wolffish from 2001 to 2023 suggests a limited overall availability of benthic food resources in the mouth of Chupa Inlet, where the fish spend their summer feeding period. The patchy distribution of settlements of various mollusc species and epifauna in this area, along with interannual differences in their abundance, significantly influence the occurrence of prey items in the wolffish diet.

The analysis of long-term variability in the occurrence of different prey species in the wolffish diet allows for certain assumptions about the causes of change in the structure of its trophic relationships within the study area. In the early 2000s, some species of epibenthos (such as crabs *H. araneus*, hermit crabs *P. pubescens*, and less often chitons *T. marmorea*) were quite common in the wolffish diet. However, by approximately 2010–2012, the frequency of occurrence of these prey items in wolffish stomachs sharply decreased, while the frequency of occurrence of the mollusc *S. groenlandicus*, which inhabits silty sand, increased. Around the same time, the occurrence of the ascidian *S. rustica* in the wolffish diet also began to increase. It is known that in the White Sea these ascidians can form clusters on the surface of the shells of dead bivalves *S. groenlandi-*

cus, usually in association with other epibionts (Yakovis et al. 2008; Yakovis and Artemieva 2017). It is possible that this relationship might partly explain the increase in the occurrence of these two species in the wolffish diet. It should be noted that, according to observations made by divers at the sites where wolffish were caught, clusters of ascidians were also found in the study area on rocky outcrops and stones, where the infauna was absent (our unpublished observations).

Regarding the dynamics in the occurrence frequency of molluscs of the genus *Musculus*, it should be noted that these bivalves often use the tunic of ascidians as a substrate for settlement (Yakovis and Artemieva 2017), which may explain their increased co-occurrence with ascidians in the wolffish diet during the period from 2014 to 2019. The subsequent shift in the wolffish feeding habits from consuming epifauna (crustaceans) to consuming infauna (molluscs) is most likely related to some successional changes in benthic communities caused by the movement of bottom sediments. For example, the reduction in the role of epifauna in the wolffish diet may have occurred due to sand accumulation in certain areas of the summer feeding grounds. It is known that sublittoral sand masses can be transported over fairly long distances (Robert et al. 2021), leading to the formation of silty sand lenses that could have caused the disappearance of epibenthic organisms from the wolffish diet.

It is worth noting that the first "crisis" marked by an increase in the proportion of fish with empty stomachs (2010–2014) coincides with a decrease in the frequency of occurrence of epibenthic species and an increase in this indicator for *S. groenlandicus*, which inhabits sandy-silty substrates. The second "crisis" in wolffish feeding intensity (2019–2021) may also be linked to sand deposition in the shallow coastal areas of the sublittoral zone in the study area of Chupa Inlet. Thus, the observed multi-year variability in the feeding intensity of adult wolffish, in our opinion, reflects the current dynamic state of the benthic food base for this species in Chupa Inlet. In order to further analyze the causes of change in the trophic relationships of wolffish, a detailed study of its diet is needed, combined with an assessment of the number of feeding fish and an evaluation of the abundance of key prey species in the benthic biocenoses in specific areas of wolffish feeding grounds in Chupa Inlet.

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REFERENCES

Albikovskaya L.K. 1983. Feeding characteristics of wolffishes in the Labrador – Newfoundland region. *NAFO Scientific Counsil Studies*, **6**: 35–38.

Altukhov K.A., Mikhailovskaya F.B., Mukhomediyarov F.B., Nadezhin V.M., Novikov P.I. and Palenichko Z.G. 1958. Fishes of the White Sea. Gosudarstvennoe izdatelstvo Karelskoy ASSR, Petrozavodsk, 160 p. [In Russian].

Barsukov V.V. 1953. Towards knowledge of the reproduction biology of the White Sea wolffish (*Anarhichas lupus* L.). *Zoologicheskii Zhurnal*, **32**(6): 1211–1216. [In Russian].

Barsukov V.V. 1956. White Sea wolffish (*Anarhichas lupus maris-albi* Barsukov). *Voprosy Ikhtiologii*, **6**: 129–136. [In Russian].

Barsukov V.V. 1959. Fauna SSSR. Sem. zubatok (Anarhichadidae) [Fauna of USSR. The wolffish family (Anarhichadidae)]. Vol. 5(5). Izdatelstvo Akademii Nauk SSSR, Moscow-Leningrad, 171 p. [In Russian; English translation, 1972, Indian National Scientific Documentation Centre, New Dehli].

Barsukov V.V. 1986. Anarhichadidae. In: P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (Eds). Fishes of the North-Eastern Atlantic and the Mediterranean. UNESCO, Paris: 1113–1116.

Barsukov V.V. and Nizovtsev G.P. 1960. On feeding of Barents Sea wolffishes (*Anarhichas latifrons* Steenstrup et Hallgrimsson, *A. minor* Olafsen, *A. lupus* L.). *Trudy Murmanskogo Morskogo Bioiogicheskogo Instituta*, **2**(6): 203–206. [In Russian].

Beukema J.J., Dekker R., Essink K. and Michaelis H. 2001. Synchronized reproductive success in the main bivalve species in the Wadden Sea: causes and consequences. *Marine Ecology Progress Series*, **211**: 143–155. https://doi.org/10.3354/meps211143

Borutskiy E.V. (Ed.). 1974. Methodical guide for study of feeding and food relationships of fish in nature. Moscow, Nauka, 254 p. [In Russian].

Brotskaya V.A., Zhdanova N.N. and Semyonova N.L. 1963. Bottom fauna of the Velikaya salma and the adjoining regions of the Kandalaksha Bay of the White Sea. *Reports of the White Sea biological station of the Moscow State University*, **2**: 159–181. [In Russian].

Büttger H., Asmus H., Asmus R., Buschbaum C., Dittmann S. and Nehls G. 2008. Community dynamics of intertidal soft-bottom mussel beds over two decades. *Helgoland Marine Research*, **62**: 23–36. https://doi.org/10.1007/s10152-007-0099-y

Cleveland W.S. and Loader C. 1996. Smoothing by Local Regression: Principles and Methods. In: W. Härdle and M.G. Schimek (Eds). Statistical Theory and Computational Aspects of Smoothing. Contributions to Statistics. Physica-Verlag Heidelberg: 10–49. https://doi.org/10.1007/978-3-642-48425-4_2

Fromentin J.M., Ibanez F., Dauvin J.C., Dewarumez J.M. and Elkaim B. 1997. Long-term changes of four macrobenthic assemblages from 1978 to 1992. *Journal of the Marine Biological Association of the United Kingdom*, **77**(2): 287–310. https://doi.org/10.1017/S002531540007168X

Gerasimova A.V. and Maximovich N.V. 1988. The structure and production of the settlement and biocenosis *Arctica islandica* (L.) in Chupa Inlet (White Sea). *Vestnik Leningradskogo Universiteta*, Series 3, **2**: 3–11. [In Russian].

Gerasimova A.V. and Maximovich N.V. 2000. Analysis of long-term changes in the bivalve population structural characteristics (White Sea). *Vestnik Sankt-Petersburgskogo Universiteta*, Series 3, **2**: 24–27. [In Russian].

Gerasimova A.V. and Maximovich N.V. 2001. Ecology of *Arctica islandica* L. and *Serripes groenlandicus* Briguiere in the White Sea. *Vestnik Sankt-Petersburgskogo Universiteta*, Series 3, **4**: 87–91. [In Russian].

Gerasimova A.V. and Maximovich N.V. 2013. Age-size structure of common bivalve mollusc populations in the White Sea: the causes of instability. *Hydrobiologia*, **706**: 119–137. https://doi.org/10.1007/s10750-0121415-3

Golikov A.N., Averintsev V.G., Babkov A.I., Kuntsevich Z.V., Luleev V.I., Matveeva E.V., Menshutkina T.V., Novikov O.K., Petryashev V.V., Potin V.V., Smirnov I.S., Fedyakov V.V. and Shoshina E.V. 1978. Changes in quantitative characteristics in the composition and structure of bottom biocenoses of some bays of the Chupa Inlet of the White Sea over 10 years (1967–1977). In: L.Ya. Borkin (Ed.). Morphology, systematics and evolution of animals. Zoologicheskiy Institut, Leningrad: 54–56. [In Russian].

Golikov A.N., Averintsev V.G., Babkov A.I., Menshutkina T.V., Fedyakov V.V. and Shoshina E.V. 1982. Biocenoses of the Palkin Inlet in the White Sea. In: O.A. Scarlato (Ed.). Marine invertebrates of coastal biocenoses of the Arctic Ocean and the Pacific Ocean. Zoologicheskiy Institut, Leningrad: 3–11. [In Russian].

Golikov A.N., Maximovich N.V. and Sirenko B.I. 1988. On distribution, growth and reproduction of *Mytilus edulis* L. with reference to settlement off the Sonostrov Island (the White Sea). In: O.A. Scarlato (Ed.). Hydrobiological peculiarities of the south-eastern part of the Kandalaksha Bay in connection with the mussel aquaculture in the White Sea. Zoologicheskiy Institut, Leningrad: 97–108. [In Russian].

Golikov A.N., Scarlato O.A., Buzhinskaja G.N., Vasilenko S.V., Golikov A.A., Perestenko L.P. and Sirenko B.I. 1986. Changes in benthos of the Possjet Bay (Japan Sea) over the last 20 years as a result of accumulation of organic matter in bottom sediments. *Oceanology*, **26**(1): 131–135. [In Russian].

Golikov A.N., Scarlato O.A., Galtsova V. and Menshutkina T.V. 1985a. Ecosystems of the Chupa Inlet of the White Sea and their seasonal dynamics. In: O.A. Scarlato (Ed.). Biocenoses of the Chupa Inlet of the White Sea and their seasonal dynamics. Nauka, Leningrad: 5–83. [In Russian].

Golikov A.N., Scarlato O.A., Maximovich N.V., Matveeva T.A. and Fedyakov V.V. 1985b. Fauna and ecology of shell molluscs in the Chupa Inlet of the White Sea. In: O.A. Scarlato (Ed.). Biocenoses of the Chupa Inlet of the White Sea and their seasonal dynamics. Nauka, Leningrad: 185–229. [In Russian].

Hagen N.T. and Mann K.H. 1992. Functional response of the predators American lobster *Homarus americanus* (Milne-Edwards) and Atlantic wolffish *Anarhichas lupus* (L.) to increasing numbers of the green sea urchin *Strongylocentrotus droebachiensis* (Müller). *Journal of Experimental Marine Biology and Ecology*, **159**: 89–112. https://doi.org/10.1016/0022-0981(92)90260-H

Johannesen E., Lindstrøm U., Michalsen K., Skern-Mauritzen M., Fauchald P., Bogstad B. and Dolgov A. 2012. Feeding in a heterogeneous environment: spatial dynamics in summer foraging Barents Sea cod. *Marine Ecology Progress Series*, **458**: 181–197. https://doi.org/10.3354/meps09818

Jónsson G. 1982. Contribution to the biology of catfish (*Anarhichas lupus*) at Iceland. *Rit Fiskideildar*, **6**, 2–26.

Keats D.W., South G.R. and Steele D.H. 1985. Reproduction and egg guarding by Atlantic wolffish (*Anarhichas lupus*: Anarhicidae) and ocean pout (*Macrozoarces americanus*: Zoarcidae) in Newfoundland waters. *Canadian Journal of Zoology*, **63**: 2565–2568. https://doi.org/10.1139/z85-382

Keats D.W., Steele D.H. and South G.R. 1986. Atlantic wolffish (*Anarhichas lupus* L.; Pisces: Anarhichidae) predation on green sea urchins (*Strongylocentrotus droebachiensis* (O.F. Mull.); Echinodermata: Echinoidea) in eastern Newfoundland. *Canadian Journal of Zoology*, **64**: 1920–1925. https://doi.org/10.1139/z86-288

Khaitov V. 2013. Life in an unstable house: community dynamics in changing mussel beds. *Hydrobiologia*, **706**(1): 139–158. https://doi.org/10.1007/s10750-012-1283-x

Kudersky L.A. 1966. Benthic fauna of the Onega Bay, the White Sea. *Trudy Karelskogo otdeleniya GosNIORH*, **4**(2): 204–371. [In Russian].

Kudersky L.A. and Rusanova M.N. 1963. Feeding of demersal fish in the western part of the White Sea. *Uchenye zapiski Karelskogo pedagogicheskogo instituta*, **15**: 221–300. [In Russian].

Liao Y. and Lucas M.C. 2000. Diet of the common wolffish *Anarhichas lupus* in the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, **80**: 181–182. https://doi.org/10.1017/S0025315499001745

Lukanin V.V. and Oshurkov V.V. 1981. The structure of intertidal mussel settlements in Kandalaksha Bay of the White Sea. *Biologia morya*, **5**: 33–38. [In Russian].

Lukanin V.V., Naumov A.D. and Fedyakov V.V. 1986. Dynamics of the size-frequency structure of blue mussel (*Mytilus edulis* L.) beds in the White Sea. In: O.A. Scarlato (Ed.). Ecological investigations of the benthic organisms of the White Sea. Zoologicheskiy Institut, Leningrad: 50–63. [In Russian].

Lukanin V.V., Oshurkov V.V. and Berger V.Ya. 1983. On the distribution and stocks of blue mussel in the Kandalaksha Bay of the White Sea. In: O.A. Scarlato (Ed.). The results and perspectives of investigation of biological resources of the White Sea. Zoologicheskiy Institut, Leningrad: 49–55. [In Russian].

Maximovich N.V. and Gerasimova A.V. 2007. Distribution and resources of bivalves in Chupa Inlet (Kandalaksha Bay, White Sea). *Sbornik nauchnykh trudov FGNU "GosNIORKH"*, **337**: 570–579. [In Russian].

Mukhomediyarov F.B. 1963. Biology and fishery of the noncommercial fishes in the coastal waters of the Karelia. In: Z.G. Palenichko (Ed.). Papers on the comprehensive studies of the White Sea. Izdatelstvo Akademii Naus SSSR, Moscow–Leningrad: 131–143. [In Russian].

Naumov A.D. 2006. Clams of the White Sea. Ecological and faunistic analysis. Zoologicheskiy Institut, Saint Petersburg, 367 p. [In Russian].

Naumov A.D., Babkov A.I. and Fedyakov V.V. 1986. Biocenoses of the Kolvitsa Inlet of the Kandalaksha Bay of the White Sea. In: O.A. Scarlato (Ed.). Ecological investigations of the benthic organisms of the White Sea. Zoologicheskiy Institut, Leningrad: 91–122. [In Russian].

Nikolaev A.P. 1951. Fish species of Pomor and Karelia Coasts of the White Sea. *Izvestiya Karelo-Finskogo Filiala Akademii Nauk SSSR*, **3**: 93–99. [In Russian].

Orlova E.L., Karamushko L.I., Berestovsky E.G. and Kireeva E.A. 1989. Studies on feeding in the Atlantic wolffish, *Anarhichas lupus*, and the spotted wolffish, *A.minor*, under experimental conditions. *Journal of Ichthyology*, **29**: 91–101.

Oshurkov V.V. and Lukanin V.V. 1982. The sublittoral mussel settlements in Kandalaksha Bay of the White Sea. *Vestnik Leningradskogo Universiteta*, **15**: 5–11. [In Russian].

Pavlov D.A. 1994. Fertilization in the wolfish *Anarhichas lupus*: external or internal? *Journal of Ichthyology*, **34**: 140–151.

Pavlov D.A., Dzerzhinskiy K.F. and Radzikhovskaya E.K. 1992. Assessing the quality of roe from White Sea wolfish, *Anarhichas lupus marisalbi*, obtained under experimental conditions. *Journal of Ichthyology*, **32**(1): 88–104.

Pavlov D.A. and Moksness E. 1994. Production and quality of eggs obtained from wolffish (*Anarhichas lupus* L.) reared in captivity. *Aquaculture*, **122**: 295–312. https://doi.org/10.1016/0044-8486(94)90339-5

Pavlov D.A. and Novikov G.G. 1986. On the development of biotechnology for rearing of White Sea wolffish, *Anarhichas lupus marisalbi*. 1. Experience of obtaining mature sex products, incubation of eggs and rearing of young fish. *Journal of Ichthyology*, **26**: 95–106.

Pavlov D.A. and Novikov G.G. 1993. Life history and peculiarities of common wolffish (*Anarhichas lupus*) in the White Sea. *ICES Journal of Marine Science*, **50**: 271–277. https://doi.org/10.1006/jmsc.1993.1029

Pavlov D.A. and Radzikhovskaya E.K. 1991. Reproduction biology of White Sea wolffish *Anarhichas lupus marisalbi* (based on experimental data). *Journal of Ichthyology*, **31**(7): 52–62.

Petersen G.H. 1978. Life cycles and population dynamics of marine benthic bivalves from the Disko Bugt area of West Greenland. *Ophelia*, **17**: 95–120. https://doi.org/10.1080/00785326.1978.10425475

R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Robert A.E., Quillien N., Bacha M., Caulle C., Nexer M., Parent B., Garlan T. and Desroy N. 2021. Sediment migrations drive the dynamic of macrobenthic ecosystems in subtidal sandy bedforms. *Marine Pollution Bulletin*, **171**: 112695. https://doi.org/10.1016/j.marpolbul.2021.112695

Rusanova M.N. 1963. Short notes on biology of some mass invertebrate species in the vicinity of the cape Kartesh. In: Z.G. Palenichko (Ed.). Materials of integrated research of the White Sea. Vol.2. Izdatelstvo Academii Nauk SSSR, Moscow–Leningrad: 53–65. [In Russian].

Schückel U., Ehrich S. and Kröncke I. 2010. Temporal variability of three different macrofauna communities in the northern North Sea. *Estuarine, Coastal and Shelf Science*, **89**(1): 1–11. https://doi.org/10.1016/j.ecss.2010.04.006

Sell A.F. and Kröncke I. 2013. Correlations between benthic habitats and demersal assemblages—a case study on the Dogger Bank (North Sea). *Journal of Sea Research*, **80**: 12–24. https://doi.org/10.1016/j.seares.2013.01.007

Sukhotin A.A. and Berger V.Ja. 2013. Long-term monitoring studies as a powerful tool in marine ecosystem research. *Hydrobiologia*, **706**: 1–9. https://doi.org/10.1007/s10750-013-1456-2

Templeman W. 1985. Stomach contents of Atlantic Wolffish (*Anarhichas lupus*) from the Northwest Atlantic. *NAFO Scientific Council Studies*, **8**: 49–51.

Townhill B.L., Holt R.E., Bogstad B., Durant J.M., Pinnegar J.K., Dolgov A.V., Yaragina N.A., Johannesen E. and Ottersen G. 2021. Diets of the Barents Sea cod (*Gadus morhua*) from the 1930s to 2018. *Earth System Science Data*, **13**: 1361–1370. https://doi.org/10.5194/essd-13-1361-2021

Varfolomeeva M. and Naumov A.D. 2013. Long-term temporal and spatial variation of macrobenthos in the intertidal soft-bottom flats of two small bights (Chupa Inlet, Kandalaksha Bay, White Sea). *Hydrobiologia*, **706**: 175–189. https://doi.org/10.1007/s10750-012-1341-4

Yakovis E. and Artemieva A. 2017. Cockles, barnacles and ascidians compose a subtidal facilitation cascade with multiple hierarchical levels of foundation species. *Scientific reports*, **7**(1): 237. https://doi.org/10.1038/s41598-017-00260-2

Yakovis E.L., Artemieva A.V., Shunatova N.N. and Varfolomeeva M.A. 2008. Multiple foundation species shape benthic habitat islands. *Oecologia*, **155**: 785–795. https://doi.org/10.1007/s00442-007-0945-2

Yershov P.N. 2010a. Population structure, growth and diet of Atlantic wolffish *Anarhichas lupus marisalbi* Barsukov, 1956 in the Kandalaksha Bay of the White Sea. *Proceedings of the Zoological Institute RAS*, **314**(3): 343–356. [In Russian]. https://doi.org/10.31610/trudyzin/2010.314.3.343

Yershov P.N. 2010b. Long-term changes in the food composition of the shorthorn sculpin *Myoxocephalus scorpius* (Linnaeus, 1758) in the Kandalaksha Bay of the White Sea. *Vestnik Sankt-Petersburgskogo Universiteta*, Series 3, **2**: 55–62. [In Russian].

Wood S.N. 2017. Generalized Additive Models: An Introduction with R (Second Edition). New York, Chapman and Hall/CRC, 496 p. https://doi.org/10.1201/9781315370279

WoRMS Editorial Board. 2024. World Register of Marine Species. Available from https://www.marinespecies.org (accessed 06 July 2024).