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Stability of the spatio-temporal structure of helminth infestations in the Kamchatka Sable

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Abstract. This paper presents the results of helminthological monitoring of the Kamchatka sable (*M. zibellina kamtschadalica* Birula, 1916) across nine districts of Kamchatka Krai from 1952 to 2022. Previous research, based on helminthological dissections of 10,053 predator carcasses from 1952 to 1992, established that the Prevalence Rate (PR) — the percentage of infected individuals in a sample — for eleven background helminth species differs across all districts. These proportions were designated by us as the Specific Infestation Pressure (SIP). This study examines augmented quantitative and qualitative characteristics of the four previously identified SIP types in sables, with five subtypes, each represented by distinct variants in the nine studied districts. The dynamics of helminth PR values are demonstrated, and evidence is provided for the stability of the SIP from the beginning of observations, not only across each eleven-year cycle corresponding to sable population cycles but also across different time periods up to 1980, 1992, 2002, 2018, and 2022.

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Keywords: Kamchatka Krai, Kamchatka sable, parasites, helminths, helminthological dissection, Prevalence Rate (PR), Specific Infestation Pressure (SIP)

Стабильность пространственно-временной структуры гельминтозных инвазий камчатского соболя

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Аннотация. Представлены результаты гельминтологического мониторинга камчатского соболя в девяти районах Камчатского края с 1952 по 2022 г. Ранее, по материалам гельминтологических вскрытий 10 053 тушек хищника за 1952–1992 гг., установлено, что соотношение величины ЭИ (экстенсивности инвазии — процента зараженных особей в исследуемой группе) одиннадцати фоновых гельминтов во всех районах отличается. Эти соотношения обозначены нами как «специфический инвазионный пресс» (СИП). В данной работе рассматриваются дополненные количественные и качественные характеристики выделенных нами ранее четырех типов СИП соболей с пятью подтипами, которые представлены отдельными вариантами в каждом из девяти изученных районов. Показана динамика значений ЭИ гельминтов и приведены доказательства стабильности СИП с начала наблюдений не только в каждые одиннадцать лет, соответствующие циклам численности соболя, но и в разные по продолжительности отрезки времени по 1980, 1992, 2002, 2018 и 2022 годы.

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Ключевые слова: Камчатский край, Камчатский соболь, паразиты, гельминты, гельминтологическое вскрытие, экстенсивность инвазии (ЭИ), специфический инвазионный пресс (СИП)

Introduction

Research of parasite-host relationships in vertebrates has predominantly focused on small, abundant, and easily collected hosts, such as rodents, freshwater fish, amphibians, and occasionally birds (Tokobaev, Morev 1968; Nadtochij et al. 1971; Babaev 1973; Kovalchuk 1983; Scott 1987; Haukisalmi et al. 1988; Spratt 1990; Roberts et al. 1992; Ieshko 1994; Romashova 2002). Among larger examined animals, the most typical are wild species hunted for meat or fur. Significant databases have been compiled on the diversity of helminth species infecting these hosts, including the intensity and dynamics of infection, and the geographical distributions of parasites: (Petrov 1927; 1928; Afanas'ev 1941; Troitskaya 1967; Hansson 1970; Kovalchuk 1979; Custer, Pence 1981; Tranbenkova 1996; 2003; 2016; Sidorovich, Anisimova 1997; Koehler et al 2009). These studies confirm the pathogenic effects of certain helminth species on fur-bearing animals (Grakov 1962; Anderson 1971; Monakhov, Trushin 2001; Petrov et al. 2011).

The parasitic helminths found in these fur-bearing animals influence host population dynamics, and, consequently, the structure and homeostasis of the biogeocenosis. To our knowledge, no systematic studies describing the long-term (multi-decadal) structure of parasitic helminth populations in large vertebrates have been conducted previously. This study presents the results of multi-decade monitoring of helminth communities in the Kamchatka sable (*M. zibellina kamtschadalica* Birula, 1916).

Materials and methods

The Kamchatka sable inhabits the Kamchatka Peninsula and the continental part of Kamchatka Krai, an area divided into ten administrative districts (Fig. 1).

The entire study area spans approximately 1,600 km from 51° N to 65° N. The peninsula itself is about 1,200 km long, while the continental portion extends 400 km inland.

The peninsula's maximum width is 400 km and it connects to the mainland at approxi-

mately 60° N. The climate of coastal districts is moderated by the Sea of Okhotsk, the Bering Sea, and the Pacific Ocean, becoming progressively more continental inland.

The vast territory of each administrative district, combined with its coastal or continental position, relief, and other geographical features, creates significant ecological and geographical divergence.

This study examines helminth infections in the Kamchatka sable across these ten districts. The large spatial extent and distinct physical characteristics of each district enabled us to distinguish between their respective parasite communities.

Furthermore, until 1980, all sable specimens were tagged only with the administrative district of origin, not the specific collection site.

The eastern coastal districts, from South to North, are Ust-Bolsheretsky, Sobolevsky, Bystrinsky, and Tigilski (Fig. 1). In these areas, sables inhabit tundra and river floodplains. Further inland, they occupy birch forests and cedar-birch habitats. Bystrinsky District features a higher abundance of spruce, while areas further north are marked by birch-spruce mixed forests.

The western coastal districts include Yelizovsky, Ust-Kamchatsky, and Karaginsky Districts (Fig. 1). In Yelizovsky District, the primary habitats are extensive birch forests with cedar-birch areas. Sables in Ust-Kamchatsky District inhabit spruce forests ('spruce islands'), as well as mixed forests, and river floodplains. Further North in Karaginsky District, sables are found in tundra with sparse forests and in river floodplains.

Milkovsky District is located in the central part of the peninsula within the Kamchatka River Basin. Its habitats are the most diverse of all districts, encompassing river floodplains, birch forests, spruce-birch forests, and mixed spruce forests.

In the continental part of Kamchatka Krai, the Penzhinsky District supports sables in river floodplains and tundra within the Penzhina River Basin, on the flanks of the Koryaksky and Okhoto-Kolymsky Uplands. The other

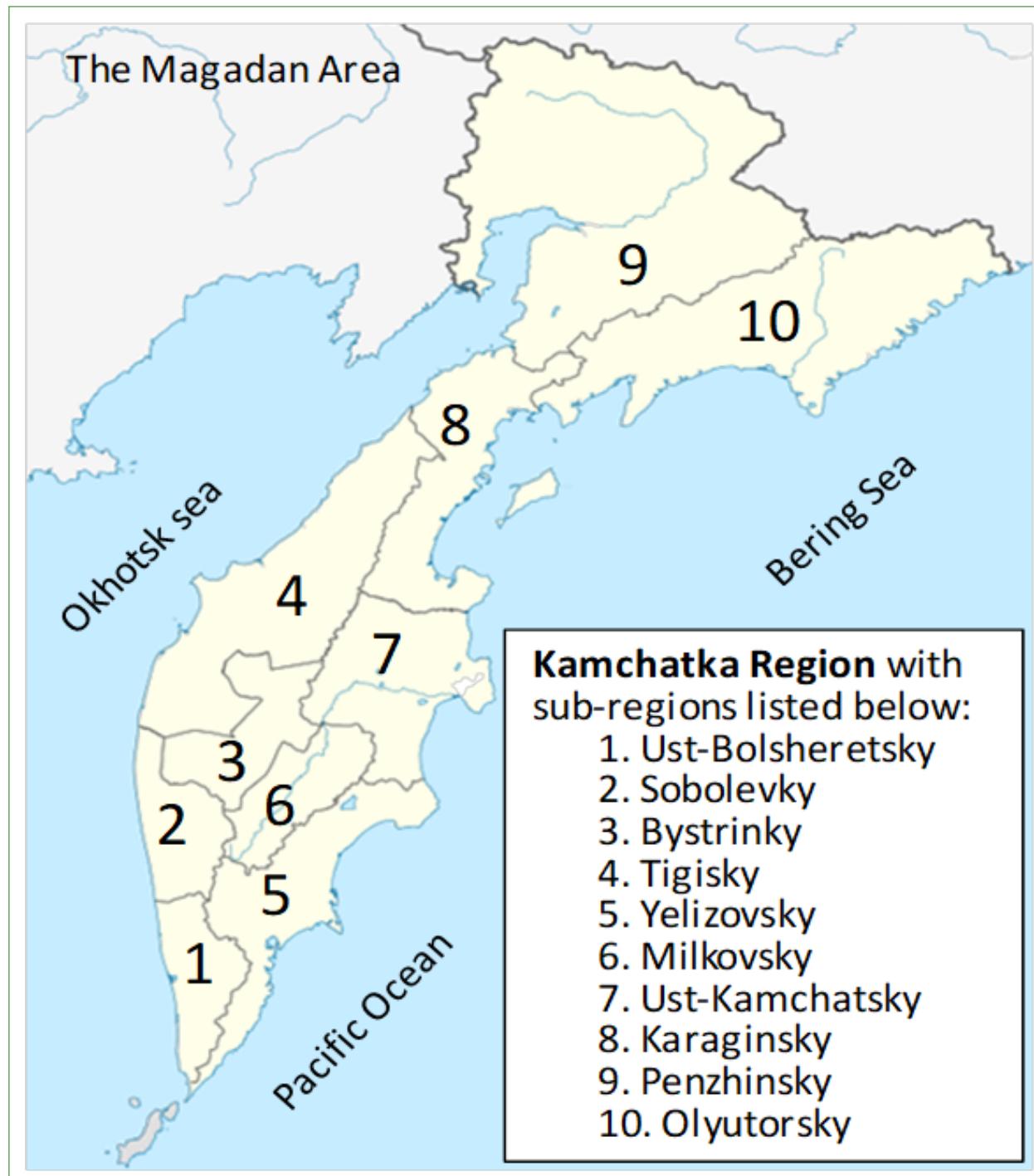


Fig. 1. Study area: Kamchatka Region with administrative districts drawn. Avtor Fig. 1 A. Ilgen, 2019

Рис. 1. Область исследования: Камчатский край с обозначенными административными районами. Автор рисунка 1 А. Илген

continental district, Olyutorsky, contains a small, isolated sable population in coastal forests. Only 13 specimens were examined from this region; given this small sample size, this population was excluded from our analysis of Specific Infestation Pressure (SIP).

Our long-term study of sable populations and helminths, initiated in 1952, involves

annual surveys of sables harvested during the winter hunting season from November to February. Until 1989, this research was conducted within the Kamchatka Branch of the All-Union Research Institute of Game Management and Fur Farming Named After B. M. Zhirkov. Since then, monitoring has continued under the Kamchatka Branch of

the Pacific Institute of Geography, Far Eastern Branch of the Russian Academy of Sciences. All results presented here are based on observations of helminth infections during the fall-winter season.

As helminth studies did not start simultaneously for all districts, the duration of monitoring and the number of studied specimens vary. A summary of all the study periods and the number of examined specimens up to 2022 is provided in Table 1.

Of the total number of specimens (13,901), the 13,601 were examined using the 'incomplete helminthological dissection' which involves the dissection of the intestines, stomach, esophagus, trachea, and lungs (Skryabin 1928; Ivashkin et al. 1971).

This method was selected after the 'complete helminthological dissection' of 300 specimens revealed helminths exclusively in

the trachea, lungs, stomach, and intestines, with no parasites found in other tissues and organs.

In a limited number of cases, however, additional organs were examined; specifically, the sinuses were investigated in 150 sable specimens.

For all specimens, data on sex, body fat condition (assessed on a 5-point scale), and age range were recorded. Age was categorized as 'juvenile', '1–2 years old', or 'older than 3 years', determined by the degree of skull suture fusion. For female sables, fertility was assessed by counting the number of mature corpora lutea in the ovaries.

To investigate the presence of *Trichinella nativa* larvae, diaphragmatic, hip, and tongue muscles from 1,814 sable specimens collected between 1980 and 1984 were examined. Tissues were digested in 0.5 % acid-pepsin solu-

Table 1
Duration of monitoring and number of sable carcasses examined in Kamchatka Krai from 1952 to 2022

Таблица 1

Продолжительность наблюдений и количество вскрытых тушек соболей в Камчатском крае с 1952 по 2022 г.

Administrative district	Monitoring period	Years of examination*	Number of sable carcasses
Kamchatka Peninsula			
<i>Western coast</i>			
Ust-Bolsheretsky	1966–2022	40	903
Sobolevsky	1959–2022	45	1,198
Bystrinsky	1956–2021	48	1,166
Tigilsky	1956–2022	57	2,303
<i>Central part of the peninsula</i>			
Milkovsky	1952–2022	65	3,708
<i>Eastern coast</i>			
Yelizovsky	1953–2020	59	2,720
Ust-Kamchatsky	1956–2020	44	1,081
Karaginsky	1975–1993	14	298
Continental part of Kamchatka Krai			
Penzhinsky	1956–2007	18	511
Olyutorsky	1969–1970 & 1984–1985	2	13
Summary			
Kamchatka Krai Coordinates: 51°07'–64°56' N, Area: 464,275 sq.m. (WIKIPEDIA)		Min – 2	Total: 13,901
		Max – 65	

*Number of years in which sable carcasses, harvested during the autumn-winter hunting seasons, were examined.

* Число лет вскрытых тушек соболей, добытых в осенне-зимние сезоны промысла.

tion for 24 hours and subsequently inspected under a microscope at 60x magnification using transmitted light. Archived data from 1,476 specimens from the Bystrinsky, Yelizovsky, and Milkovsky Districts were also reviewed. Larvae of other parasitic helminths were not targeted in this investigation.

The primary metric used was the prevalence rate (PR) of a given helminth species, defined as the percentage of infected individuals within the examined sample.

This study analyzes the long-term mean PR values of helminths across different districts of Kamchatka Krai for specific observation periods. This includes the proportion of the mean PR of individual helminth species constituting the Specific Infestation Pressure (SIP) in sables across different time periods from the start of observations in each of the nine studied administrative districts.

For each helminth, species identification was confirmed. The proportion of the mean PR values of helminths contributing to the SIP was compared across districts for given observation periods. Additionally, the overall prevalence rate (OPR) — the percentage of sables infected with any helminth — and the intensity of infestation (II) — the number of individual parasites of a specific helminth species in infected hosts — were quantitatively assessed.

To clarify the infestation rates of sables with rare helminth species, we analyzed the results of annual studies comprising at least 27 sable carcasses. The analysis of large commercial samples of sable carcasses, harvested annually during winter hunting seasons, provides statistically reliable data on the long-term variability of helminth infestations in this predator, including for relatively rare species (Akhmedov, Rojtman 1986).

Statistical analyses were performed using descriptive statistics in Microsoft Excel 2019.

Results and discussion

The helminth fauna of the Kamchatka sable comprises 20 species, of which 14 are specific to mustelids and 6 are non-specific. Among the specific helminths, 10–11 are considered

background species, being observed in sables more or less regularly. The remaining species are rare, very rare, or known only from literature records (Tranbenkova 2006). Depending on the species, background helminths are observed either annually or at intervals of one to two, or even four, years.

The initial discovery and development of a conceptual framework systematically describing the variability in the extent of helminth infestation in the Kamchatka sable across different geographical areas were established in 1993. We refer to this parasite-host dynamic as 'infestation pressure'. By that time, we had analyzed 10,053 sable specimens collected during hunting seasons from 1952 to 1992, identifying 11 common, or background, helminth species. Among these, two nematode species — *Crenosoma petrowi* Morosow, 1939 and *C. vulpis* (Dujardin, 1874) Railliet, 1915 — are considered within the SIP as a single genus, *Crenosoma* (Tranbenkova 1996; 2006). Consequently, when listing the helminth species constituting the SIP, we indicate 10 taxonomic units.

The Specific Infestation Pressure (SIP) is a systematic grouping of these 11 background helminth species, defined by their prevalence rate (PR = percentage of infected individuals in the studied sample). Published work up to 1980 identified 13 parasitic helminth species in the Kamchatka sable (Kontrimavichus 1969). In addition to these, we have documented a further 7 helminth species that are non-specific to sables (Tranbenkova 1996; 2006).

We selected the 11 most common species reliably identified in the Kamchatka sable for inclusion in the SIP system. Of these, five are specific to Mustelidae, another five are specific to Canidae, Ursidae, and Felidae, and one is specific to marine mammals. Based on their PR and frequency of occurrence, we categorized these 11 species into three groups: 'mass', 'common', and 'conditionally rare', as detailed in Table 2.

Table 2 presents the list of background helminths in sables and illustrates the heterogeneity of their prevalence rates across different administrative districts of Kamchatka Krai.

Table 2
Minimum and maximum Mean Prevalence Rate (PR) of background helminth species in sables across different districts of Kamchatka Krai based on monitoring data from 1952 to 2022

Таблица 2
Минимальная и максимальная средняя ЭИ фоновых видов гельминтов у соболей в разных районах Камчатского края по материалам мониторинга с 1952 по 2022 г.

Helminth species (location in host)	Mean PR (%)			
	Max M±m%	Administrative districts	Min M±m%	Administrative districts
Mass species				
<i>Soboliphyme baturini</i> Petrow, 1930; (stomach)	70.28 ± 3.59	Ust-Bolsheretsky	0.9 ± 0.55	Karaginsky
<i>Baylisascaris devosi</i> Sprent, 1968; (intestine)	28.19 ± 4.35 28.71 ± 1.67	Karaginsky Milkovsky	0.89 ± 0.31	Ust-Bolsheretsky
Common species				
<i>Taenia martis</i> (Zeder, 1803) Freeman, 1956; (intestine)	18.66 ± 2.55	Sobolevsky	7.69 ± 3.19	Karaginsky
<i>Thominx aerophilus</i> (Creplin, 1839) Skrjabin et Schikhobalova, 1954; (trachea, lungs)	17.74 ± 1.77	Milkovsky	0.54 ± 0.38	Penzhinsky
<i>Genus Crenosoma</i> Molin, 1861*; (trachea, lungs)	13.21 ± 1.89	Yelizovsky	5.59 ± 2.0	Penzhinsky
Conditionally rare species				
<i>Mesocestoides kirbyi</i> Chandler, 1944; (intestine)	2.82 ± 1.1	Ust-Bolsheretsky	0.66 ± 0.47	Karaginsky
<i>Filaroides martis</i> (Werner, 1782); (lungs)	4.67 ± 1.22	Bystrinsky	0.52 ± 0.38	Penzhinsky
<i>Anisakis simplex</i> Dujardin, 1845; (larvae)**; (stomach, intestine)	3.81 ± 0.83	Sobolevsky	0.27 ± 0.19	Ust-Kamchatsky
<i>Capillaria putorii</i> (Rudolphi, 1819) Travassos, 1915***; (stomach)	2.52 ± 1.42	Ust-Kamchatsky	0.15 ± 0.11	Yelizovsky
<i>Trichinella nativa</i> Britov et Boev, 1972 (larvae)***; (diaphragm, tongue muscles, etc.)	6.53	Karaginsky	0.38	Ust-Bolsheretsky

* The sable in Kamchatka is recorded as a host for two species — *Crenosoma petrowi* Morosow, 1939 and *C. vulpis* (Dujardin, 1874) Railliet, 1915 (Kontrimavichus 1969; Kozlov 1977). In dissection records up to 1992, only the genus name *Crenosoma* was used (Tranbenkova 1996; 2003).

** *A. simplex* larvae enter the gastrointestinal tract of sables with local salmonid species. Their remains were found in autumn and winter in 4.6–32.3 % of animals on the peninsula, and in spring and summer in nearly 10.0 %. In Penzhinsky District, the figure was 2.1 % (Belov 1977; Valentsev 1982). Gaps in its detection can last 1–3 years, and rarely longer.

*** Detection gaps may exceed three years.

* - Соболь на Камчатке указан в числе хозяев двух видов - *C. petrowi* Morosow, 1939 и *C. vulpis* (Dujardin, 1874) Railliet, 1915 (Козлов 1977; Контимавичюс 1969). В журналах вскрытий до 1992 г. использовалось только название рода *Crenosoma* (Транбенкова 1996; 2003).

** - *A. simplex* larvae попадает в желудочно-кишечный тракт соболей с местными видами лососевых. Их остатки найдены осенью и зимой у 4,6 - 32,3 %, а весной и летом почти у 10,0 % зверьков на территории полуострова. В Пенжинском районе у 2,1 % (Белов 1977; Валенцев 1982). Перерывы в ее обнаружении могут составлять 1-3 года и редко больше.

*** - Возможны перерывы в обнаружении более 3 лет.

Mass species of helminths are observed in sables annually and often exhibit high II. Individual animals can harbor tens to hundreds of specimens. Gaps in detection rarely exceed one year. Their mean PR varies from 0.5 % to 70–80 %, depending on the administrative district.

Common species infect the predator regularly but not necessarily intensively. Their mean long-term PR does not exceed 25 %, and the mean II is typically no more than five specimens. Detection intervals range from one to three years, though they are often found annually.

Conditionally rare helminth species are not observed in sables every year, with detection gaps reaching four years or more. The mean PR of conditionally rare helminths is consistently below 4 %, and II is substantially less than one. A conditionally rare, non-specific species for mustelids is the immature larval nematode *A. Simplex* Dujardin, 1845, a parasite of marine mammals that is occasionally found in sables in some areas.

The number of helminth species and the II decrease at higher latitudes. In the southern and central parts of the Kamchatka Peninsula, we found 11 common species; in northern areas, 10 species; and in the northernmost Penzhinsky District, only 8 species. The OPR in southern areas is twice that of the northern peninsula and three times higher than in Penzhinsky District (Tranbenkova 2006). For example, by 2022, the OPR of sables was 65.39 % in Milkovsky District (central peninsula) compared to 23.11 % in Penzhinsky District.

Systematic longitudinal gradients in helminth prevalence are also evident, even where the maximum distance between hunting lands in southern Kamchatka is approximately 200 km or less. In the south, the OPR with all helminths by 2022 was 80.76 % on the western coast (Ust-Bolsheretsky District) and 76.52 % in Sobolevsky District, compared to 68.14 % on the eastern coast (Yelizovsky District). Longitudinal differences are less pronounced in the north, with the OPR of 46.31 % in the western coastal Tigilsky District versus 43.66 % in the eastern Karaginsky District.

As previously described, the term ‘infestation pressure’ (introduced in 1992) refers to a unique set of prevalence rates for common parasitic helminth species. This set, specifically the ratio of infestation intensities among different helminth species, remains constant and unique for each administrative region of Kamchatka (Tranbenkova 1996; 2000; 2016). We later renamed this stable system ‘Specific Infestation Pressure’ (SIP) to distinguish it from the more general use of ‘infestation pressure’, which often refers to the negative physiological, growth, and reproductive impacts of helminths on their hosts.

We define the structure of SIP by: (1) the assemblage of helminth species found in each district; (2) the prevalence rate for each species; and (3) the ratios of infestation intensities. This paper demonstrates that while SIP varies dynamically in space and time, its core structure remains constant.

In our opinion, the SIP structure is a ranked list of background helminths (mass, common, and conditionally rare) by their absolute mean PR values. Its stability is defined by the complete or near-complete invariance in the sequence of PR values for the mass and common helminth species that act as dominants and subdominants within the SIP. The role of associated species with low PR values is negligible for individualizing the SIP and is not considered here.

Since 1992, we have proposed several revisions to the description of these parasite-host systems and the SIP (Tranbenkova 2000; 2006). The main characteristics of SIP were formulated in 2010 based on the monitoring of helminth infestations in 12,619 sable carcasses (Tranbenkova 2014). Subsequent analyses of data from 1952 to 2015 and 2017 led to revisions and additions, including information on its structural persistence over time (Tranbenkova 2018). A comparison of SIP across administrative districts for 11-year cycles up to 2017 confirmed an absolutely stable spatio-temporal structure in most western coastal districts, a less pronounced stability on the eastern coast, and a very weak expression in the northern Karaginsky and Penzhinsky

Ust-Bolsheretsky, 1966- 2022 SIP MD-S-h-(a)

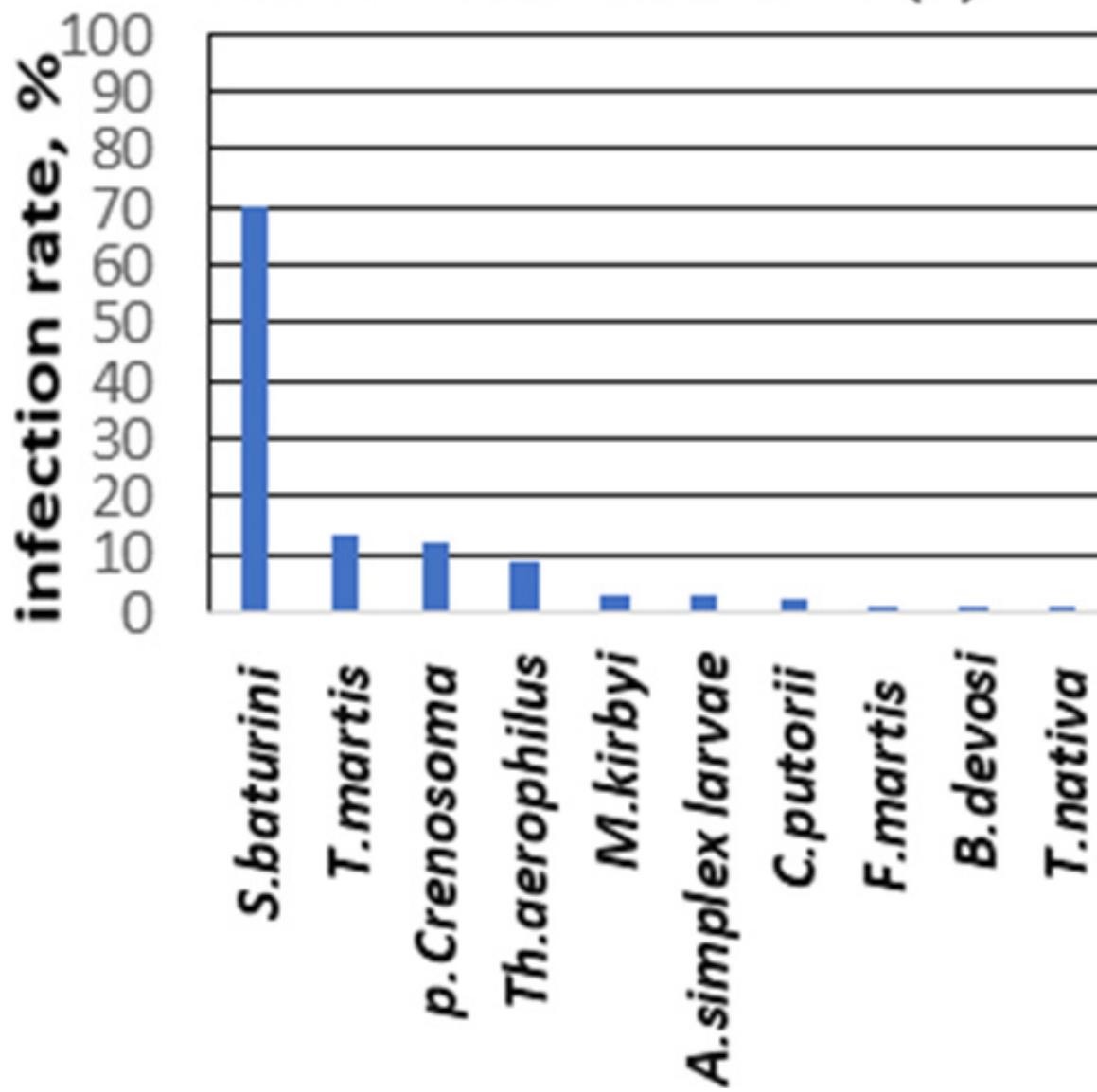


Fig. 2. Diagram of SIP. Type I Monodominant (MD), Subtype — MD-S-h Variant MD-S-h-(a), Ust-Bolsheretsky district

Рис. 2. Диаграмма СИП. Тип I Монодоминант (MD), Подтип — MD-S-h Вариант MD-S-h-(a), Усть-Большерецкий район

Districts (Tranbenkova 2018). These 11-year cycles correspond to documented 'large' cycles in Kamchatka sable population dynamics (Vershinin, Belov 1973; Valentsev, Fil 2012). In 2022, analysis of 13,888 sable carcasses further clarified SIP characteristics and provided new evidence of its stability.

We classify the main SIP types by the number of dominant helminth species pres-

ent. A 'Monodominant' (MD) type has one dominant species, a 'Bi-dominant' (BD) type has two, and a 'No Dominant' (ND) type has none. A transitional 'Passing' (P) type falls between dominant and non-dominant states. The SIP name includes a letter from the dominant species (e.g., 'S' for *Soboliphyme baturini* Petrow, 1930), followed by a code for its quantitative structure: 'h' for homogeneous

Sobolevsky, 1959-2022 SIP MD-S-h-(b)

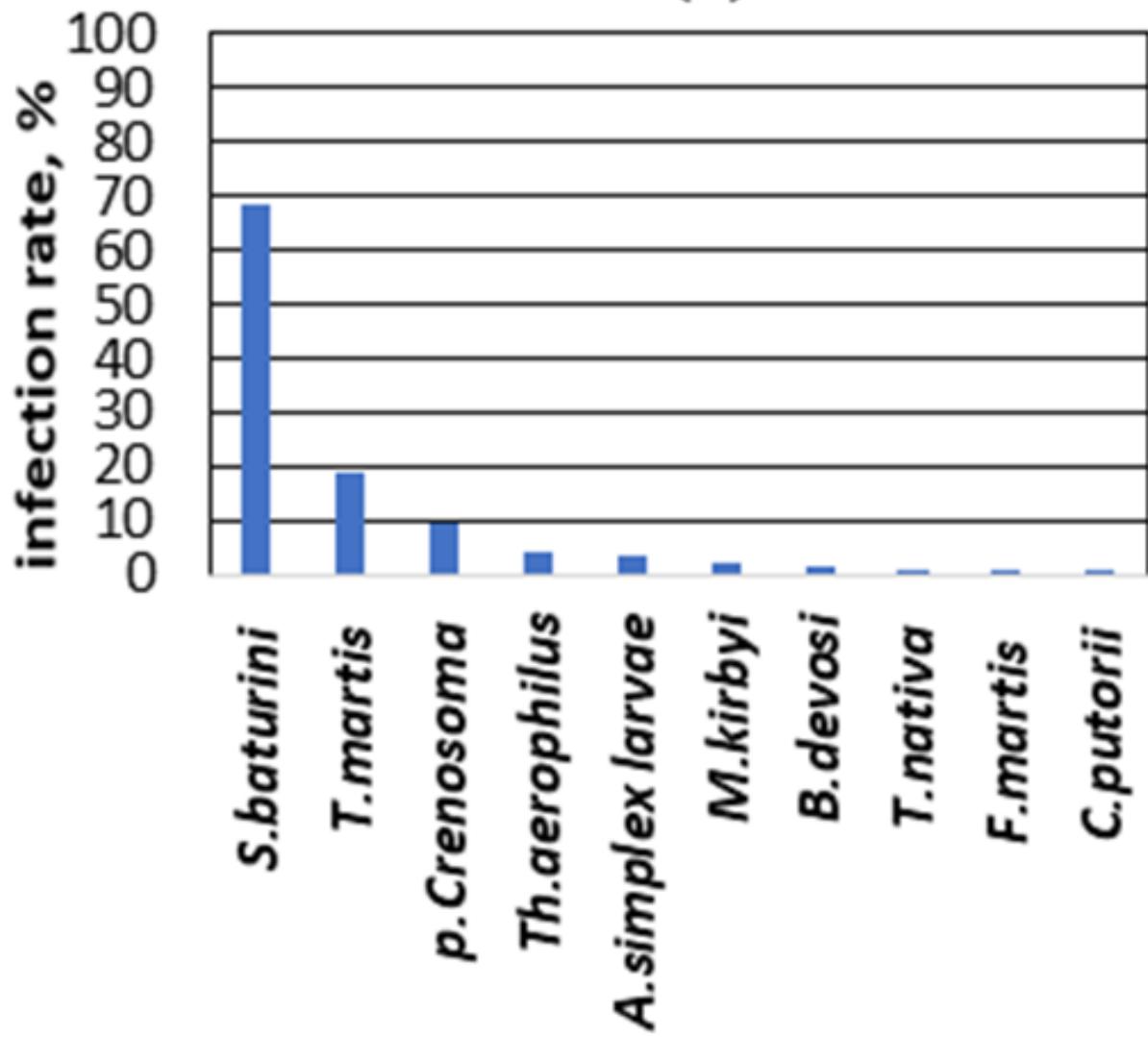


Fig. 3. Diagram of SIP. Type I Monodominant (MD), *Subtype* — MD-S-h Variant MD-S-h-(b), Sobolevsky district

Рис. 3. Диаграмма СИП. Тип I Монодоминант (MD), *Подтип* — MD-S-h Вариант MD-S-h-(b), Соболевский район

(where $\geq 74\%$ of parasites are from one dominant and one subdominant species) and 'hh' for heterogeneous (where the combined PR of the dominant and primary subdominant is $< 72\%$, typically with four subdominant species). A variant indicator in parentheses (a-i) corresponds to the surveyed areas where each SIP variant was found.

When describing the SIP structure, subdominant species are listed in descending order of their PR value. Consequently, all SIP

types, subtypes, and variants are distinguished by the PR values of dominants and subdominants and their descending order. The four main SIP types we have identified — Monodominant (MD), Bi-dominant (BD), Passing (P), and No Dominant (ND) — are represented across nine districts by four distinct subtypes with nine variants. These include three MD subtypes with five variants, two P subtypes with one variant each, and one variant each for the BD and ND types. Due to differences in the

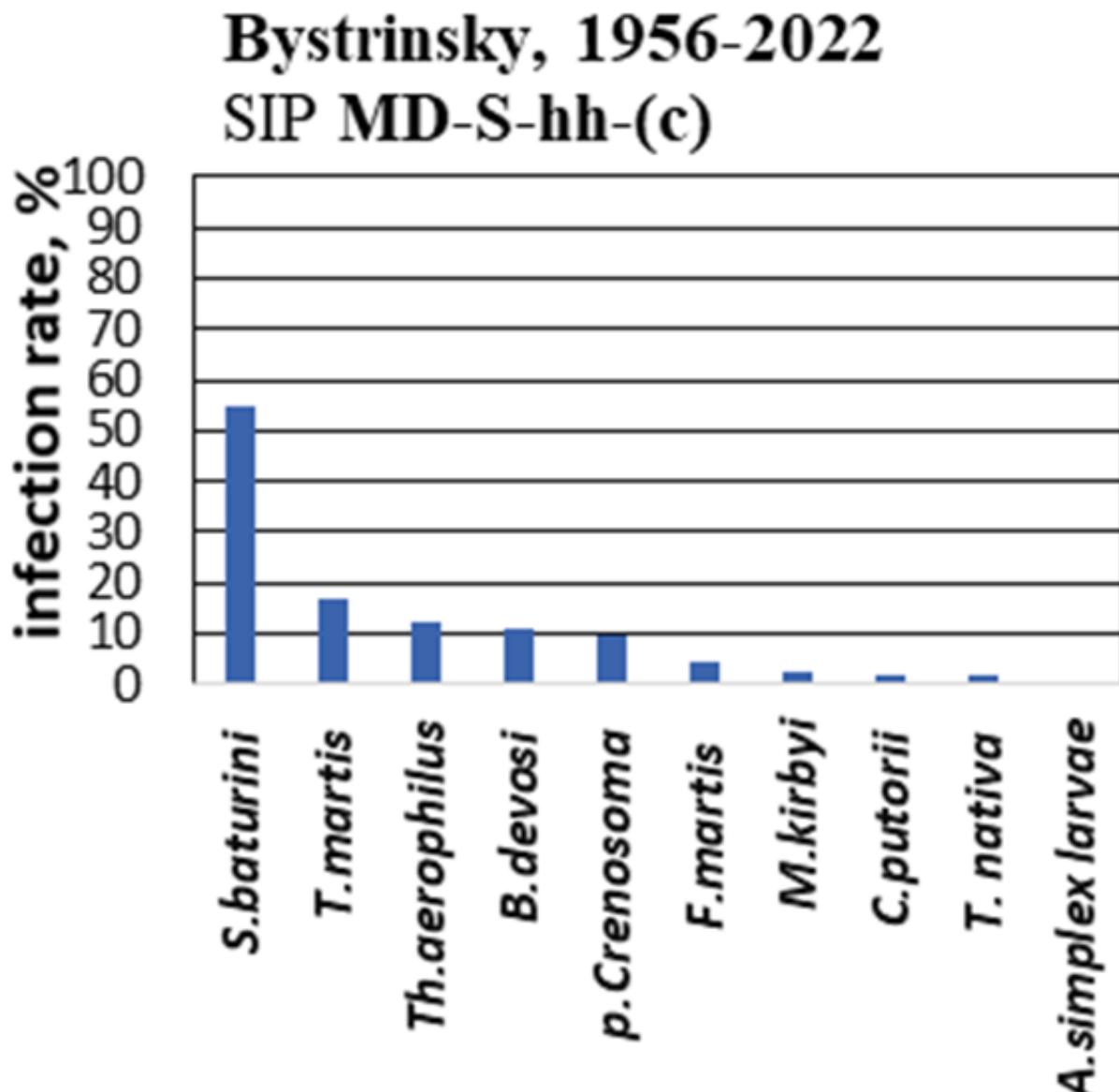


Fig. 4. Diagram of SIP. Type I Monodominant (MD), *Subtype* — MD-S-hh Variant MD-S-hh-(c), Bistrinsky district

Рис. 4. Диаграмма СИП. Тип I Монодоминант (MD), *Подтип* — MD-S-hh Вариант MD-S-hh-(c), Быстринский район

PR of dominant and subdominant helminths, the SIP structure is unique to each district.

A list of the nine SIP variants follows, with descriptions and the ranges of mean PR values for 1980, 1992, 2002, 2015, 2018, and 2022. These periods were selected to assess how the documented increase in sable infestation by certain helminths since the late 20th century has influenced their mean PR values and, consequently, the structural proportions that define the SIP.

Type I — Monodominant (MD)

This type is characterized by the presence of a single dominant species from the 'mass'

category, typically, *S. baturini* and, in one case, *B. devosi*. The PR of sables with the dominant type of helminth is 2 to 9 times higher than with subdominants. We define five variants within three subtypes of the monodominant SIP.

Subtype 1 — MD-S-h. A homogeneous subtype with one dominant species, *S. baturini*. Two variants of this subtype are found in the southern part of the western coast of the Kamchatka Peninsula (Ust-Bolsheretsky and Sobolevsky Districts).

1. MD-S-h-(a). For this SIP variant, the PR of the dominant species *S. baturini* ranges

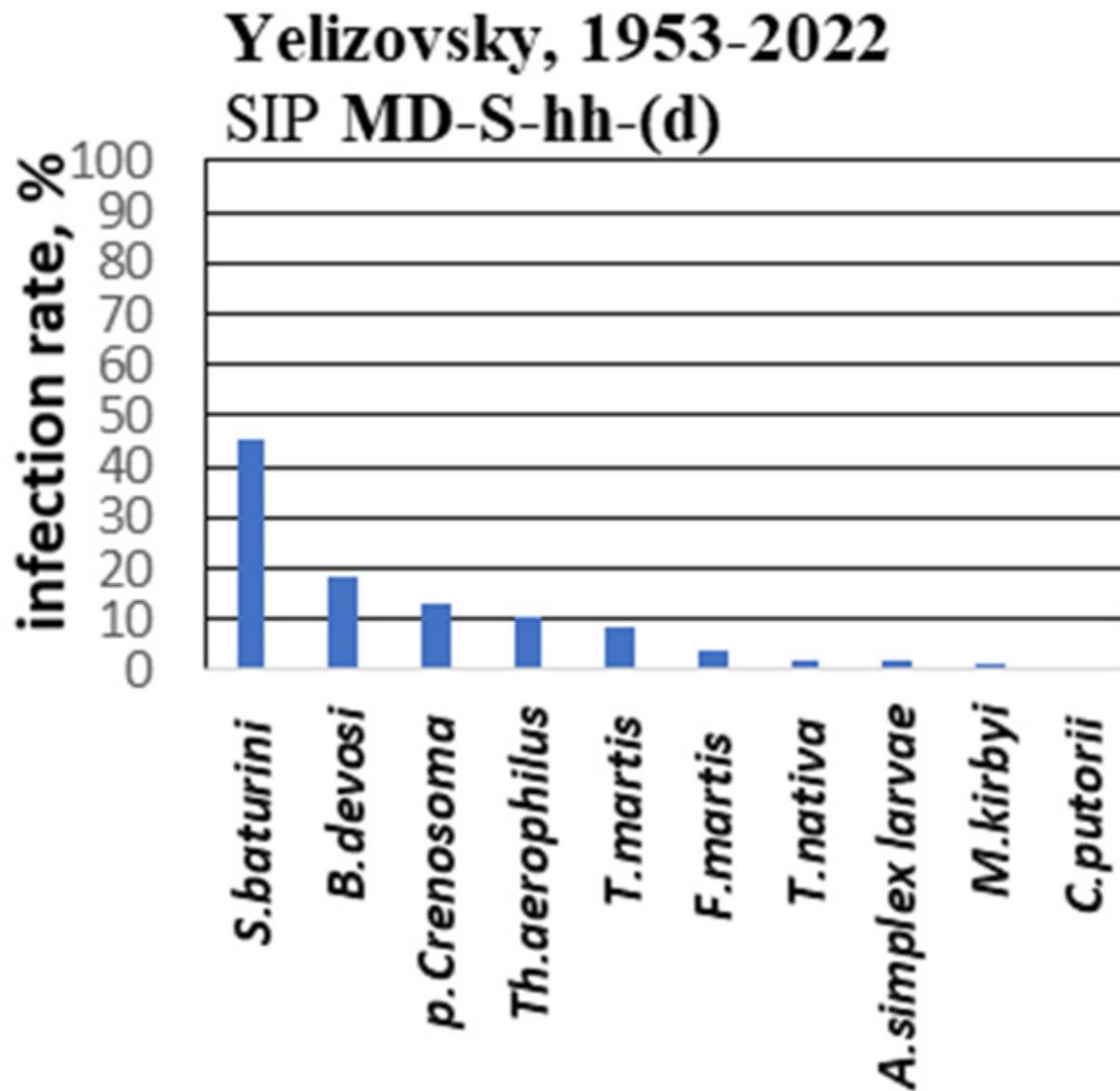


Fig. 5. Diagram of SIP. Type I Monodominant (MD), *Subtype* — MD-S-hh Variant MD-S-hh-(d), Yelizovsky district

Рис. 5. Диаграмма СИП. Тип I Монодоминант (MD), *Подтип* — MD-S-hh Вариант MD-S-hh-(d), Елизовский район

from 52.81 to 70.28 %. Its PR is 2.42 to 5.74 times higher than the maximum PR observed for sub-dominant helminth species. Three subdominant helminth species were identified in the Ust-Bolsheretsky District (Fig. 2). These are common sable parasites, with the genus *Crenosoma* having the highest PR values, followed in descending order by *T. martis* and *Th. Aerophilus*.

2. MD-S-h-(b). For this SIP variant, the PR of the dominant species *S. baturini* ranges from 58.7 to 68.25 %. Two subdominant species of helminth were identified in the Sobo-

levsky District (Fig. 3). The mean PR values of *S. baturini* is 3.67 to 6.99 times higher than those for the subdominant species.

Subtype 2 — MD-S-hh. A heterogeneous subtype with the dominant species *S. baturini*. The PR of the dominant is less than 55 %, and four subdominant helminth species are present: *T. martis*, g. *Crenosoma*, *Th. Aerophilus*, and *B. devosi*.

This subtype is divided into two variants: found in the middle part of the Central Ridge and the southern part of the eastern coast, respectively (Bystrinsky and Yelizovsky Districts).

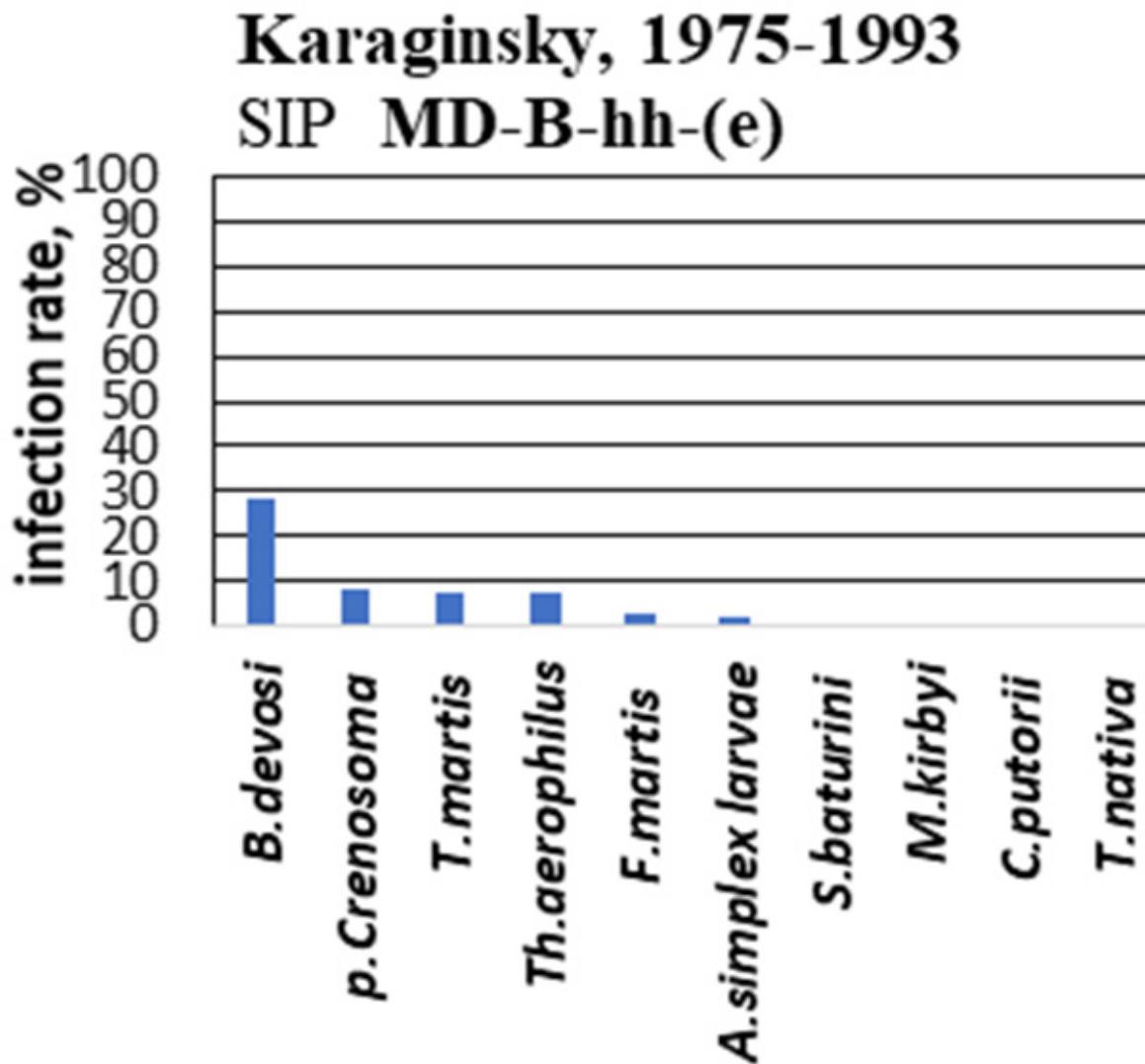


Fig. 6. Diagram of SIP. Type I Monodominant (MD), *Subtype* — MD-B-hh Variant MD-B-hh-(e), Karaginsky district

Рис. 6. Диаграмма СИП. Тип I Монодоминант (MD), *Подтип* — MD-B-hh Вариант MD-B-hh-(e), Карагинский район

3. MD-S-hh-(c). For this SIP variant, the PR value for *S. baturini* is from 47.46 % to 54.63 %. Its PR is 3.28 to 6.54 times higher than the maximum PR observed for sub-dominant helminth species (Bystrinsky District) (Fig. 4).

4. MD-S-hh-(d). The PR for *S. baturini* ranges from 40.91 % to 45.20 %. Its PR is 2.18 to 7.53 times higher than that of the subdominant species (Yelizovsky District).

Both variants share the same four subdominants: three common (*T. martis*, g. *Crenosoma*, *Th. Aerophilus*) and one mass species *B. devosi*. In the Bystrinsky District (western coast), the PR of the subdominant *B. devosi* is the lowest among the other subdominants.

In Yelizovsky District (southern east coast), the PR of the subdominant *B. devosi* is almost equal to that of the other key subdominants of genus *Crenosoma* (Fig. 5).

Subtype 3 — MD-B-hh. A heterogeneous version with the dominant nematode *B. devosi*.

5. MD-B-hh-(e). A single variant with a PR of *B. devosi* at 28.19 %, which is 3.31 to 3.8 times higher than PR for the subdominant helminth species. There are three types of subdominants, similar to SIP MD-S-h-(a). However, their PR values are significantly lower than in all four previous monodominant SIP variants (Fig. 6). This variant was found in the

Milkovsky, 1952-2022 SIP BD-SB-hh-(f)

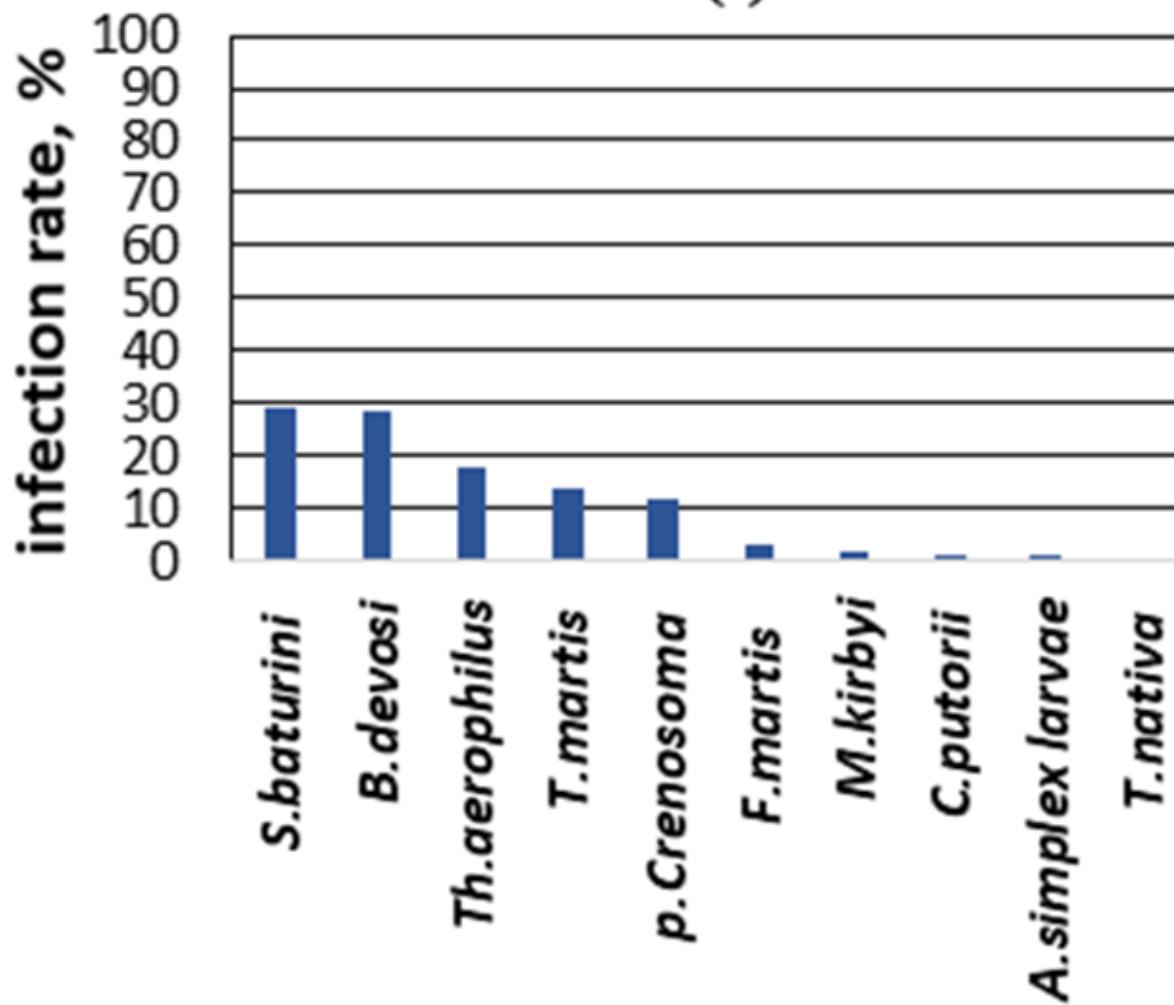


Fig. 7. Diagram of SIP. Type II Bi-dominant (BD) Variant BD-SB-hh-(f), Milkovsky district

Рис. 7. Диаграмма СИП. Тип II Бидоминант (BD) Вариант BD-SB-hh-(f), Мильковский район

north-eastern part of the Kamchatka Peninsula (Karaginsky District).

Type II — Bi-dominant (BD-SB-hh)

A heterogeneous type with two co-dominant species, *S. baturini* and *B. devosi*. The mean PR for each is below 33 %. Three subdominant parasitic nematode species are present, with the highest PR values for *Th. aerophilus*, followed by *g. Crenosoma* and *T. martis*. This type is found in the central part of the Kamchatka Peninsula (Milkovsky District) and is represented by a single variant.

6. BD-SB-hh-(f). A single variant. The PR for *S. baturini* is from 26.12 to 32.92 %, which

is 1.65 to 3.5 times higher than that for the subdominant species. The PR for *B. devosi* ranges from 26.31 % to 28.71, which is 1.62 to 3.05 times higher than that of the subdominant species (Fig. 7).

Type III — Passing (P-hh)

A heterogeneous type with one dominant species, where the mean long-term PR value for the dominant is less than 25 %. This SIP type is found in two subregions: the northern part of western coast (Tigilsky District), with *S. baturini* as the dominant (*Subtype — P-S-hh*), and the continental part of Kamchatka Krai (Penzhinsky District), with the cestode *T. mar-*

Tigilsky, 1956-2022

SIP P-S-hh-(g)

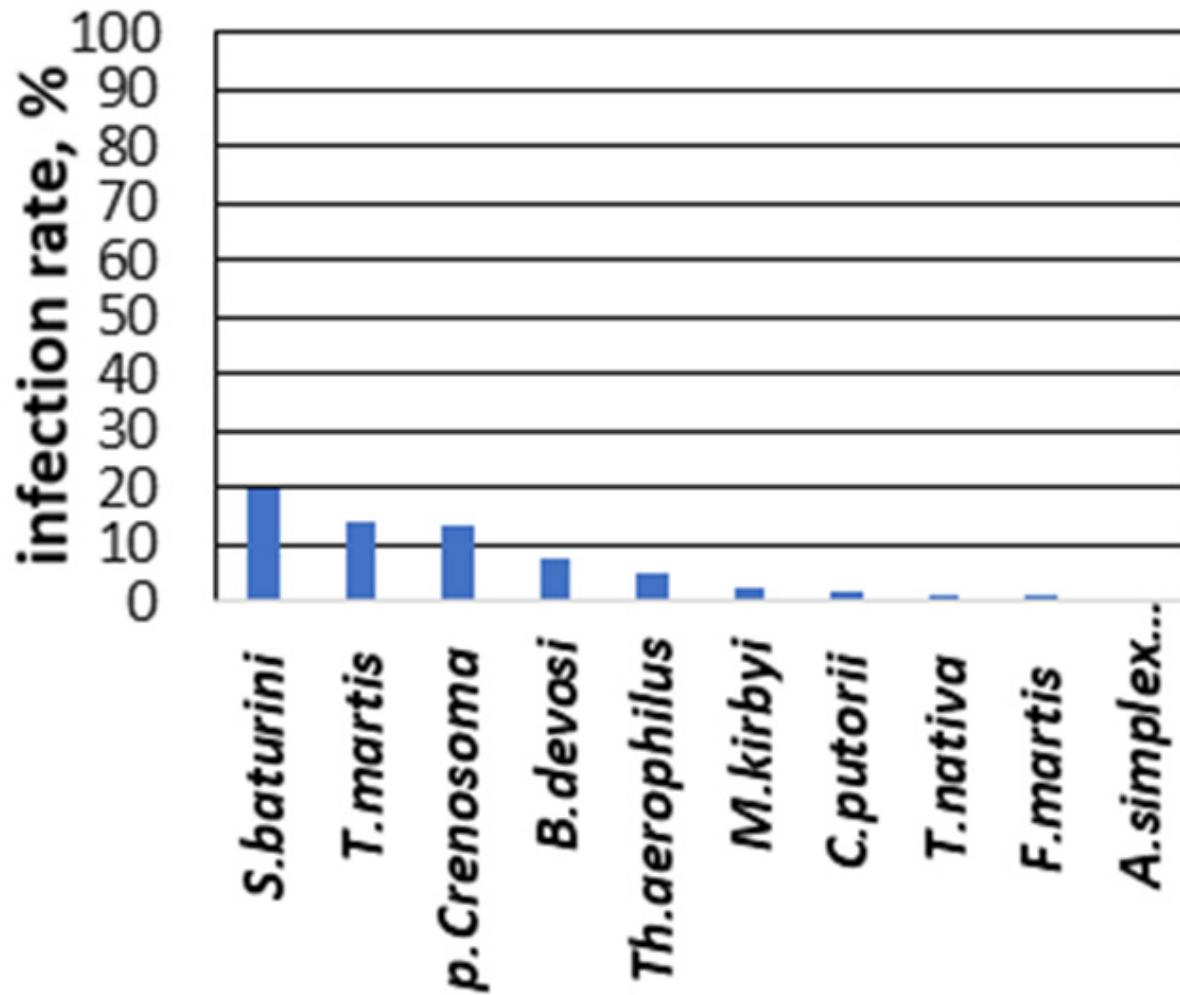


Fig. 8. Diagram of SIP. Type III Passing (P-hh), *Subtype* — P-S-hh Variant P-S-hh-(g), Tigilsky district

Рис. 8. Диаграмма СИП. Тип III Переходный (P-hh), *Подтип* — P-S-hh Вариант P-S-hh-(g), Тигильский район

is as the dominant (*Subtype* — **P-T-hh**). Each subtype is represented by one variant.

7. (**P-S-hh-(g)**). The PR for *S. baturini* ranges from 19.71 to 22.58 %, with four subdominant helminth species. The PR of the dominant species is 1.2 to 1.56 times higher than that of the subdominant species (Tigilsky District) (Fig. 8).

Subtype — **P-T-hh**. That subtype is also represented by a single variant.

8. **P-T-hh-(h)**. The PR for *T. martis* is from 1.57 to 12.95 %, with two subdominant hel-

minth species present: *g. Crenosoma* and *B. devosi*. The PR value of the dominant species is 2.0 times higher than that of the subdominant species (Penzhinsky District) (Fig. 9).

Type IV — No Dominant (ND-hh)

A heterogeneous type with no dominant species, found in the central part of the eastern coast of the Kamchatka peninsula (Ust-Kamchatsky District). This type is represented by a single variant.

9. **ND-hh-(i)**. Five subdominant helminth species are present. PR values for the sub-

Penzhinsky, 1956-1996 SIP P-T-hh-(h)

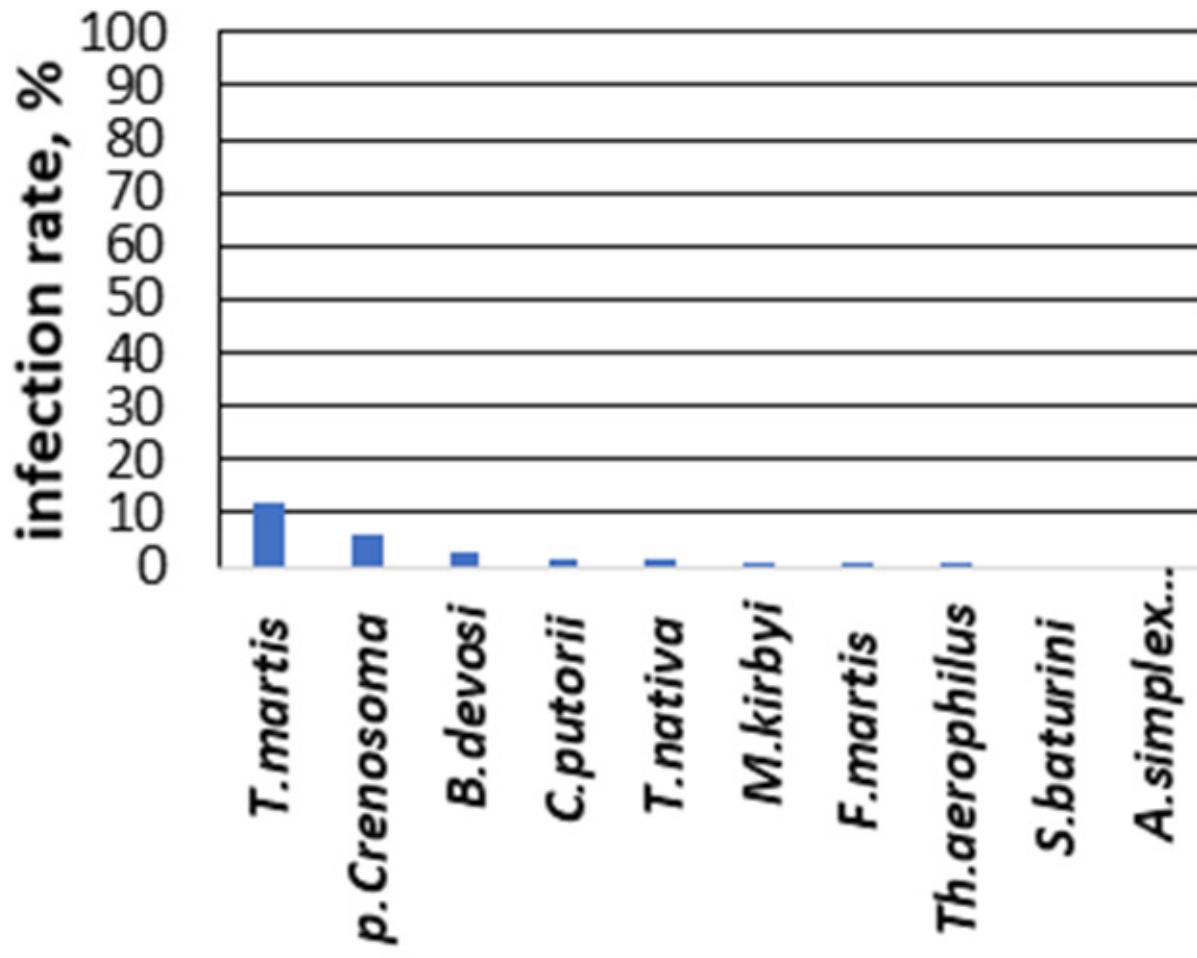


Fig. 9. Diagram of SIP. Type III Passing (P-hh), *Subtype* — P-T-hh Variant P-T-hh-(h), Penzhinsky district

Рис. 9. Диаграмма СИП. Тип III Переходный (P-hh), *Подтип* — P-T-hh Вариант P-T-hh-(h), Пенжинский район

dominant helminth species are 2.99 to 9.69 higher than those for the associated species (Ust-Kamchatsky District) (Fig. 10).

As evidenced by the description of the SIP across different regions of Kamchatka Krai, the primary components of its composition are the mass and common helminth species. The dominant role in seven of the nine SIP variants is played by the mass species *S. baturini* and *B. devosi*, and in only one variant by the common species *T. martis*.

Subdominants in the SIP are consistently common species across all variants, although

in some areas, mass species also appear as subdominants (e.g., *B. devosi* in the mono-dominant heterogeneous subtype MD-S-hh). Depending on the geographic coordinates, mass species may even be relegated to the status of associated species, as observed for *S. baturini* in the north-eastern Karaginsky District.

These characteristics of the SIP are largely determined by systematic variability in the prevalence rates of the two dominant helminth species, *S. baturini* and *B. devosi*, along a south-west to north-east gradient across the

Ust-Kamchatsky, 1956-2022

SIP ND-hh-(i)

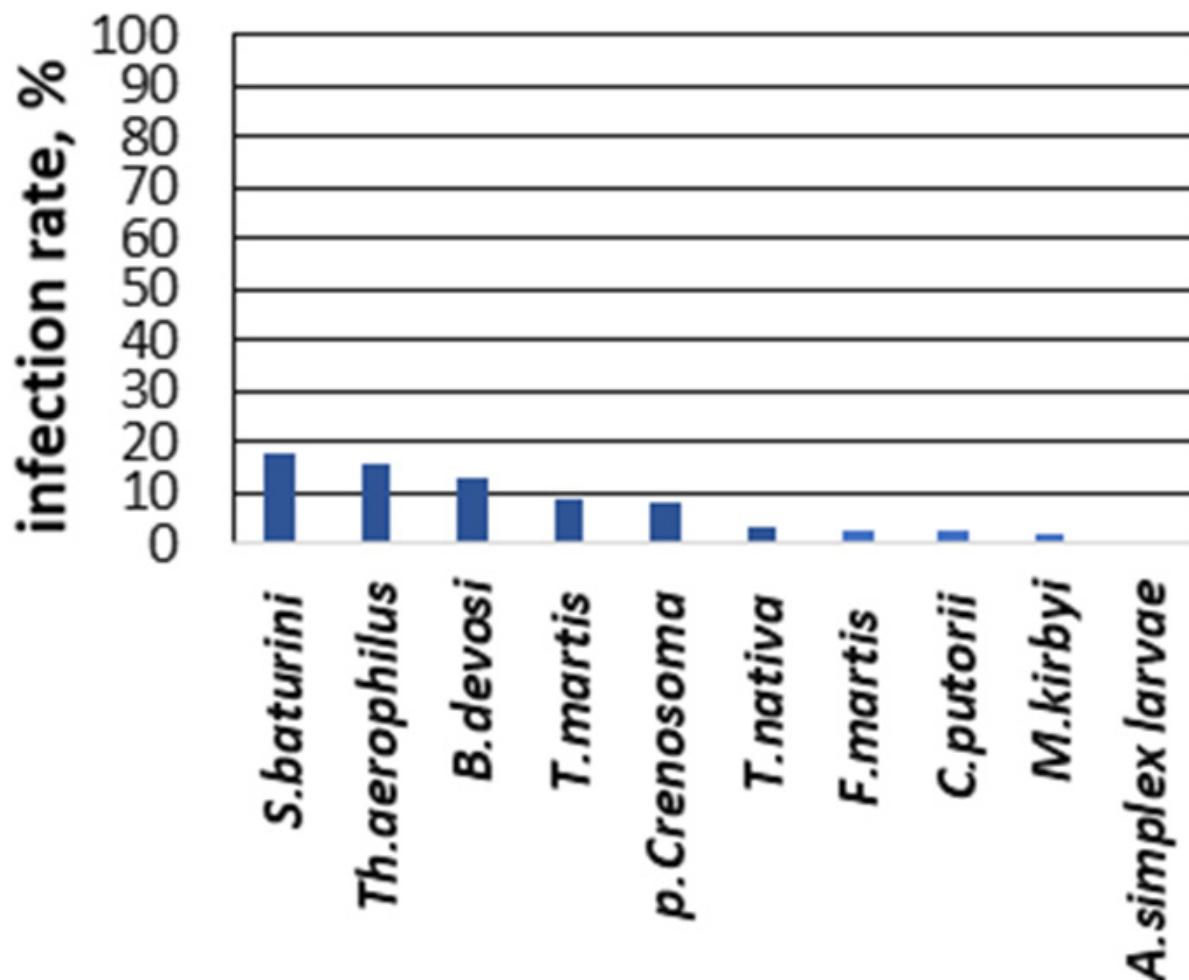


Fig. 10. Diagram of SIP. Type IV No dominants (ND-hh) Variant ND-hh-(i), Ust-Kamchatsky district

Рис. 10. Диаграмма СИП. Тип IV Нет доминанта (ND-hh) Вариант ND-hh-(i), Усть-Камчатский район

Kamchatka Peninsula — from Ust-Bolsheretsky and Sobolevsky Districts to Karaginsky. The maximum and minimum PR for *S. baturini* is higher on the western coast compared to equivalent latitudes on the eastern coast and decreases towards the north (Table 3).

This table, which demonstrates the differences in PR values for the mass species *S. baturini* and *B. devosi* between the western and eastern coasts, illustrates the geographical determinism of their dominance within the SIP. The nematode *S. baturini* is the sole dominant species in the SIP for sables in three districts

on the southern and central western coast — Ust-Bolsheretsky (Table 4, SIP MD-S-h-(a)), Sobolevsky (Table 5, SIP MD-S-h-(b)), and Bystrinsky (Table 6, SIP MD-S-hh-(c)) — and in one district on the southern east coast, Yelizovsky (Table 7, SIP MD-S-hh-(d)).

At the north of the east coast (Tigilsky District), the PR for this nematode decreases, and its dominance becomes 'conditional' (Table 8).

In the central part of the Kamchatka Peninsula (Milkovsky District), *S. baturini* is one of two co-dominant nematode species, the second being *B. devosi* (Table 9).

Table 3

Summary data on the Overall Prevalence Rate (OPR%) of sables with helminths and the proportion (%) contributed by the mass nematode species *S. baturini* and *B. devosi* in the northern and southern parts of both coasts of the Kamchatka Peninsula from 1953 to 2022

Таблица 3

Сводные данные показателей суммарной зараженности (ОИ%) соболей гельминтами и доли (%) в ее составе массовых видов нематод *S. baturini* и *B. devosi* на севере и юге обоих побережий полуострова Камчатка в период с 1953 по 2022 г.

Geographical location, district name	<i>S. baturini</i>		<i>B. devosi</i>	
	Mean long-term PR%	Proportion (%) of total helminths	Mean long-term PR%	Proportion (%) of total helminths
	M±m		M±m	
<i>Western coast</i>				
Southern part, Ust-Bolsheretsky	70.28 ± 3.59	86.18 ± 2.94	0.89 ± 0.31	1.21 ± 0.44
Northern part, Tigilsky	19.71 ± 2.73	34.41 ± 3.98	7.77 ± 1.29	16.33 ± 2.63
<i>Eastern coast</i>				
Southern part, Yelizovsky	45.20 ± 3.42	62.32 ± 3.82	18.63 ± 2.46	26.66 ± 3.31
Northern part, Karaginsky	0.79 ± 0.55	1.40 ± 0.95	28.19 ± 4.35	61.56 ± 7.25

The other nematode, *B. devosi*, is the dominant species in the north-eastern part of the Kamchatka Peninsula (Karaginsky District) (Table 10).

As previously indicated, a comparison of sable helminth infestations across districts at 11-year intervals until 2017 demonstrated that the SIP possesses a notably stable spatio-temporal structure (Tranbenkova 2018). The stability of the SIP variants was categorized as follows:

1. Maximum stable. The homogeneous monodominant variants **MD-S-h-(a)** and **MD-S-h-(b)** on the southern western coast.

2. Quite stable. The heterogeneous monodominant variants **MD-S-hh-(c)**, **MD-S-hh-(d)**, the **MD-B-hh-(e)** subtype, and the bi-dominant type **BD-SB-hh-(f)** from the central western coast, southern and northern eastern coast, and central peninsula.

3. Relatively stable. The transitional type variants **P-S-hh-(g)** (Tigilsky District), **P-T-hh-(h)** (Penzhinsky District) (Table 11), and the no-dominant type **ND-hh-(i)** (Ust-Kamchatsky District) (Table 12) from the northern and central eastern coast and the northern continental part of the region (Penzhinsky District).

The stability is demonstrated by the proportions of PR values for dominant and subdominant helminths in the SIP across the nine districts from the start of observations through 1980, 1992, 2002, 2015, 2018, and 2022 (Tables 4–12). Shorter intervals were chosen after 2015 due to a relatively rapid increase in helminth infestation rates in some areas in recent years, which could potentially alter the PR proportions and thus the SIP structure.

In all tables, the sum of PR values for each helminth species serves as an indicator of structural constancy, making the quantitative distinctions between dominants, subdominants, and associated species clearly visible. For instance, the proportions of PR values for the three subdominants in the Ust-Bolsheretsky District (SIP **MD-S-h-(a)**) has remained nearly constant across all observed periods (Table 4). The order of subdominants by PR (after the dominant *S. baturini*) is consistently genus *Crenosoma*, followed by *T. martis* and *Th. aerophilus*, with a single exception where *T. martis* temporarily displaced genus *Crenosoma*. Similarly, in Sobolevsky District (SIP **MD-S-h-(b)**), the proportion of PR values for the dominant *S. baturini* and the

Table 4

Таблица 4

Ust-Bolsheretsky District. SIP MD-S-h-(a)

Усть-Большерецкий район. СИП МД-С-х-(а)

Observation period from 1959 up to:	Total infestation by all helminths (OPR %)	Infestation of sables with helminths comprising the SIP (PR %)						Associated species		
		Dominant	Subdominant species							
	<i>S. baturini</i>	<i>g. Crenosoma</i>	<i>T. martis</i>	<i>Th. aerophilus</i>	<i>M. kirbyi</i>	<i>A. simplex larvae</i>	<i>C. putorii</i>	<i>B. devosi</i>	<i>F. martis</i>	<i>T. nativa</i>
1980	65.72	52.81	21.83	7.80	6.60	5.03	0.26		1.25	0.69
1992	71.27	57.28	17.48	7.94	6.31	3.20	0.39	0.56	1.69	0.99
2002	73.88	62.24	14.13	8.40	6.92	2.50	1.97	0.59	1.32	1.21
2015	78.73	69.32	12.15	11.22	8.83	2.58	1.82	2.3	1.03	0.84
2018	80.23	69.87	12.17	11.62	8.64	3.15	2.43	1.6	0.97	0.80
2022	80.76	70.28	12.07	12.98	8.46	2.82	2.59	2.4	0.89	1.03
Total:	450.59	381.8	89.83	59.96	45.76	19.28	9.46	7.45	7.15	5.56

Table 5

Таблица 5

Observation period from 1959 up to:	Total infestation by all helminths (OPR %)	Infestation of sables with helminths comprising the SIP (PR %)						Associated species		
		Dominant	Subdominant species							
	<i>S. baturini</i>	<i>T. martis</i>	<i>g. Crenosoma</i>	<i>Th. aerophilus</i>	<i>A. simplex larvae</i>	<i>B. devosi</i>	<i>M. kirbyi</i>	<i>F. martis</i>	<i>C. putorii</i>	<i>T. nativa</i>
1980	70.07	61.78	13.80	13.08	3.65		3.25	0.85	0.09	
1992	69.88	59.81	13.97	12.72	2.77	3.85	2.26	0.97	0.37	0.74
2002	69.66	59.70	13.80	11.11	3.53	4.48	2.00	1.0	0.30	0.0
2015	75.02	66.38	17.1	10.35	4.01	3.67	1.6	1.71	0.27	0.33
2018	75.60	67.16	17.70	10.11	1.91	4.04	1.9	1.67	0.6	0.32
2022	76.52	68.25	18.66	9.76	4.22	3.81	1.81	2.12	0.57	0.30
Total:	436.75	383.08	95.03	67.13	20.09	19.85	12.82	8.32	2.20	0.95

Table 6

Таблица 6

Bystrinsky District. SIP MD-S-hh-(c)

Быстринский район. СИП МД-С-хх-(с)

Observation period from 1956 up to:	Total infestation by all helminths (OPR %)	Dominant						Subdominant species						Infestation of sables with helminths comprising the SIP (PR %)						Associated species											
		<i>S. baturini</i>			<i>T. martis</i>			<i>g. Crenosoma</i>			<i>Th. aerophilus</i>			<i>B. devosi</i>			<i>F. martis</i>			<i>M. kirbyi</i>			<i>C. putorii</i>			<i>A. simplex larvae</i>			<i>T. nativa</i>		
1980	65.14	50.37	9.09	14.36		10.35		11.40		2.74		3.25																			
1992	67.73	49.79	13.43	10.48		9.20		7.80		3.67		3.19		0.0		0.0		0.0										1.52			
2002	68.16	47.46	13.69	9.94		8.81		8.90		3.05		2.77		0.20		0.0															
2015	70.45	51.59	15.35	9.49		10.76		9.58		3.33		2.87		1.93		0.52															
2018	71.86	53.44	15.75	9.78		11.69		10.06		4.22		2.60		2.16		0.47															
2022	72.84	54.63	16.67	9.64		12.05		11.15		4.67		2.44		1.97		0.51															
Total:	416.18	307.28	83.98	63.69		62.86		58.89		21.68		17.12		6.26		1.5															

Table 7

Таблица 7

Yelizovsky District. SIP MD-S-hh-(d)

Елизовский район. СИП МД-С-хх-(д)

Observation period from 1953 up to:	Total infestation by all helminths (OPR %)	Dominant						Subdominant species						Infestation of sables with helminths comprising the SIP (PR %)						Associated species								
		<i>S. baturini</i>			<i>g. Crenosoma</i>			<i>B. devosi</i>			<i>Th. aerophilus</i>			<i>T. martis</i>			<i>F. martis</i>			<i>M. kirbyi</i>			<i>C. putorii</i>			<i>T. nativa</i>		
1980	60.99	43.89	20.15	7.56		11.36		5.83		0.11		0.49		0.25														
1992	63.43	42.04	16.3	12.51		9.12		6.98		2.89		0.68		1.39		0.0		1.68										
2002	63.45	40.91	15.03	14.39		8.23		6.96		2.63		0.88		1.5		0.0												
2015	66.63	44.47	8.14	16.86		9.88		7.72		4.54		1.53		1.09		0.17												
2018	67.59	44.54	13.44	18.66		9.54		8.08		3.83		1.67		1.06		0.16												
2022	68.14	45.2	13.21	18.63		10.37		8.23		3.77		1.64		1.04		0.15												
Total:	390.23	260.95	86.27	88.61		58.5		43.8		16.97		6.89		6.33		0.48												

Table 8

Таблица 8

Tigilsky District. SIP P-S-hh-(g)

Тигильский район. СИП P-S-hh-(g)

Observation period from 1956 up to:	Total infestation by all helminths (OPR %)	Infestation of sables with helminths comprising the SIP (PR %)								Associated species
		Dominant				Subdominant species				
	<i>S. baturini</i>	<i>g. Crenosoma</i>	<i>T. martis</i>	<i>B. devosi</i>	<i>Th. aerophilus</i>	<i>M. kirbyi</i>	<i>C. putorii</i>	<i>F. martis</i>	A. simplex larvae	<i>T. nativa</i>
1980	42.16	21.69	18.08	6.5	2.05	7.85	2.17	0.65	0.34	
1992	47.62	22.58	17.04	11.21	4.09	6.68	2.33	0.48	0.97	0.34
2002	46.58	21.16	15.69	11.22	5.83	6.15	2.1	0.48	0.88	0.26
2015	47.94	21.58	13.79	13.75	8.59	5.03	3.06	1.46	1.35	0.9
2018	46.98	20.47	13.12	14.18	8.11	5.03	2.59	1.13	1.1	0.63
2022	46.31	19.71	13.04	14.03	7.77	4.87	2.45	1.97	1.04	0.71
Total:	277.59	127.19	90.76	70.89	36.44	35.61	14.7	6.17	5.68	2.84

Table 9

Таблица 9

Milkovsky District. SIP BD-SB-hh-(f)
Мильковский район. СИП BD-SB-hh-(f)

Observation period from 1952 up to:	Total infestation by all helminths (OPR %)	Infestation of sables with helminths comprising the SIP (PR %)								Associated species
		Dominant				Subdominant species				
	<i>S. baturini</i>	<i>B. devosi</i>	<i>Th. aerophilus</i>	<i>g. Crenosoma</i>	<i>T. martis</i>	<i>F. martis</i>	<i>M. kirbyi</i>	<i>C. putorii</i>	A. simplex larvae	<i>T. nativa</i>
1980	61.48	32.92	28.64	16.62	15.48	9.4	1.39	1.12	0.32	0.31
1992	61.01	28.59	26.5	15.11	14.55	10.31	2.23	1.26	0.6	0.77
2002	60.03	26.12	26.31	15.28	13.45	10.39	2.01	1.1	0.5	0.67
2015	63.53	28.76	27.25	15.61	12.09	12.53	2.77	1.51	1.39	0.65
2018	64.59	28.95	28.26	16.66	11.81	13.65	3.29	1.75	1.31	1.13
2022	65.39	29.25	28.71	17.74	11.82	14.05	3.38	1.83	1.15	1.41
Total:	376.03	174.59	165.67	97.02	79.2	70.33	15.07	8.57	5.27	4.94

Table 10

Таблица 10

Karaginsky District. SIP MD-B-hh-(e)

Observation period from 1975 up to:	Total infestation by all helminths (OPR %)	Infestation of sables with helminths comprising the SIP (PR %)						Associated species			
		Dominant <i>B. devosi</i>	g. <i>Crenosoma</i>	<i>T. martis</i>	<i>Th. aerophilus</i>	<i>E. martis</i>	<i>A. simplex larvae</i>	<i>S. baturini</i>	<i>M. kirbyi</i>	<i>C. putorii</i>	<i>T. nativa</i>
1992	43.43	27.79	8.40	8.06	7.46	2.91	2.24	0.85	0.46		6.53
2002	43.66	28.19	7.80	7.80	7.41	2.70	1.92	0.79	0.66	0.0	
Total:	87.09	55.98	16.20	15.86	14.87	5.61	4.16	1.64	1.12	0.0	

Table 11

Таблица 11

Penzhinsky District. SIP P-T-hh-(h)

Observation period from 1956 up to:	Total infestation by all helminths (OPR %)	Infestation of sables with helminths comprising the SIP (PR %)						Associated species		
		Dominant <i>T. martis</i>	Subdominant species g. <i>Crenosoma</i>	<i>B. devosi</i>	<i>C. putorii</i>	<i>F. martis</i>	<i>Th. aerophilus</i>	<i>M. kirbyi</i>	<i>T. nativa</i>	
no 1980	14.11	1.57	6.53	2.63	0.22	1.27	0.43	0.0		
no 1992	25.13	12.95	6.69	3.16	1.68	0.64	0.66	0.67	1.33	
no 2002	23.11	11.19	5.59	2.83	1.38	0.52	0.54	0.75		
Total:	62.35	25.71	18.81	8.62	3.28	2.43	1.63	1.42		

Table 12

Таблица 12

Ust-Kamchatsky District. SIP ND-hh-(i)

Observation period from 1956 up to:	Total infestation by all helminths (OPR %)	Infestation of sables with helminths comprising the SIP (PR %)						Associated species			
		Subdominant species <i>Th. aerophilus</i>	<i>S. baturini</i>	<i>B. devosi</i>	g. <i>Crenosoma</i>	<i>T. martis</i>	<i>C. putorii</i>	<i>F. martis</i>	<i>M. kirbyi</i>	<i>A. simplex larvae</i>	<i>T. nativa</i>
1980	44.41	16.19	11.85	12.17	11.43	5.48	0.27	0.75	1.67		
1992	45.21	14.23	10.0	10.73	10.67	9.19	2.35	1.81	1.24	0.45	3.22
2002	42.36	13.33	9.02	10.85	9.68	8.1	1.76	1.62	1.04	0.31	
2015	46.8	13.38	14.04	13.47	8.14	8.84	2.75	1.57	2.05	0.3	
2018	48.97	16.1	17.31	13.23	8.43	9.72	2.59	2.5	2.35	0.35	
2022	49.27	16.02	18.06	12.93	8.24	9.12	2.52	2.72	2.14	0.27	
Total:	277.02	89.25	80.28	73.38	56.59	50.45	12.24	10.97	10.49	1.68	

two subdominants (*T. martis* and genus *Crenosoma*) remained unchanged throughout the study (Table 5).

Consequently, the analysis of the SIP structure in Ust-Bolsheretsky and Sobolevsky Districts over intervals of 9, 19, 24, 35, 37, and 40 years confirmed the results of the earlier 11-year cycle analysis (Tranbenkova 2018), affirming the 'maximum stability' of the **MD-S-h-(a)** and **MD-S-h-(b)** variants.

The classification as 'quite stable' was also confirmed for the four variants **MD-S-hh-(c)**, **MD-S-hh-(d)**, **MD-B-hh-(e)**, and **BD-SB-hh-(f)** (Tables 6, 7, 10, and 9). Across all periods, the difference between the PR of the dominants (*S. baturini* and *B. devosi*) and the subdominants corresponded to their descriptions, although the absolute PR values of subdominants occasionally deviated from the general downward trend.

Both transitional type SIP variants (**P-S-hh-(g)** in Tigilsky District and **P-T-hh-(h)** in Penzhinsky District) were classified as 'relatively stable'. The PR proportions between dominants and subdominants correspond to the type description, and the order of subdominant species is preserved (Table 10, Table 11). However, due to shorter observation periods (Karaginsky: 1975–1993; Penzhinsky: 1956–1995), a more confident assessment of their stability is not yet possible.

Concurrently with the structural analysis, we examined the dynamics of sable infestation, specifically the PR of individual helminth species and the overall PR. As shown in the supporting tables (Tables 4–12), the overall helminth PR has increased in almost all areas of Kamchatka Krai.

The most pronounced increase occurred in the southern half of the western and eastern coasts (Ust-Bolsheretsky, Sobolevsky, Bystinsky, and Yelizovsky Districts). In the first three districts, the increase was driven predominantly by the dominant nematode *S. baturini* and the subdominants *T. martis* and *Th. aerophilus*. In Yelizovsky District, the increase in PR for these helminths was less pronounced, and a notable decrease in infestation with lung nematodes of the ge-

nus *Crenosoma* was observed. In contrast, no trend toward increased overall PR was noted in the northern districts (Karaginsky and Penzhinsky, Tables 10 and 11). We posit that the duration of studies in these northern areas is currently insufficient for drawing definitive conclusions about long-term trends in helminth infestation.

Conclusions

First, the Specific Infestation Pressure (SIP) is a conceptual framework designed to systematically describe the variability in helminth species composition and the extent of infestation in the Kamchatka sable across different administrative (geographical) subregions of Kamchatka Krai.

Second, as evidenced by the description of all nine SIP variants, the structure — defined by the descending order of dominant and subdominant helminth species according to their prevalence rate (PR) — is unique to each district and is not replicated in any other (Tables 4–12).

Third, such a distinct pattern is not apparent among the associated species. While it is clear they contribute to the overall prevalence rate (OPR) in each district, their individual PR values are low to very low (less than 1%). Consequently, the dynamics and specific role of each associated species within the SIP remain unclear and warrant further investigation for a complete description.

Fourth, a key argument supporting the validity of the SIP concept is its stability. The structural parameters consistently align with the same type and variant across different time periods, including 11-year sable population cycles and intervals ranging from 9 to 40 years from the start of observations in each district from 1980 up to 2022.

Fifth, the observed constancy of the structure, to a greater or lesser degree depending on its classification as 'maximum', 'quite', and 'relatively' stable, coupled with the dynamism of its individual components, indicates the capacity of the SIP for homeostasis. This suggests it functions as an integral part of broader natural biocenotic mechanisms regulating sable populations in Kamchatka Krai.

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