

# Spatial Distribution and Composition of Populations of the Bivalve *Tetrarca boucardi* (Jousseume, 1894) (Arcidae) in Vostok Bay, Sea of Japan

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**Abstract**—The vertical distribution of the bivalve *Tetrarca boucardi* is studied at several sites in Vostok Bay, which largely characterize the diversity of biotopes of the upper subtidal zone of Peter the Great Bay (the Sea of Japan). In this part of the species range, at a depth of 0.5–10 m, *T. boucardi* forms stable perennial populations, in which there is the regular replenishment by juveniles; the population lifetime apparently many times exceeds the bivalve's individual lifespan. The maximum shell length of *T. boucardi* is 74 mm; the maximum individual age is 19 years. The most abundant accumulations of *T. boucardi* with a biomass of 530 g/m<sup>2</sup> (36.7% of the total biomass of macrozoobenthos) are found in shallow water at a depth of about 3 m in semi-protected inner parts of the bay, which are well warmed in summer. For the first time, it is found that relatively sheltered habitats on wave-exposed rock reefs mainly at a depth of 0.5–1.5 m are also favorable for the species (average biomass, 72.7 g/m<sup>2</sup>; 11.2%). *T. boucardi* also occurred on soft bottoms at a depth of 1–10 m (average biomass, 22.2 g/m<sup>2</sup>; about 2%) in druses of large bivalves *Modiolus kurilensis* and *Crenomytilus grayanus*. Local differences in the abundance and composition of *T. boucardi* populations are discussed in relation to the habitat conditions.

**Keywords:** bivalve mollusk *Tetrarca boucardi*, vertical distribution, size and age composition, habitat conditions, associated fauna, Peter the Great Bay, Sea of Japan

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## INTRODUCTION

The bivalve *Tetrarca boucardi* (Jousseume, 1894) is an Asian Pacific subtropical-low-boreal species, which is distributed from Taiwan almost to the northern border of Primorsky krai [8, 17, 23, 28, 29]. The species is common on the Pacific and Sea of Japan coasts of the Japanese Islands; it has also been recorded at Kunashir Island [13, 27, 28, 30]. North of Peter the Great Bay along the mainland coast of Russia, no dense aggregations of *T. boucardi* but only rare single specimens or juveniles were found, as on the South Kuril shoal and at Sakhalin Island [6]. In Peter the Great Bay (the Sea of Japan), this species is a common element of the fauna of shallow and second-order bays [16, 24]. In semi-protected inlets of Possyet and Vostok bays, *T. boucardi* is the leading species of the biocenosis of *Crenomytilus grayanus* (*Modiolus difficilis*) + *Tetrarca boucardi*, forming aggregations together with *C. grayanus* and/or *Modiolus kurilensis* on boulders and rocks. Apparently, these mollusks also have a significant role in some other benthic communities, where relatively high indices of their abundance were observed [3]. Despite its frequent findings and high

local abundance, the population biology of *T. boucardi* is virtually unstudied. Most studies that mention this species are primarily concerned with the biology of bivalves as a whole. There is fragmentary information about the occurrence in plankton and the morphology of larvae, the sperm ultrastructure, resistance to changes in water salinity, as well as about the morphological and functional features of the digestive gland of *T. boucardi* [1, 5, 14, 26]. The objectives of this study are to clarify the current picture of the spatial distribution of *T. boucardi* in Peter the Great Bay of the Sea of Japan, as well as to analyze the size and age composition of local populations, reflecting the characteristics of reproduction of the mollusk population in this part of the range.

## MATERIALS AND METHODS

The studies were performed in April 2020 in Vostok Bay (Peter the Great Bay, Sea of Japan; 42°53' N, 132°45' E) (Fig. 1). Published data [16] and the results of our long-term observations of the distribution of benthic fauna in the bay showed that *Tetrarca boucardi*

occurs on almost all hard bottoms in very few numbers, but forms aggregations only in a few localities. Hence, the spatial distribution was analyzed at three extensive sites differing in environmental conditions. Site 1 was a gently sloping (average slope of about 2°) silted bottom in the shallow innermost part of Tikhaya Zavod Inlet, which is protected from strong winds and waves of the open sea. Site 2 was located near the pier of the Vostok Biological Station of Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences; it had a greater bottom slope than in the first site (about 7° on average) and was characterized by more active hydrodynamics due to waves reflected from the opposite shore of the bay in stormy weather. Site 3 is one of the rock reefs of the bay, which is subject to the periodic significant impacts of waves, especially during the passage of summer–fall cyclones. Surveys were conducted on transects located from the water's edge to the maximum depth of the distribution of *T. boucardi*. Three transects were performed at site 1 and two transects at site 2; the distance between transects was 100 m. At site 3, two long (about 150 m) transects were made along and across the reef. The plots on the bottom were visually marked along transects, which were uniform in terms of substrate type and inhabitants [15]. Within the plots, the numbers of *T. boucardi* and associated large epibenthic forms of macrozoobenthos (below, referred to as zoobenthos) were randomly counted in 30 1-m<sup>2</sup> counting frames. These data were used to calculate the average population density of mollusks and other invertebrates. In addition, at each station, all animals were collected from 5–8 frames (area, 1.0 and 0.01 m<sup>2</sup>) in order to characterize the size and age composition of *T. boucardi* and to correct data on the abundance of small forms of zoobenthos. The shell length was measured with a caliper to the nearest 1 mm; after removing epibionts, the live body weight of *T. boucardi* was estimated for each specimen. For other invertebrates, the average body weight was estimated by weighing 30–50 randomly collected specimens. The shell length measurements were used to analyze the size composition of *T. boucardi* from different habitats, the biomass was calculated using body-weight data. The individual age of *T. boucardi* was estimated from marks on the outer surface of the shell and on a transverse saw cut. In most cases, these marks are clearly distinguishable visually and are formed annually [9, 11].

Statistical data were processed on a PC using the SPSS 17 software package. When comparing the size and age composition of mollusks at the three sites, a nonparametric Kruskal–Wallis test was used. A posteriori comparisons were made using a Mann–Whitney test with adjusted a significance level of  $p < 0.05$ .

## RESULTS

### *Spatial Distribution*

At site 1, three zones can be conventionally distinguished according to the biotope type and zoobenthos abundance. Coarse sand with pebbles, gravel, shell debris, and macroalgae *Sargassum* sp. extended for 3–37 m from the coastline to a depth of 1 m. Hermit crabs and a few (less than 1 ind. per 5 m<sup>2</sup>) gastropods *Littorina* spp., *Tegula rustica*, *Boreotrophon candelabrum*, and *Cryptonatica janthostoma* occurred in this biotope. Only 4 individuals of *Tetrarca boucardi* were found in a large area, attached by a byssus to objects of anthropogenic origin. The biomass of the zoobenthos averaged 2.3 g/m<sup>2</sup>.

At a depth of 1–3 m, a belt of the seagrass *Zostera* was observed; boulders of various sizes occurred sometimes as heaps or as a more or less gentle talus slope. The biomass of zoobenthos was on average 1424.7 g/m<sup>2</sup>. This biotope supports the largest population of *T. boucardi* at the top of the bay with a population density of  $83.1 \pm 62.0$  ind./m<sup>2</sup> (maximum value, 219 ind./m<sup>2</sup>) and a biomass of  $522.9 \pm 397.8$  g/m<sup>2</sup> (maximum, 1381.8 g/m<sup>2</sup>), which made up 36.7% of the total biomass of zoobenthos. The mollusks usually formed dense clusters, which looked like brushes, overgrowing the upper and lateral surfaces of several neighboring boulders with one layer (Fig. 2a). Occasionally, several large specimens of *Modiolus kurilensis* were interspersed in such an accumulation, but more often individuals of *M. kurilensis* were located between the boulders, more or less submerged in gravel and fine clastic, sometimes heavily silted sediment. This species was second in biomass among invertebrates in this bottom habitat (198.2 g/m<sup>2</sup>); the population density of *M. kurilensis* was significantly lower than that of *T. boucardi* ( $2.2 \pm 2.0$  ind./m<sup>2</sup>) and comparable with that of equally common but smaller hermit crabs *Pagurus* spp. ( $9.9 \pm 9.0$  ind./m<sup>2</sup>), gastropods *T. rustica* ( $5.7 \pm 4.5$  ind./m<sup>2</sup>) and *B. candelabrum* ( $2.1 \pm 2.0$  ind./m<sup>2</sup>), the starfish *Patiria pectinifera* ( $4.5 \pm 3.8$  ind./m<sup>2</sup>), the sea urchin *Strongylocentrotus intermedius* ( $3.9 \pm 3.4$  ind./m<sup>2</sup>), and serpulid polychaetes. Much less frequent were the sea urchin *Mesocentrotus nudus*, the holothurian *Apostichopus japonicus*, the sea squirt *Styela clava*, the mollusks *Azumapecten farreri*, *Crenomytilus grayanus*, and *Mitrella burchardi*, as well as the spider crab *Pugettia quadridens* (1 specimen per 2–10 m<sup>2</sup>). The population density of other invertebrates (sponges, bryozoans, decapods, ascidians, etc.) did not exceed 0.1 ind./m<sup>2</sup> (colony/m<sup>2</sup>). The length of the boulder zone along transects varied from 5 to 84 m.

Seaward of the boulder talus to the maximum depth (about 6 m), the slope of the bottom decreased, boulders became more and more rare; mixed druses of *C. grayanus* and *M. kurilensis* were common on silty sand (Fig. 2b). The biomass of zoobenthos was

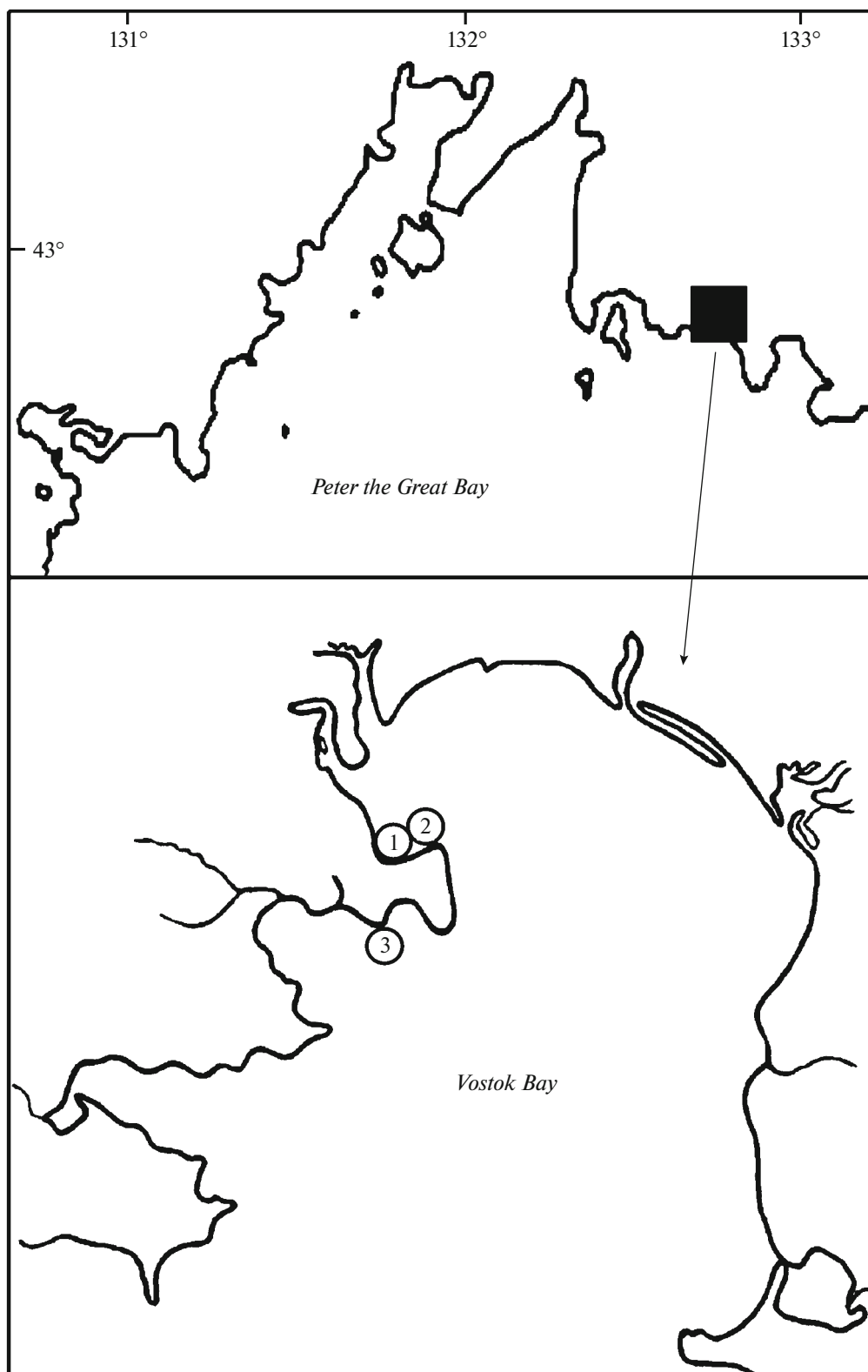
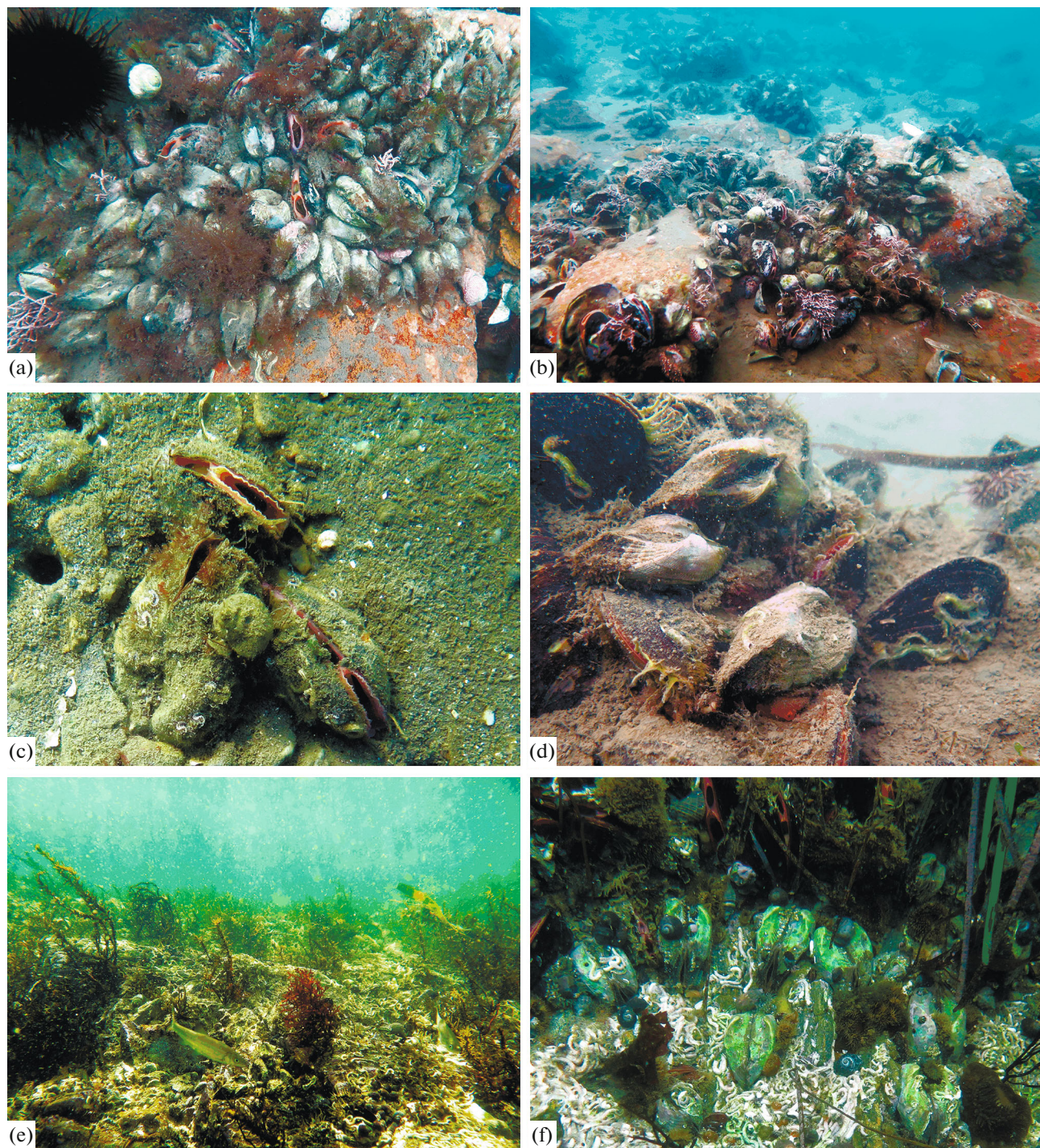


Fig. 1. A schematic map showing the survey areas in Vostok Bay. 1–3, The location of study sites and populations of *Tetrarca boucardi*.



**Fig. 2.** Appearance of aggregations of the bivalve mollusk *Tetrarca boucardi* in different biotopes. (a, b) Site 1, the innermost part of the bay, boulders, silty sand; (c, d), site 2, at Vostok Biological Station, silty sand; (e, f) site 3, a wave-exposed rocky reef.

881.3 g/m<sup>2</sup>. The population density of *T. boucardi*, which occurred in this zone on boulders and, to a lesser extent, in mytilid druses, was several times lower than at a depth of 1–3 m (average,  $8.1 \pm 7.9$  ind./m<sup>2</sup>; maximum, 45 ind./m<sup>2</sup>). The biomass was  $51.1 \pm 49.8$  g/m<sup>2</sup> (maximum, 283.5 g/m<sup>2</sup>), or 5.8% of the total biomass

of zoobenthos. The abundance of *T. boucardi* was lower compared to the large and locally most abundant Gray mussel, for which the above parameters were on average  $18.0 \pm 14.3$  ind./m<sup>2</sup> and  $535.0 \pm 499.7$  g/m<sup>2</sup>, respectively. The population density of *M. kurilensis* did not exceed  $3.1 \pm 3.0$  ind./m<sup>2</sup>, while the biomass

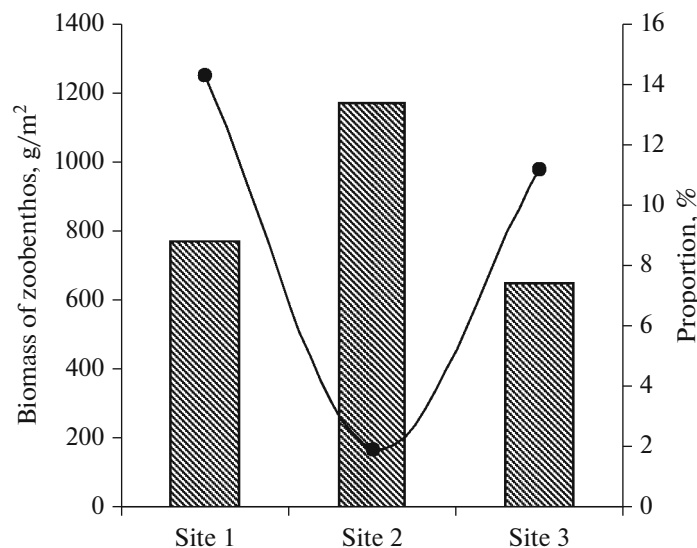


Fig. 3. Proportion of *Tetrarca boucardi* in the zoobenthic community at sites 1, 2, and 3. The bars show the average biomass of zoobenthos, g/m<sup>2</sup>; the line indicates the biomass of *T. boucardi*, % of the average biomass of zoobenthos.

did not exceed  $274.2 \pm 244.4$  g/m<sup>2</sup>. The octopus *Enteroctopus dofleini* disappeared from the zoobenthos; the scallop *Mizuhopecten yessoensis* (1 specimen per 10 m<sup>2</sup>) was found on silty sand between mytilid druses. The average population density of *T. boucardi* in this part of the bay was generally about 30 ind./m<sup>2</sup>; the biomass reached 190.3 g/m<sup>2</sup>, or about 14.3% of the total biomass of the zoobenthos (Fig. 3).

At site 2, the bottom slope was more significant, the maximum depth was greater than in the nearby innermost part of the bay. No stone-boulder ridge was observed, the bottom was consistently silty sand with small pebbles and shell debris. Therefore, only two vertical zones can be conventionally distinguished at site 2. At a distance of almost 15–20 m from the shore to a depth of about 1 m, the zoobenthos consisted of numerous mud shrimps *Upogebia issaeffi*, the starfish *Patiria pectinifera*, hermit crabs, gastropods *Natica*, *Littorina*, and very few specimens of *Tegula*, as well as small crabs. *T. boucardi* was not found; the zoobenthos biomass was 5.7 g/m<sup>2</sup>.

The other zone was located below to a maximum depth of 9–10 m. The bulk of the zoobenthos was large mytilids, sea urchins *S. intermedius* and *M. nudus*, and some other forms. The biomass of zoobenthos was on average 1167.1 g/m<sup>2</sup>. At the upper boundary of this extensive zone, single specimens and small druses of 2–3 adults of *M. kurilensis* were observed; equally few individuals of *T. boucardi* were attached to them (Fig. 2c). With increasing depth, the siltation of the bottom gradually increased; Gray mussels appeared in the druses of *M. kurilensis*, the proportion of Gray mussels gradually increased, as did the size and occurrence of the aggregations (Fig. 2d). The abundance of *T. boucardi* also increased but this was observed only to

a depth of 3.0–3.5 m; at greater depths, it again decreased. Thus, the population density of *T. boucardi* was about 2 ind. per 5 m<sup>2</sup> at a depth of 1.0–1.5 m,  $5.0 \pm 4.8$  ind./m<sup>2</sup> at 3–4 m, 1 ind. per 2 m<sup>2</sup> at 6 m; at a depth of 9–10 m, where the outer boundary of the distribution of mytilid druses lay and there were no hard substrates necessary for the attachment of *T. boucardi*, only its juveniles that had settled in the preceding year were found. The biomass of *T. boucardi* was 4.1, 50.6, 5.1, and about 0.5 g/m<sup>2</sup>, respectively. The average values of the population density and biomass of the species were 2.2 ind./m<sup>2</sup> and 22.2 g/m<sup>2</sup>, respectively. The estimates are rather modest (1.9% of the total biomass of the zoobenthos), compared to the abundance of other invertebrates in this part of the bay (Fig. 3). The most abundant species were *M. kurilensis* ( $8.3 \pm 7.7$  ind./m<sup>2</sup> and  $497.0 \pm 459.3$  g/m<sup>2</sup>), the sea urchin *S. intermedius* (1.2 ind./m<sup>2</sup> and 35.3 g/m<sup>2</sup>), and Gray mussel (about 2 ind./m<sup>2</sup> and 40 g/m<sup>2</sup>). Hermit crabs and the sea star *Patiria* (1–2 ind./m<sup>2</sup>) were ubiquitous, but their biomass, as a rule, did not exceed 1.4–8.4 g/m<sup>2</sup>. The biomass of gastropods, crustaceans, polychaetes, and other small organisms was less than 1.0 g/m<sup>2</sup>.

Site 3 was a stony ridge of submerged and protruding small rocks and a system of gullies, the depth of which gradually decreased when moving from the seaward deep part of the reef to the shore. The extensive shallow reef flat and the reef slope differed in the composition and abundance of zoobenthos; therefore, two zones of habitat of *T. boucardi* could be conventionally distinguished. In the first zone (Fig. 2e), extending from the lower intertidal boundary to a depth of 50–70 cm, the biomass of the zoobenthos averaged 105.6 g/m<sup>2</sup>. The highest population density (up to 350 ind./m<sup>2</sup>)

was found for small sedentary serpulid polychaetes (biomass,  $21.3 \pm 19.7$  g/m<sup>2</sup>). Their calcareous tubes free from seedlings of the brown alga *Sargassum* sp. almost completely covered the rocks. *Littorina* sp. were found everywhere on open rocks and in crevices (population density,  $93.8 \pm 79.7$  ind./m<sup>2</sup>; biomass  $17.8 \pm 11.9$  g/m<sup>2</sup>). The barnacle *Chthamalus dalli* was also numerous; however, like some other small invertebrates, its biomass was relatively low. In terms of biomass, *M. kurilensis* was predominant ( $31.2 \pm 29.0$  g/m<sup>2</sup>) with a population density of about 1 ind./m<sup>2</sup>. *T. boucardi*, like *M. kurilensis*, usually settled in small gullies, using the roughness of the rocky substrate to attach. The population density of the species was higher than that of *M. kurilensis* ( $5.5 \pm 4.5$  ind./m<sup>2</sup>), while the biomass was lower ( $28.7 \pm 22.8$  g/m<sup>2</sup>).

Outside of this zone, sea grass plants of *Phyllospadix iwatensis* grew in places protected from the direct impact of waves on the reef crest and slope, on fringing rocks, and in the deepest gullies up to 1.0–1.5 m. The abundant macrofauna was associated with the seagrass vegetation, its average biomass was 1188.8 g/m<sup>2</sup>. The zoobenthos was dominated by *M. kurilensis* with a biomass of  $460.1 \pm 369.6$  g/m<sup>2</sup> and a population density of  $7.0 \pm 6.6$  ind./m<sup>2</sup>. The biomass of the sea urchin *S. intermedius* ( $224.2 \pm 198.0$  g/m<sup>2</sup>) and the bivalve *Mytilisepta keenae* ( $132.3 \pm 129.7$  g/m<sup>2</sup>) was significant. *T. boucardi* was also abundant (Figs. 2f, 3), with the maximum density sometimes exceeding 100 ind./m<sup>2</sup> and a biomass of up to 597.0 g/m<sup>2</sup> (on average,  $116.7 \pm 117.6$  g/m<sup>2</sup>). In relatively sheltered places, single specimens of Gray mussel, the sea urchin *M. nudus*, and colonies of the sponge *Halichondria* sp. were found. Other invertebrates (gastropods, chitons, polychaetes, sea anemones, and crustaceans), although quite common, made up a relatively small proportion of the total biomass of the community (9.1%; about 109 g/m<sup>2</sup>) (Fig. 3). Below the *Phyllospadix* belt, macrobenthos was almost lacking on descending rock ridges and gullies extending seaward, as well as on rock blocks on the reef flanks somewhat more protected from direct waves. From a depth of 4–5 m, single specimens of Gray mussel and barnacles were found. Only juveniles of *T. boucardi* were recorded in small numbers in mytilid aggregations at the base of the slope at a depth of 10–12 m.

#### Size Composition of Populations

At site 1, at the top of the bay, *T. boucardi* had a shell length of 11 to 60 mm (Fig. 4). Individuals of less than 30 mm in size were rather few (about 17%), the most abundant were those with a shell length of 41–44 mm (more than 22%). In the size-frequency distribution, a shift towards the predominance of relatively large individuals was observed.

At site 2, the shell length of *T. boucardi* varied more widely from 16 to 74 mm. In the size-frequency distribution, it is conditionally possible to distinguish two groups of individuals with a shell length of less than 30 mm and from 30 to 60 mm. Specimens with a shell length of more than 60 mm constituted almost 4% of the population.

On the wave-exposed rocky reef at site 3, the population of *T. boucardi* consisted of individuals with a shell length of 18 to 55 mm. The size-frequency distribution was unimodal; mollusks 36–38 mm in size were predominant (about 30%) in terms of abundance.

Multiple comparisons of mollusk samples from different sites in the bay using the Kruskal–Wallis test revealed a significant difference in their size composition ( $P < 0.05$ ).

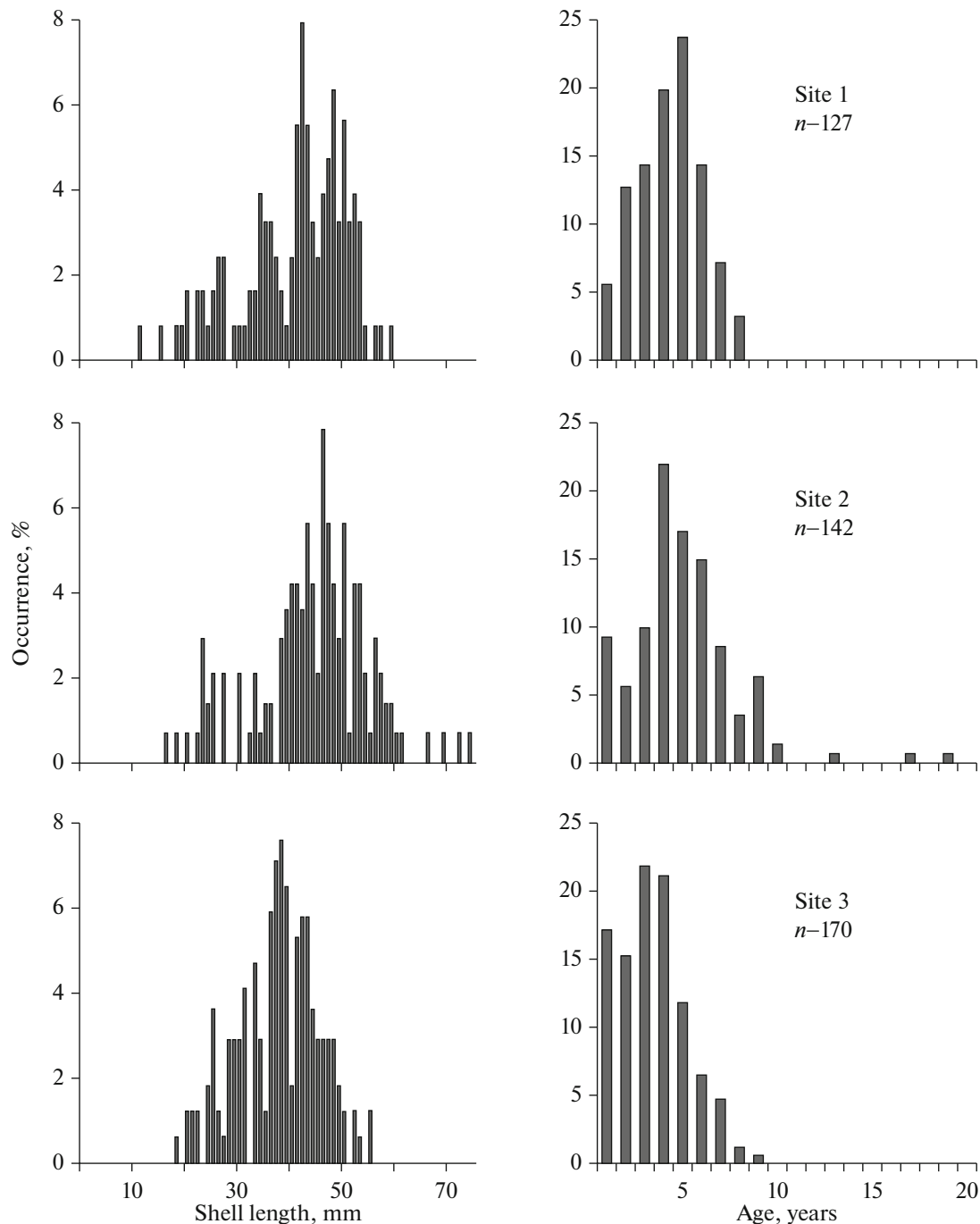
#### Age Composition of Populations

At site 1, the *T. boucardi* population was represented by individuals of 1 to 8 years old (Fig. 4). Four- and 5-year-old mollusks were noticeably predominant (43.3%) in abundance. At site 2, individuals of 1 to 19 years old were recorded. The main part of the population (97.9%) was made up of 1–10-year-old mollusks. The highest abundance (53.5%) was found for 4–6-year-old individuals. At site 3, the *T. boucardi* population consisted of individuals aged 1 to 9 years. The bulk of the population (75.3%) was 1–4-year-old mollusks.

Comparison of samples from different parts of the bay showed a significant (paired Mann–Whitney test;  $P < 0.05$ ) difference in the age composition of *T. boucardi* at site 3 from that of sites 1 and 2, for which the difference was random ( $P = 0.051$ ).

## DISCUSSION

The spatial distribution of benthic organisms is determined by a complex of environmental factors, among which temperature, substrate type, and hydrodynamic activity are of great importance. A large array of field and experimental evidence obtained at different levels of organization of living systems indicate a close relationship between the distribution of aquatic organisms and their thermopathy (see, for example, [7, 23, 32]). On the long-term scale, temperature is a rather conservative environmental factor for any geographic locality. Therefore, it is not surprising that the current distribution of *Tetrarca boucardi* exhibits characteristic features that were observed 50–60 years ago when studying the composition, structure, and distribution of bottom biocenoses in coastal waters of Peter the Great Bay [24]: this warm-loving species forms the densest populations in the well-warmed innermost parts of shallow bays and gulfs. In Possyet Bay, *T. boucardi* was the leading species, forming abundant populations (biomass, up to 1.2 kg/m<sup>2</sup>) in semi-protected



**Fig. 4.** The size (left) and age (right) composition of populations of *Tetrarca boucardi* at sites 1, 2, and 3.

bays predominantly on hard bottoms at a relatively shallow depth of 1.5–3.0 m [3, 23, 24]. A mixed population of mollusks, in which *T. boucardi* was the leading form, was previously reported at the top of Vostok Bay (site 1), where the upper water layers warm up to 23–25°C in summer [25]. The biomass of *T. boucardi* in this area reached almost 1.5 kg/m<sup>2</sup> [16]. We also recorded the former population, although with a slightly lower biomass of the mollusk.

The results of the study showed that below 3.0–3.5 m the number of *T. boucardi* gradually decreased. This was especially clearly evident at site 2, which is characterized by the relatively consistent character of the biotope, stable water salinity, the absence of wave action, and high abundance of large mytilids, which provide a potentially suitable substrate for attachment of the mollusk [20]. The temperature conditions change markedly with depth. At a depth of about 5 m, a ther-

moocline is observed; as a result, the water temperature, for example, in July–August, is 2–4°C lower than at the surface, 16–18°C ([25]; my own long-term observations). Here and down to a depth of 10 m, the most favorable temperature for *T. boucardi*, which is comparable to the surface temperature, is observed for a very short period of time, because in late August–early September the water is already mixed to form a homothermal layer. With a further increase in depth and, accordingly, with a decrease in the water temperature to 12–13°C at the 20-m isobath, the abundance of *T. boucardi* decreases even more rapidly. Hence, the findings of the species at a depth of more than 10 m in wave-protected areas in Peter the Great Bay are rather few and rare, although it is not ruled out that this is largely due to the growing shortage of favorable substrate.

On open-sea shores and wave-exposed rocks, the abundance of *T. boucardi* is low: very few adult individuals as well as juveniles are usually found ([24]; present study). However, we found aggregations of this species on the reef flat of rock reefs from the lower intertidal boundary to a depth of 1.5 m. The age composition and the relatively high proportion of juveniles at site 3 (Fig. 4b) indicate the regular replenishment of spat and high spat survival. This is due to the fact that the shallow water of the reef is, to a great extent, protected by a belt of the seagrass *Phyllospadix iwatensis* from being actively mixed with the adjacent open water of the bay; in spring and summer, water in subtidal and tidal pools and gullies warms up faster and more significantly than in other habitats. In addition, juvenile mollusks are concentrated under a canopy of *P. iwatensis* vegetation within the tangled roots, which apparently prevent them from being eaten by predators. Likewise, for example, the network of byssal threads of Gray mussels and the periostracal bristles of *M. kurilensis* are conducive to the survival of their juveniles [20, 22].

According to the classification of subtidal bionomic types [15], the surveyed reef falls under the category of moderately protected shores. In summer and fall, in stormy weather, when cyclones move from the south and southwest, the inhabitants of the reef experience increased hydrodynamic impact. In some years, typhoons are especially strong. In this case, large waves hit with force onto the frontal part of the reef, cover the reef, and rapidly spread over the reef flat, washing away animals and plants and fine sediment from gullies and cracks, together with its inhabitants. After a storm, numerous single individuals of *T. boucardi* along with other epi- and infaunal animals are usually found cast ashore. In addition, aggregates of several bivalves with an attached tuft of the seagrass *P. iwatensis* occurred, which helps the mollusks to be transported via currents over long distances. This indicates that the abundance and lifespan of *T. boucardi* on the rock reef significantly depend on the frequency and strength of wave action in stormy weather. The

maximum age of *T. boucardi* in this habitat was 8 years, which is significantly lower than the previously reported lifespan of the species, 20 years [10].

The lifespan of *T. boucardi* at site 1 was also relatively low (9 years), which is much lower than the lifetime of this population. The location of the population in the well-warmed and wave-protected innermost part (top) of the bay ensures the regular, although less abundant replenishment of juveniles, compared to the exposed reef. A very high crowding of mollusks was observed on stones within clusters of mollusks (“brushes”) at the top of the bay, which was not recorded in any other place. Their numbers and lifespan in this biotope are largely determined by factors related to the population density. Suffice it to say that most mollusks older than three years have an almost penetrating injury of the shell as a result of the constant mechanical rubbing of valves in contact. The destruction of the calcite shell is also facilitated by the weakly acidic environment, which is usually characteristic of shallow silty sediment with a high content of humic compounds [4].

Hard bottom substrates (rocks, boulders) typical for sites 1 and 3 are absent at site 2. For settlement, byssal attachment onto the substrate, and subsequent life, juveniles of *T. boucardi* use the only relatively stable surface, viz., shells of *M. kurilensis* and Gray mussels. This substrate is favorable for *T. boucardi* at the early stages of the mollusk. The periostracal bristles, which completely cover the shell of relatively young *M. kurilensis* and are present at the shell apex in old individuals, protect the juveniles of various invertebrates concentrating within the bristles from being eaten by fish, crustaceans, and other predators [20]. As *T. boucardi* grows, an increasingly larger area is required for attachment of the byssus, which in this species is a massive and powerful strand, in contrast to numerous thin threads of the mytilid byssus ending in a tiny disc, the sole [2, 12, 21, 23, 31]. The bristly areas of the shell of *M. kurilensis* turn out to be unsuitable for maturing *T. boucardi* to attach to them, while bristle-free areas of old individuals are often occupied by other organisms or are submerged in sediment to some extent [19, 20]. Some of the growing mollusks discard the byssus and crawl to another place in search of favorable conditions, while others die. In general, despite the high population density of *M. kurilensis* and Gray mussels, the favorable substrate for the attachment of *T. boucardi* is fairly limited at site 2, which is a factor that reduces its abundance. On the other hand, the relatively low population density of *T. boucardi* in the absence of adverse wave action is conducive to the fact that in this biotope mollusks of the species have an intact shell, reach large body sizes, and their lifespan is almost 2 times higher than in other habitats.

Thus, the results of the study indicate that in Peter the Great Bay of the Sea of Japan, *T. boucardi* lives not



only in wave-sheltered areas but also along relatively open shores. The mollusk forms stable perennial populations with the regular replenishment of juveniles; it is a dominant, leading, or merely trivial species of the benthic community, constituting 2 to 26% of the total biomass of the associated zoobenthos. The most abundant local populations of *T. boucardi* are confined to hard bottoms, suitable for strong byssal attachment. On soft bottoms, *T. boucardi* can be found where a sufficiently stable substrate is available for spat to settle, viz., druses of Gray mussel and *M. kurilensis*, objects of anthropogenic origin projecting above the bottom, or in the case of the introduction of mollusks washed off rocks and boulders in stormy weather. It is possible that the dispersal of *T. boucardi* also occurs in early spring via ice floes carried away from shallow water and via plants and animals frozen in the ice. In Peter the Great Bay, the mollusks form mass aggregations at depths of up to 3–4 m, but are also found at depths of up to 20 m. In the coastal waters of Japan at a depth of 140–200 m and at Moneron Island (near the southwestern coast of Sakhalin Island) at a depth of 40–80 m, only young one-year-old specimens and empty shells of *T. boucardi* were found [18, 28]. Apparently, the habitat conditions in these regions are suitable for the formation of stable multi-aged populations of the mollusk.

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#### COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interests.* I declare no conflict of interest.

*Statement on the welfare of animals.* All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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