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SHRIMPS OF THE GENUS *PALAEMON* (CRUSTACEA, DECAPODA, PALAEMONIDAE) OF THE EUROPEAN SEAS

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Shrimps of the genus *Palaemon* (the family Palaemonidae) are among the most active invasive shrimps. To date, six species from this genus inhabit the shelf of seas washing Europe from the Gulf of Bothnia in the north to the Don River mouth in the southeast. Due to global warming and enhanced development of shipping which facilitated the transfer of larvae of these shrimps with ballast water, five out of six species significantly expanded their ranges in a historically short period of time. One of them, *Palaemon macrodactylus*, that was a south-boreal Western Pacific species, became a cosmopolitan. Only *Palaemon xiphias*, a symbiont of a seagrass *Posidonia oceanica*, has preserved its classic Mediterranean–Lusitanian range. The article provides data on the morphology of each of six species and the identification key. Also, the paper describes the history of the formation of new ranges, size composition, features of reproductive biology, and food composition of each species.

Keywords: shrimps, *Palaemon*, invasion, range, European seas, Black Sea

One of the most pressing problems of both theoretical and applied hydrobiology, as well as zoogeography, is the invasion of new species into already existing hydrocenoses and the formation of new ranges for species that seemed to be quite endemic. This process is continuous and unstoppable. For example, 76 species of aquatic and semiaquatic animals and plants have penetrated into water bodies of countries of the Baltic Sea basin since the early XIX century [Olenin, 2005]. The largest water bodies of the Kaliningrad region can serve as evidence of this. Thus, in recent decades, species from the Caspian, Black, and Mediterranean seas and from waters of East Asia and America have penetrated into main water bodies of the region – the Curonian and Vistula lagoons. Out of seven Decapoda species that inhabit water bodies of the Kaliningrad region today (those include two species of shrimps, two species of crabs, and three species of crayfish), the native ones are only a shrimp *Crangon crangon* and one species of crayfish.

The introduction of other two species of crayfish results from accidental or intentional acclimatization. The signal crayfish *Pacifastacus leniusculus*, native to western areas of North America (the Canadian province of British Columbia and the US states of Washington, Oregon, and Idaho), occurs in the Kaliningrad region only in Yantarnoe Lake (Sinyavinsky quarry, formerly Walter amber quarry) located

between Yantarny and Sinyavino villages. The spiny-cheek crayfish *Orconectes limosus* is of North American origin as well. It was introduced to Europe in 1890 and colonized all types of water bodies in 21 countries, including Poland, Lithuania, and Belarus. Precisely this species turned out to be a carrier of an oomycete *Aphanomyces astaci*, the causative agent of crayfish plague, and this became a classic case of barbaric acclimatization with catastrophic consequences.

Procambarus clarkii (a so-called red swamp crayfish from Florida) is widely distributed and beloved by aquarists for its bright coloring. This species can carry crayfish plague, is very aggressive towards other crayfish, and actively digs the bottom. It is already clear that the distribution of this American crayfish was a mistake with very unpleasant consequences [Aklehnovich, Razlutskij, 2013; Laurent, 1997; Westman, 2003].

A crab *Rhithropanopeus harrisii* is also of American origin. Its native range is believed to cover fresh and estuarine waters off the eastern coast of North America from the southwest of the Gulf of St. Lawrence (Canada) to Veracruz (Mexico) [Williams, 1984]. Assumably, it migrated from there to waters of the western US. In 1874, the species was registered in Europe [Turoboyski, 1973].

The mitten crab *Eriocheir chinensis* was introduced to Europe from the Yellow Sea in 1912 at the larval stage with ballast water and was found in the Aller River (Germany). From there, it distributed widely in rivers and canals of all Europe from Germany and France to the Mediterranean Sea. In waters of the Kaliningrad region, it was first recorded in 1935 [Bacevièius, Gasiûnaitë, 2008]. In the Black Sea, it was found in 1998, and in the White Sea, in 2010 [Kitaiskii mokhnatorukii krab, 2023].

A shrimp *Palaemon elegans* appeared in waters of the Kaliningrad region in 2002. The first single specimens were caught in the sea almost at the water's edge near Kulikovo village. A year later, it was already caught in relatively large quantities in the Vistula Lagoon, at the Baltic Spit, in a so-called hydro harbor, and in ditches of the Baltiysk forts. The range of this species and other taxonomic, ecological, and faunistic data about it are provided below. There, we would like to note that two more *Palaemon* representatives were found in Polish waters: *P. adspersus* and *P. macrodactylus*. They have not yet been recorded in the Kaliningrad region, but at least the second one may penetrate there in the near future. This governed the necessity to make a "tool" for their rapid and reliable detection in our waters.

The author hopes that this work will be useful as a guide for a wide range of hydrobiologists interested in active invasive species of hydrobionts which include not only representatives of the genus *Palaemon*. Therefore, we considered it necessary to precede the information directly on these species with data on the body morphology of caridean shrimps.

Body structure of caridean shrimps. Shrimps belong to higher crustaceans which are characterized by a constant number of body segments (21); within higher crustaceans, shrimps belong to the order Decapoda, suborder Pleocyemata, and infraorder Caridea [De Grave, Fransen, 2011]. This is a large group of marine, brackish-water, and freshwater arthropods accounting for 3.5 thousand species. The main morphological characters distinguishing them from representatives of other orders of higher crustaceans are structural features of the cephalothoracic shell (carapace). From above and from the sides, it covers the five-segmented head (cephalon) and the eight-segmented thorax. Together, they form the cephalothorax. The lateral surfaces of the carapace (branchiostegites) form the outer walls of the branchial chamber enclosed between the inner surfaces of the branchiostegites and the wall of the cephalothorax. The cephalothorax bears appendages (limbs or their derivatives). Those are divided into three groups. The front five pairs are located within the cephalon. These are two pairs of flagella (antennules and antennae) performing the functions of sensory organs (touch and chemical sense organs) and three pairs

of jaws (mandibles and two pairs of maxillae). The thorax bears eight pairs of appendages; the first three ones perform the function of maxillipeds, and five pairs of the walking legs, or pereiopods, perform the locomotor function. The first three pairs (in all representatives of the suborder Dendrobranchiata and in Stenopodidea from Pleocyemata) or two pairs (in Caridea) are armed with claws.

In the gill chamber of decapods, each somite of the thorax and (or) its appendages initially bear four gills named according to their position. The gill sitting on the wall of the segment above the articulated coxa (the first segment of the limb) of this segment is called a pleurobranch. A pair of gills attached to the articular membrane between the body wall and the coxa are arthrobranchs. A gill sitting on the coxa outgrowth serving to ventilate the gill chamber (the epipodit) is called a podobranch.

There are three main types of gills: phyllobranchia, trichobranchia, and dendrobranchia. Phyllobranchia have the simplest structure. This is a stack of leaf-shaped gills sitting in pairs along the axial blood vessel. Trichobranchia are bundles of filiform gills around the axial vessel of the gill. Dendrobranchia are formed by primarily paired gills subdivided into tree-like dissected bundles [McLaughlin, 1980]. Shrimp of the family Palaemonidae to which the genus *Palaemon* belongs have phyllobranchia.

The terminology used to describe shrimps is shown in Fig. 1.

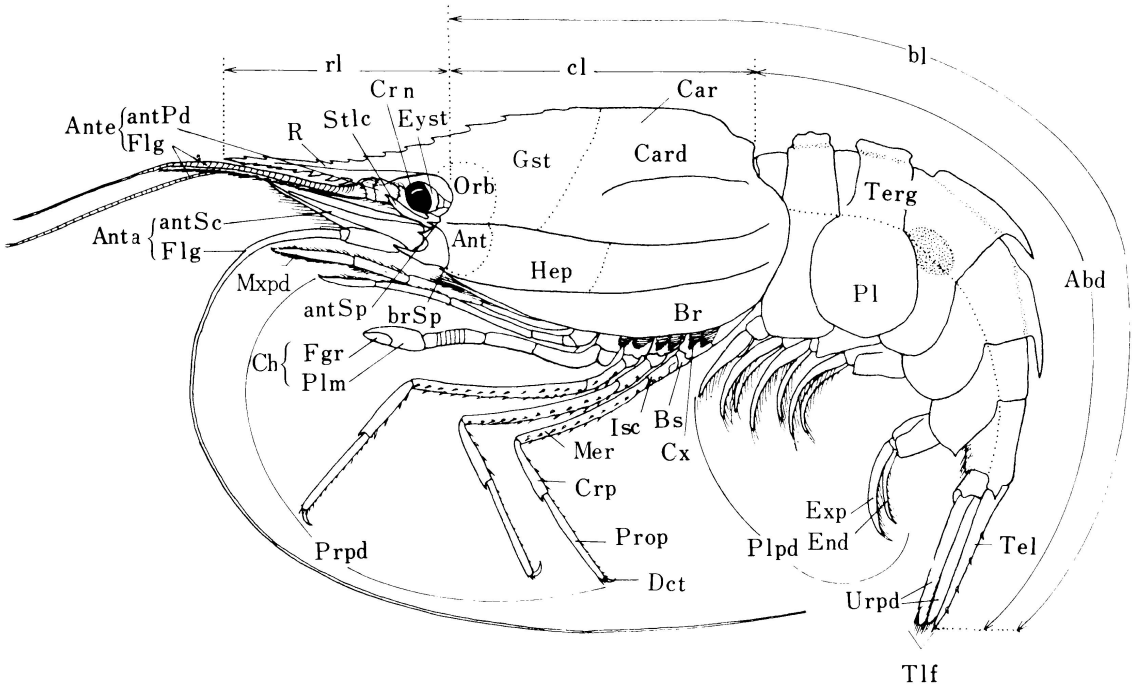

Fig. 1. Terminology used in the identification of shrimps (after [Baba et al., 1986], with additions). AntPd, antennular peduncle; antSC, antennal scale; antSp, antennal spine; bl, body length; Bra, brachial region; brSp, branchiostegal spine; Bs, basis; Car, carapace; Card, cardial region; Ch, chela; cl, carapace length; Crn, cornea; Crp, carpus; Cx, coxa; Dct, dactylus; End, endopod; Exd, exopod; Fgr, finger; Flg, flagellum; Gst, gastric region; Hep, hepatic region; Isc, ischium; Mer, merus; Mxpd, maxilliped; Orb. region, orbital region; Pl, pleuron; Plpd, pleopod; Plm, palm; Prop, propodus; Prpd, pereiopod; Rost, rostrum; rl, rostrum length; Stlc, stylocerite; Tel, telson; Terg, tergit; Tif, tail fan; Urpd, uropod

Shrimps cover a large group of decapods characterized by a unique appearance (so-called shrimp-like) and previously attributed to the former suborder Natantia of the order Decapoda. To date, they are included in the suborders Dendrobranchiata Bate, 1888 (entirely) and Pleocyemata Burkenroad, 1963 (the infraorders Procarididea Felgenhauer & Abele, 1983, Stenopodidea Spence Bate, 1888, and Caridea Dana, 1852) [De Grave, Fransen, 2011; Martin, Davis, 2001]. In September 2011, those accounted for 4,048 species [De Grave, Fransen, 2011].

Representatives of this infraorder play an extremely important role in ocean ecosystems. They inhabit the entire World Ocean from the supralittoral to the abyssal zone; they colonized freshwater basins on the Earth's surface and beneath it (in caves). Among them, there are burrowing and shelter-dwelling shrimps, epibenthic, bottom-dwelling, and pelagic ones. They can be commensals and have very complex relationships with other representatives of the fauna (for example, cleaner shrimps from different taxonomic groups, snapping shrimps from the family Alpheidae cohabiting with fish, or shrimps from the subfamily Pontoniinae which are coral symbionts). The role of shrimps in food webs, as well as their role as objects of fishing and mariculture, is well known.

And, as mentioned above, some of them play a significant role as invasive species. Out of them, representatives of the family Palaemonidae absolutely dominate – the largest family of shrimps (981 species, of which 41 are *Palaemon* ones [De Grave, Fransen, 2011]).

The family Palaemonidae covers shrimps with no longitudinal sutures along the entire length of the carapace. The telson bears two or three pairs of spines. Antennules have two completely separated flagella and an additional branch (the third one). Mandibles usually with a cutting process. Maxilla 1 with an unusually large median lobe of the coxa; maxilla 2 without or with one-two endites (internal branches of the limb). The exopodite of maxilliped 1 with a flagellum. Maxilliped 2 bears no large and tightly seating setae on the marginal segment; the maxilliped's third segment from the end is fused with the second one and with the wider following segment. Pleopods 2 of males have a copulatory organ (appendix masculina, the male process) [Chace, Bruce, 1993].

The family is divided into two subfamilies: Palaemoninae and Pontoniinae. Representatives of the first one usually have the posterior margin of the telson armed with two pairs of spines and bearing two or more submedial setae; maxillipeds 3 usually have two arthrobranchs.

Diagnosis of the genus *Palaemon* (after [Chace, Bruce, 1993; Kobyakova, Dolgopol'skaya, 1969]). The rostrum without a protruding basal ridge; on the anterior margin of the carapace, there are two spines: the upper antennal and the lower branchiostegal. In some species, the branchiostegal spine may be slightly offset from the anterior margin of the carapace. A groove ("longitudinal suture") extends backwards from the branchiostegal spine slightly curving downwards. There is no spine in the liver area of the carapace ("liver spine"). The fourth thoracic sternite has a thin median process; mandibles normally have a two- or three-segmented palp. Three posterior pairs of pereiopods have a simple finger which is shorter than the propodus. The endopodite of pleopods 1 of a male has no marginal protrusion.

As already mentioned, in the world fauna, 41 species of *Palaemon* shrimps are currently known. This genus is very widespread in the World Ocean. Its representatives usually inhabit the littoral zone. In water basins with very poorly developed tidal phenomena, its species are found from the water's edge. *Palaemon* representatives inhabit saline water, brackish water, and freshwater of tropical and temperate climate zones. Some species have limited commercial value, primarily as a bait for hook fishing.

To date, there are 6 species of this genus in European seas.

Key to identify shrimp species of the genus *Palaemon* from European waters

(after [D'Udekem d'Acoz et al., 2005; Kulish, 2021], with additions)

1. Branchiostegal spine located on the anterior margin of the carapace 2
– Branchiostegal spine slightly offset from the anterior margin of the carapace . . . . *Palaemon xiphias* Risso, 1816
2. Rostrum not curved or slightly curved upwards, not very thinned distally, and armed with teeth along 85–100% of its dorsal margin; merus of pereiopods 2 shorter than the carpus or equal to it 3
– Rostrum noticeably curved upwards and thinned distally; armed with teeth along 50–65% of its dorsal margin (*i. e.*, one third of the distal part of the dorsal margin is unarmed); merus of pereiopods 2 is 1.25 times the length of the carpus; the rostrum usually with 6–8 dorsal teeth (excluding the subapical one), 2 of which are located on the cephalothorax behind the orbital margin; the distance between the first and second teeth 1.5 times greater than between the second and third ones; mandibular palp three-segmented; dactylus of pereiopods 2 is 0.7 times as long as a palm or more . . . . . *Palaemon serratus* (Pennant, 1777)
3. Not less than 7 (usually more) dorsal teeth (excluding the subapical one); 2 or 3 of them are located on the cephalothorax behind the orbital margin; the posterior margin of the dorsal teeth is directed obliquely upward; in just-caught specimens, the lower half of the rostrum has no red pigment spots 4
– There are fewer dorsal teeth (usually 5–6, excluding the subapical one); one of them is located on the cephalothorax behind the orbital margin, and the second is often located right on it; the posterior margin of the dorsal teeth is directed parallel to the dorsal side of the rostrum; in just-caught specimens, the lower half of the rostrum with red pigment spots; mandibular palp three-segmented; dactylus of pereiopods 2 is 0.8 times the length of a palm . . . . . *Palaemon adspersus* Rathke, 1837
4. Rostrum usually with 7–9 dorsal teeth (excluding the subapical one) 5
– Rostrum usually with 10–12 dorsal teeth (excluding the subapical one); 2 or 3 of them are located on the cephalothorax behind the orbital margin; the distance between the first and second teeth is 1.5–2 times greater than between the second and third ones; the proximal part of the rostrum is not very convex ventrally; the short branch of the external flagellum of antennules is equal to their peduncle; dactylus of pereiopods 2 is 0.7 times the length of a palm; mandibular palp three-segmented; dactylus of pereiopods 3 very slender, approximately 0.9 times as long as the carpus . . . . . *Palaemon macrodactylus* Rathbun, 1902
5. Two posterior dorsal teeth located on the cephalothorax behind the orbital margin; the distance between the first and second teeth 1.5 times greater than between the second and third ones; the proximal part of the rostrum protrudes noticeably ventrally (but not always); the short branch of the external flagellum of antennules is 0.7 times as long as their peduncle; mandibular palp three-segmented; dactylus of pereiopods 2, possibly, longer and slenderer on soft substrates than on hard ones . . . . . *Palaemon longirostris* H. Milne Edwards, 1837
– Three posterior dorsal teeth located on the cephalothorax behind the orbital margin; the distance between the first and second teeth equal to the distance between the second and third ones; the proximal part of the rostrum protrudes strongly ventrally; the short branch of the external flagellum of antennules fused for approximately 50% of its length; the dactylus of pereiopods 2 is 0.4 times the length of the palm; mandibular palp two-segmented . . . . . *Palaemon elegans* Rathke, 1837

Ecological and faunistic characteristics of shrimp of the genus *Palaemon* in European waters

***Palaemon adspersus* (Rathke, 1837)** (Fig. 2A). **Diagnosis** (after [Köhn, Gosselck, 1989], with additions). The length of the rostrum is approximately equal to the length of the carapace; the distal part of the rostrum extends beyond the level of the distal margin of the scaphocerites by approximately the length of the section in front of the distal tooth of the rostrum ventral side. The rostrum with a simple or double apical end, armed from above with five-six, rarely seven teeth, one of which, the most posterior, is on the carapace, behind the orbital margin. The rostrum lower (ventral) side is armed with three, rarely four teeth, with dark brown, to black, chromatophores (according to [D'Udekem d'Acoz et al., 2005], with red spots). Its width is not greater than the width of the upper half of the rostrum. Antennae with two flagella, the outer one with a flagella-like outgrowth fused with the base of the flagella. Mandibles with a three-segmented palp. The length of the claw fingers is ¾ the length of its palm, and the carpus of the pereiopod 2 is shorter than the merus.

Range. The range covers Eastern Atlantic, where the species reaches N60°, the Irish Sea, and the Atlantic waters of Morocco. In the Mediterranean Basin, it is found in the Western Mediterranean, the Alboran, Adriatic, Ionian, and Aegean seas, in the Sea of Marmara, and in the Eastern Mediterranean (Levant) [D'Udekem d'Acoz, 1999]. It inhabits the Black Sea and Sea of Azov [Kulish et al., 2018]. In 1930, *P. adspersus* was accidentally introduced in the Caspian Sea and stayed there. In the Baltic Sea, the species is distributed up to the Southern Finland [Köhn, Gosselck, 1989] and Gdansk [Inyang, 1977/78a, b], and is absent only in the Gulf of Bothnia [D'Udekem d'Acoz, 1999]. It is quite common (but not abundant) in the Bay of Gdansk: there, in summer 1975–1976, the density of the shrimp varied 1 to 17 specimens *per* 100 m^2 at a depth of 1–3 m [Wiktor et al., 1980]. Its low abundance in the Bay of Gdansk is confirmed by other researchers as well [Lapińska, Shaniawska, 2006]. This species inhabits depths of 0.1–10 m together with shrimps *Crangon crangon* and *P. elegans* making up only 2% of the total abundance of caught shrimps of the three species. It has not yet been registered in waters of the Kaliningrad region (our unpublished observations since 2002). The Bay of Gdansk seems to be the eastern border of *P. adspersus* distribution in the Southern Baltic.

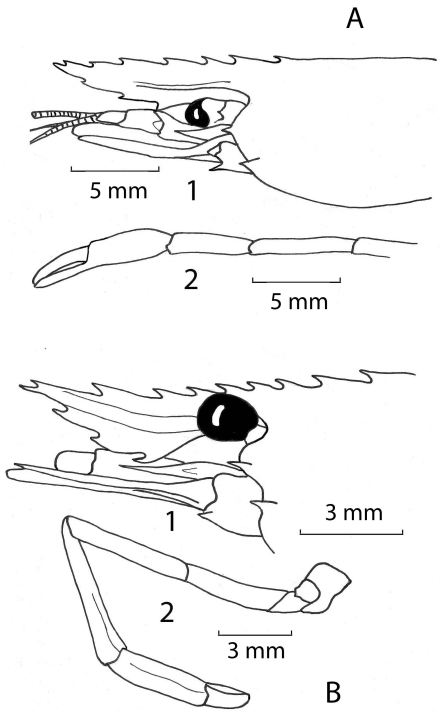

Fig. 2. A, *Palaemon adspersus*; B, *Palaemon elegans*: 1, cephalothorax, side view; 2, the 2nd pereiopods

Ecological characteristics. A shallow-water shrimp. In the northern Black Sea and in the Sea of Azov, it is associated with eelgrass beds [Evchenko et al., 2015] which is likely to result from the fact that it is most abundant in the shallowest areas of lagoons and estuaries inhabiting thickets of *Zostera marina*, *Ruppia* sp., and *Potamogeton* sp. [Kobyakova, Dolgopol'skaya, 1969]. Accordingly, this shrimp prefers relatively soft sediments. In this part of its range, *P. adspersus* is a commercial species; the latest known estimate reports that its stock is 100 t [Evchenko et al., 2015]. Off the southern coast

of the Black Sea (Sinop Peninsula, Turkey), it is found in almost the same conditions. Since the material was sampled in January–February, the shrimp occurred at depths of about 30 m, where its abundance was very low; it migrated to the shore only at relatively high water temperature [Bilgin, Samsun, 2006]. The connection of *P. adspersus* with thickets, primarily *Zostera* ones, is also observed in other parts of its range. M. Gutu [1980] reports that the species was found in its thickets off the coast of Romania, and A. Berglund [1983] reports that it was encountered in Gulmar Fjord (western coast of Sweden), in Northern Denmark, and in waters of France from its northern coast to Arcachon (the southern area of the Bay of Biscay). In such cases, this shrimp was registered on sandy sediments, but it was also recorded in rocky depressions of the intertidal zone filled with water, among brown algae (*Fucus* sp.). In the Gulf of Gdansk, it is noted at depths of 0.5–1.0 m and also among thickets [Lapińska, Shaniawska, 2006; Wiktor et al., 1980]. Euryhaline species. It occurs in water with salinity from 5.5‰ (according to [Köhn, Gosselck, 1989]) or from 7–8‰ to oceanic values [Berglund, 1983; Kobyakova, Dolgopol'skaya, 1969], but prefers brackish-water habitats.

It is difficult to describe in detail *P. adspersus* size composition both because its size varies from region to region and because various researchers measure it differently and do not always report how they determined it. We found no conversion factors from the length of the carapace to the total body length.

The timing of the reproductive period is also very variable. Specifically, in a shallow (the depth averages 0.8 m) lagoon of Missolonghi (the Mediterranean Sea, N38°15′, E21°05′), abundant in aquatic vegetation and organic matter accumulated in the substrate, egg-bearing females are found from January to mid-June. Their highest abundance is registered in April. The duration of egg incubation depends on water temperature: at the beginning of the reproductive period, at +13 °C, it takes 42–47 days, and in the middle, when the value is about +20 °C, it takes 22–25 days. The reproductive period is limited to August, for water temperature reaches its maximum at this time. Year-round observations of fluctuations in the size composition have shown as follows: during the first six months of life, both males and females reach a total body length of 21 mm, and at the age of 1 year, both are of 24 mm. Then, the growth of males slows down; by 3 years (the maximum age), males have a body length of 48 mm, and females, 54 mm (assumably, the total body length was measured from the posterior margin of the orbits to the posterior margin of the telson). In winter, the growth almost stops [Klaoudatos, Tsevis, 1987]. These researchers indicate referring to literature sources that in waters of Denmark and Eastern Germany, the reproductive period lasts from May to late August. The mean realized fecundity of *P. adspersus* off the southern coast of the Black Sea is (1,963 ± 144) eggs (the range is 758–3,710). The mean egg sizes (short–long axis) at initial and late stages of embryonic development are 0.58–0.74 and 0.62–0.85 mm, respectively [Bilgin, Samsun, 2006].

In different parts of the range, biological parameters of this species vary, and this also affects the lifespan: it can exceed 3 years. The end of the reproductive period in mid-June, when water temperature is higher than +21 °C, suggests why *P. adspersus* range is limited to temperate and subtropical climatic zones: reproductive activity is possible at water temperature within +13…+20 °C [Klaoudatos, Tsevis, 1987].

Its diet includes detritus, algae, polychaetes, crustaceans, small molluscs, and juvenile fish [Köhn, Gosselck, 1989]. N. Inyang [1977/78b] expands the list of plant remains (in addition to algae, it contains diatoms and *Zostera*). When listing crustaceans, the researcher indicates the occurrence of decapods, as well as copepods, amphipods, and mysids, which together make up about 40% of all the food consumed. The second place is occupied by detritus (35.7%), and the third one, by polychaetes (18.3%).

To study food composition of *P. adspersus* in the Black Sea, the shrimp was sampled in the area of the Lebyazhy Islands of the Karkinitsky Bay, at a depth of less than 1.5 m, in September 2016, from commercial trap nets [Burukovsky, 2019]. The specimens had a body length (from the posterior margin of the orbits to the end of the telson) of 31.5–58.1 mm (males were of 33.9–44.1 mm, with a mode of 37 mm). The sex ratio was approximately 1 : 8 (11.7% of males and 82.3% of females). Females were represented by two groups: shrimps with gonads at maturity stage II had a modal size of 37 mm, and shrimps with gonads at maturity stage III, 47 mm. Therefore, in September, some of females already mated and molted, and vitellogenesis began in their gonads.

It turned out that *P. adspersus* is a benthic feeder and an euryphagous species. Its food spectrum covers a wide range of food objects: from detritus and plant remains to gastropods, higher crustaceans, including shrimps, and fish. In terms of the way it obtains food, it is primarily a gatherer – a detritivore and necrophage, with 70% of the volume of the virtual food lump occupied by detritus and corpses of higher crustaceans. At the same time, towards polychaetes, it behaves as an attacking predator, and towards gastropods, as a grazing one [Burukovsky, 2022a]. Comparison of food composition of this shrimp in the Karkinitsky Bay [Burukovsky, 2019] with that in the Baltic Sea [Inyang, 1977/78b], in Atlantic waters [Figueras, 1986], and Mediterranean waters [Guerao, 1993–1994] of the coast of Spain reveals its spatial and temporal quasi-stability. Based on all of the above, *P. adspersus* should be classified as an opportunistic predator of the subtidal zone [Burukovsky, 2019, 2022a].

It has not yet been encountered off the coast of the Kaliningrad region. The reason is probably as follows. In terms of temperature and salinity, waters washing the shores of this region are similar to those in the neighboring Gulf of Gdansk. However, sediments differ: along the coast of the Kaliningrad region, those are of accumulative origin and are composed of sands brought by a longshore current from the southwest. The bottom of coastal shallows is also composed by medium-sized sands with an admixture of gravel. There is almost no silt in sediments [Blashchizhin, 1976]. Apparently, due to this, there are no permanent *Zostera* and *Fucus* thickets in waters. In some areas, storms regularly wash ashore thickets of both *Zostera* and *Fucus*. It is believed to indicate the temporary nature of their existence [Gubareva et al., 2006]. Probably, this is why *P. adspersus* larvae (undoubtedly carried by the current into our waters) cannot find conditions there for the formation of permanent settlements.

***Palaemon elegans* Rathke, 1837** (Fig. 2B). **Diagnosis** (after [Köhn, Gosselck, 1989], with additions). The rostrum is straight or slightly curved upwards. The maximum width of its lower plate is greater than that of the upper one. The rostrum is approximately equal in length to the carapace; its distal end usually does not extend beyond the distal margin of the scaphocerites and is most often bifurcated. The dorsal side of the rostrum bears seven to ten teeth, usually eight-nine. Out of them, three (rarely two) are located on the carapace behind the eye orbit. The lower side of the rostrum is armed with three-four teeth. Mandibles have a two-segmented palp (not a three-segmented one, as in other European species of the genus *Palaemon*). The carpus of the pereiopod 2 is usually longer than the merus and shorter than the claw. The length of the claw fingers is noticeably shorter than the length of its palm.

Range (after [D'Udekem d'Acoz, 1999], with additions). It covers Eastern Atlantic. In the north, the shrimp inhabits areas from the south and east of Norway, where it reaches N60°. In the east, the distribution limit is the Baltic Sea (up to the Gulf of Finland [Katajisto et al., 2013]), all coasts of Britain, waters along the southern coast of the North Sea, the Bay of Biscay, waters of Galicia (Spain), Portugal, Southwestern Spain, and Atlantic waters of Morocco. *P. elegans* was found on the Argen Bank (Mauritania) [Schaffmeister et al., 2006]. At one time, the shrimp was also believed to inhabit

the Cape Verde islands and areas along the entire tropical coast of Western Africa [Fransen, 2023]; later, it was proven that this is *P. vicinus* – a species closely related to *P. elegans* [Ashelby, 2009]. It is registered off Madeira Island, the Azores, and Canary Islands. It inhabits all the seas in the Mediterranean Basin, and also it occurs in the Black Sea and Sea of Azov [Borcea, 1929; Caspers, 1951; Kobyakova, Dolgopol'skaya, 1969; Gutu, 1980]. In 1954–1956, during the acclimatization of the mullet in the Aral Sea, *P. elegans* accidentally penetrated there from the Caspian Sea and formed in the Aral Sea dense commercial aggregations [Kobyakova, Dolgopol'skaya, 1969; Vinogradov, 1968]. It survived the death of the Aral Sea and two crisis situations in the remaining "stub." It survived until the early XXI century. Unfortunately, the researcher does not report whether the shrimp occurs there now [Plotnikov, 2021].

It is found in continental waters of Israel and Iraq, where, the same as in the Caspian Sea, it penetrated because of accidental introduction [Plotnikov, 2021].

Outside the Atlantic Ocean basin, *P. elegans* was registered in the Suez Canal. There, it was among so-called Lessepsian migrants named after an engineer Ferdinand de Lesseps, who built the Suez Canal between the Mediterranean and Red seas (opened in 1869). Therefore, it is not accidentally recorded in the Red and Arabian seas and in Persian Gulf.

Ecological characteristics. It inhabits depths from the water's edge down to 5 m and prefers seagrass thickets and depressions of the rocky substrate where there is water during low tide [D'Udekem d'Acoz, 1999; Gutu, 1980]. A marine species, but also occurring in brackish water and freshwater. Mostly confirming this, H. Caspers [1951] adds as follows: off the coast of Bulgaria, single small individuals are found at depths down to 18 m. Off the coast of Romania, it is found at depths of 6–12 m on silty–sandy bottom together with *Crangon crangon* [Borcea, 1929].

P. elegans from the Sea of Azov is called a rockpool shrimp [Evchenko et al., 2015; Kulish et al., 2018], as it prefers relatively hard bottoms, stone accumulations, and baths on rocky littorals [Berglund, 1983; Kobyakova, Dolgopol'skaya, 1969]. However, the same as *P. adspersus*, this species can inhabit seagrass thickets, often together with *P. adspersus*. In the Sea of Azov, it is noted everywhere: from the Perekop Bay to the Kerch Strait. In this water body, its usual length in catches is 7–8 cm (the technique of measurement is not reported), and weight is up to 2.5 g. There, *P. elegans* inhabits the coastal zone among stones and algae, especially *Cystoseira* and *Zostera*.

In waters of Morocco, egg bearing lasts February to July [Lagardére, 1971]. Off the coast of Bulgaria and in the Sea of Azov, the shrimp reproduces May to August, and the peak of spawning occurs in the second half of May – in June [Caspers, 1951; Evchenko et al., 2015]. A female lays 160–3,600 eggs on pleopods carrying them for 1–1.5 months [Evchenko et al., 2015]. During summer, each female is capable of carrying eggs 3–4 times. Off the southern coast of the Black Sea, the mean fecundity of *P. elegans* is (1,057 ± 88) eggs (the range is 308–2,628). The mean egg sizes (short–long axis) at initial and late stages of embryonic development are 0.45–0.57 and 0.48–0.71 mm, respectively [Bilgin, Samsun, 2006].

The exact timing of the reproductive season of the shrimp in waters of the Kaliningrad region has not yet been established. However, it is clear that females can spawn there at least three times during summer.

In the Gulf of Gdansk located to the west of the Kaliningrad region, *P. elegans* is especially abundant on hard and rocky substrates or near concrete piers. The species is often found among filamentous green and brown algae growing on hard substrates [Janas, 2005].

In waters of the Kaliningrad region, it is distributed along the entire coast; this species has inhabited the entire Russian area of the Vistula Lagoon, as well as ditches and canals of the Baltiysk old forts. Its biotope is similar to that described above. In summer, both in the sea and in the lagoon, the shrimp is recorded at shallow depths from the water's edge; in the lagoon, it definitely prefers harder substrates. For example, it is abundant in the so-called hydro harbor of the Baltic Spit, where it inhabits almost the water's edge: cavities under dilapidated concrete lining of edges of the hydro harbor and aggregations of filamentous algae (own observations). The strip along the sea coast, where *P. elegans* is not so abundant, but also occurs, is characterized by medium-sized sands with an admixture of gravel [Blashchizhin, 1976]. The species tolerates significant desalination and withstands salinity fluctuations up to 35‰ and even up to 45‰ (at a temperature of +10 °C). In the Baltic Sea, it occurs at salinity from 15–20‰ (at its western border, in the Kattegat area) to 6–8‰ (in the Baltic Sea) and even to 2‰ (in the Gulf of Bothnia) [Janas, Mańkucka, 2010]. Larvae prefer stable temperatures of about +18 °C for their normal development [Inyang, 1977/78a, b]. In the Black Sea, the shrimp performs seasonal migrations moving from shallows to depths down to 30 m [Kobyakova, Dolgopol'skaya, 1969; Evchenko et al., 2015].

In the Kaliningrad Gulf and Primorskaya Bay of the Vistula Lagoon, the length of the shrimp carapace varied 2.1 to 11.8 mm. Considering the shape of the size composition curves, the total lifespan of *P. elegans* reaches three years. Sex differentiation occurs in the first year of life. Males were not recorded among three-year-old individuals. Assumably, they do not survive (at least, most of them) to this age. Females grow faster than males, and in size groups of 7–8 mm, there are already no males. Juveniles begin to appear in July, but mass replenishment of shrimp settlements occurs in September [Tsigvintsev, 2008].

In the Vistula Lagoon, detritus and plant remains prevailed in full stomachs of *P. elegans*. Detritus looked as a grayish-brown suspension or flakes, and in full stomachs, as a flocculent mass.

Plant remains were represented by higher plants with leaf scraps and their periphyton and by algae. Living plants were not noted among plant remains. They always bore traces of more or less prolonged maceration. In periphyton, diatoms, green algae, and blue-green algae were found belonging to five classes: Pennatophyceae, Centrophyceae, Chlorophyceae, Chlorococcophyceae, and Hormogoniophycea. A total of 23 species were identified.

Most often, shrimps of all size groups contain detritus (88.9%) and chironomid larvae (52.1%). In the virtual food lump, detritus prevailed (making up ⅔ of its volume, 70.4%), as well as plant remains (17.6%). These two food objects, along with periphyton algae, occupy 99.8% of the reconstructed mean volume of the food lump.

Consequently, *P. elegans* is a typical epibenthic shrimp behaving in the Vistula Lagoon as a benthic feeder which prefers a pretty narrow range of bottom objects. Its food also includes planktonic organisms (single cyclops and rotifers), but they are accidental. Detritus and plant remains, accompanied by periphyton algae, completely dominate the shrimp stomachs. In the Vistula Lagoon, *P. elegans* seems to serve currently as the main consumer of detritus of plant origin at different stages of its formation – together with associated periphyton. Apparently, *P. elegans* has no serious competitors among autochthonous species of the lagoon [Burukovsky, 2012, 2022b]. It does not compete with another, "older" invader of the Vistula Lagoon: the crab *Rhithropanopeus harrisii* which prefers there living higher plants with no signs of periphyton [Burukovsky, 2022a].

***Palaemon longirostris* H. Milne Edwards, 1837** (Fig. 3). **Diagnosis** (after [Smaldon, 1993; Zooplankton and Micronekton, 2023]). The rostrum straight or slightly curved upwards and protruding beyond the scaphocerite; end of the rostrum sometimes bifurcated and armed with seven-eight dorsal and three-four (rarely five) ventral teeth. Two dorsal teeth are located behind the posterior margin of the orbits; the distance between the first and second teeth is approximately 1.5 times greater than between the second and remaining distal teeth.

The carapace with antennal and branchiostegal spines. Antennae have three flagella; the short branch of the external flagellum is approximately 0.66 (⅔) the length of the antennular peduncle and merges with the long flagellum for approximately ⅓ of its length. The outer margin of the stylocerite straight or slightly convex; its anterior margin convex. The scaphocerites reach the distal half of the carpus of pereiopods 2, sometimes extend somewhat further; the apical spine does not extend beyond the distal margin of the lamellar part of the scaphocerite. Maxillepedes 3 with the exopodite. Mandibles with a three-segmented palp. The finger of pereiopods 2 is approximately 0.4–0.5 times the length of the palm of the claw, but is variable; the carpus is equal in length to the merus or slightly longer. Telson with two pairs of lateral spines.

Note. In 1968, the species *Palaemon garciacidi* was described [Zariquiey Álvarez, 1968]. Its range was limited to waters of Southern Portugal and Southeastern Spain and to the Atlantic waters of Morocco [D'Udekem d'Acoz, 1999]. Interestingly, J.-P. Lagardére [1971] noted that the variability of the rostrum structure in this species overlaps with that of *P. longirostris*. Therefore, he considered *P. garciacidi* Zariquiey Álvarez, 1968 to be not an independent species, but a subspecies *P. longirostris* sp. *garciacidi* Zariquiey Álvarez, 1968. A comparative morphological and genetic study of shrimps from different populations attributed to these two taxa showed that *P. longirostris* and *P. garciacidi* should be considered one species, and the differences between shrimps from various habitats do not exceed the limits of interpopulation variability [Cartaxana, 2015]. Based on the priority criterion, this is *P. longirostris*.

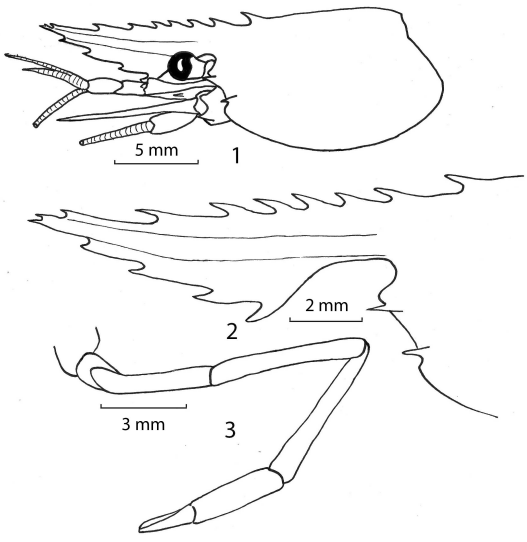

Fig. 3. *Palaemon longirostris*: 1, cephalothorax, side view; 2, rostrum, side view; 3, the 2nd pereiopods

Range. The species inhabits the Eastern Atlantic, where it is recorded from Northeastern Germany to Morocco [D'Udekem d'Acoz, 1999; Lagardére, 1971]. Within this area, it is occasionally found south, southeast, and southwest of England [Smaldon, 1993]. The shrimp is registered in the Bay of Biscay and in Portuguese waters. There are poorly confirmed signals that it occurs in various parts of the Mediterranean, *inter alia* off the Aegean coast of Turkey and in waters of Israel. It was recently noted off the southern coast of the Black Sea (Sinop Peninsula) [Sezgin et al., 2007] and off the southwestern coast of the Crimea, in the estuary of the Chernaya River, at a depth of 3–4 m, on silted shell rock [Statkevich, 2019]. Assumably, *P. longirostris* has already settled in the Black Sea, and its new findings should be expected.

The size of egg-bearing females (the carapace length) is 7.1 to 14.6 mm. In waters of England, they spawn April–May to August [Smaldon, 1993]. Further south, in France, in the Gironde River, egg-bearing females begin to occur earlier, March to July, and spawn at least once a season. They carry 78–1,391 eggs on pleopods; the mean value is (547 ± 234) eggs [Béguer et al., 2010]. Off the coast of France, *P. longirostris* is considered a commercial species with an annual catch of 36–82 t [Béguer, 2010]. Further south, in waters of Morocco, the reproductive period begins earlier, in January, and lasts until July, with a peak in April–May [Lagardére, 1971].

This species tends to act as a predator preferring the most accessible food objects. Juveniles in the Gironde estuary feed mainly on copepods (*Eurytemora affinis* and *Acartia bifilosa*) and adult mysids (*Mesopodopsis slabberi* and *Neomysis integer*). At the same time, they can feed on amphipods (*Gammarus zaddachi*), polychaetes, juvenile decapods, and detritus. There is a tendency to necrophagy. Larvae feed on diatoms [Béguer, 2010].

***Palaemon macrodactylus* Rathbun, 1902** (Fig. 4). **Diagnosis** (after [D'Udekem d'Acoz et al., 2005]). The rostrum straight and extending beyond the distal margin of the antennular peduncle; rather narrow in its proximal third. Its dorsal side armed with 9–15 teeth, most often 10–12 (excluding the subapical one). Two-three teeth of the dorsal series located on the carapace behind the level of the orbits. The first tooth separated from the second one by a distance 1.5–2 times (sometimes more) exceeding the distance between the second and third teeth. The size of the gap between the teeth gradually increases from front to back. The distance between two distal teeth approximately equal to that between two proximal ones (or less). The dorsal teeth of the rostrum directed obliquely upwards. The ventral side of the rostrum armed with three-five teeth. There is a branchiostegal spine on the anterior margin of the carapace. The short branch of the outer flagellum of the antennule is equal in length to the antennular peduncle. Mandibular palps three-segmented. The length of the claw fingers is 0.7 of the palm length. The length of the propodus of pereiopods 2 is equal to the length of the carpus. On pereiopods 3–4, the length of the fingers is almost equal to the length of the carpus.

History of the formation of the modern range of the species. The homeland of *P. macrodactylus* is the Far East. There, the northern border of its range is Peter the Great Bay. Further south, the shrimp is found off the coast of South Korea and China, up to the Yangtze River mouth, and inhabits waters of Japan [Ashelby et al., 2013; Marin, 2013]. It is described from waters of Taiwan as well [Chan, Yu, 1985].

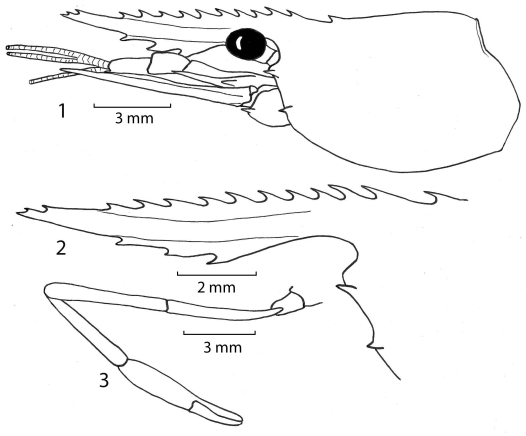

Fig. 4. *Palaemon macrodactylus*: 1, cephalothorax, side view; 2, rostrum, side view; 3, the 2nd pereiopods

The first data on *P. macrodactylus* outside its native range were published by W. Newman in 1963 (cited after: [Ashelby et al., 2013]), *prior* to its finding in waters of Taiwan. It was recorded in San Francisco Bay, and it was already a settled species at that time there. W. Newman believed that *P. macrodactylus* had been inhabiting this area since at least 1954 and was introduced to San Francisco Bay during the Korean War. Anyway, it was recorded there in commercial quantities in 1957 and was used as a fishing bait [Ashelby et al., 2013]. To date, this species is distributed in the Eastern Pacific as far north

as Boundary Bay (it is located on the border between the Canadian province of British Columbia and the US state of Washington) and as far south as the Los Peñasquitos Lagoon (San Diego County, 120 miles south of Los Angeles) [Ashelby et al., 2013].

In the 1960–1970s, *P. macrodactylus* was registered in Australia. The history of its occurrence there remains unclear. First, it was noted in Mannering Lake in the state of New South Wales (Southeastern Australia), and later, it was encountered in the vicinity of Port Adelaide on the southern coast of the continent. Moreover, it is assumed that the settlement in Southeastern Australia has not survived to this day [Ashelby et al., 2013].

In the 1990s, the shrimp appeared in European waters. It was first found in the River Thames. Currently, *P. macrodactylus* has settled in a vast area of the Northeastern Atlantic: from the southern area of the North Sea in the north to Southern Spain [Ashelby et al., 2013; D'Udekem d'Acoz et al., 2005; González-Ortegón et al., 2006]. It is still unclear how the species penetrated into the Northeastern Atlantic: directly from Asia or from San Francisco.

As for the Baltic Sea, in the paper [Ashelby et al., 2013], the researchers note that this sea can be considered a risk region for *P. macrodactylus* introduction.

In 2002, the shrimp was found in waters of Romania (Black Sea), in the Port of Constanța, and then in Bulgaria, in the brackish-water Lake Varna which is connected to the sea [Micu, Niţă, 2009; Raykov et al., 2010]. As assumed, the species was carried there from Rotterdam with ballast water.

Around the same time (at least, since 2001), *P. macrodactylus* was registered in the New York estuary network. In the first samples taken that year, there were egg-bearing females, *i. e.*, it was already an established settlement. The region is characterized by such a high density of shipping that it was impossible to determine where this species came from: San Francisco or new settlements in European waters [Ashelby et al., 2013; Warkentine, Rachlin, 2010].

In the same 2001, there was a report on *P. macrodactylus* record in the Southeastern Atlantic, in the port of Mar del Plata (Argentina). There, the shrimp inhabits waters with a mean salinity of 32–33.7‰; it has already distributed over 120 km to the south and to the north, to the borders of Uruguay [Spivak et al., 2006].

In 2005, the species was registered in the Mediterranean Sea: first, in its western part, in waters of the Balearic Islands [Ashelby et al., 2013]; in May 2012, in the Venice lagoon (the northern Adriatic Sea, Italy) [Cavraro et al., 2014]. After this, the "conquest" of the Black Sea was only a matter of time. Indeed, in 2009, the shrimp was noted in Bulgaria, in the above-mentioned Lake Varna formed as a result of global geological shifts and connected to the sea; then, it was recorded in waters of Romania [Micu, Niţă, 2009]. Finally, in July 2018, *P. macrodactylus* was first caught in waters of the European Russia: in the Kerch Strait area (Sea of Azov, coast of the Chushka Spit, Krasnodar Krai) [Timofeev et al., 2019]. A few years later, its settlements were found in the Don River estuary [Matishov et al., 2022]. Consequently, the species definitely settled in the Black Sea and Sea of Azov.

To date, *P. macrodactylus* can be considered a cosmopolitan of temperate and subtropical waters, although in the south of the Asian part of its range, it reaches tropics in waters of China and Taiwan. It can be assumed that the "conquest" of the World Ocean by this species is not yet complete.

Ecological characteristics. Undoubtedly, successful distribution of this species may result not only from significantly developed shipping, but also from its tolerance to a wide range of temperatures and salinities and to hypoxic conditions. Moreover, *P. macrodactylus* is a great osmoregulator

and, accordingly, can inhabit freshwater or almost freshwater areas, as in California, and areas with completely marine conditions, as in Mar del Plata [Spivak et al., 2006].

In waters of the Northern Europe, *P. macrodactylus* prefers brackish estuaries, where it inhabits areas of port walls and yacht moorings, as well as spots where floating garbage and a reed (*Phragmites australis*) are accumulated. This is probably why this species, the same as *P. adspersus*, has not yet penetrated into waters of the Kaliningrad region and Lithuania (due to features of currents and sedimentogenesis of these areas, see above).

The peculiarities of life cycle vary greatly from area to area. In the native part of the species range, the breeding season lasts mid-April to early October; in California, egg-bearing females occur May to August; and in Argentina, the breeding season is confined to the southern summer, October to March. Two-year-old *P. macrodactylus* females lay their eggs on pleopods earlier than one-year-old females. One-year-old shrimps lay less than 1,000 eggs, and older ones lay 500 to 2,800. Representatives of each age group can produce at least two generations *per* year, while in laboratory-controlled conditions, they can spawn five to nine times in a row.

The growth rate of females is the highest in the first year of life with a spurt (acceleration) before spawning. The next year, growth slows down. Sexual differences emerge when the shrimps reach the length of 20 mm; females grow faster than males and are larger. Lifespan in Japanese waters is two-three years. In Mar del Plata, the species lives less than in the native part of its range, and this is due to stressful conditions of their habitat in highly saline water [Ashelby et al., 2013].

Stomachs of *P. macrodactylus* contain remains of mysids, copepods, amphipods, barnacles (Balanidae), polychaetes, small bivalves, fish larvae, and insects. They account for 75–93% of stomach contents [Ashelby et al., 2013]. Therefore, the species is considered omnivorous, although it seems clear that it is, first of all, a predator and, possibly, a predator-gatherer (according to [Burukovsky, 2022b]).

***Palaemon serratus* (Pennant, 1777)** (Fig. 5). **Diagnosis** (after [Smaldon, 1993]). The rostrum noticeably curved upwards; its end usually bidentate. In adults, dorsal teeth do not reach the distal third of the rostrum. Six or seven dorsal teeth, and four-five ventral ones; two dorsal teeth located behind the posterior margin of the orbits. The carapace with antennal and branchiostegal spines. Antennae have three flagella; the short branch of the outer flagellum of antennules is approximately 0.85 times the length of the antennular peduncle, and the fused part of the flagellum is 0.20–0.25 times the length of the long flagellum. The outer margin of the stylocerite is convex, but may be slightly concave; in very large individuals, the anterior margin of the stylocerite is convex, and the apical spine is long and strong. The scaphocerite reaches half the length of fingers of pereiopods 2 or the distal end of the finger in juveniles; the apical spine of the scaphocerite does not extend beyond the anterior margin of its plate. Maxillipeds 3 reach half the length of the scaphocerite or are slightly shorter; there is the exopodite. Mandibles with three-segmented palps. Dactylus of pereiopods 2 equals 0.5 times the length of the propodus; merus is 1.25 times the length of the carpus. Telson with two pairs of lateral spines.

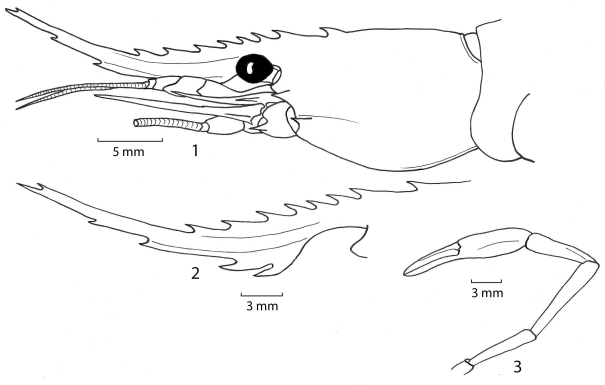

Fig. 5. *Palaemon serratus*: 1, cephalothorax, side view; 2, rostrum, side view; 3, distal part of the 2nd pereiopod

Range. Off the coast of Britain, it is common in the south, southwest, and west and rare in the northeast, although single specimens have been recorded off Northumberland. The shrimp was encountered off the western, southwestern, and southeastern shores of Ireland [Smaldon, 1993]. It occurs in the North Sea, in waters of France: off both coasts of the Cotentin Peninsula and in the Bay of Biscay. *P. serratus* was registered off the coast of Northern Spain (Galicia) and Portugal, off the southwestern coast of Spain, Canary Islands, and the Madeira. It was noted off the coast of Morocco up to Western Sahara. The species was found almost everywhere in the Mediterranean Basin, Sea of Marmara, and Black Sea. Interestingly, *P. serratus* is quite rare in the Black Sea. It was reported from the coast of the Crimea, Lake Varna, and Sukhumi Bay [Kobyakova, Dolgopol'skaya, 1969]; also, it was recorded in underwater karst caves of the Western Crimea (Cape Tarkhankut) [Kovtun, Makarov, 2011].

Ecological characteristics. The shrimp is common along rocky shores, in tidal baths, but often also near shores unprotected and moderately protected from waves, as well as in the subtidal zone among algae (in South Wales, England, among *Laminaria digitata* and *Fucus serratus* [Grenfell, 2013]), and in *Zostera* thickets. *P. serratus* can occur in the same tidal baths as *P. elegans*, but it does not go as far into the littoral zone as the second species [Smaldon, 1993].

It inhabits depths from the water's edge down to 40 m, where it spends winter months. At these depths, females prefer rocky substrates, and males choose silty soils. In summer, the shrimp migrates to estuaries and reaches there the peak of abundance by September; then, is goes back. The reason is this species actively avoids open sea areas (water is too cold in winter and warm in summer). Males are the first to migrate both to estuaries and back [Grenfell, 2013].

The maximum total length is 110 mm; usually, it is slightly less than 100 mm (for some reason, the total body length was measured by this author from the posterior margin of the orbits to the posterior margin of the sixth abdominal segment, and not the telson, as is accepted by most researchers. – *R. B.*). The species is characterized by sexual dimorphism of body size. The mean size of males is 7.5 cm; females, 9 cm. One of the reasons is that males reach sexual maturity at the age of 6–7 months, while females reach sexual maturity at 9–10 months [Grenfell, 2013].

In British waters, the breeding season lasts usually November to June, with some large females laying their eggs in July, August, and September [Smaldon, 1993]. In the Ebro River delta (the Western Mediterranean), the breeding season begins in August, when females with mature gonads appear in shallows overgrown with *Zostera*. However, the proportion of egg-bearing females is low there. They may migrate to other habitats [Guerao, Ribera, 2000].

***Palaemon xiphias* Risso, 1816** (Fig. 6). **Diagnosis.** The anterior end of the rostrum always extends beyond the anterior margin of the scaphocerite, and its distal part is curved upward. The rostrum has seven dorsal teeth (rarely eight or six), one subterminal, and five ventral (rarely four). Two posterior dorsal teeth are located on the carapace behind the posterior margin of the orbits. The branch of the short flagellum of the antennule is fused for approximately ⅕ of its length. The palp of the mandible is three-segmented. The claw finger of the pereiopods 2 is significantly longer than the palm of the claw and slightly longer than the carpus. The branchiostegal tooth is located at a distance from the anterior margin of the carapace [Lagardére, 1971; Pesta, 1918].

Range. An inhabitant of the Eastern Atlantic, including water areas of Canary Islands and Madeira. It is registered almost everywhere in the Mediterranean Sea: in the Alboran, Adriatic, Aegean, and Ionian seas and off the coast of Northern Africa from Egypt to Morocco. Wherever it is found, it is closely related to thickets of a seagrass, primarily *Posidonia oceanica* and to a lesser extent *Zostera marina*

and *Cymodocea nodosa*. In fact, the range of this species is limited to the range of *Posidonia*: the Mediterranean Sea and nearby areas of the Eastern Atlantic [Posidoniya, 2023].

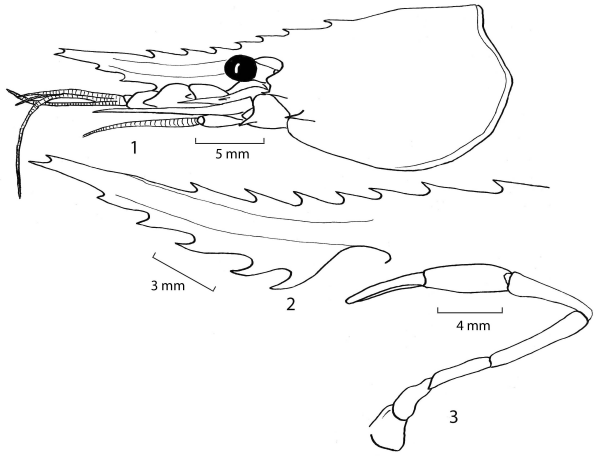

Fig. 6. *Palaemon xiphias*: 1, cephalothorax, side view; 2, rostrum, side view; 3, the 2nd pereiopods

Ecological characteristics. *Posidonia* usually grows in large colonies forming, together with other seagrasses, unique underwater meadows in sea bays and bights at depths from the littoral zone down to 30 m, sometimes even down to 50 m. Wherever these sea meadows are mentioned, *P. xiphias* is mentioned as well. This species is often called *Posidonia* prawn. In the Adriatic Sea, the shrimp is found at depths of 2 to 6 m. In this area, it begins laying eggs on pleopods in May–June [Karlovac, 1969; Pesta, 1918]. The size composition and reproductive biology of this species were best studied in 1989–1990 in the Western Mediterranean: in the Alfacs Bay near the Ebro River delta (Spain) [Guerao et al., 1994]. There, the total body length measured from the end of the rostrum to the end of the telson, was 21–70 mm in females and 19–50 mm in males.

The shrimp growth was observed during the whole year and was faster in summer than in winter. Sexual dimorphism in size composition was noted throughout life, starting with the smallest sizes. In overwintered individuals, especially in females, the growth rate decreases in May which coincides with the beginning of the reproductive season. Already in June, more than 90% of females with a body length of 48–66 mm lay their eggs on pleopods. In October, very few large females remain in the population. A chiasm is formed between them and the next generation of females with the greatest length of 46 mm. Then, the reproductive season ends. The lifespan of *P. xiphias* is 14–17 months. The main part of each generation is born in July. Females can lay eggs on pleopods two to five times depending on water temperature. At +21 °C, embryonic development lasts for 20 days, and at +28 °C, for 12 days. The number of eggs on pleopods varied from 318 in a female with a body length of 37.9 mm to 2,750 in a shrimp with a body length of 69 mm [Guerao et al., 1994].

In terms of food composition, *P. xiphias* is a benthic feeder. Its stomachs most often contain bottom-dwelling higher crustaceans (amphipods, mysids, and isopods); along with them, although much less frequently, bivalves, gastropods, polychaetes, and echinoderms occur. Detritus is found in every second or third stomach. Copepods are recorded quite often (in every third or fourth stomach) (these might be bottom-dwelling harpacticoids. – *R. B.*). The frequency of their occurrence is the highest in juveniles and decreases by 4 times with a gain in the body size of the shrimp. The same is true for the frequency of occurrence of mysids. Other higher crustaceans are more common in larger individuals. Not very often, plant remains are also noted in stomachs [Guerao, 1995]; their role is sharply reduced during winter, when they are replaced chiefly by bottom animals [Sitts, Knight, 1979].

DISCUSSION

Currently, six shrimp species of the genus *Palaemon* inhabit European waters from the Gulf of Bothnia to the Sea of Azov. The set of six objects is not easy to analyze: there are relatively few items for this. On the other hand, it seems that the stimulus (or, precisely, the set of such stimuli) for the emergence

of processes in the environment driving the formation of modern habitats of these species was common: global warming which opened the way for European species of the genus *Palaemon* to the north and the presence of permanent routes for "carriers" of reservoirs for their larvae – ships with their ballast water.

As a result, these six species are divided, conventionally, into three groups: a cosmopolitan *P. macrodactylus*, a persistent native of the Mediterranean–Lusitanian zoogeographic area *P. xiphias*, and four other species that cannot be attributed to either the first or second group.

The aboriginality of *P. xiphias* is determined by a clear external factor: symbiosis with a higher plant *Posidonia oceanica*, one of the most interesting species of marine herbaceous plants (so-called seagrasses) common along the coast of the Mediterranean Sea and nearby areas of the Atlantic Ocean. This underwater grass has all the characters of a land plant: it has roots (very long ones, 1.5 m, to hold on more tightly to the seabed), leaves (ribbons up to 0.5 m), stems (those are also roots, only above-the-sand ones, and also up to 1.5 m long), flowers, seeds, and fruits. The area of *Posidonia* underwater meadows in the Mediterranean Sea alone is 3% of its surface area (75,000 km^2) [Posidoniya, 2023]. *P. xiphias* distribution and features of its biology are inseparably connected with these underwater meadows, and *vice versa*: this *Palaemon* species is not known outside *Posidonia* colonies. Accordingly, until *Posidonia oceanica* penetrates into the Black Sea, *P. xiphias* will not occur there. Assumably, in the foreseeable future, there will be no replenishment of *Palaemon* fauna of the Black Sea.

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КРЕВЕТКИ РОДА *PALAEMON* (CRUSTACEA, DECAPODA, PALAEMONIDAE) ЕВРОПЕЙСКИХ МОРЕЙ

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Креветки рода *Palaemon* (семейство Palaemonidae) — одни из самых активных инвазивных видов креветок. На шельфе морей, омывающих Европу от Ботнического залива на севере и до устья Дона на юго-востоке, сегодня обитают шесть видов креветок из данного рода. В результате глобального потепления и усиленного развития судоходства, облегчивших перемещение личинок этих креветок с балластными водами, в исторически краткий промежуток времени пять из шести видов существенно увеличили размеры своих ареалов, а один из них, *Palaemon macrodactylus*, из южнобореального западнопацифического вида превратился в космополита. Лишь *Palaemon xiphias*, симбионт морской травы *Posidonia oceanica*, сохранил свой классический средиземноморско-лузитанский ареал. В статье представлены сведения о морфологии, истории формирования новых ареалов, размерах, особенностях репродуктивной биологии и составе пищи каждого вида, а также приведены ключи для определения.

Ключевые слова: креветки, *Palaemon*, инвазия, ареал, европейские воды, Чёрное море