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TROPHIC RELATIONSHIPS IN THE *ZOOPLANKTON – GELATINOUS ZOOPLANKTON* FOOD CHAIN IN THE SHELF AREAS OF THE CRIMEAN COAST OF THE BLACK SEA

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The seasonal and spatial dynamics of the key trophic characteristics were studied (food spectrum, feeding rate, and predatory impact on mesozooplankton) for populations of the jellyfish *Aurelia aurita* (Linnaeus, 1758) and ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865. The investigation was carried out during four cruises of the RV "Professor Vodyanitsky" in the shelf areas of Crimean Peninsula in January to October 2016. The area was divided into inner (depth of < 50 m) and outer (51–150 m) shelves. To study the food spectrum and feeding rate of gelatinous predators, the composition of food items in the gastric cavity was analyzed under a binocular microscope. Daily ration (R, mg C·ind.$^{-1}$·day^{-1}) was calculated by the formula: $R = B_z \times DT^{-1} \times 24$, where B_z is zooplankton biomass in the predator gastric cavity (mg), and DT is zooplankton digestion time (h). Predatory impact of gelatinous zooplankton was estimated by the values of daily ration and mesozooplankton biomass. Zooplankton was sampled with a Juday plankton net with mouth diameter of 38 cm and mesh size of 140 µm. Vertical net hauls were performed: at the inner shelf stations, from the sea surface down to the bottom; at the outer shelf stations, down to the boundary of the hydrogen sulfide zone ($\delta_t = 16.2$ conventional units according to a Sea-Bird probe). In the samples fixed with 4 % formalin solution, zooplankton abundance, its taxonomic composition, and size–age structure were quantified by standard method. In the food spectrum of the jellyfish, seasonal differences were revealed: predominance of Bivalvia veligers in winter and spring and wide species composition of Crustacea and other groups of prey in summer. The feeding rates of the studied species were similar: specific daily rations in winter, spring, and autumn did not exceed tenth of a percent of the carbon content in the body. Both species fed at a maximum rate in summer on the outer shelf: the specific rations reached 12.9 and 5.1 % C of the body for the jellyfish and ctenophore, respectively. *A. aurita* and *M. leidyi* populations consumed 0.2 to 5 % of the fodder zooplankton biomass *per* day; it did not result in a drastic reduction in zooplankton abundance and provided favorable feeding conditions for small planktivorous pelagic fish.

Keywords: gelatinous zooplankton, *Aurelia aurita*, *Mnemiopsis leidyi*, daily ration, ingestion

In the ecosystem, representatives of gelatinous zooplankton act as potential food competitors of small pelagic fish: their food relations and common food spectrum determine a fodder base for fish, their food supply, and, as a result, fish stocks. Based on the observed coincidence of the rations of gelatinous zooplankton and small pelagic fish (Crustacea and other zooplankton prey), researchers assume the following: with a decrease in pelagic fish stock – either due to overfishing or due to effect of climatic and other factors – gelatinous zooplankton can not only become competitors for small pelagic fish, but also functionally replace the latter ones. This is what happened in the Black Sea during the outbreak of the invasive ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 (Gucu, 2002 ; Oguz et al., 2008). Moreover, gelatinous zooplankton consumes fish eggs and larvae, and its predation may limit the recruitment of small pelagic fish (Condon et al., 2013 ; Richardson et al., 2009). One of the approaches to analyze the food relations between small pelagic fish and gelatinous zooplankton can be a quantitative assessment of the feeding rate of gelatinous zooplankton and the degree of food supply for small pelagic fish, which is indicated by species diversity, abundance of eggs and larvae of separate species, and abundance of feeding individuals in populations.

The aim of this work was to study seasonal and spatial peculiarities of the feeding of two mass gelatinous zooplankton species in the Black Sea – *Aurelia aurita* (Linnaeus, 1758) and *M. leidyi* – and the feeding rate of their populations of the key food resource – zooplankton – in the coastal areas of Crimea (the Black Sea). Such a complete survey of the spatial distribution and seasonal dynamics of gelatinous zooplankton and such an investigation of trophic relationships in the *zooplankton – gelatinous zooplankton* system on the Crimean Peninsula shelf were performed for the first time.

MATERIAL AND METHODS

The studies were carried out in 2016, during four cruises of the RV "Professor Vodyanitsky": the 83rd (winter, January to February), 84th (spring, April), 86th (early summer, June), and 90th (autumn, October). The research covered the coastal areas of Crimea (the Black Sea) from the Cape Tarkhankut to Kerch (Fig. 1). All the stations were located on the shelf. For the analysis, those were divided into stations of the inner (depth of < 50 m) and outer (51–200 m) shelves.

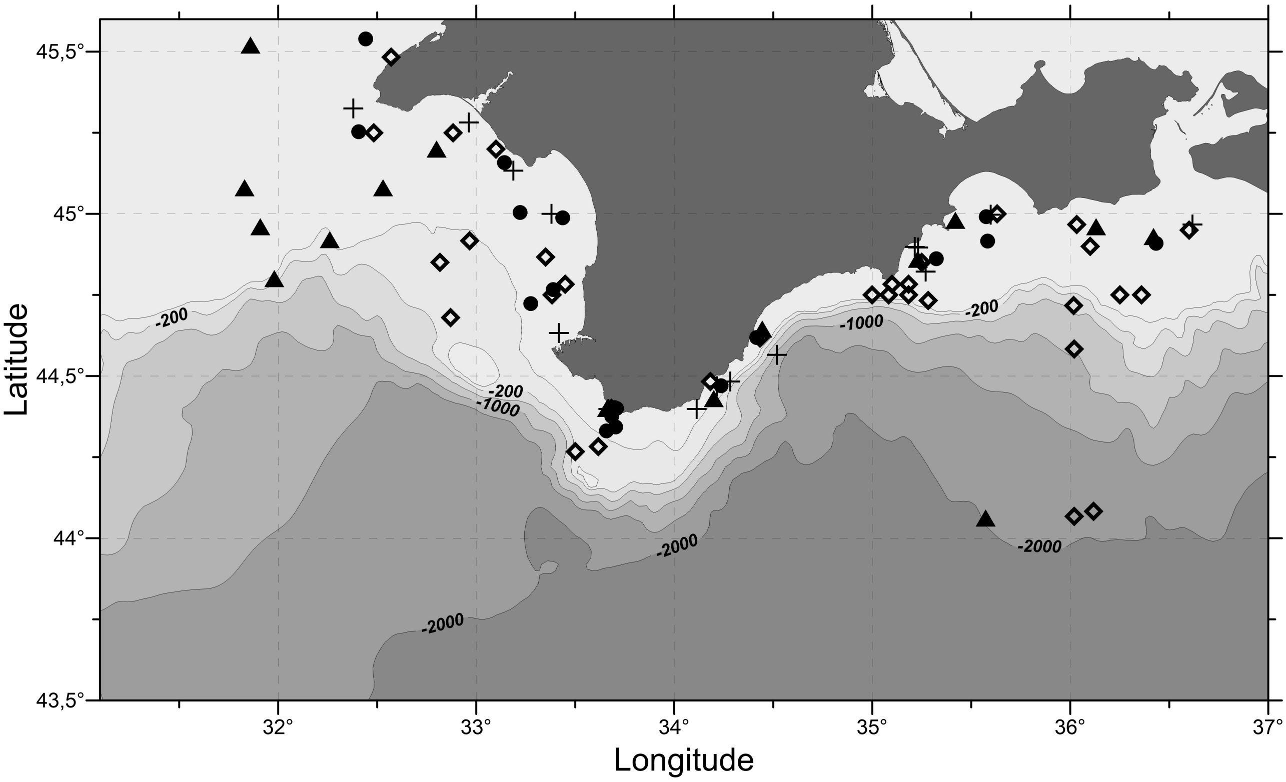

Fig. 1. Map of stations sampled in the inshore waters off the Crimean coast in January – February (+), April (●), June (◊), and October (▲) 2016

The sampling areas in every cruise, temperature conditions, and the number of stations are given in Table 1.

Table 1. Research conditions in the 83rd, 84th, 86th, and 90th cruises of the RV "Professor Vodyanitsky" in January – October 2016 (the number of stations is given for gelatinous zooplankton / mesoplankton)

Cruise No.	Dates	Surface layer temperature, °C	Number of stations	Coordinates
83	28.01–02.02	+7.5…+9.6	17 / 11	N44.23° – N45.5°, E32.22° – E36.26°
84	19.04–27.04	+10.1…+11.9	29 / 15	N45.41° – N44.18°, E36.25° – E32.24°
86	08.06–18.06	+18.4…+21.7	45 / 8	N43.26° – N45.5°, E32.01° – E36.36°
90	25.09–01.10	+13.2…+15.0	26 / 5	N44.24° – N45.49°, E31.50° – E36.30°

Sampling and processing of gelatinous macroplankton were carried out according to the method described earlier (Anninsky, 2009 ; Finenko et al., 2013). Abundance was expressed in ind.·m^{-2}; biomass, in g·m^{-2} wet weight. To study the food spectrum and the feeding rate of gelatinous predators in the sea, all sampled specimens were examined in the laboratory under a microscope immediately after being caught. The composition of food items in the gastric cavity of animals was determined down to the species level and stage of development. Daily ration (R, mg·ind.$^{-1}$·day^{-1}) was calculated by the formula:

$$R = B_z \times DT^{-1} \times 24 \,, \tag{1}$$

where B_z is zooplankton wet biomass in the predator gastric cavity, mg;

DT is zooplankton digestion time, h.

For the jellyfish, the digestion time was quantified by the formula involving the food biomass in the gastric cavity (B_z, mg) and the weight of the animal (WW, g). Importantly, a conversion factor k_t was introduced when converting the digestion time of crustacean zooplankton from +20 °C to the temperature recorded in the sea (Vinberg, 1956), and a conversion factor k_{sp} was introduced for an increase in the digestion time of Bivalvia veligers (2.67) compared to that of crustacean zooplankton (Hansson et al., 2005):

$$DT = 1.81 \times B_z^{0.122} \times WW^{-0.193} \times k_t \times k_{sp} \,. \tag{2}$$

The second conversion factor was not introduced when large *A. aurita* (> 150 mm) had less than 5 veligers in the gastric cavity. In these cases, the digestion time was equated to the digestion time of crustacean zooplankton.

For *M. leidyi*, the digestion time was calculated according to data of (Finenko et al., 2010), with the temperature correction when converting the values from +20 °C to the temperature recorded in the sea (Vinberg, 1956).

For *A. aurita*, the minimum food requirements (the required amount of assimilated food to compensate for the respiratory needs) were estimated by the formula:

$$Q = 0.00936 \times WW^{0.84} \times 0.535 k_t \times 24 \,, \tag{3}$$

where Q is the respiratory rate at the temperature studied, mg C·ind.$^{-1}$·day^{-1};

WW is the wet weight, g;

0.535 is the conversion factor from mL O_2 to mg C;

k_t is the conversion factor to convert the values from +20 °C to the temperature registered (Anninsky & Timofte, 2009).

For *M. leidyi*, the respiratory needs were quantified by formulas relating the ctenophore respiratory rate to the dry body weight at the temperature recorded (Abolmasova, 2001).

Predatory impact by two species – *A. aurita* and *M. leidyi* – was estimated based on the daily rations of the population and zooplankton biomass. Zooplankton was sampled with a Juday plankton net with mouth diameter of 38 cm and mesh size of 140 μm. Vertical net hauls were performed: at the inner shelf stations, from the sea surface down to the bottom; at the outer shelf stations, down to the boundary of the hydrogen sulfide zone determined by an isopycnal (δ_t = 16.2 conventional units according to a Sea-Bird probe). In the samples fixed with 4 % formalin solution, zooplankton abundance, its taxonomic composition, and size–age structure were quantified by standard method.

To convert linear dimensions of separate mesozooplankton species into units of wet biomass, the size–weight ratios known for the Black Sea species were used (Petipa, 1957). When recalculating rations and other indicators into carbon units, it was assumed as follows: for zooplankton, the dry weight is 20 % of the wet weight, and the carbon content is 40 % of the dry weight (Arashkevich et al., 2014); for gelatinous zooplankton, the values are 2.2 % and 4 %, respectively (Finenko et al., 2003). The material obtained was processed in Surfer, Microsoft Excel, and Grapher software. The significance of statistical differences between the samples was assessed by Student's *t*-test. In each case, mean value ± standard error of the mean (*SE*) is given.

RESULTS

Seasonal and spatial dynamics of gelatinous zooplankton. In both areas studied in all the seasons, abundance of *A. aurita* significantly exceeded abundance of the ctenophore (Fig. 2). On the outer shelf, *A. aurita* reached its maximum development in spring and early summer (about 30 ind.·m^{-2}; biomass 800 g·m^{-2} wet weight), when the population included individuals of both the previous year generation and the current one.

Intensive reproduction was observed in spring in shallow coastal areas: about 40 % of the population was formed by gelatinous zooplankton of the new generation (< 10 mm). On the outer shelf, a rapid growth of gelatinous zooplankton was recorded in spring which led to an increase in the ratio of 11–50-mm animals compared to their ratio in winter – a rise from 10 to 40 % of total abundance. In summer, this group prevailed in both areas. In autumn at shallow stations, the size structure of *A. aurita* population was limited to two groups (11–50 and 51–100 mm). In the second area, it was more diverse (4 groups): large, 101–200-mm animals formed up to 30 % of total abundance.

M. leidyi was registered in plankton of both areas during the entire study period with abundance 4 to 10 times lower than that of *A. aurita*, with a maximum at the stations of the inner shelf in autumn. In winter, adult, mature individuals prevailed in both areas; by spring, their ratio on the inner shelf decreased due to the death of part of the population. In summer and autumn, the ratio of larvae (≤ 10 mm) in the population reached 90 %. On the outer shelf in all the seasons, the population was represented by large mature individuals with an oral-aboral length of > 30 mm.

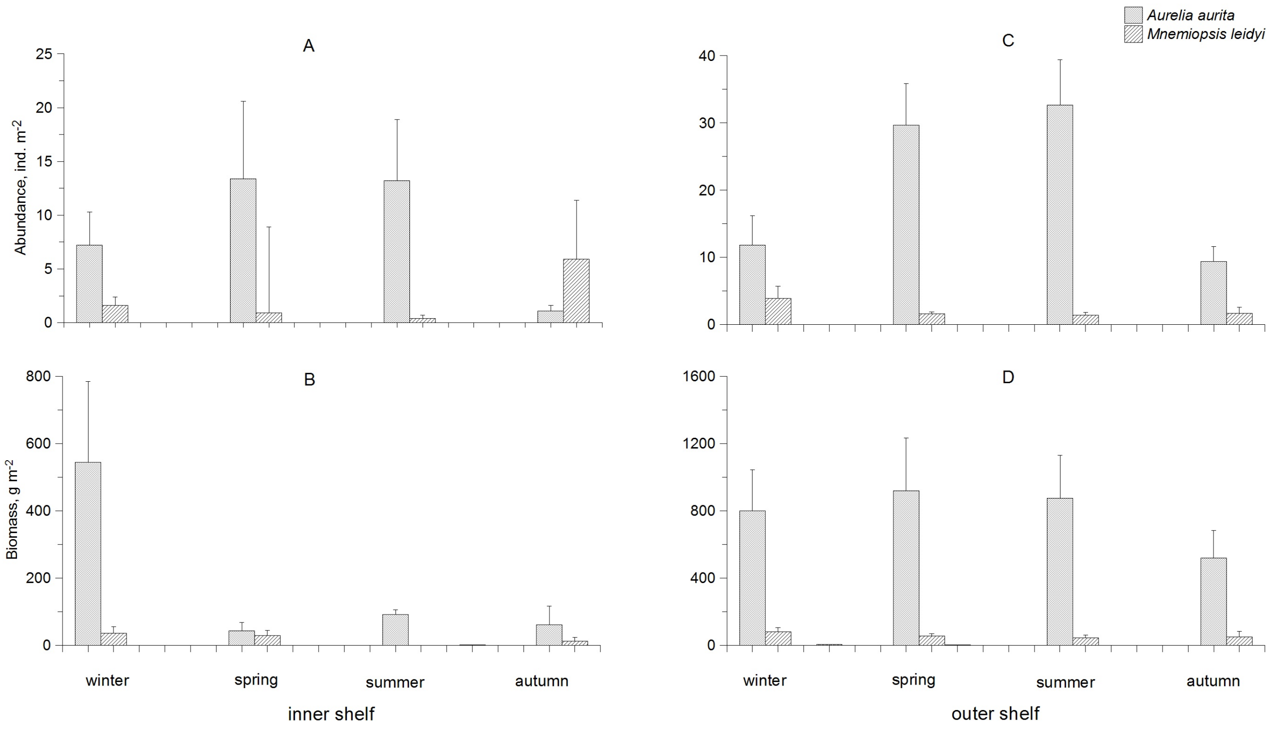

Fig. 2. Abundance (ind.·m^{-2}) (A, C) and biomass (g·m^{-2}) (B, D) of two gelatinous species in different areas and seasons of 2016

Fodder zooplankton biomass. For gelatinous zooplankton, the main food resource are small crustaceans (Copepoda and Cladocera) and pelagic larvae of benthic animals, as well as *Oikopleura*, *Sagitta*, and Rotifera. On the outer shelf, fodder zooplankton biomass in winter, spring, and summer was several times higher than the values recorded during these seasons on the inner shelf (Table 2). In autumn (in October), the values of fodder zooplankton biomass in two water areas were the same.

Table 2. Seasonal variability of the wet biomass of fodder zooplankton (mg·m^{-3}) and individual taxa in inner and outer shelf areas off the Crimean coast in 2016 (*n* denotes the number of stations)

Season	Area	*n*	Copepoda	Cladocera	*Oikopleura dioica*	*Parasagitta setosa*	Mero-plankton	Fodder zooplankton
Winter	Inner shelf	11	11.77 ± 2.4	0	0.19 ± 0.1	0.21 ± 0.1	1.01 ± 0.3	13.28 ± 2.5
	Outer shelf	1	30.53	0	0.03	28.01	0.14	58.70
Spring	Inner shelf	9	40.28 ± 7.4	0.11 ± 0.1	0.57 ± 0.1	6.40 ± 5.7	5.75 ± 0.6	53.42 ± 10.5
	Outer shelf	5	69.64 ± 13.6	0	0.08 ± 0.01	140.56 ± 122.7	3.73 ± 1.6	214.02 ± 123.5
Summer	Inner shelf	8	13.50 ± 3.6	3.23 ± 1.5	4.09 ± 1.7	0.05 ± 0.04	19.27 ± 6.9	40.21 ± 10.9
	Outer shelf	9	29.59 ± 6.4	0.43 ± 0.1	1.39 ± 0.4	31.08 ± 16.7	1.19 ± 0.4	63.67 ± 21.9
Autumn	Inner shelf	4	22.16 ± 2.5	0.12 ± 0.05	0.30 ± 0.2	13.51 ± 8.3	7.52 ± 6.0	43.62 ± 15.2
	Outer shelf	5	24.22 ± 2.2	0.01 ± 0.01	1.93 ± 1.0	16.18 ± 3.4	0.55 ± 0.1	42.88 ± 5.7

Zooplankton was represented by species and groups common for the Black Sea, with their ratio depending on the season. In winter, Copepoda accounted for 89 and 52 % of biomass on the inner and outer shelves, respectively. In subsequent seasons, their ratio gradually decreased on the inner shelf and varied widely (11 to 50 %) on the outer one. Acartiidae prevailed in the first area; *Calanus euxinus* Hulsemann, 1991 prevailed in the second. In autumn, *Paracalanus parvus* Claus, 1863 prevailed out of Copepoda in both areas (> 60 % of Copepoda biomass).

Cladocera made up a small ratio of zooplankton in both areas (0.2–1.0 %) during most of the study period; their maximum relative biomass (8 %) was registered on the inner shelf in early summer. In fodder zooplankton biomass on the inner shelf, in contrast to that on the outer one, a significant contribution was made by larvae of benthic animals (8–48 % in different seasons), with a maximum in early summer. On the outer shelf, *Parasagitta setosa* J. Müller, 1847 was a key component of fodder zooplankton: this species reached 50 % of fodder zooplankton biomass in some seasons.

Feeding of gelatinous zooplankton, food supply, and predatory impact on the zooplankton community. During the study period, the main component of jellyfish ration was Bivalvia veligers and Crustacea. In winter, *A. aurita* food spectrum was poor. Despite the fact that the ratio of meroplankton in fodder zooplankton total biomass was low, Bivalvia veligers accounted for up to 80 % of the prey abundance on the outer shelf. Among crustaceans, small ratios of *Acartia clausi* Giesbrecht, 1889 and *Oithona davisae* Ferrari F. D. & Orsi, 1984 were registered, as well as Copepoda nauplii and Rotifera. In spring, summer, and autumn, Crustacea mostly prevailed (Fig. 3). In summer, the food spectrum of *A. aurita* expanded both due to an increase in the number of crustacean species consumed [*Centropages ponticus* Karavaev, 1895, *P. parvus*, and *Pleopis polyphemoides* (Leuckart, 1859)] and due to consumption of other groups of prey (Gastropoda larvae, *P. setosa*, and *Oikopleura (Vexillaria) dioica* Fol, 1872).

In summer, a peculiarity of *A. aurita* food composition was the presence in the gastric cavity of a diatom *Coscinodiscus granii* Gough, 1905 in large number in some areas (in the western one – the Karkinitsky Bay; in the northeastern one). In general, during the entire study period, except for winter, Crustacea formed the basis of *A. aurita* ration in both water areas.

Unlike *A. aurita*, *M. leidyi* clearly preferred crustaceans. Those accounted for up to 70 % of the total prey abundance in the gastric cavity at the stations on both inner and outer shelves in different seasons.

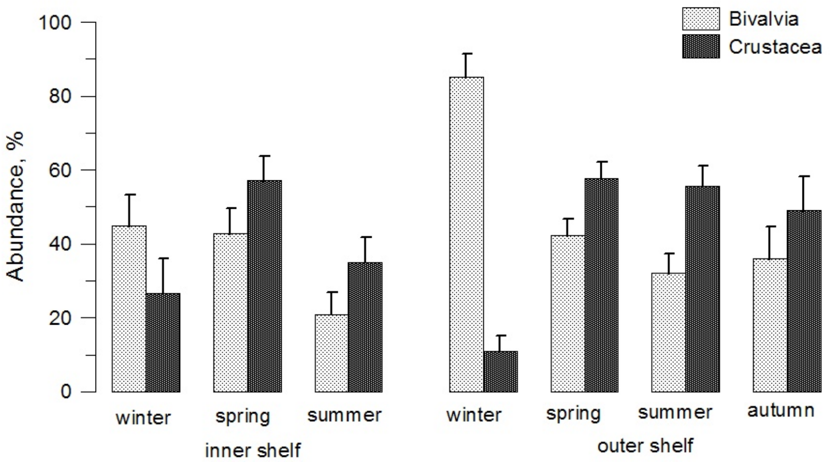

Fig. 3. Variability of *A. aurita* food composition (% of total abundance in the gastric cavity) in different seasons and areas of the Crimean shelf in 2016

In *A. aurita* population, the abundance of feeding individuals varied seasonally. Specifically, in winter and spring, it was maximum in both areas (96–98 %), while in summer and autumn, the value did not exceed 70 %. On the inner shelf, *A. aurita* stopped feeding in autumn.

Unlike *A. aurita*, 100 % of the studied *M. leidyi* had food in the gastric cavity in all the seasons.

In both areas, the values of *A. aurita* daily ration varied by an order of magnitude during the study period. The minimum ones were registered at shallow stations in spring [(0.010 ± 0.002) mg C·ind.$^{-1}$·day^{-1}], when the mean size of an individual in the population is minimal (Table 3).

Table 3. Diameter (D, mm), carbon content (C, mg·ind.$^{-1}$), prey abundance in the gastric cavity (N, ind.), daily ration (R, mg C·ind.$^{-1}$·day^{-1}), and specific daily ration (R/C, %·ind.$^{-1}$·day^{-1}) for *A. aurita* in inshore areas of the Black Sea (*n* denotes the number of measurements)

Season	Area	*n*	D	C	N	R	R/C
Winter	Inner shelf	15	116.9 ± 8.6	87.2 ± 16.2	10.2 ± 3.0	0.031 ± 0.021	0.03 ± 0.01
	Outer shelf	20	125 ± 9.4	88.9 ± 16.9	16.7 ± 4.4	0.017 ± 0.010	0.08 ± 0.04
Spring	Inner shelf	31	25.3 ± 4.2	2.9 ± 1.2	7.7 ± 1.8	0.010 ± 0.002	3.97 ± 0.63
	Outer shelf	51	52.5 ± 3.0	9.9 ± 1.9	15.7 ± 1.2	0.100 ± 0.010	2.11 ± 0.19
Summer	Inner shelf	25	60.8 ± 5.1	11.4 ± 5.24	11.8 ± 5.4	0.100 ± 0.020	2.85 ± 0.84
	Outer shelf	48	50.2 ± 2.7	6.8 ± 1.0	11.9 ± 1.7	0.250 ± 0.040	12.9 ± 3.1
Autumn	Inner shelf	20	0	0	0	0	0
	Outer shelf	27	80.8 ± 7.8	30.2 ± 8.4	19.1 ± 4.5	0.05 ± 0.01	0.32 ± 0.10

The rations were the highest in summer on both inner and outer shelves. The prey abundance in the gastric cavity ranged ~ 8 to 19 ind., with no clear relationships with either the season or spot of study ($p > 0.5$). The minimum values of the specific daily ration were recorded in winter at low temperature, low zooplankton biomass, and predominance of large animals in the population. Due to the differences in the structure of the jellyfish population by areas, in the shallow water area in spring, the specific daily ration was twice as high as the ration on the outer shelf. On the outer shelf in summer, *A. aurita* specific ration reached its maximum values: (12.9 ± 3.1) % C_{body}·day^{-1}.

The ration values increased with a rise in water temperature: on average, animals with carbon content of 10 mg consumed in winter 0.12 % C_{body}·day^{-1}; in spring, 0.56 % C_{body}·day^{-1}; and in summer, 3 % C_{body}·day^{-1} at a temperature of +8, +10, and +20 °C, respectively.

In different seasons, the feeding rate of the ctenophore was slightly higher than that of *A. aurita* individuals. Specifically, the ranges in daily rations were (0.01 ± 0.002) to (0.25 ± 0.04) mg C·ind.$^{-1}$·day^{-1} for *A. aurita* and (0.018 ± 0.009) to (0.40 ± 0.15) mg C·ind.$^{-1}$·day^{-1} for *M. leidyi*. Importantly, a small number of measurements for the ctenophore allows us to highlight a trend, but not statistically significant differences (Tables 3 and 4).

The feeding rate of the studied species did not differ significantly as well: in winter, spring, and autumn, the specific daily rations did not exceed tenth of a percent of the carbon content in the body. Both species fed at a maximum rate in summer in the area of the outer shelf: the rations reached 12.9 and 5.1 % C of the body for *A. aurita* and ctenophore, respectively.

The minimum daily food requirements of *A. aurita*, which were calculated as a respiration rate under given temperature conditions, ranged 1.9 to 10 % C of the body. The degree of food supply for *A. aurita* indicated by the ratio between respiratory needs (Q, mg C·ind.$^{-1}$·day^{-1}) and feeding rate (R, mg C·ind.$^{-1}$·day^{-1}) varied seasonally (Fig. 4).

Table 4. Length (L, mm), carbon content (C, mg·ind.$^{-1}$), prey abundance in the gastric cavity (N, ind.), daily ration (R, mg C·ind.$^{-1}$·day^{-1}), and specific daily ration (R/C, %·ind.$^{-1}$·day^{-1}) for *M. leidyi* in inshore areas of the Black Sea (*n* denotes the number of measurements)

Season	Area	*n*	L	C	N	R	R/C
Winter	Inner shelf	4	33.5 ± 6.5	16.7 ± 8.9	7.4 ± 3.8	0.018 ± 0.009	0.19 ± 0.11
	Outer shelf	14	37.4 ± 4.7	13.2 ± 3.6	11.0 ± 4.6	0.03 ± 0.01	0.13 ± 0.04
Spring	Inner shelf	6	41.3 ± 7.9	12.6 ± 5.1	19.2 ± 5.5	0.066 ± 0.025	0.28 ± 0.12
	Outer shelf	8	62.7 ± 5.6	29.0 ± 6.8	21.8 ± 5.3	0.262 ± 0.103	0.43 ± 0.19
Summer	Inner shelf	0	0	0	0	0	0
	Outer shelf	3	56.3 ± 13.9	35.4 ± 18.0	27.0 ± 14.8	0.404 ± 0.152	5.10 ± 3.72
Autumn	Inner shelf	1	92	89.5	19	0.370	0.40
	Outer shelf	4	54.2 ± 9.0	32.5 ± 16.3	9.0 ± 7.0	0.032 ± 0.071	0.21 ± 0.09

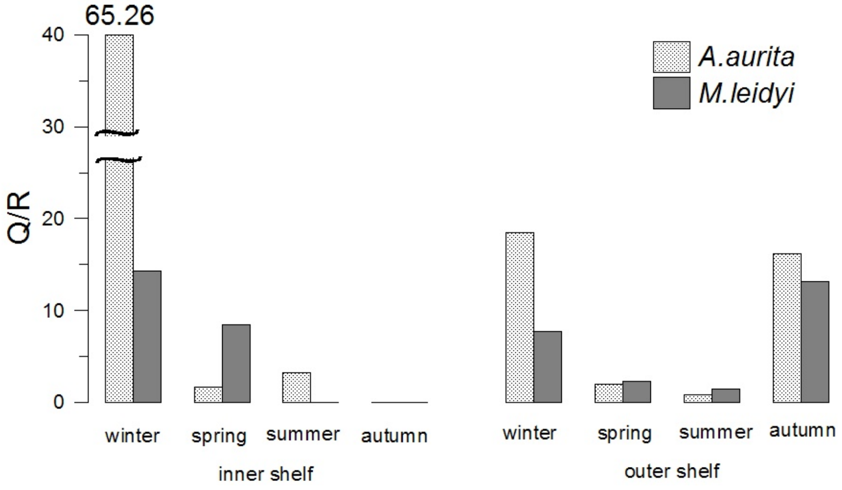

Fig. 4. Seasonal dynamics of the relationship between respiration rate (Q, mg C·ind.$^{-1}$·day^{-1}) and daily ration (R, mg C·ind.$^{-1}$·day^{-1}) for *A. aurita* and *M. leidyi*

On the inner shelf in winter, respiratory needs were dozens of times higher than daily rations. In spring and summer, *A. aurita* were better supplied with food (Q/R ranged 1.64 to 3.27). On the outer shelf in summer, the daily rations of the population were higher than the food requirements. Thus, during most of the year, *A. aurita* could not compensate for its minimum food requirements solely with mesozooplankton. There were practically no differences in the degree of food supply by area, except for winter, when the population on the inner shelf was less supplied; it is associated with low feeding rate due to low zooplankton concentration. *M. leidyi* was better supplied with food in spring and summer on the outer shelf (Q/R values were 2.1 and 1.5, respectively) and experienced less food shortage during the entire study period than *A. aurita*.

Predatory impact for *A. aurita* population, which was calculated based on the values of ration and zooplankton biomass, varied 0.22 to ~ 5 % of zooplankton biomass *per* day. The value of the predatory impact for the ctenophore population was an order of magnitude lower (0.02 to 0.29) due to its small abundance in the study period (Fig. 5). Unfortunately, the time of intensive growth and development of *M. leidyi* population (late June till September), when the predatory impact is maximum, was not covered by our investigation.

In general, predatory impact of gelatinous zooplankton in the coastal areas of Crimea in winter, spring, and early summer was 0.35–1.3 %; in autumn, it reached ~ 5 % of zooplankton biomass *per* day. Considering the fact that the specific production of Copepoda – the main food resource for gelatinous zooplankton – is 10 % of biomass *per* day, we can conclude as follows: the predatory impact of gelatinous zooplankton in the studied areas varied within 3.5–50 % of daily production and could not result in a decrease in the zooplankton community biomass.

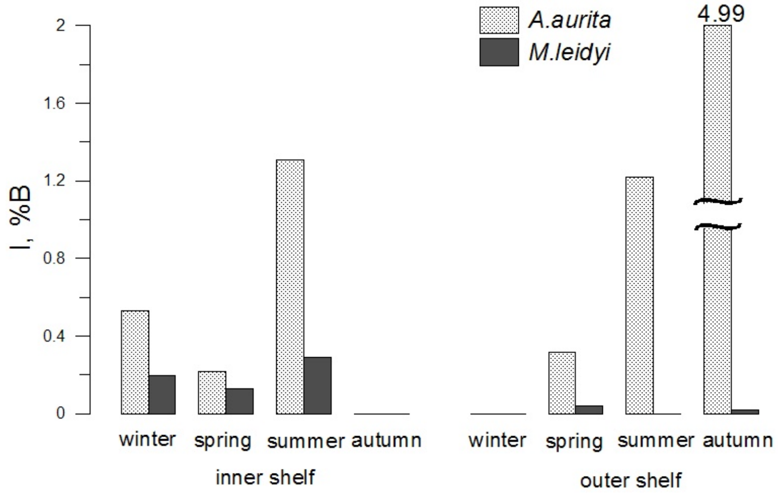

Fig. 5. Seasonal dynamics of predatory impact of *A. aurita* and *M. leidyi* populations on mesoplankton biomass

DISCUSSION

Based on monitoring observations in the Sevastopol shelf area, as well as on studies carried out in 2013–2016 on the Crimean shelf, an increase is clearly seen in *A. aurita* biomass in recent years compared to that in the early 2000s, when *A. aurita* wet biomass in the period of its maximum development was 200–300 $g \cdot m^{-2}$ (Anninsky et al., 2011). As for the shelf areas off the Crimean coast in 2016, we can conclude the following: on the inner shelf, maximum *A. aurita* biomass was (544 ± 296) $g \cdot m^{-2}$, and on the outer shelf, (800 ± 281) $g \cdot m^{-2}$. In contrast, *M. leidyi* population density in coastal areas decreased. In recent years, the mean summer (May to September) ctenophore biomass in the Sevastopol shelf area does not exceed 100 $g \cdot m^{-2}$, whilst in the 2000s, it reached 300 $g \cdot m^{-2}$. In the summer of 2004–2009, the mean population density in the Black Sea coastal areas near Sevastopol was (198.2 ± 43.7) $ind. \cdot m^{-2}$; in 2010–2014, it was (54.5 ± 14.0) $ind. \cdot m^{-2}$ (Finenko et al., 2018b). Our study in 2016, as mentioned above, did not cover the period of mass development of the ctenophore, and its abundance and biomass values were much lower.

In different seasons of 2016, *A. aurita* specific feeding rate in the coastal areas of Crimea varied within 0.03–12.9 % C of the body (see Table 3). In the Black Sea open areas in autumn 2010, daily rations were estimated at 2 % C (Anninsky et al., 2013). In the coastal area in the spring of 2013, those varied within 1–3 % C (Datsyk et al., 2015). In our studies carried out in different seasons, the range in values was wide due to seasonal and spatial peculiarities of the structure of *A. aurita* population, as well as due to temperature and food conditions. Seasonal differences in *A. aurita* daily rations in the coastal areas of Crimea practically coincide with the results of laboratory experiments: those showed that at natural mesoplankton concentrations, daily rations varied 0.1 to 10.0 % of the carbon content in the body of the jellyfish (Anninsky et al., 2020).

Earlier, the degree of food supply for *A. aurita* population was assessed. The studies were carried out in autumn and spring in the Black Sea coastal and deep-water areas (Anninsky & Timofte, 2009 ; Anninsky & Datsyk, 2013 ; Datsyk et al., 2015). Based on this assessment, in these seasons, the food requirements of the jellyfish exceeded predatory impact on mesoplankton approximately twice. In winter, according to our study, the difference between respiratory needs and ration is much higher and amounts to dozens of times. In spring and summer, these differences vary 2–4 times depending on the area; on the outer shelf in summer, those reach a minimum value (~ 0.8 times). Thus, for most of the life cycle, *A. aurita* cannot compensate for its minimum food requirements with mesoplankton and, apparently, uses alternative food sources. In the literature, the issue of alternative food sources for this species is actively discussed (Anninsky et al., 2020 ; Malej et al., 2006 ; Olesen et al., 1994 ; Stoecker et al., 1987). In laboratory experiments, it was established that microzooplankton can be a key component of *A. aurita* ration (Stoecker et al., 1987). Based on the fact that microzooplankton biomass and production in the coastal areas of Crimea in separate periods reach values comparable with the corresponding indicators for mesozooplankton (Finenko et al., 2006) and given its longer digestion time, it can be assumed as follows: microzooplankton can serve as an additional food source for *A. aurita*. The issue of the use of phyto- and bacterioplankton, as well as dissolved organic matter, by the jellyfish is also discussed, but there is still no unambiguous position (Malej et al., 2006 ; Purcell et al., 2007 ; Richardson et al., 2009 ; Shick, 1975). As already mentioned, in the western and eastern areas of the shelf in the summer of 2016, in the gastric cavity of the jellyfish, we found an alga *Coscinodiscus granii* in large number: it accounted for 40–45 % of the total number of prey. Importantly, the presence of “empty” cell membranes and leaked contents of chloroplasts indicated that in some cases, phytoplankton digestion was successful. However, its ratio in the daily ration calculated by carbon was insignificant (< 1 %).

For an adult ctenophore, the imbalance between food requirements and the amount of mesoplankton consumed in winter and autumn is not as great as for the jellyfish. Apparently, for most of the life cycle, the animals not only compensate for their respiratory needs, but also have enough food for growth and reproduction due to mesoplankton. During the first few days, at the larval stage, the main food source for *M. leidyi* is microzooplankton (Finenko et al., 2008 ; Sullivan & Gifford, 2004). However, already at the transitional stage, mesoplankton prevails over microzooplankton (Finenko et al., 2008).

In the study period, the main contributor to the predatory impact on zooplankton by gelatinous zooplankton was *A. aurita*. Nevertheless, the predatory impact of two mass species (*A. aurita* and *M. leidyi*) on mesoplankton in winter, spring, and summer was low (0.7–2.0 % of zooplankton biomass *per* day). It increased in autumn in the area of the outer shelf up to 7 %, but it could not lead to a cardinal reduction in the zooplankton community abundance. The same conclusion is drawn by the data in (Shushkina & Arnautov, 1985): even in the years of *A. aurita* maximum development (in the 1980s), the population could consume only 5–7 % of zooplankton biomass *per* day, or 50–70 % of its daily production.

Low values of zooplankton predatory impact by *A. aurita*, close to those obtained by us, were registered in the Sevastopol shelf area and in the Black Sea open areas earlier (Datsyk et al., 2015). The lack of correlation between biomass of gelatinous predators and biomass of mesoplankton and its individual taxonomic groups (Arashkevich et al., 2015) confirms our conclusion: at this stage, gelatinous zooplankton does not control the quantitative development of the zooplankton community. Apparently, the values of zooplankton abundance and biomass are now determined not by predation of gelatinous zooplankton, but by variability of the ratio of productivity and mortality due to effect of other factors. At the same time, there was a transformation of the pelagic ecosystem of the Black Sea: it returned to the classical type of *zooplankton – fish – planktophages* functioning after the period of *zooplankton – Mnemiopsis* interaction during the “explosion” of this invasive ctenophore (that time, the trophic chain leading to fish was greatly reduced).

In recent years, a decrease in the predatory impact of gelatinous zooplankton on fodder zooplankton in the Black Sea coastal areas (Finenko et al., 2013, 2018a) combined with climate changes in the region has led to an improvement in food supply for larvae of thermophilic fish species. It resulted in an increase in their survival, a rise both in species diversity and duration of the spawning period, and forming of favorable conditions for embryonic and postembryonic development (Klimova & Podrezova, 2018).

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ТРОФИЧЕСКИЕ ОТНОШЕНИЯ В ПИЩЕВОЙ ЦЕПИ ЗООПЛАНКТОН — ЖЕЛЕТЕЛЫЕ В ШЕЛЬФОВЫХ РАЙОНАХ КРЫМСКОГО ПОБЕРЕЖЬЯ ЧЁРНОГО МОРЯ

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В четырёх рейсах НИС «Профессор Водяницкий» в январе — октябре 2016 г. исследована сезонная и пространственная динамика основных трофических характеристик (пищевой спектр, интенсивность питания и выедания мезозоопланктона) популяций двух видов желетелых (медузы *Aurelia aurita* (Linnaeus, 1758) и гребневика *Mnemiopsis leidyi* A. Agassiz, 1865) на шельфе Крымского полуострова. Район работ был разделён на внутренний (глубина менее 50 м) и внешний (51–200 м) шельф. Для изучения спектра питания и скорости потребления пищи желетелыми хищниками под бинокуляром определяли состав пищевых объектов в гастральной полости животных. Суточный рацион (R, мг·экз.$^{-1}$·сут$^{-1}$) рассчитывали по формуле $R = B_z \times DT^{-1} \times 24$, где B_z — биомасса зоопланктона в гастральной полости хищника (мг), а DT — время переваривания зоопланктона (ч). Выедание зоопланктона оценивали по величинам суточных рационов популяции и по биомассе мезозоопланктона. Зоопланктон отбирали планктонной сетью Джеди с диаметром входного отверстия 38 см и размером ячеи 140 мкм. Вертикальными ловами на станциях внутреннего шельфа облавливали слой от поверхности до дна, на внешнем шельфе — до границы сероводородной зоны, определяемой по изопикне (по данным зонда Sea-Bird, $\delta_t = 16{,}2$ усл. ед.). В фиксированных 4%-ным раствором формалина пробах по стандартной методике определяли численность зоопланктона, его таксономический состав и размерно-возрастную структуру. Выявлены сезонные различия в пищевом спектре медуз — преобладание велигеров двустворчатых моллюсков в зимне-весенний период и широкий видовой состав ракообразных и других групп жертв летом. Интенсивность питания двух изученных видов была близкой: удельные суточные рационы зимой, весной и осенью не превышали десятых долей процента содержания углерода в теле. С максимальной скоростью оба вида питались летом в районе внешнего шельфа: рационы достигали 12,9 и 5,1 % С тела у медуз и гребневиков соответственно. Популяции *A. aurita* и *M. leidyi* выедали от 0,2 до 5,0 % биомассы кормового зоопланктона в сутки, что не приводило к кардинальному сокращению численности зоопланктонного сообщества и обеспечивало благоприятные пищевые условия для мелких планктоноядных пелагических рыб.

Ключевые слова: желетелый зоопланктон, *Aurelia aurita*, *Mnemiopsis leidyi*, суточный рацион, выедание