Turk. J. Fish.& Aquat. Sci. 26(7), TRJFAS27516
https://doi.org/10.4194/TRJFAS27516

Turkish Journal of FISHERIES and AQUATIC SCIENCES

PROOF
RESEARCH PAPER

Gradients of Plankton and Its Bioluminescence Across the Northern Shelf of the Black Sea (2011-2023)

Sergey A. Piontkovski[1,*], Irina M. Serikova[2], Yuliya A. Zagorodnyaya[2], Elena Yu. Georgieva[2], Ivan A. Minsky[1,2], Alexandr V. Melnik[2]

[1]Sevastopol State University, Russian Federation, 299051, Sevastopol, 33 Universitetskaya Str.
[2]A.O. Kovalevsky Institute of Biology of the Southern Seas, RAS, Russian Federation, 299051, Sevastopol, 2 Nakhimov Ave.

How to Cite

Piontkovski, S.A., Serikova, I.M., Zagorodnyaya, Y.A., Georgieva, E.Y., Minsky, I.A., Melnik, A.V. (2026). Gradients of Plankton and Its Bioluminescence Across the Northern Shelf of the Black Sea (2011-2023). *Turkish Journal of Fisheries and Aquatic Sciences*, *26(7)*, *TRJFAS27516.* https://doi.org/10.4194/TRJFAS27516

Article History
Received 10 December 2024
Accepted 20 November 2025
First Online 12 February 2026

Corresponding Author
E-mail: spiontkovski@mail.ru

Keywords
Black Sea
Phytoplankton
Bioluminescence
Zooplankton
Ecosystem

Abstract

The distribution of shelf resources is spatially heterogeneous. In this respect, understanding their spatiotemporal gradients is of fundamental importance, since it helps update models and resource management. Data from six summer expeditions carried out from 2011 to 2023 were used to estimate along-shelf and cross-shelf spatial gradients of bioluminescence intensity, phytoplankton, and zooplankton biomass in the upper mixed layer and down to the seasonal thermocline. Plankton samples were collected along transects and oceanographic station grids. The spatial gradients varied from twofold to two orders of magnitude. The ratio of scale of the cross-shelf to along-shelf gradient was a multiple of six. It indicated the cross-shelf gradient's dominant role in mediating the pelagic community's spatial structure. The ratio of scales with equal gradients should be considered when monitoring pelagic shelf ecosystems.

Introduction

Management of shelf resources and monitoring the health of its ecosystems are important goals of the states owning the shelf (Halpern et al., 2016; Sherman, 2014; Sherman et al., 2018). Shelf ecosystems ensure the majority of the world's fish catches (Pauly et al., 2002), however, the distribution of shelf resources is spatially heterogeneous. Understanding their spatiotemporal gradients is of fundamental importance since it helps optimize simulation models, forecast models, and resource management.

The gradient of spatial distribution is a vector indicating the direction of change in a certain parameter in coordinate space. The simplest examples are maps of physical, chemical and biological parameters at various scales: from micro-distribution to the scale of the World Ocean. In the latter case, the maps are based on data collected through single expeditions, or their amalgamation. Published maps revealed the location of oligotrophic zones, latitudinal gradients of species diversity, the bipolar distribution of plankton biomass, and etc. (Hillebrand, 2004). Along with the gradients measured on board, satellite monitoring is widely used. Global maps of chlorophyll-a concentration and primary production are characteristic examples (Behrenfeld et al., 2006; Tagliabue et al., 2021).

Studies of gradients on a regional scale are often based on measurements carried out in the form of grids of oceanographic stations. Grids and subgrid measurements make it possible to identify the contribution of multiple-scale components to the spatial heterogeneity of the field (Piontkovski et al., 2022). Along with two-dimensional cross-sections of the field, one-dimensional (horizontal) ones are broadly used (Aiken, 1980; Spooner et al., 2020). A simplified scheme for assessing the contribution of multiple-scale components consists of a characteristic trend and deviations from it. The presence of monotonous trends (positive or negative) makes it possible for specialists to approximate the parameter values along the trend vector, hundreds of kilometers away from the starting point.

Studies of trends help identify zones of potential aggregation of pelagic fish and assess their stocks (Ballón et al., 2011; Bastos-Filho et al., 2021). In this regard, the plankton communities of the northern part of the Black Sea shelf are of particular interest. They exhibit significant gradients along the shelf (from its highly productive western part to the low-productivity of the eastern part) and across the shelf, due to significant changes in the shelf width (from hundreds of meters throughout its central part, to hundreds of kilometers in the western part). For example, remote sensing of chlorophyll-a concentration in the summer season indicated a spatial gradient attaining two orders of magnitude from the shallow waters of the northwestern Black Sea to the adjacent deep waters (Shapiro et al., 2010).

Summer expeditions of the Russian Academy of Sciences make it possible to estimate the gradients of plankton on the scale of the Crimean shelf, which was the goal of our research. We analyzed the along-shelf and cross-shelf gradients and the ratio of the spatial scale (vertical-to-horizontal) where these gradients are equal. The characteristics of the plankton community were represented by phytoplankton biomass, bioluminescence intensity and biomass of forage zooplankton. All these parameters are widely used in monitoring plankton communities of the World Ocean and its shelf (Letendre et al., 2023; Moline et al., 2005).

Materials and Methods

The bathymetric characteristics of the Black Sea shelf (with its boundary along the 200-meter isobath) were taken from published sources and maps. The collection of plankton samples and bioluminescent potential soundings was carried out during the summer expeditions of 2011-2023 (Table 1, Figure 1).

Due to the fact that the aforementioned expeditions were carried out within the framework of various state programs, the set of measured parameters differed between cruises, which created difficulties in comparative analysis of materials and led to a fragmental pattern of data used in the approximation of trends.

Temperature, electrical conductivity and hydrostatic pressure at a depth, ranging from 0 to 500 m, were measured predominantly using the "IDRONAUT

Table 1. General information on expeditions

r/v "Professor Vodyanitski" cruise No.	Time of expeditions	Number of station with BP casts	Number of station with plankton sampling
70	19.08-28.08.2011	19	40
87	30.06-18.07.2016	28	0
96	19.07-09.08.2017	23	49
102	09.06-01.07.2018	20	44
108	11.07-03.08.2019	38	40
128	03.08-21.08.2023	19	8

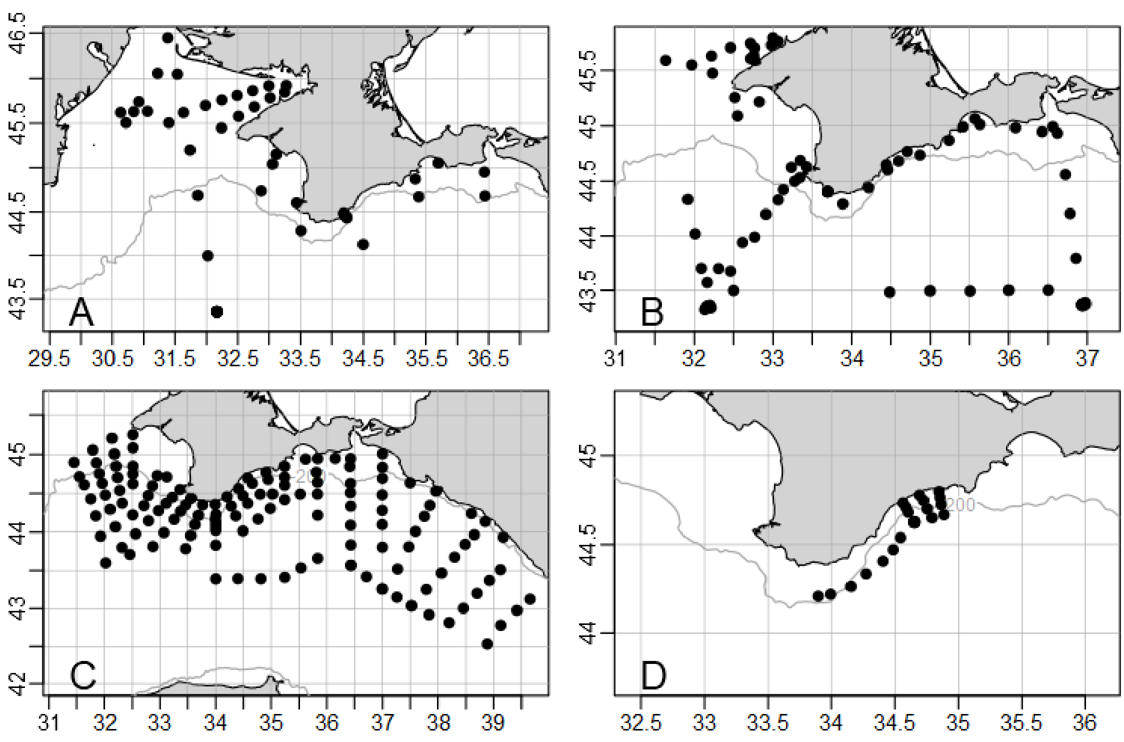

Figure 1. Examples of transects and station grids, r/v "Professor Vodyanitski", cruise No. 70, 96, 102, and 128 (A-D).

OCEAN SEVEN 320 Plus M" probe and using the "SBE-911 Plus" probe, in some cases. Data on the concentration of phosphates, nitrates and silica were taken from the archived expedition reports.

The "Salpa-M" bathyphotometer was used to measure the bioluminescent potential (BP), which characterizes the maximum luminescent energy of all organisms:

$$BP= \int B(t)dt,$$

Where B(t) is the intensity of light emission during the flash (t).

The device allows synchronous measurements of mechanically stimulated bioluminescence in the range of 10^{-13} to 10^{-8} W cm^{-2} L^{-1}, hydrostatic pressure, temperature, electrical conductivity, turbidity and photosynthetically active radiation. The resolution during instrument deployment at a speed of 1.2 m s^{-1} was 0.25 m.

The two liter Niskin water bottle samples were concentrated by reverse filtration through track membrane filters with a pore diameter of 1 µm and fixed with Lugol's solution (0.1 ml per 50 ml of sample). The species composition and sizes of cells were determined in a Naumann chamber, under a XY-B2 microscope.

Forage zooplankton, which is formed mainly by copepods, contributes to the diet of small pelagic fish of the Black Sea shelf. Zooplankton samples collected with a Juday plankton net with an entrance diameter of 36 cm and a mesh size of 140 µm were fixed with a neutral formalin solution with a 4% concentration. Samples were processed in a Bogorov chamber, in which the taxonomic composition, size of organisms and their abundance were estimated. To convert size and abundance to biomass, the size-weight ratios known for Black Sea species were applied (Kovalev et al., 1995). The regression analysis allowed us to assess the statistical significance of along-shelf and cross-shelf trends.

Results

Thermohaline Structure and Dynamics of Waters

Data from the summer expeditions, on one hand, pointed to the known properties of the thermohaline structure of shelf waters and on the other, supplemented them with new details of mesoscale variability. In July through August, we observed the warmest surface waters (25-27°C). The difference in surface temperature was 2-4°C between the eastern and western parts of the shelf, versus a 0.5-1.5°C difference throughout cross-shelf sections. The thickness of the upper mixed layer (of 10-20 m) corresponded to the climatic norm for the region. A characteristic property of the spatial structure were "tongues" of low salinity in the surface layer (with isohaline 18.1%o), stretching along the eastern part of the shelf (Figure 2). These "tongues" originate at the Caucasian coast, due to river runoff and low-salinity waters coming from the Kerch Strait.

Common features of nutrient distribution throughout cross-shelf transects were the negative trends of phosphate, nitrate and silicon concentrations in the surface layer. One of the episodes with normalized trends is shown in Figure 2. The concentration decrease attained one order of magnitude, in absolute values. Regarding the dynamics of waters in the summer time, cyclonic vorticity corresponding to large-scale circulation prevailed. Along the shelf, mesoscale and submesoscale eddies of cyclonic and anticyclonic origin were traced. Anticyclones dominated and exhibited orbital velocities ranging from 25 to 30 cm s^{-1} (Artamonov et al., 2020). Also, short-term episodes of coastal upwellings, with a decrease in temperature of 4-6°C at the surface were noted.

Bioluminescence

The along-shelf and cross-shelf gradients are evident on the map which averaged six summer cruises (Figure 3). In particular, it showed a general weakening of BP along the northern Black Sea shelf, eastward, as well as a negative cross-shelf gradient, most pronounced in the northwestern part of the sea.

The two to six-fold BP decrease was observed along the transects of the 96th, 70th, and 128th cruises. The gradients varied from 1.5 to 5 10^{-12} W cm^{-2} L^{-1} km^{-1}. Figure 4 exemplifies the BP trends in the upper 20 m layer on the along-shelf transects directed eastward. Trends were statistically significant at $P \leq 0.05$, in all cases.

A 6 –to- 17-fold BP decrease was observed in the cross-shelf transects which spanned a depth range from 31 to 2000 m (Figure 5). The gradients varied from 6 to $15*10^{-12}$ W cm^{-2} L^{-1} km^{-1}. They were calculated for the 175 km transect of the 96^{s} cruise and the 310 km transect of the 70th cruise. However, no BP trend was observed on the 128th cruise transect across the continental slope. The absence may be due to their short length as well as the pronounced mesoscale variability of BP in this region.

Overall, the ratio of spatial scales (across-to-along the shelf) with BP decline of one order of magnitude, was equal to six. This shows that cross-shelf gradients exceed along-shelf gradients, six-fold. In terms of taxonomy, it might be noted that BP gradients were mediated by the distribution of luminous Dinophyceae, which were represented by 22 taxa in the summer (Evstigneev et al., 2024).

Phytoplankton

Since mechanically stimulated bioluminescence of the Black Sea epipelagic community is generated mainly by phytoplankton, it seems useful to consider the large-

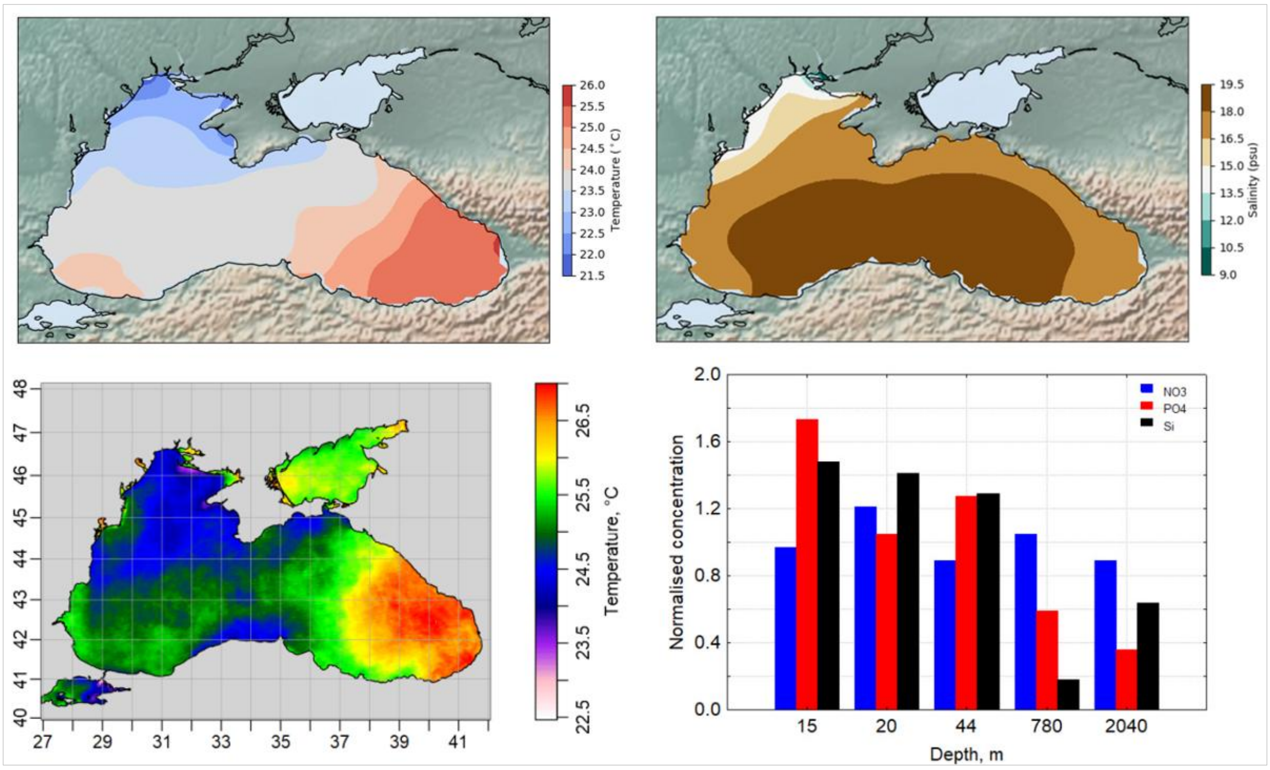

Figure 2. Thermohaline structure of waters. Upper figures: average climatic distribution of temperature and salinity at the sea surface in August 1950-2020 (http://bod-mhi.ru/ru/climaticAtlas_2020.shtml). Mid left figure: sea surface temperature in summer 2011 (http://dvs.net.ru/mp/data/201108bs_sst_ru.shtml). Mid right figure: A cross-shelf gradient of phosphate, nitrate and silicon concentrations (0 m) on the northwestern shelf; calculated according to Rodionova (2012). The ordinate axis shows concentrations normalized to the average. Bottom left figure: salinity in summer, at 25m and 100m. Red and blue circles stand for mesoscale anticyclonic and cyclonic eddies, respectively. The black bold line stands for the boundary of the Rim Current (Artamonov et al., 2020).

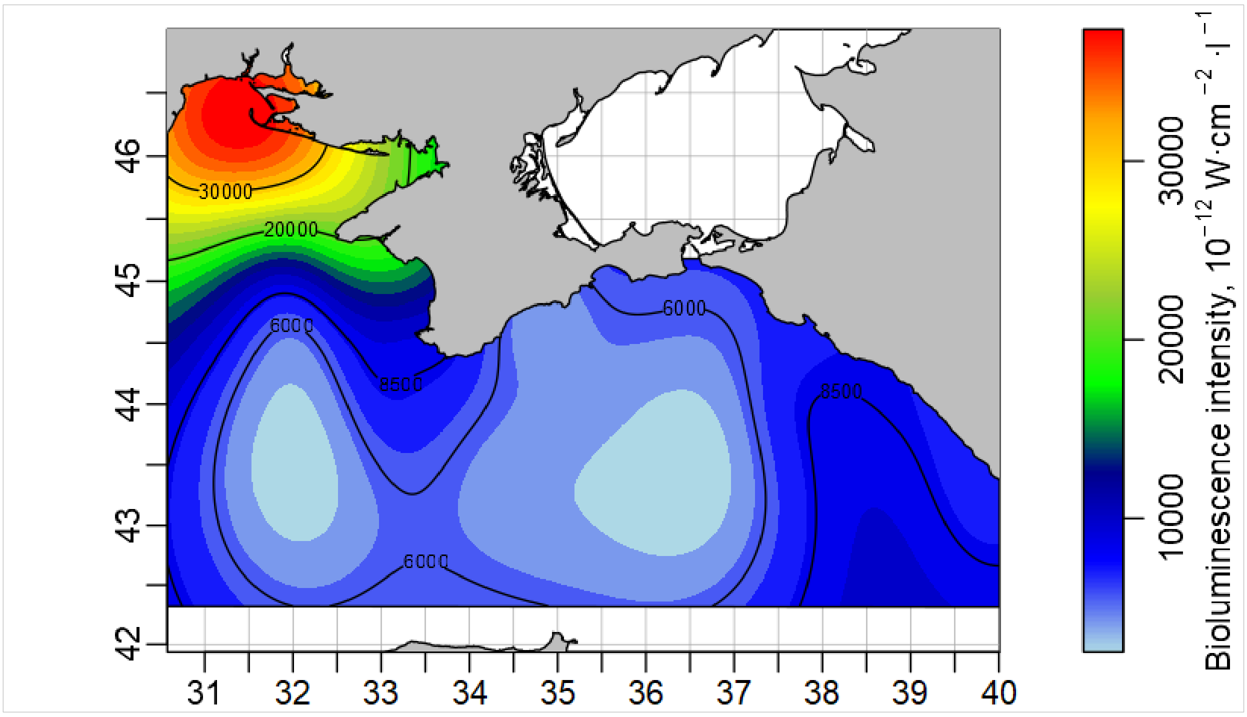

Figure 3. Spatial distribution of BP (10^{-12} W cm^{-2} L^{-1}) according to direct contact measurements in the 0-20 m layer (cruise No.70, 87, 96, 102, 108, and 128).

scale spatial trend of chlorophyll-a biomass (as an indicator of phytoplankton biomass) and Dinophyceae biomass as the main bioluminescent fraction of phytoplankton. Comparisons of chlorophyll-a and BP at night stations of the 70th cruise (i.e. during a period of stability of its vertical structure) showed high correlation elucidated in layers: 1-5, 1-34, 10-60 m, at r= 0.75, 0.78, and 0.71, respectively (Evstigneev et al., 2019). According to remotely sensed data, the distribution of chlorophyll-a elucidates the productive northwestern shelf and less productive central and northeastern regions. The gradients of Dinophyceae biomass and their luminous fractions are pronounced as well, especially along the northwestern shelf (Figure 6).

The cross-shelf transect from the 70th cruise over depths from 14 to 2150 m showed a decrease in the total phytoplankton abundance and the biomass of the luminous Dinophyceae by two orders of magnitude. The biomass decline corresponded to 0.71 mg m^{-3} km^{-1}, in gradient units. The total phytoplankton biomass decreased two-fold, which corresponded to 1.74 mg m^{-3} km^{-1}. The highest gradients were noted for the total abundance of phytoplankton, the biomass of Dinophyceae and its luminous fraction (Figure 6). On the along-shelf transect (with 8 stations), a significant Dinophyceae biomass trend was revealed (at P= 0.05), which decreased two-fold eastward, corresponding to 0.15 mg m^{-3} km^{-1} of gradient units. Overall, the cross-shelf gradients of Dinophyceae biomass exceed the along-shelf ones. The ratio of the spatial scales (across shelf-to along the shelf) at which the biomass declined by one order of magnitude was equal to nine.

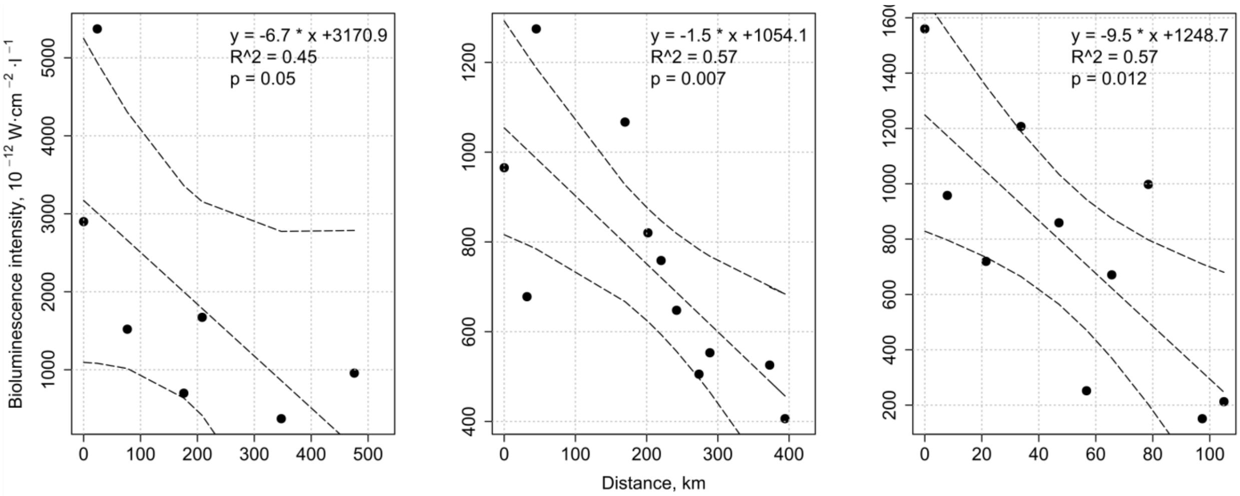

Figure 4. Bioluminescence on transects. Eastward trends of bioluminescent potential in the 0-20 m layer at stations along the Crimean shelf: in the 70th, 96th and 128th cruises (from left to right).

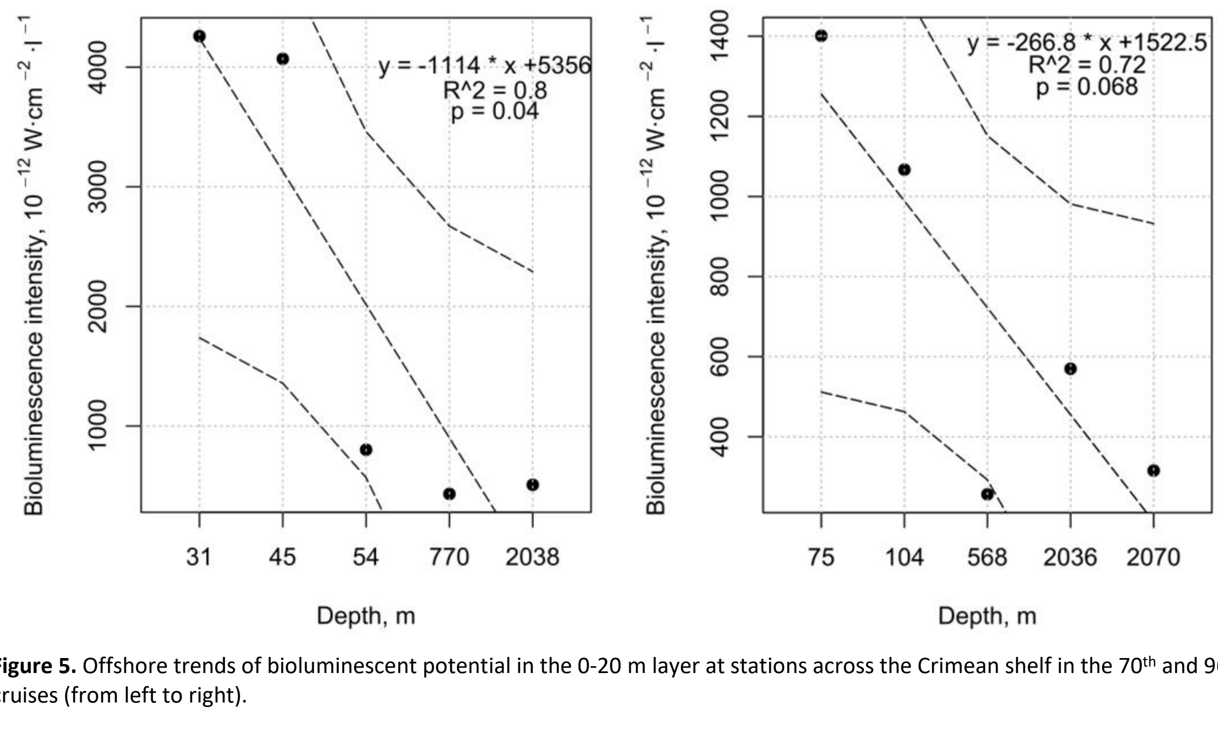

Figure 5. Offshore trends of bioluminescent potential in the 0-20 m layer at stations across the Crimean shelf in the 70th and 96th cruises (from left to right).

Contact measurements based on the processing of samples from the 96th cruise revealed an along-shelf gradient of the total biomass of phytoplankton with a threefold decrease and diatoms with a twentyfold decrease, eastward (at P≤0.01). No significant trends were found in the distribution of Dinophyceae biomass. Deviations from the trend were associated with the spatial heterogeneity of phytoplankton distribution. The cross-shelf transect of the 128th cruise, which spanned the continental slope, did not show a statistically significant trend in the distribution of biomass of various phytoplankton groups; however, the decline could be visually observed, seaward. A phytoplankton biomass decline was also traced in the cross-shelf transect of the 102nd cruise (Figure 7).

In general, the comparison of BP gradients, phytoplankton biomass and its taxonomic groups showed their similarities, as well as their differences. Thus, on the 310 km cross-shelf transect of the 70th cruise, the BP decreased 17 times in the upper 20 m layer while the biomass of dinoflagellates decreased 12 times. On the 450 km along-shelf transect of the 96th cruise, the BP decreased 2.3 times, the total phytoplankton biomass decreased three times, the biomass of dinoflagellates decreased 1.6 times, eastward. Partly, this could be associated with a spatial heterogeneity of the vertical structure of the BP and phytoplankton in the summer. Another factor involved could be a general decrease in the biomass of *Noctiluca scintillans* (Macartney) Kofoid and Swezy, 1921, which

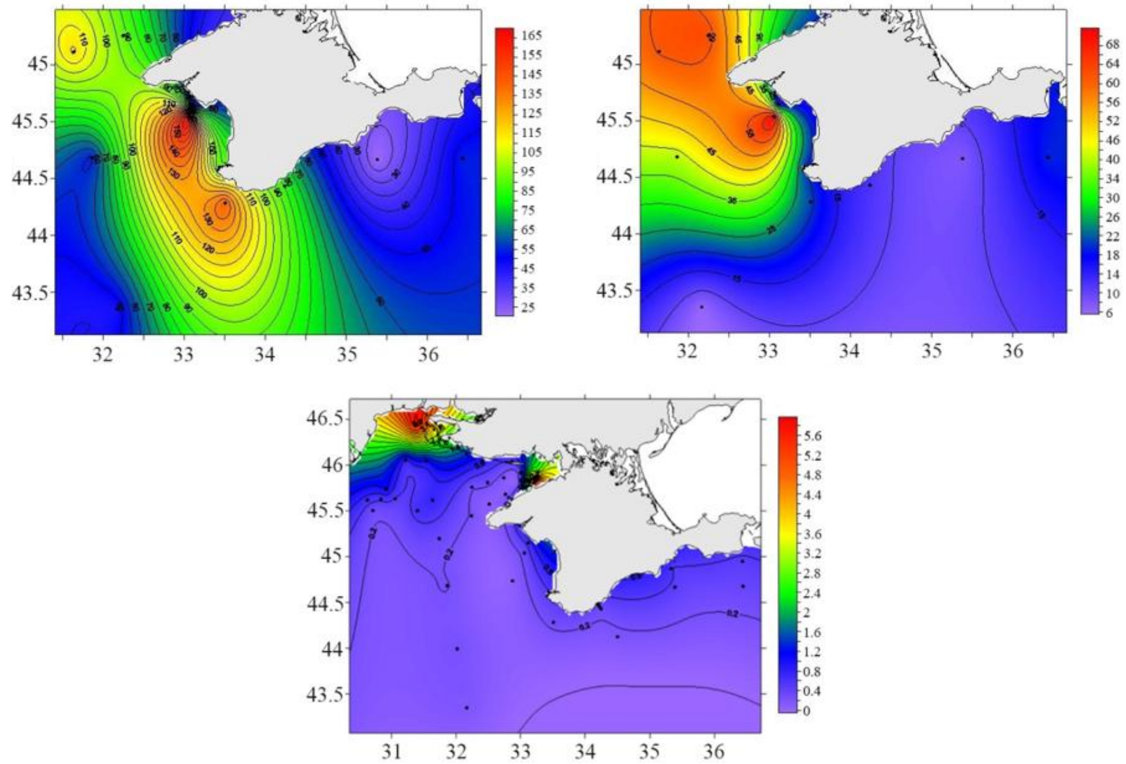

Figure 6. Spatial distribution of phytoplankton. Upper right panel: total biomass of Dinophyceae (70th cruise, Bryantseva et al., 2014). Upper left panel: biomass of bioluminescent Dinophyceae Bottom panel: chlorophyll-a concentration, mg m^{-3} (70th cruise).

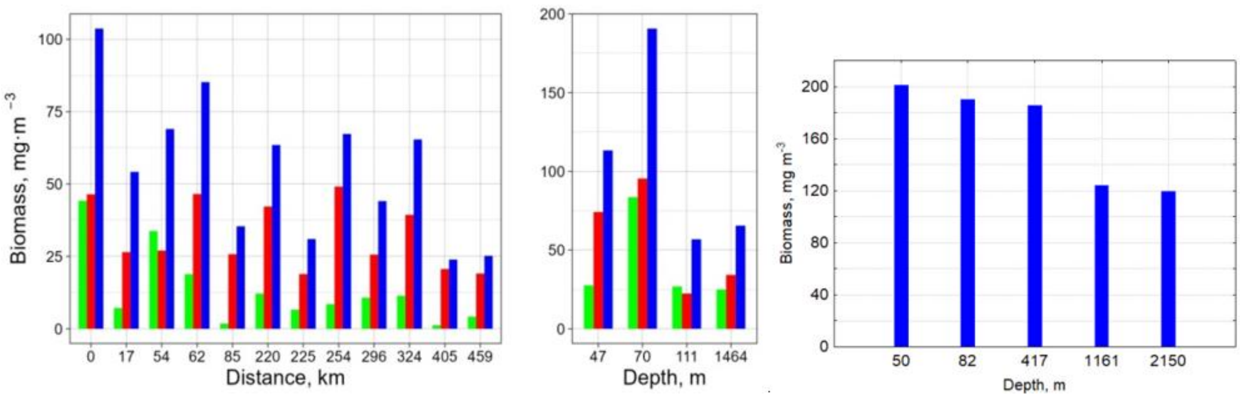

Figure 7. Distribution of phytoplankton biomass at the surface on offshore cross-shelf transects of the 96th cruise (left panel), 128th cruise (middle panel) and 102nd cruise (right panel). Green color: Bacillariophyceae, red color: Dinophyceae, and blue color: total phytoplankton biomass.

are the most luminous algae of the Black Sea. On the 70th cruise cross-shelf transect, the *Noctiluca* biomass decreased by several orders of magnitude (from 44.7 to 0.1 mg m^{-3}). Eight years later, in the same area, (during the 108th cruise survey), the biomass decrease was nearly the same (from 46.2 to 0.2 mg m^{-3}).

Zooplankton

Due to trophic interactions in the plankton community, zooplankton acts as a factor regulating the abundance of phytoplankton and its BP. Also, bioluminescent organisms contribute to the food and non-food fractions of zooplankton. Both along-shelf and cross-shelf trends were found in the distribution of the forage zooplankton biomass (Figure 8). In the first case, a tenfold decrease was observed in the eastward transect, directed from the highly productive northwestern part of the shelf to the Kerch Strait. In the second case, the cross-shelf trend can be traced in two transects (western and eastern). Thus, in the longest (western) transect, a tenfold decrease towards the open sea was noted, which corresponded to 0.12 mg m^{-3} km^{-1}, in gradient units. The ratio of the spatial scales (the cross-shelf -to- along-shelf transects) with equal biomass gradients, was equal to 10.

Along the Crimean shelf, the main contribution to the total biomass of forage zooplankton comes from copepods (41-48%) and chaetognaths (12-49%). The latter are represented by one species - *Parasagitta setosa* (J.Muller, 1847). The biomass of non-forage zooplankton is dominated by jellyfish *Aurelia aurita* (Linnaeus, 1758) which exceeded the biomass of forage zooplankton by 2-3 times, in carbon units (Piontkovski et al., 2024; Zagorodnyaya et al., 2023).

Discussion

The highest gradients of BP and phytoplankton biomass were observed on cross-shelf transects (from the shallow part of the shelf, seaward), along which the enrichment of the upper layer with nutrients (phosphates, nitrates and silicon) exhibited declining trends (Figure 2). A twofold decline in the concentration of chlorophyll-a measured *in situ* was noted in the summer of 2017 on the north-eastern shelf, on the transect to the open sea (Arashkevich et al., 2017). In general, the spatial gradients of BP depend on the biomass of the luminous Dinophyceae, during all seasons. For instance, a four-year monthly time series at a coastal station near Sevastopol showed a high correlation (r= 0.91, at P= 0.01) between BP and the total biomass of Dinophyceae (Bryantseva et al., 2014).

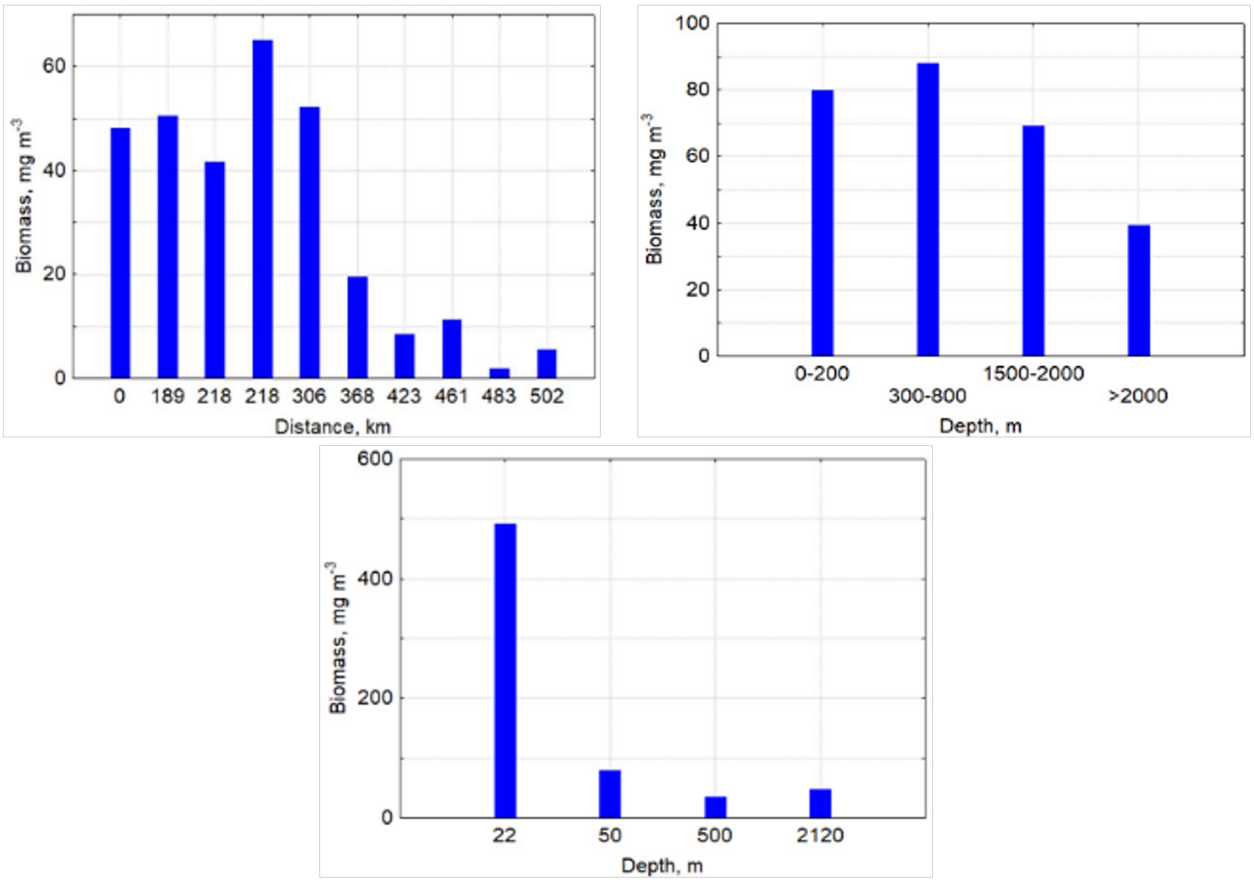

Figure 8. Distribution of a forage zooplankton biomass. Upper left panel: along-shelf biomass trend (west to east) in the 0-15, 0-57 m layer (96th cruise). The distance from the initial station of the transect is shown on the X-axis. Upper right panel: cross-shelf biomass trend on the northwestern shelf (70th cruise). The depths (on the X-axis) are ranked into four classes. Bottom panel: cross-shelf biomass trend off the eastern coast of Crimea (70th cruise).

Also, cross-shelf gradients were reported for the distribution of ichthyoplankton, in which anchovy eggs dominated in the upper mixed layer, in the summer. Based on map studies, a negative trend was evident. In the central part of the shelf anchovy egg abundance indicated a five to tenfold decrease on cross-shelf transects. Also, the species diversity of ichthyoplankton decreased twofold (Klimova et al., 2021, 2022).

Overall, our plots point to the presence of two main constituents of spatial heterogeneity: a linear trend and deviations from it. The latter are caused by mesoscale variability mediated by meanders of currents, cyclonic and anticyclonic eddies (Kubryakov et al., 2023), which are most numerous in summer. For instance, the water mass transport of shelf waters by the Sevastopol anticyclonic eddy seaward, is comparable (in volume) to the volume of waters of the entire northwestern shelf (Zhou et al., 2014). In terms of coastal dynamics, the along-shelf and cross-shelf gradients of plankton biomass are affected by water mass transport by the coastal current. Its direction fits that of the Rim Current and incorporates cross-shelf water mass transport modulated by eddies and meanders (Kubryakov et al., 2023; Shapiro et al., 2010).

We treated the 2011-2023 expeditions as replicas of spatial gradient estimates. The approach seems to be appropriate, since no statistically significant interannual trends of BP, phyto- and zooplankton biomass were observed along the Crimean shelf (Piontkovski et al., 2024). Pronounced deviations of plankton spatial gradients from the aforementioned trends are associated with mesoscale physical dynamics. The plankton biomass variance in central, versus peripheral areas of eddies attains several folds (Melnikov et al., 2024). The "mesoscale noise" generates situations when the along-shelf or cross-shelf trends reported by a certain expedition are not confirmed by the next one.

An anthropogenic influence (through the concentration of surface active anthropogenic compounds, petroleum hydrocarbons, and etc.) impacts the along-shelf and cross-shelf gradients of plankton. High concentrations of petroleum hydrocarbons (>50 µg L^{-1}) suppress bioluminescence of phytoplankton and growth rates of zooplankton, potentially to lethal effects (Avila et al., 2010). On the scale of the Crimean shelf, the concentration of nitrates, nitrites and other compounds largely depends on runoff volumes, offshore.

The contribution of trophic interactions to the formation of spatial trends can be assessed indirectly, since data on the rate of food consumption in the trophic cascade are based on experimental studies or calculations of daily rations based on the analysis of the stomachs of fish and crustaceans. For example, significant aggregations of anchovy and sprat on the shelf with copepods dominating in their diets (Bişiniqu et al., 2017) indirectly points to grazing as a significant factor in the reduction of forage zooplankton biomass in the region. Also, the abundance of gelatinous zooplankton (primarily jellyfish *Aurelia aurita*) acts as a factor reducing the biomass of forage zooplankton, since jellyfish feed on it.

In the formation of along-shelf and cross-shelf gradients, physical and biological factors could act both in combination and in parallel to one another (independently). An example of the latter is the distribution of coastal cladocerans (*Penilia avirostris, Pleopsis polyphemoides, Pseudevadne tergestina*), which constitute high abundance everywhere along the shelf, during the summer. However, their abundance markedly declines in the open sea, due to unfavorable conditions. The seasonal cycle of their abundance has an "explosive" pattern, with a short-term maximum at the end of July or in August (Piontkovski et al., 2012).

Animation in the eNATL60 cross-shelf exchange model (E-NATL 60, 2024) demonstrates magnitudes of hydrophysical spatiotemporal variability and points to the inadequacy of long-term field surveys which could last several weeks. In this respect, satellite monitoring provides more adequate estimates. However, this approach is limited by the ability to measure plankton community parameters at trophic levels above primary producers. Also, estimates of chlorophyll-a concentration from satellite images (as an indicator of phytoplankton biomass) are associated with marked errors, especially in Crimean shelf waters (Churilova et al., 2017). Continuous records of plankton characteristics using towed recorders (undulating over depth) could improve the quality of shelf water monitoring. The approach is broadly used in other regions, to measure the spatial distribution of hydrophysical parameters, phytoplankton, zooplankton and bioluminescence (Aiken et al., 2000; Bracher et al., 2020; Ollevier et al., 2023). Continuous records are especially important for studies of cross-shelf gradients, which dominate the formation of the spatial structure of the epipelagic plankton community of the Crimean shelf.

Conclusions

Spatial (along-shelf and cross-shelf) gradients of bioluminescent potential in the upper 20-meter layer of the Crimean shelf varied from 1.5 to 15×10^{-12} W cm^{-2} L^{-1} km^{-1}. These gradients were mediated by the distribution of luminous Dinophyceae, which were represented by over 20 taxa. Also, significant gradients were observed in the distribution of nutrients, phyto- and zooplankton biomass. These gradients varied from twofold to two orders of magnitude. The ratio of the scale of the cross-shelf to the along-shelf horizontal gradient was a multiple of six. It indicated the dominant role of the cross-shelf gradient in mediating the spatial structure of the pelagic community. The ratio of scales should be taken into account when monitoring the shelf epipelagic ecosystems.

Ethical Statement

This work does not contain a description of any research using people or animals as objects.

Funding Information

This work was carried out within the framework of state assignments of the Federal State Budgetary Institution of Science FRC IBSS No. 124030400057-4, No. 124022400148-4 and SevSU No. FEFM-2023-0005. Expeditionary research was carried out in the Center for Collective Use of the R/V “Professor Vodyanitski” of the Federal State Budgetary Institution of Science FRC IBSS.

Author Contribution

SAP: conceptualization; formal analysis; investigation; IMS: formal analysis; investigation; visualization; YAZ: formal analysis; investigation; visualization; EYG: formal analysis; investigation; visualization; IAM: formal analysis; investigation; visualization; AVM: formal analysis; investigation; visualization.

Conflict of Interest

The authors declare that they have no known competing financial or non-financial, professional, or personal conflicts that could have appeared to influence the work reported in this paper.

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