



Pelagic Biophysical Coupling at the Thermocline Level in a Coastal Sea

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Abstract. Marine phytoplankton photosynthetic efficiency is regulated by light and nutrient availability, which are both
25 modulated by physical processes in the stratified water column. The ecological impact of such forcings depends on the
alignment of biological and physical processes across comparable spatial and temporal scales. During summer stratification
in the southern Adriatic Sea, internal island-trapped wave (ITW) induces vertical thermocline oscillations of up to 30 meters.
In order to investigate their influence on net primary production, field campaigns were conducted during stratification
periods from 2021 to 2023. The aim of this research was to quantify net primary production rates, to relate them to
30 biophysical conditions of the water column and to characterize biophysical coupling within the thermocline. Six *in situ* ¹⁴C
primary production experiments were conducted, while high-resolution datasets on plankton community structure and
physico-chemical parameters were obtained. Results revealed a strong biophysical coupling in the thermocline layer driven
by the interaction between ITW, plankton communities and broader food web dynamics. The ITWs were associated with
increased nutrient concentrations and light availability in the thermocline layer, coinciding with enhanced photosynthetic



35 activity and primary production rates, particularly for pico- and nanophytoplankton. Net primary production was regulated by resource availability, zooplankton grazing and microbial recycling, highlighting the importance of trophic interactions under ITW forcing. This study demonstrates that ITW can modulate net primary production, therefore enhancing productivity in the stratified oligotrophic ecosystems. Such biophysical coupling at small spatio-temporal scale may play a vital role in regulating ecosystem functioning under climate change-driven prolonged stratification.

40 **1 Introduction**

Marine primary production is mediated by photoautotrophic organisms that facilitate photosynthesis to convert inorganic carbon into organic matter. Primary producers form the basis of the marine food web and play a pivotal role in global biogeochemical cycles, particularly the carbon cycle (Falkowski et al., 1998). Although comprising about 0.2% of the global primary producer biomass, marine phytoplankton are responsible for roughly half of global annual primary production (Field et al., 1998; Falkowski et al., 1998). The photosynthetic efficiency of phytoplankton depends on physiological acclimation to the light and nutrient availability within the water column (Dugdale 1967; Lewis et al., 1984; Cullen 1990; Geider et al., 1998; Moore et al., 2013).

Dynamics of abiotic environmental factors are modulated by physical processes within and between water masses (Sverdrup 1953; Denman, 1994; Mann and Lazier 2005). For instance, vertical and horizontal circulation patterns determine transfer of available nutrients (Dugdale 1967; Williams and Follows 2003; Freilich and Mahadevan, 2019) and also shape the underwater light environment (Sverdrup, 1953; Lewis et al., 1984). Moreover, physical forcings facilitate vertical and horizontal phytoplankton redistribution (Margalef, 1978; Denman, and Gargett 1983; Holloway, 1984; Franks, 1992), thus influencing net primary production (NPP) by transporting them to regions with enhanced irradiance or increased nutrient supply (Lewis et al., 1984; McGillicuddy et al., 1998). Conversely, in a stratified water column which is devoid of turbulence, phytoplankton may remain confined within water masses of distinct temperature and salinity, where reduced vertical exchange and temperature-dependent physiological responses can influence their metabolic rates (Eppley, 1972; Behrenfeld et al., 2008)

Physical processes occur over a wide range of spatio-temporal scales, and their biological relevance depends on the correspondence between these scales and those of phytoplankton growth and turnover rates (Harris, 1980; Harris, and Trimbee 1986; Denman, 1994). For instance, submesoscale processes (0.1–10 km) such as upwelling, downwelling, fronts and internal waves, lasting over hours to days may strongly influence phytoplankton because their temporal and spatial scales closely match phytoplankton growth and turnover timescales, unlike mesoscale processes (10–100 km) that typically evolve over weeks to months (Harris, 1980; Mahadevan, 2016; Lévy et al., 2018).

To understand localized variations in primary production, it is crucial to assess the presence of physical drivers that operate at scales comparable to cell-based processes (Harris, 1986; Freilich et al., 2022). For instance, unique biological and physical interactions enhance primary production at islands in oligotrophic open ocean regions (De Falco et al., 2022, 2024), a



phenomenon known as the Island Mass Effect (IME) (Doty and Oguri 1956; De Falco et al., 2022, 2024). One of these processes is internal island-trapped wave (ITW) (Longuet-Higgins, 1967; Mysak, 1967; Hogg, 1980; Brink, 1999), a special type of coastal trapped wave (Huthnance, 1978) that can enhance primary production through nutrient transport to the euphotic zone (Pan et al., 2012), changes in light properties (Holloway and Denman, 1989; Gaxiola-Castro et al., 2002; Evans et al., 2008), and vertical displacement of phytoplankton (Orr and Mignerey 2003). ITWs have been observed at only a few locations globally; Bermuda in the central Atlantic Ocean (Brink, 1999), Hawaii in the central Pacific (Luther 1985), Gotland in the Baltic Sea (Pizarro and Shaffer 1998), Mallorca Island in the western Mediterranean (Jordi et al., 2009), the Saint Pierre and Miquelon archipelago in the northwestern Atlantic Ocean (Lazure et al., 2018) and at Lastovo Island (hereafter, Lastovo) in the southern Adriatic Sea (Mihanović et al., 2009).

The Mediterranean Sea, including the Adriatic, exhibits seasonal stratification of the water column with winters marked by vertical mixing and summers by stable stratification controlled by salinity and temperature gradients (D’Ortenzio et al., 2005). Global oceans, under the influence of climate change, exhibit an increase in the intensity and duration of water column stratification (Li et al., 2020) and the expansion of oligotrophic areas (Polovina et al., 2008). These changes impact the Adriatic Sea as well, with increased sea surface temperature and prolonged stratification related to more frequent heatwaves (Coma et al., 2009; da Costa et al., 2024; Verri et al., 2024; Denamiel 2025).

Since ITWs are biologically relevant physical process, their effect on the plankton community and NPP at Lastovo was studied during summer expeditions of ISLAND project, from 2021 to 2023 (Ljubešić et al., 2024). The effects of ITWs on physics, nutrient dynamics and the plankton community were reported by Ljubešić et al. (2024). Furthermore, oxygen-based NPP estimates showed increased productivity rates in the thermocline layer. However, impacts of ITWs on NPP using direct productivity measurements have not yet been reported. Therefore, the aims of this study are to: (1) quantify the *in situ* ^{14}C primary production in an oligotrophic, stratified island ecosystem of the southern Adriatic Sea; (2) relate *in situ* primary production to the environmental conditions across depth layers of the stratified water column; (3) characterize biophysical coupling within the thermocline layer of a dynamically stratified ecosystem influenced by ITW.

2 Materials and methods

2.1 Study site and ITW characterization

The Adriatic Sea is a semi-enclosed basin in the northeastern Mediterranean Sea with a pronounced north-south gradient in trophic status and primary production rates (Matek and Ljubešić 2024). Primary production hotspots are documented, such as Palagruža Sill where upwelling occurs (Zore-Armanda 1984; Marasović et al., 1999; Turchetto et al., 2000). However, Lastovo could be another productivity hotspot facilitated by ITWs. They propagate clockwise around the island with a 24-hour period and their resonant excitation depends on island geometry, water column stratification properties (thermocline depth and density difference) and the strength of physical forcings (diurnal barotropical tides or diurnal wind) (Mihanović et al., 2014). ITWs introduce advection and convection processes to an otherwise static stratified water column, and cause



thermocline vertical oscillations that can reach up to 30 m under a strong diurnal wind (Orlić et al., 2011). Such oscillations could enhance NPP in an oligotrophic region such as the study area during summer stratification by transporting nutrients upward or redistributing phytoplankton vertically and exposing them to enhanced irradiance. Field campaigns in southern Adriatic Sea were carried out in July 2021, June and July 2022 and July 2023, when the occurrence of pronounced ITW events was expected (Mihanović et al., 2014). Research was conducted at the opposite sides of Lastovo: northern islet Maslovnjak (station M1) and southern Cape Struga (stations S0, S1), as well as at Korčula Island (hereafter, Korčula) at islet Vrhovnjak, Prižba (station P4) (Fig. 1), which was chosen as the reference site where no ITW events have been documented.

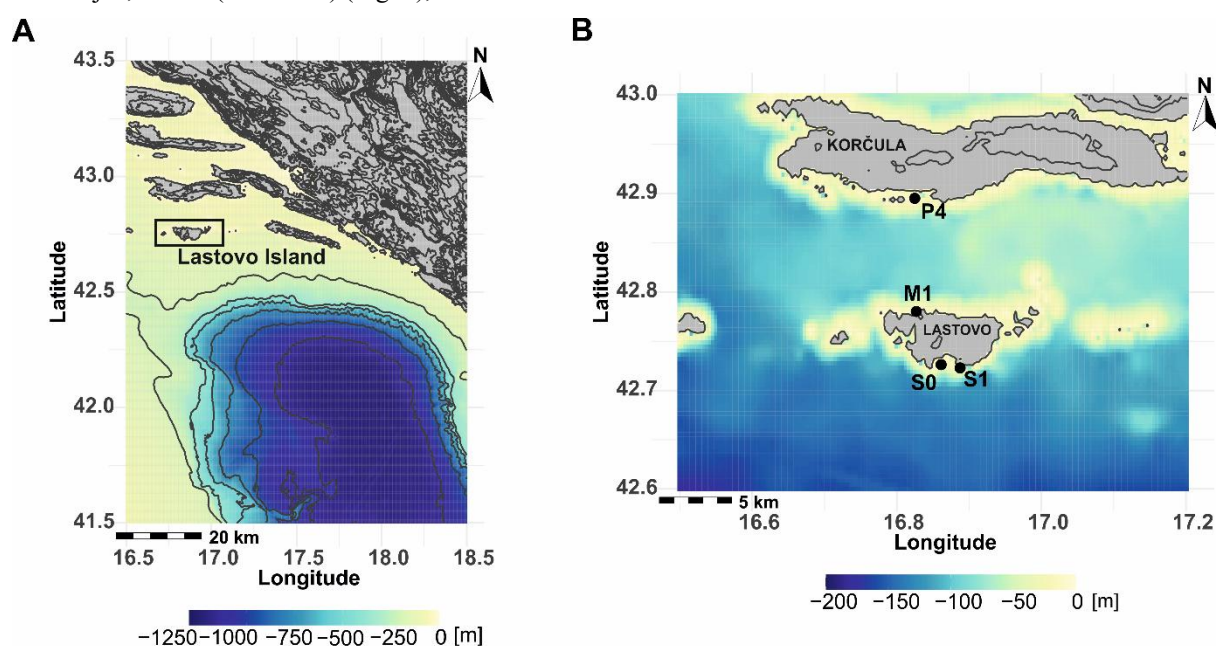


Figure 1. Study area with superimposed bathymetry: **(A)** southern Adriatic Sea and location of Lastovo Island indicated by a square; **(B)** Locations of *in situ* ^{14}C primary production experiments, including Maslovnjak (station M1) and Struga (station S0) at Lastovo Island, as well as Prižba (station P4) at Korčula Island.

ITW episodes at Lastovo during late spring 2022 and early summer 2023 were identified using *in situ* temperature data from Struga and Maslovnjak, together with wind data from the Lastovo meteorological station in 2022 and Weather Research and Forecast (WRF) model data in 2023 (Ljubešić et al., 2024), as wind measurements from the Lastovo meteorological station were not available during the summer of 2023. The main criterion was that the range of diurnal thermocline oscillations exceeded 12 m during significant diurnal episodes of the eastward wind component. A week-long ITW period was observed in early June 2022 (2–8 June 2022), coinciding with *in situ* ^{14}C primary production experiments conducted at Maslovnjak (M1) on 7 June 2022 and at Prižba (P4) on 8 June 2022 (Fig. 2). Interestingly, this ITW episode was more evident on the Maslovnjak temperature loggers than at Struga, indicating possible alongshore ITW variability during this period. Primary production incubations carried out on 4 and 8 July 2023 at Struga (S0) coincided with an intermittent ITW episode that lasted from 2 to 8 July 2023 (Fig. 3).

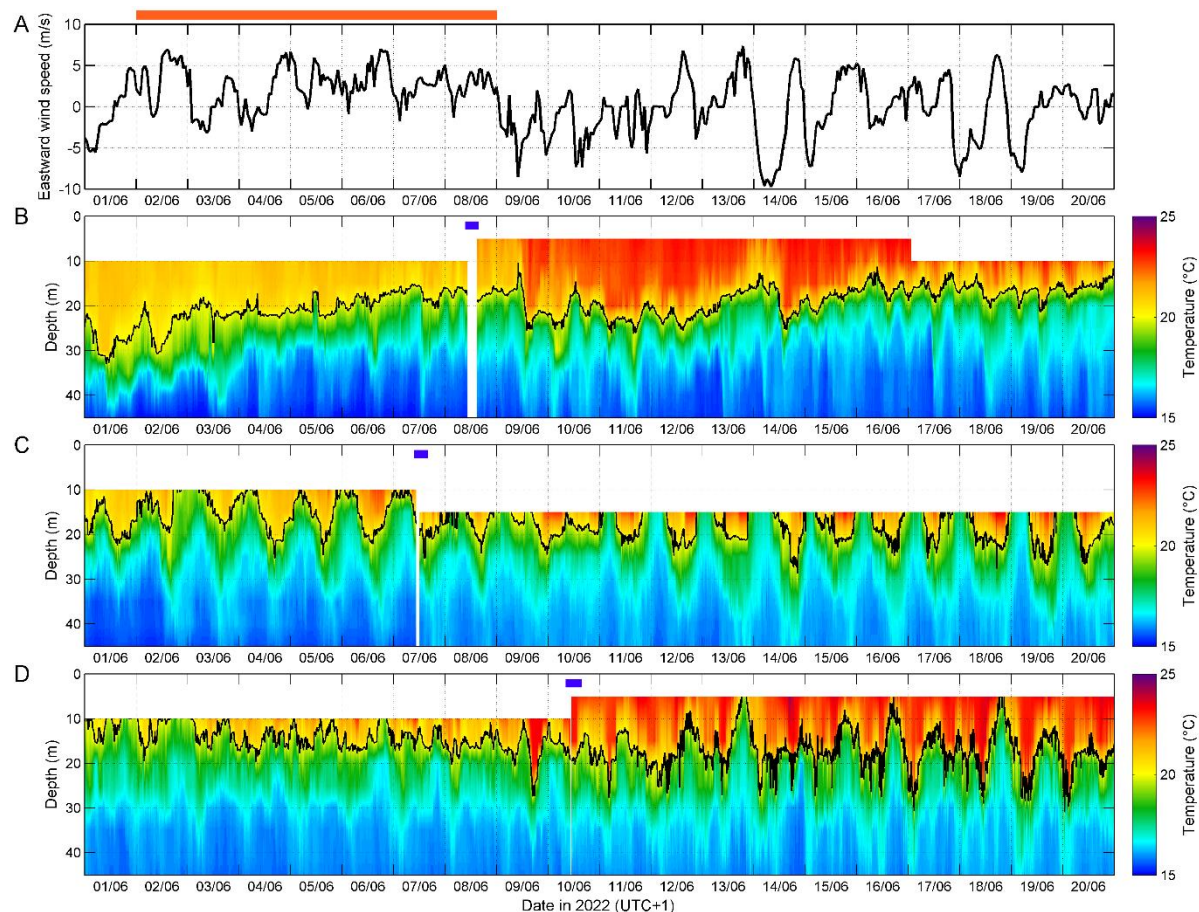


Figure 2. (A) Eastward wind speed measured at Lastovo DHMZ meteorological station, from 1 to 20 June 2022. (B) Temperature data recorded at Prižba station (P4), (C) Maslovnjak station (M1) and (D) Struga station (S1), during the same period. The ITW event coinciding with *in situ* ^{14}C primary production experiments conducted in June 2022 is denoted by orange horizontal line above panel (A). Blue horizontal lines in panels (B)–(D) denote *in situ* incubation times at corresponding stations. The thick black contour in panels (B)–(D) indicates the 20 °C isotherm.

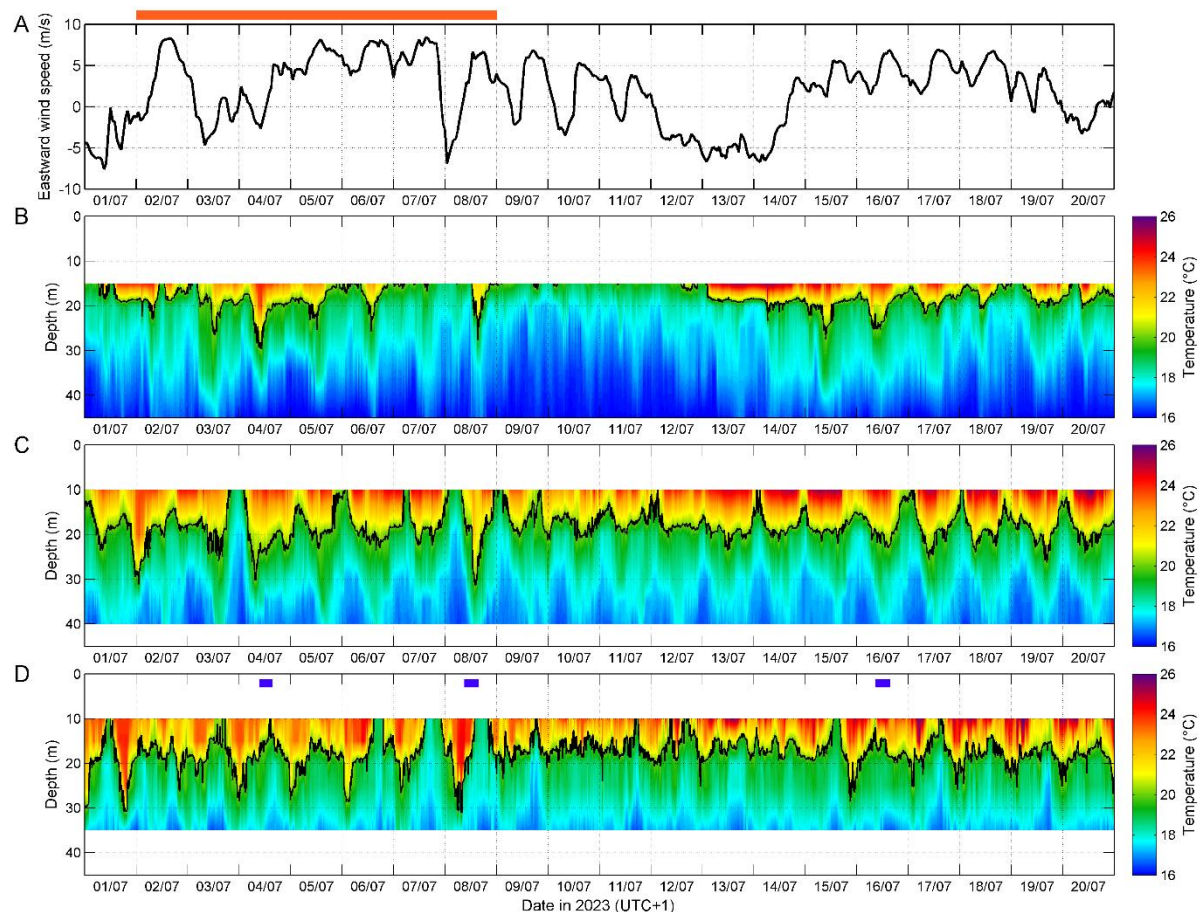


Figure 3. (A) Eastward wind speed extracted from WRF meteorological model at grid point close to Lastovo DHMZ meteorological station, from 1 to 20 July 2023. (B) Temperature data recorded at Prižba station (P4), (C) Maslovnjak station (M1) and (D) Struga station (S1) during the same period. The ITW event coinciding with *in situ* ^{14}C primary production experiments conducted in July 2023 is denoted by orange horizontal line above panel (A). Blue horizontal lines in panel (D) denote *in situ* incubation times at Struga (S0) station. The thick black contour in panels (B)–(D) indicates the 20 °C isotherm.

2.2 Field sampling and measurements

Moored measurements included temperature recorded by thermistors (HOBO Pendant Temperature/Light Data Logger), photosynthetically active radiation (PAR) measured using DEFI2-L sensors and *in situ* ^{14}C primary production experiments (Table 1). Profiles for temperature, salinity, chlorophyll *a* fluorescence (Chl F), and oxygen were measured using multi-parametric CTD (Conductivity-Temperature-Depth, SBE 19, Sea-Bird Electronics Inc., USA) with 0.5 m depth averaging. Sampling was conducted for nutrients and chlorophyll *a* (Chl *a*) analyses, as well as for plankton community composition (Table 1). High-frequency adaptive sampling strategy was guided by meteorological and oceanographic model forecasts of



ITWs (Ljubešić et al., 2024). Sampling for plankton community composition was conducted only at station S1 in July 2021
140 and July 2022 and was not performed in June 2022 or July 2023.

Nutrients were sampled in duplicates of 15 mL, filtered through a 0.2 μm PES syringe filter, fixed with 30 μL of 6 M HCl
and stored in the dark and cold until the laboratory analysis using an autoanalyzer (SEAL QuAatro segmented flow
AutoAnalyzer), resulting in phosphate, nitrate, nitrite and silicic acid concentrations [$\mu\text{mol L}^{-1}$]. Samples for Chl *a* were
145 filtered ($V = 1 \text{ L}$) through glass microfiber filters (GF/F, Whatman) with a nominal pore size of 0.7 μm . Chl *a* concentrations
[mg m^{-3}] were measured using the fluorometry method (Holm-Hansen et al., 1965). Phytoplankton, bacterioplankton and
zooplankton were sampled and analyzed as described by Matek et al. (2023) and Ljubešić et al. (2024). Microphytoplankton
($>20 \mu\text{m}$) and nanophytoplankton ($2\text{--}20 \mu\text{m}$) abundances were determined by light microscopy (cells L^{-1}), while
picophytoplankton ($<2 \mu\text{m}$), comprised of photosynthetic picoeukaryotes (PPEs), cyanobacteria and heterotrophic bacteria,
by flow cytometry (cells mL^{-1}).

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Table 1. Measurements and sampling conducted at Lastovo Island during the 2021–2023 field campaigns at Prižba (P4), Maslovnjak (M1), and Struga (S1, S0). The table summarizes depths of moored measurements (where applicable shown as initial depth : depth interval : final depth), indicates ship-based measurements and discrete sampling (marked with "x"), and lists the periods during which they were conducted. Abbreviations: PAR (photosynthetically active radiation), NPP (net primary production), T-S-Chl F-O₂ (Temperature-Salinity-Chlorophyll fluorescence-Oxygen), Chl *a* (Chlorophyll *a*).

Continuous measurements					Discrete sampling		
Moored				Ship-based			
	Temperature (Thermistors, dt = 5 min)	PAR (DEFI2-L, dt = 5 min)	<i>In situ</i> ¹⁴ C NPP experiments	T-S-Chl F-O ₂ profiles (SBE CTD, dz = 0.5 m)	Nutrients	Chl <i>a</i>	Plankton
2021	P4	5 m : 5 m : 45 m, except 25 m					
	M1	5, 10, 15, 30, 40 and 45 m					
	S1	5, 10, 20, 30, 35 and 45 m		x	x	x	x
	S0						
	<i>Period</i>	<i>June–September</i>		<i>July</i>	<i>July</i>	<i>July</i>	<i>July</i>
2022	P4	10 m : 5 m : 45 m	x	x		x	
	M1	15, 25, 30, 35, 40 and 45 m	x	x		x	
	S1	5 m : 5 m : 45 m, except 10 m	10 m and 40 m	x	x	x	x
	S0		x	x		x	
	<i>Period</i>	<i>June–September</i>	<i>July–October</i>	<i>June</i>	<i>June and July</i>	<i>July</i>	<i>July</i>
2023	P4	15, 20, 25, 35, 40 and 45 m					
	M1	10, 20, 30, 35 and 45 m		x			
	S1	10, 15, 20, 25, 30, 35 and 45 m	10 m and 30 m	x			
	S0		x	x	x	x	
	<i>Period</i>	<i>June–December</i>	<i>July</i>	<i>July</i>	<i>July</i>	<i>July</i>	

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2.3 *In situ* ^{14}C primary production experiments and concurrent measurements

A total of six *in situ* ^{14}C primary production experiments were conducted using the ^{14}C method (Nielsen 1952) along with concurrent measurements with CTD and discrete sampling for nutrients and Chl *a* analysis (Table 2). In 2022, experiments were conducted at Lastovo on 7 and 10 June at stations M1 and S0, respectively, and at Korčula on 8 June at station P4 (Table 2). Although the primary objective of these initial experiments was methodological optimization rather than targeting ITW events, an ITW event coincided with the experiment conducted at M1 (Table 2, Fig. 2). In July 2023, the experimental design was specifically aimed at capturing ITW events at station S0 by following meteorological and oceanographic model forecasts. Incubations were carried out during ITW events on 4 July (S0-04) and 8 July (S0-08), and under post-event conditions on 16 July (S0-16) (Table 2, Fig. 3). This approach in experimental design allowed temporal comparisons of primary production rates between ITW and no-ITW conditions at the same station, thereby minimizing the influence of spatial variability.

Primary production experiments were conducted by using a mooring line with an anchored floating buoy. The 100 mL glass bottles were utilized for dark and light incubations. Prior to each experiment, bottles were cleaned in 1 M HCl and dried at 60 °C. The light bottle was always placed above the dark bottle in order to prevent shading. Samples for incubation were taken with 5 L Niskin bottles, filtered through 100 µm mesh to remove zooplankton and incubated with 2.4 mM aqueous solution of ^{14}C -labelled sodium bicarbonate ($\text{NaH}^{14}\text{CO}_3$) as described in Table 2. Samples were filtered immediately after incubations using 47 mm diameter 0.2 µm pore-sized mixed cellulose ester filters (Advantec), placed in scintillation vials, rinsed with 100 µL concentrated HCl (10 M) to remove excess ^{14}C and left on an open tray for 24 h to dry. Vials were stored in the dark and at low temperature (around 4 °C) to prevent degradation or loss of ^{14}C through water-air transfer. A liquid scintillation counter (DHI A/S, Lab Products, Denmark) was used to determine ^{14}C activity (in disintegrations per minute (DPM)). During primary production experiments, the same Niskin bottle was used to collect water samples for ^{14}C incubation, nutrient analysis and Chl *a* determination. In addition, CTD casts were performed concurrently to profiles for temperature, salinity, chl F and oxygen (Table 2).

Table 2. Experimental design of *in situ* ^{14}C primary production incubations, including experiment year, station, sampling period, incubation depths, incubation duration, ITW occurrence and measurements conducted concurrently with the primary production experiments.

	Station	Period	Depths	Incubation (h:min)	Concurrent measurements			
					ITW	CTD	Nutrients	Chl <i>a</i>
2022	P4	8 June	0, 5, 10, 20, 30 and 50 m	6:05	No	x		x
	M1	7 June	0, 5, 10, 20, 30, 50 and 65 m	6:15	Yes	x		x
	S0	10 June	0, 5, 10, 20, 30, 50 and 65 m	7:30	No	x		x
2023	S0	4 July (S0-04)	0, 5, 10, 20, 30 and 65 m	5:53	Yes	x	x	x



8 July (S0-08)	0, 5, 10, 20, 30 and 65 m	6:30	Yes	x	x	x
16 July (S0-16)	0, 5, 10, 20, 30 and 65 m	6:41	No	x	x	x

2.4 Calculation of primary production rates

Daily NPP at depth z ($P_T(z)$ [mg C m^{-3}]) was calculated by applying the following equation:

$$P_T(z) = \frac{[(DPM_L - DPM_D) \times DIC \times K_1 \times K_2 \times K_3]}{DPM_D} \times T \quad (1)$$

185 where DPM_L are observed disintegrations per minute in samples incubated in light, DPM_D are observed disintegrations per minute in samples incubated in dark, DPM_{ST} is a standard value of disintegrations per minute determined in the $\text{NaH}^{14}\text{CO}_3$ solution ($9320750 \text{ DPM mL}^{-1}$), DIC is an average concentration of dissolved inorganic carbon calculated for coastal waters ($27500 \text{ mg C m}^{-3}$), K_1 is a correction coefficient for discrimination of ^{14}C (1.05) that has lower uptake compared to ^{12}C (around 5%), K_2 is a correction coefficient for respiration of organic matter (1.06) during the incubation (around 6%), K_3 is the reciprocal of the incubation time ($K_3 = 1/\text{h:min}$) and T is the photosynthetic period ($T = \text{time of sunset} - \text{time of sunrise} - 30 \text{ min}$ (margin or error)).

190 $P_T(z)$ at 0 m at station M1 and during experiment S0-04 in July 2023 were excluded from the analysis because reliable rate estimates could not be obtained. Normalized daily NPP at depth ($P^B_T(z)$ [$\text{mg C (mg Chl)}^{-1}$]) was calculated by normalizing $P_T(z)$ to biomass characterized by Chl a . Daily depth-integrated NPP ($P_{Z,T}$ [mg C m^{-2}]) was calculated by applying trapezoidal integration to vertical profiles of $P_T(z)$.

2.5 Light model

Optical properties were continuously recorded by sensors deployed on the southern cliff of Lastovo (Struga, station S1). PAR sensors [$\mu\text{mol m}^{-2} \text{s}^{-1}$] were positioned at the 10 m and 30 m depths from 6 to 23 July 2023. All sensors were placed in a horizontal position to ensure an upward orientation towards light. Raw sensor data were recorded at 5-minute intervals and subjected to low-pass filtering using a moving average to obtain 1-hour interval data. Time series with removed night values were applied to the following model in order to estimate the attenuation coefficients of PAR (K_{PAR}):

$$K_{PAR} = \left(\frac{PAR_2}{PAR_1} \right) \times -\frac{1}{\Delta z} \quad (2)$$

where PAR_1 is the measurement at 10 m, PAR_2 is the measurement at 30 m and Δz is the difference between the measured depths.

205 The light model was developed for a week when ITWs occurred during 7–13 July 2023. The model was fitted to the K_{PAR} and modeled surface irradiance (I_0):

$$I(z,t) = I_0 \times e^{-(K_{PAR}) \times \sim z} \quad (3)$$

where $\sim z$ [m] is a model depth vector, and the surface irradiance was modeled as:

$$I_0 = I_0^m \times \sin\left(\pi \times \frac{t}{D}\right) \quad (4)$$



210 where I_0^m [W m^{-2}] and D [h] are the monthly averages of surface irradiance and daylength, respectively, obtained from the Croatian Meteorological and Hydrological Service (DHMZ), and t [h] represents a 24-hour cycle.

The thermocline was analyzed using temperature data [$^{\circ}\text{C}$] from data loggers mounted at S1 station with PAR sensors, confirming that the 20 $^{\circ}\text{C}$ isotherm is a representative indicator of vertical thermocline oscillations. Depths of this isotherm (z_i [m]) and average depth of the isotherm (z_{avg}) were determined and fitted to the light model (Eq. (4)) to obtain $I(z_i, t)$ and
 215 $I(z_{avg}, t)$. These models were used to quantify the difference in the light behaviour between ITW and no-ITW periods.

2.6 Data analyses

Data analyses were performed on four datasets obtained during four field campaigns carried out in late spring or mid summer of 2021, 2022 and 2023, each addressing a different objective of the study. The datasets from July 2021 and July 2022 were used to characterize the recurrent biogeochemical structure of the summer stratified ecosystem. Although primary
 220 production was not measured during these field campaigns, the identified biogeochemical patterns provided an ecological framework for interpreting primary production measurements obtained during the June 2022 and July 2023 *in situ* experiments. Specifically, the July 2021 and July 2022 datasets included abundances of micro- and nanophytoplankton [cells L^{-1}], picophytoplankton and heterotrophic bacteria [cells mL^{-1}], nutrient concentrations [$\mu\text{mol L}^{-1}$] (phosphate, nitrate, nitrite and silicic acid), Chl a concentrations [mg m^{-3}] and CTD-derived temperature [$^{\circ}\text{C}$]. The June 2022 and July 2023 datasets
 225 comprised $P_T(z)$ [mg C m^{-3}], $P^B_T(z)$ [$\text{mg C (mg Chl)}^{-1}$], Chl a and nutrients (phosphate, nitrate and silicic acid) concentrations, CTD-measured temperature [$^{\circ}\text{C}$] and oxygen [mg L^{-1}].

Statistical analyses and visualizations were performed across sampling depths categorized into surface, thermocline and deep layers based on CTD-derived temperature profiles. Sampling depths determined during field campaigns in July 2021 and 2022 were categorized in layers as described in Matek et al. (2023) and Ljubešić et al. (2024), while incubation depths
 230 related to June 2022 and July 2023 *in situ* primary production experiments are defined in Table S1. Data visualizations were performed using the software Grapher 12 and R studio using packages "plotly" (Sievert et al., 2026), "ggplot2" (Wickham et al., 2026), "gridExtra" (Auguie, 2017) and "ggvegan" (Simpson, 2026). Statistical analyses were conducted in R studio using "vegan" package (Oksanen et al., 2026). Extreme values that were not relevant were removed from the July 2021 and July 2022 datasets by using a z-score threshold between $-1.96 < z < 1.96$. Primary production rates at 0 m at station M1 in June
 235 2022 and during experiment S0-04 in July 2023 were excluded from the analysis because reliable rate estimates could not be obtained.

Multivariate analyses, including canonical correspondence analysis (CCA) and principal component analysis (PCA), were performed to examine variability in datasets with multiple variables in a low-dimensional space. Prior to multivariate analysis, phytoplankton and bacterioplankton counts were log-transformed, while environmental data were log-transformed,
 240 normalized and standardized. Resemblance matrices were calculated using Euclidean distance for abiotic data and Manhattan distance (Bray-Curtis) similarity for biotic data. Variance inflation factors (VIFs) were calculated for each variable to eliminate those that are highly correlated ($\text{VIF} > 10$). CCA was performed separately on the July 2021 ($N = 59$) and July



2022 (N = 180) datasets to examine variability in the phytoplankton and bacterioplankton community when constrained with environmental variables. PCA was conducted separately on the combined June 2022 dataset (N = 20) and on the July 2023 dataset (N = 17) to provide an overall statistical assessment of variability in NPP and associated environmental conditions. Statistical significance of the CCA model and constrained axes was tested using analysis of variance (ANOVA) and was defined as p-value < 0.05.

To assess ITW-related effects on NPP, percentage change in $P_{Z,T}$ between ITW and no-ITW periods was calculated as:

$$PC = \frac{(ITW - (no-ITW))}{no-ITW} \times 100 \quad (5)$$

where *ITW* and *no-ITW* represent primary production rates measured under ITW and no-ITW conditions, respectively. In June 2022, percentage changes in $P_{Z,T}$ were calculated between the ITW experiment at M1 station and the experiments conducted at S0 and P4. In July 2023, the ITW experiments S0-04 and S0-08 were compared with the S0-16 experiment. Since consecutive *in situ* primary production measurements specifically targeting ITW events were conducted at the same station in July 2023, layer-specific percentage changes in $P_{Z,T}$ were additionally calculated for the surface, thermocline and deep layers to assess potential ITW-related effects throughout the water column.

To further assess ITW-related effects on environmental conditions and NPP in July 2023, descriptive comparisons of biogeochemical variables, Cliff's delta (δ) effect size and linear regression analysis were performed. Cliff's δ is a non-parametric measure of effect sizes suitable for comparisons between groups with small and uneven sample sizes. It quantifies the probability that values from one group are larger than those from another without assuming normality or equal variances. Cliff's δ ranges from -1 to 1, where values near 0 indicate negligible differences while larger absolute values indicate stronger effects. This approach allowed to quantify differences in biogeochemical variables between ITW and no-ITW conditions. To quantify how NPP was related to environmental conditions within the water column, ordinary least-squares linear regression analysis was performed, with primary production treated as the response variable and selected physical and biogeochemical variables as predictors.

3 Results

3.1 Biogeochemical regime of the stratified island ecosystem

The summer stratified ecosystem off Lastovo during 2021–2023 field campaigns was characterized by pronounced vertical gradients in environmental factors, particularly temperature and nutrient concentrations, including nitrate, phosphate and silicic acid (Fig. 4A, B). Measured water column temperatures ranged between 15–27 °C, with distinct temperature intervals defining different depth layers and confirming strong thermal stratification (Fig. 5, Table S1). These vertical gradients structured distinct ecological niches for phytoplankton and bacterioplankton communities. Specifically, higher nitrate and silicic acid concentrations were associated with greater abundances of microphytoplankton in the colder deep layer of the stratified water column, whereas increased phosphate concentrations were related to the greater abundances of smaller-sized



cells in nano- and picophytoplankton, as well as PPEs, which predominated in the warmer surface and thermocline layers
(Fig. 4A, B). Heterotrophic bacteria were mostly related to the upper warmer layers (Fig. 4A, B). Chl *a* showed the strongest
correlation with microphytoplankton, indicating formation of a DCM layer (Fig. 4A, B). Picophytoplankton exhibited a
distinct niche, with *Synechococcus* preferring warmer surface and thermocline layers, whereas *Prochlorococcus* thrived in
the colder deep layer (Fig. 4A, B). Vertical distributions of environmental variables, as well as phytoplankton and
bacterioplankton communities, were consistent throughout the two summers, suggesting recurrent ecological functioning.
According to CCA, environmental variables explained a total of 19.4% ($p = 0.005$) and 11.7% ($p = 0.002$) of the variability
in the micro- and nanophytoplankton community during July 2021 and July 2022, respectively (Fig. 4A, B). In contrast, the
variability in the picophytoplankton and bacterioplankton was more strongly constrained by environmental factors, with
44.8% ($p = 0.001$) and 88.9% ($p = 0.001$) of the total variation explained in July 2021 and July 2022, respectively. These
results suggest that picophytoplankton and bacterioplankton exhibited a stronger and prompt response to environmental
variability compared to nano- and microphytoplankton. CCA scores and eigenvalues are provided in the supplementary
material (Table S2).

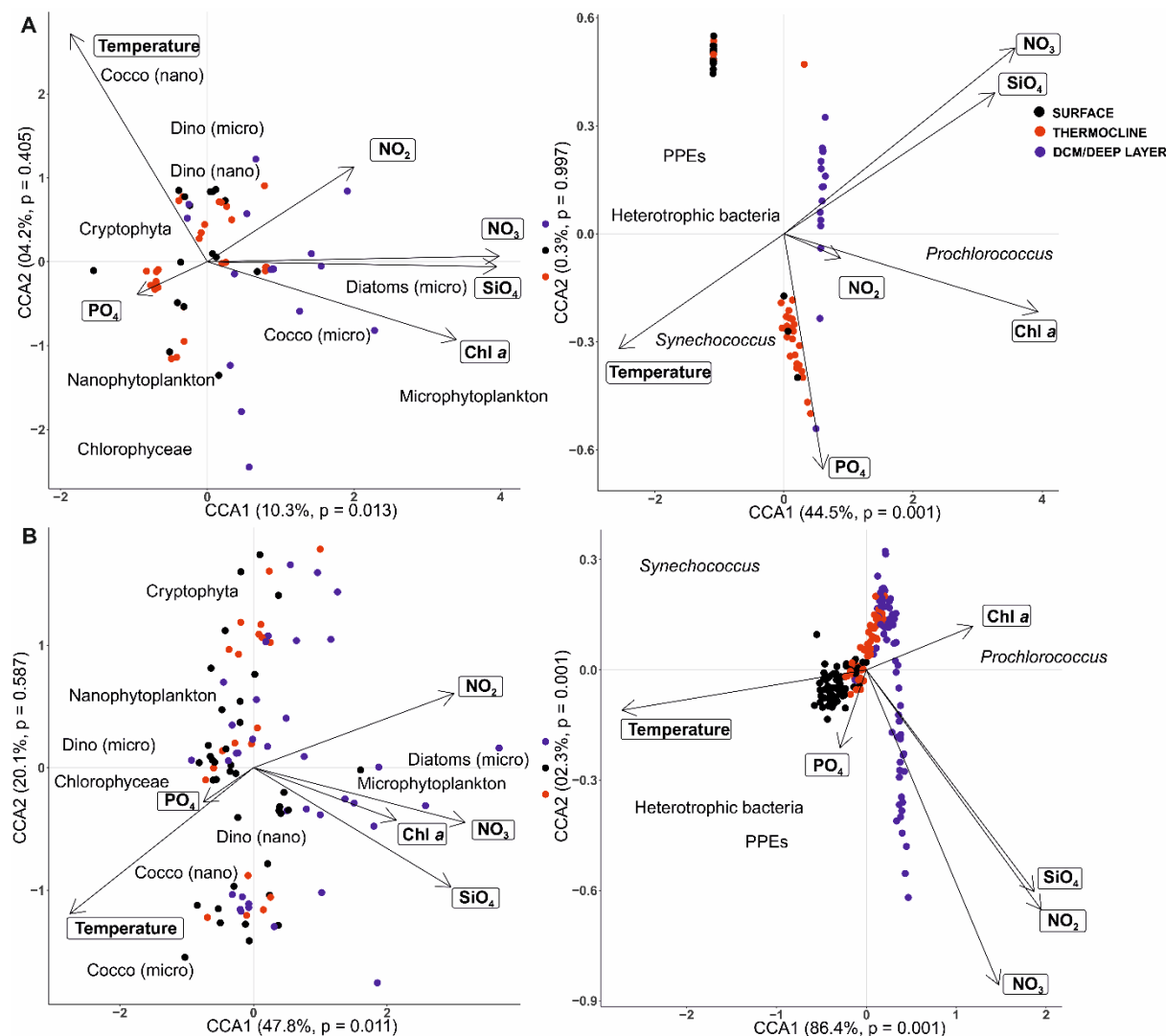


Figure 4. Canonical correspondence analysis (CCA) of phytoplankton and bacterioplankton communities constrained by environmental variables at station S1 in **(A) July 2021** and **(B) July 2022**. Environmental variables include temperature [$^{\circ}C$], nutrients [$\mu mol L^{-1}$] (phosphate (PO_4), nitrate (NO_3), nitrite (NO_2), silicic acid (SiO_4) and chlorophyll a ($Chl a$) [$mg m^{-3}$]. Microphytoplankton are represented by dinoflagellates (Dino), coccolithophores (Cocco) and diatoms [$cells L^{-1}$]; nanophytoplankton by Dino, Cocco, Chlorophyceae and Cryptophyta [$cells L^{-1}$]; picophytoplankton by *Prochlorococcus*, *Synechococcus* and photosynthetic picoeukaryotes (PPEs) [$cells mL^{-1}$]; and bacterioplankton by heterotrophic bacteria [$cells mL^{-1}$]. Points represent sample-weighted scores ($N = 59$ in July 2021, $N = 180$ in July 2022). Colours indicate depth layer: surface, thermocline, and DCM (July 2021) or surface, thermocline, and deep layer (July 2022). Arrows represent environmental variable loadings (biplot scores).

Lack of interannual variability in measured variables supports a recurrent ecosystem state, rather than a year-specific regime (Fig. 5). Each layer of the stratified water column exhibited similar distribution of physical and biogeochemical variables in July 2021 and 2022, except for $Chl a$ (Fig. 5). Observations made during *in situ* primary production experiments in July



2023 fall within the distribution range of measured variables (Fig. 5), confirming consistent biophysical coupling during summer stratification at Lastovo. These analyses provide an ecological framework for interpreting NPP rates in relation to phytoplankton community composition and the physico-chemical conditions of the stratified ecosystem.

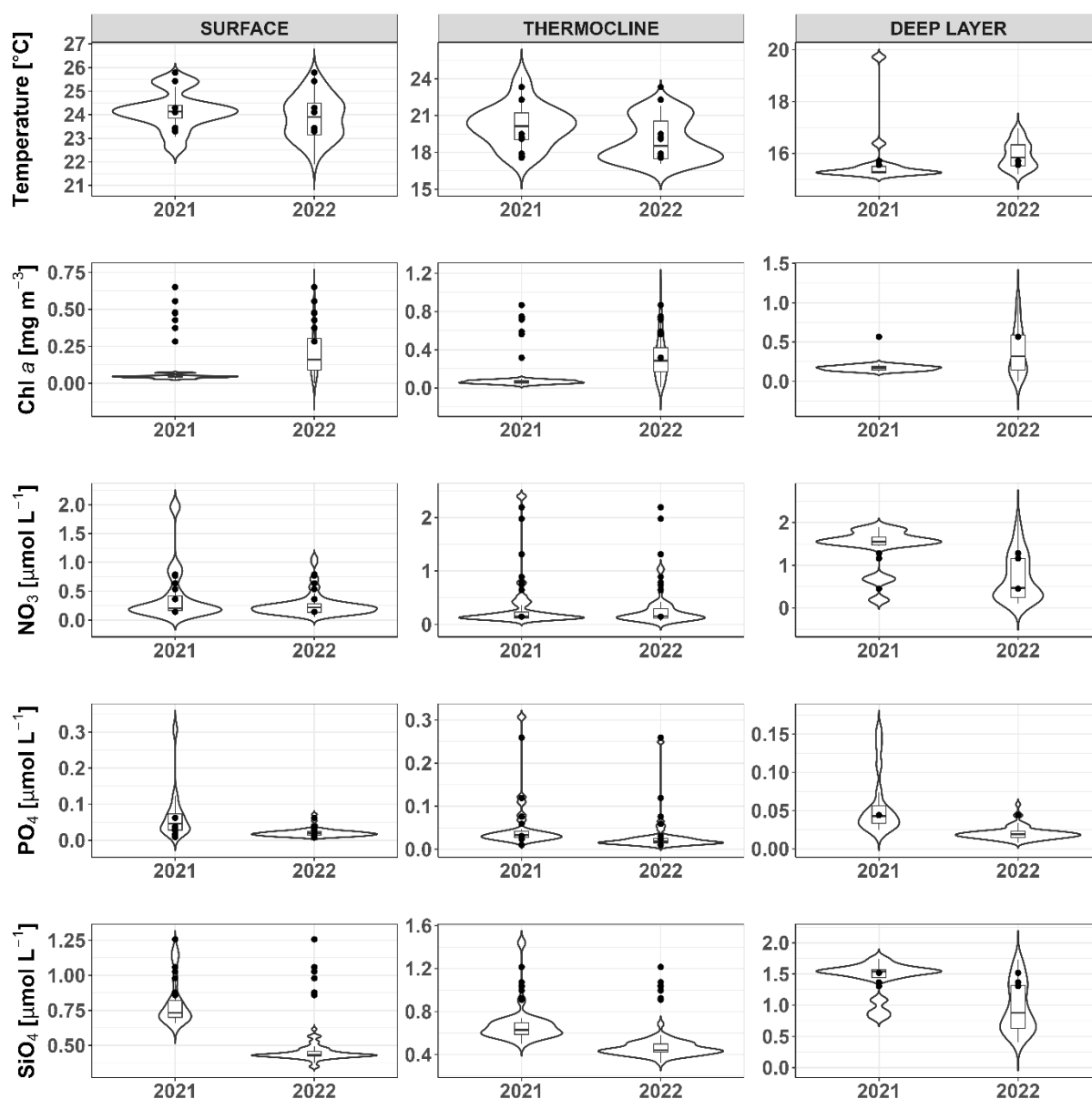


Figure 5. Interannual comparison of vertical physical and biogeochemical structure, showing July 2023 observations of temperature [°C], chlorophyll *a* [mg m⁻³] and nutrients [μmol L⁻¹] (phosphate (PO₄), nitrate (NO₃), silicic acid (SiO₄)) overlaid on the July 2021 and 2022 distributions.



3.2 Primary production in the stratified water column

Both $P^B_T(z)$ and $P_T(z)$ were higher in the surface and thermocline layers compared to the deep layer, and this trend of linear decrease in NPP with depths is consistent across all experiments (Fig. 6A, B). Chl *a* concentrations ranged up to 1.2 mg m^{-3} in July 2022 (Fig. 6A) and up to 2 mg m^{-3} in July 2023 (Fig. 6B), indicating increased biomass. A DCM formed at 50 m at stations M1 and P4 and at 65 m at station S0 during all *in situ* primary production experiments, except during S0-04 where the highest Chl *a* values occurred at 20 m and a DCM was not observed (Fig. 6A, B). $P_{Z,T}$ at Lastovo (stations M1 and S0) was almost two times higher compared to Korčula (station P4), as revealed by *in situ* experiments conducted in June 2022 (Fig. 6A). In the following year, $P_{Z,T}$ at station S0 revealed fluctuations in productivity possibly related to ITW events (Fig. 6B).

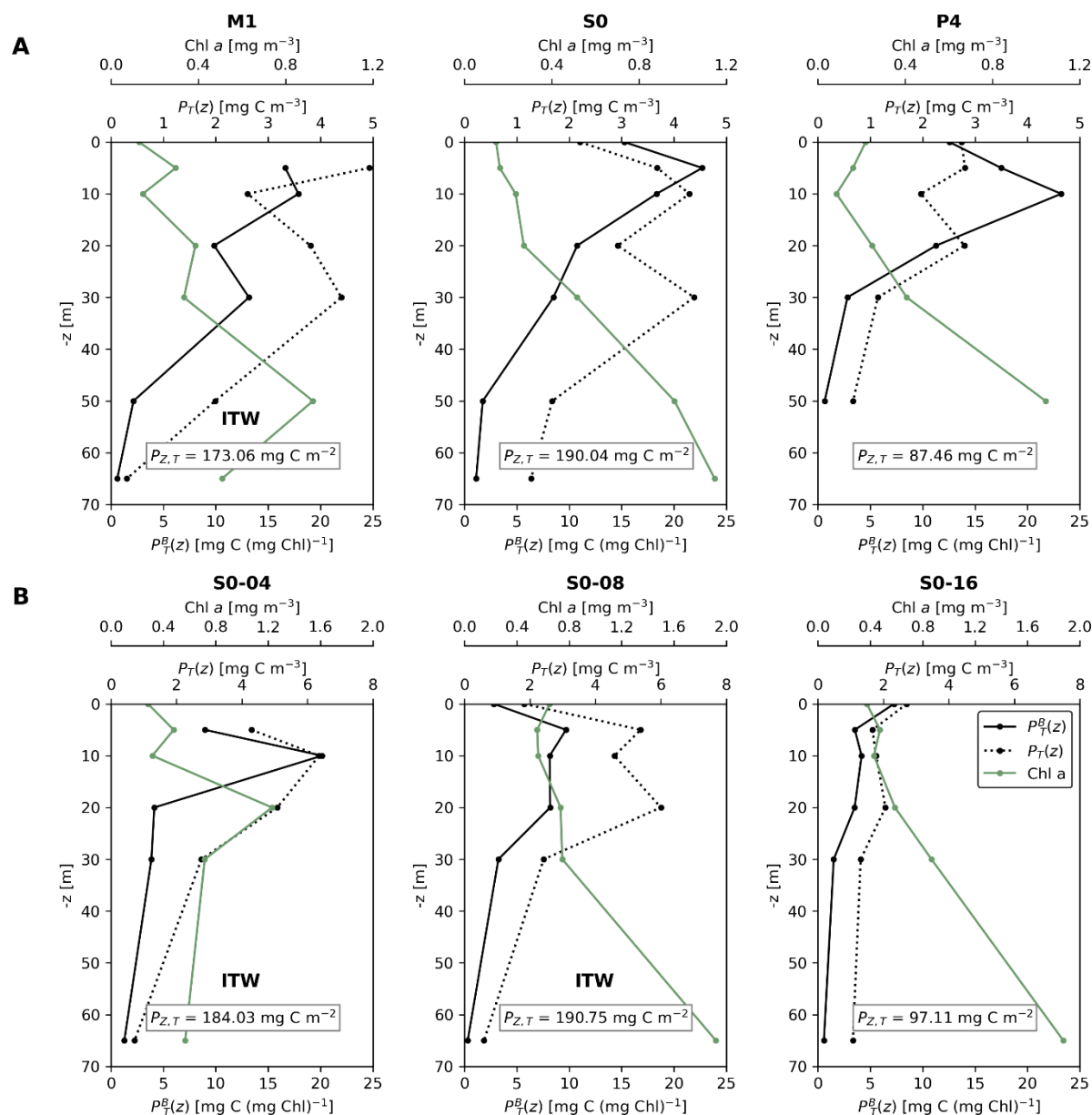


Figure 6. *In situ* ^{14}C primary production measurements with concurrent Chl *a* observations in **(A)** 2022 at stations M1, S0 and P4 on 7, 10 and 8 June, respectively, and **(B)** 2023 at station S0 on 4, 8 and 16 July (S0-04, S0-08 and S0-16, respectively). Shown are vertical profiles of daily net primary production ($P_T(z)$), and daily normalized net primary production ($P_T^B(z)$). The shaded area beneath $P_T(z)$ represents daily depth-integrated net primary production ($P_{Z,T}$).

We observed a layer-specific variability in NPP, Chl *a*, oxygen and nutrients at station S0 in July 2023 (Fig. 7). NPP was phosphate limited as indicated by very low values across the whole water column when compared to nitrates (Fig. 7). If we do not consider the high nitrate value of $4 \mu\text{mol L}^{-1}$ in the surface layer, both phosphate and nitrate concentrations were



highest in the thermocline layer. Furthermore, the surface layer had lower oxygen concentrations compared to the thermocline layer (Fig. 7). Conversely to the biomass, $P_T(z)$ and $P_T^B(z)$ were higher in the surface and thermocline layers than in the deep layer, indicating that smaller sized cells were the highest contributors to the primary production (Fig. 7). These observations were also supported by the steady biogeochemical state defined by July 2021 and July 2022 datasets (Fig. 4A, B). Therefore, we can argue that picophytoplankton (specifically *Synechococcus*) and nanophytoplankton (coccolithophores, dinoflagellates, Chlorophyceae and Cryptophyta) were the most active primary producers at the surface and the thermocline of the water column.

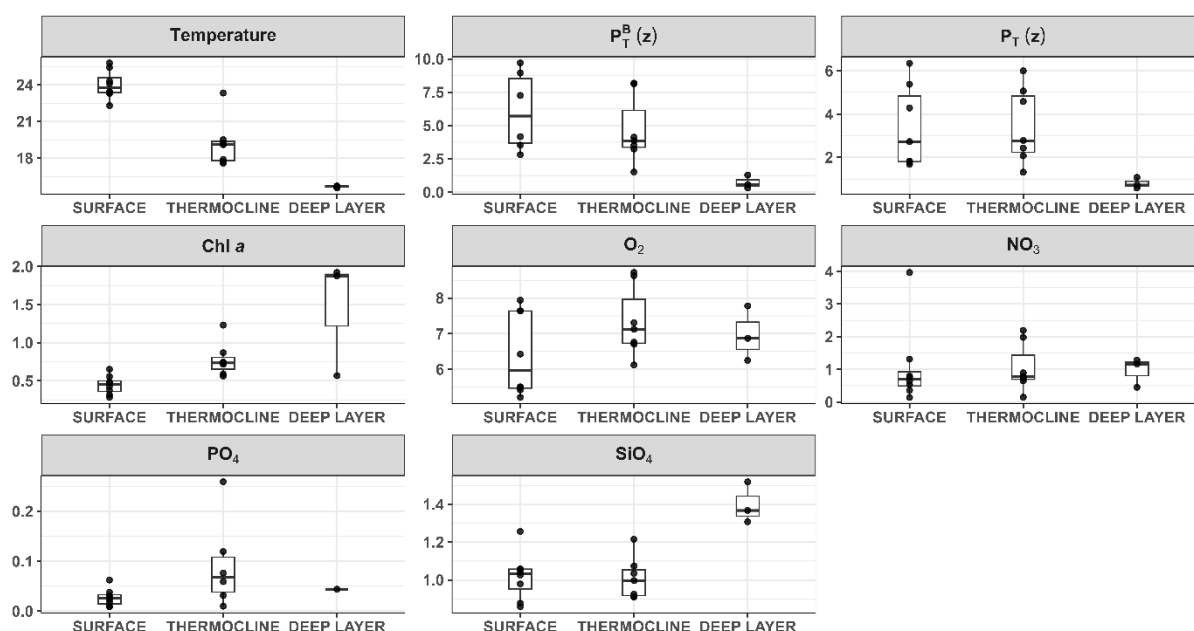


Figure 7. Layer-specific variability of data obtained in July 2023 at station S0. Shown are daily normalized net primary production at depth ($P_T^B(z)$ [mg C (mg Chl)⁻¹]), daily net primary production at depth ($P_T(z)$ [mg C m⁻³]), and simultaneously measured physical and biogeochemical variables: temperature [°C], chlorophyll *a* (Chl *a* [mg m⁻³]), oxygen (O₂ [mg L⁻¹]) and nutrients [μmol L⁻¹], including phosphate (PO₄), nitrate (NO₃) and silicic acid (SiO₄).

Photosynthetic activity, indicated by $P_T^B(z)$, was lower in the thermocline compared to the surface layer, while $P_T(z)$ remained consistent between the two layers (Fig. 5). This result suggests that primary producers in the thermocline required less energy to maintain similar rates of $P_T(z)$ as those in the surface layer, and therefore potentially higher phytoplankton physiological efficiency. Regression analysis showed that vertical distribution of temperature, Chl *a*, nitrate and oxygen significantly explained up to 56% of the layer-specific variability in $P_T^B(z)$ ($R = 0.56$, p -value = 0.047) (Table S3). The explanatory power of the regression model decreased when oxygen was excluded ($R = 0.47$, p -value = 0.047) (Table S3), highlighting its importance in explaining the variability in NPP within the stratified water column off Lastovo. In contrast to $P_T^B(z)$, the regression of $P_T(z)$ against environmental variables was not statistically significant. This suggests that $P_T^B(z)$ more



closely reflected the physiological adaptation of phytoplankton to their surroundings than $P_T(z)$, since $P_T^B(z)$ is normalized to biomass (Chl *a*) and therefore contains information on the photosynthetic capacity of each cell.

345 **3.3 Variability of the thermocline ecosystem influenced by ITW**

3.3.1 Primary production response to ITW

During the June 2022 ITW event at M1 at Lastovo, $P_{Z,T}$ was 97.9% higher than at the reference station P4 at Korčula (Table 3). In contrast, $P_{Z,T}$ at M1 was 8.9% lower than at S0 (Table 3). In July 2023, $P_{Z,T}$ was approximately 90-120% higher during ITW events than under no-ITW conditions (Table 3). Layer-specific analysis showed that this increase in $P_{Z,T}$ was confined to the thermocline layer (Table 3). Thermocline-integrated production increased by 473.1% during S0-04 and by 464.8% during S0-08 relative to S0-16, whereas production in the surface and deep layers decreased (Table 3). Consistent with these differences, total $P_{Z,T}$ during the no-ITW experiment S0-16 was approximately twofold lower than during the ITW experiments (Fig. 6B), reaching values comparable to those observed at Korčula, where ITWs were not documented (Fig. 6A).

355 **Table 3.** Percentage change in daily depth-integrated net primary production ($P_{Z,T}$ [mg C m⁻²]) between ITW (M1 in June 2022, S0-04 and S0-08 in July 2023) and no-ITW conditions (S0 and P4 in June 2022, and S0-16 in July 2023), presented for the entire water column (total), and for July 2023 only, separately for the surface, thermocline and deep layers.

Percentage change in $P_{Z,T}$ [%] (Eq. (5))					
Year	ITW vs no ITW	Total	Surface	Thermocline	Deep layer
June 2022	M1 vs P4	97.9			
	M1 vs S0	-8.9			
July 2023	S0-04 vs S0-16	89.5	-78.1	473.1	-32.5
	S0-08 vs S0-16	96.4	-7.9	464.8	-44.2

3.3.2 Environmental variability associated with ITW

360 Effect sizes based on Cliff's δ were used to evaluate the direction and magnitude of differences in NPP rates and concurrent environmental variables between ITW and no-ITW conditions in the surface and thermocline layers in July 2023 (Fig. 6, Table 3, Fig. S1). In the thermocline layer, ITW conditions were associated with higher NPP rates and nutrient concentrations, together with lower dissolved oxygen concentrations (Fig. 8). All measured nutrients showed positive effect sizes during ITW conditions, with the strongest change observed for phosphate (Fig. 8). Temperature variability increased in the thermocline layer, reflecting vertical oscillations driven by ITWs (Fig. S1). Nutrient variability also increased in the thermocline layer, with broader ranges and higher median concentrations of nitrate, phosphate and silicic acid during ITW conditions (Fig. S1). Dissolved oxygen decreased across the water column during ITWs, with the lowest value recorded in the surface layer (Fig. S1). Chl *a* values were higher in the surface layer and correspondingly lower in the thermocline layer during ITW events (Fig. 8), suggesting a redistribution of biomass between these layers. Specifically, prior to ITW events,



370 Chl *a* ranged between 0.283–0.479 mg m⁻³ in the surface layer and 0.588–1.229 mg m⁻³ in the thermocline layer. During ITWs, these ranges shifted to 0.555–0.651 mg m⁻³ and 0.563–0.748 mg m⁻³, respectively.

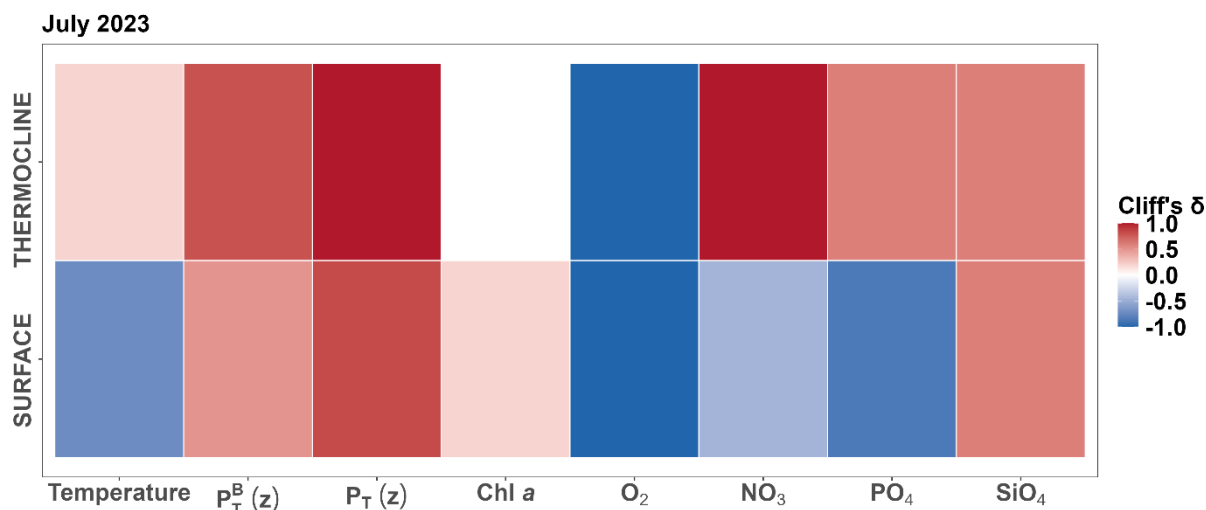


Figure 8. Effect sizes (Cliff's δ) for primary production rates and concurrent environmental variables measured under ITW and no-ITW conditions in July 2023 at station S0, for the surface ($N = 7$) and thermocline ($N = 8$) layers. Variables include temperature [°C], daily normalized net primary production at depth ($P_T^B(z)$ [mg C (mg Chl)⁻¹]), daily net primary production at depth ($P_T(z)$ [mg C m⁻³]), chlorophyll *a* (Chl *a* [mg m⁻³]), oxygen [mg L⁻¹] and nutrients [μ mol L⁻¹], including nitrate (NO₃), phosphate (PO₄) and silicic acid (SiO₄). Higher values of measured variables during ITWs are denoted by red color, blue color indicates higher values during no-ITW conditions, while white color represents no difference in measured variables.

PCA further confirmed that higher $P_T^B(z)$ and $P_T(z)$ values were generally associated with the surface and thermocline layers (Fig. S2A, B), specifically during ITW conditions (Fig. S2B). In July 2023, the no-ITW experiment S0-16 formed a separate cluster from the ITW experiments S0-04 and S0-08 (Fig. S2B). The trend of increase in $P_T^B(z)$, $P_T(z)$ and phosphate concentrations during ITW events in the thermocline layer (Fig. S2B) suggests a link between ITW-driven nutrient dynamics and NPP. PCA eigenvalues and scores for PC1 and PC2 axes are provided in the supplementary material (Table S4).

3.3.3 Underwater light field

385 Model of underwater light field was developed to examine light properties at the time of *in situ* primary production experiments in July 2023, particularly during ITW event. PAR and K_{PAR} were fitted to the light model $I(z,t)$ (equation 3). PAR measured at the station S1 from 6 to 13 July 2023 (Table 1) spanned from 3.10 μ mol m⁻²s⁻¹ to 642.65 μ mol m⁻²s⁻¹ at 10 m depth (Fig. S3), with a mean value of 319.56 ± 200.92 μ mol m⁻²s⁻¹. At 30 m depth, PAR ranged from 2.35 μ mol m⁻²s⁻¹ to 156.52 μ mol m⁻²s⁻¹ (Fig. S3), with a mean value of 73.75 ± 50.68 μ mol m⁻²s⁻¹. Estimated K_{PAR} (Eq. (3)) ranged from 0.04 m⁻¹ to 0.11 m⁻¹ (Fig. S3), with a mean value of 0.08 ± 0.01 m⁻¹, elucidating an optically transparent water column. Because the thermocline layer was of primary interest, the 20 °C isotherm depths at S1, used as a proxy for the vertical position of the thermocline, were superimposed on the $I(z,t)$ model output (Fig. 9A). During ITW episode (7–8 July 2023), thermocline depths oscillated approximately from the 5 m to 25 m depths (Fig. 9A).



395 The light model $I(z,t)$ with superimposed 20 °C isotherm depths confirmed that thermocline oscillations generated by ITWs can bring this layer into the shallower parts of the water column at the time of the high surface irradiance in the afternoon at station S1 (Fig. 9A). To quantify the extent of excess light available to phytoplankton during ITW events, light was modeled at the 20 °C isotherm depth ($I(z_i,t)$, representing the thermocline oscillations during ITWs) and at the average isotherm depth ($I(z_{avg},t)$, reflecting a no-ITW scenario) (Fig. 9B). Light levels at the average isotherm depth did not exceed $\sim 90 \text{ W m}^{-2}$ (Fig. 9B), indicating substantially lower light availability within the thermocline layer than at the surface, where irradiance was estimated at $\sim 300 \text{ W m}^{-2}$ (Fig. 9A). During ITWs, irradiance in the thermocline layer reached up to 150 W m^{-2} (Fig. 9B), suggesting enhanced light availability due to pronounced thermocline oscillations (Fig. 9A).

400 Assuming that the average isotherm depth represents no-ITW conditions with no diurnal thermocline oscillations, it is evident that ITWs exposed the thermocline layer to substantially higher light levels. These observations were quantified using the difference between $I(z_i,t)$ and $I(z_{avg},t)$, confirming that the strongest response occurred in early July 2023, when irradiance difference reached 70 W m^{-2} (Fig. 9C). These results suggest that ITWs could influence the phytoplankton community by vertically displacing water masses toward the surface, thereby increasing their light exposure and enhancing photosynthetic activity.

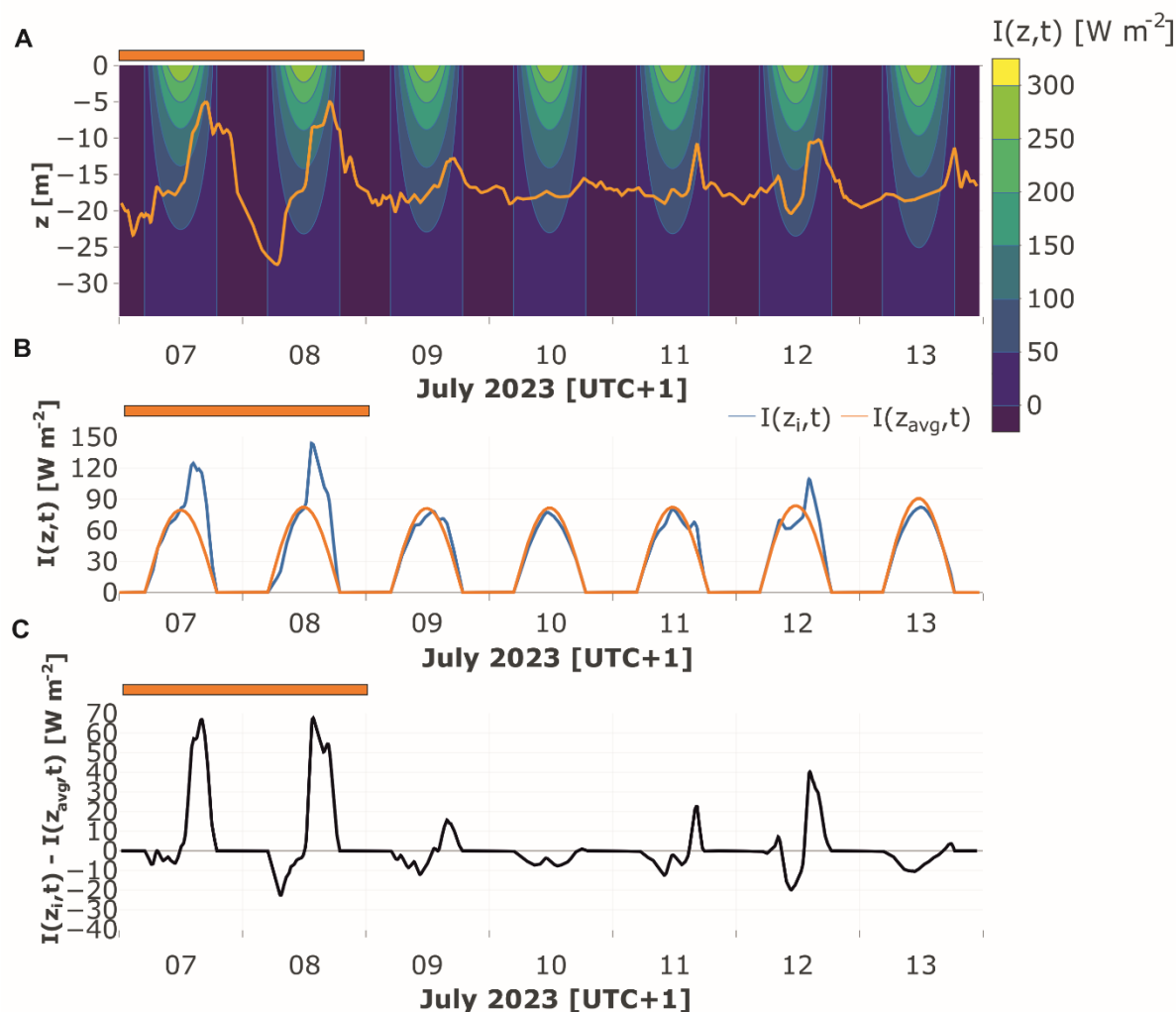


Figure 9. Underwater light field at the southern cliff Struga (S1 station) at the Lastovo Island during 7–13 July 2023. ITW period is indicated by the orange line. Shown are **(A)** modeled light ($I(z,t)$ [W m⁻²]) with thermocline isotherm depths overlaid (red line), **(B)** light modeled at the thermocline isotherm depths ($I(z_i,t)$ [W m⁻²]) and at the average thermocline depth ($I(z_{avg},t)$ [W m⁻²]), **(C)** difference between $I(z_i,t)$ and $I(z_{avg},t)$ [W m⁻²].

4 Discussion

4.1 Ecosystem off the island of Lastovo under stratified conditions

Water column properties at Lastovo during the summer (Fig. 5) are characteristic of a stratified ecosystem (Mena et al., 2019; Zheng et al., 2025), with a developing thermocline in the surface layer and DCM confined to the deeper layers. In the Adriatic Sea, the water column structure undergoes pronounced seasonal changes. Stratification develops during summer due



to temperature and salinity gradients, while wind-driven mixing breaks it during the winter (D’Ortenzio et al., 2005). Specifically, the southern Adriatic Sea starts to stratify in April and reaches maximum stability in August (Viličić et al., 1989), which is congruent with the temperature time-series data obtained at Lastovo (Matek et al., 2023; Ljubešić et al., 2024; Hartkamp, 2025).

The Adriatic Sea is characterized by low phosphate concentrations ($< 0.2 \mu\text{mol L}^{-1}$) (Viličić et al., 1989), thus primary production at Lastovo is phosphate-limited (Pojed and Kveder 1977; Marasović et al., 2005), as confirmed by our observations as well (Fig. 7). Concentrations of phosphate, nitrate and silicic acid also agree with observations made for the southern Adriatic Sea (Viličić and Stojanoski 1987; Viličić et al., 1989, 2008). Chl *a* concentrations in the open southern Adriatic Sea range from 0.17 mg m^{-3} to 1.1 mg m^{-3} (Socal et al., 1999; Turchetto et al., 2000), which is consistent with the concentrations reported in this study (Fig. 7). Moreover, the biogeochemical regime that is driving the vertical distribution of phytoplankton and bacterioplankton communities at Lastovo (Fig. 4) is typical for a stratified ecosystem. Nanophytoplankton is more abundant in the upper layers compared to the microphytoplankton, while *Prochlorococcus* and *Synechococcus* exhibit specific niches (Šilović et al., 2011, Mena et al., 2019) as observed in this study, where *Prochlorococcus* was more dominant in the deep layer, whereas *Synechococcus* was more abundant at the surface and the thermocline (Fig. 4A, B).

4.2 Primary production in the oligotrophic southern Adriatic Sea

Although data on primary production rates in the southern Adriatic Sea are limited (Matek and Ljubešić 2024), existing records are congruent with our observations (Fig. 6A, B). In the stratified Ionian Sea, primary production reached 184 mg C m^{-2} , which agrees well with the values observed in this study, especially at stations M1 and S0 during June 2022, and during S0-04 and S0-08 experiments in July 2023 (Fig. 6A, B). On the other hand, La Ferla et al. (2005) reported $P_{Z,T}$ at 249 mg C m^{-2} in the South Adriatic, which is similar to the primary production rate observed at Palagruža Sill, reported at 236 mg C m^{-2} (Turchetto et al., 2000) and notably exceeding $P_{Z,T}$ at Lastovo and Korčula (Fig. 6A, B). However, Palagruža Sill is known to be influenced by upwelling during the summer that facilitates nutrient transport to the euphotic zone and creates a localized area of increased primary production within an otherwise oligotrophic system (Zore-Armanda 1984). Values reported for the Ionian Sea might also be influenced by circulation dynamics known as the Bimodal Adriatic-Ionian Oscillation (BiOS) (Civitarese et al., 2010), a phenomenon underlying decadal variations in primary production in the southern Adriatic Sea (Marasović et al., 1995; Grbec et al., 2009).

All reported values for the southern Adriatic Sea are notably lower compared to the eutrophic northern Adriatic Sea that is influenced by strong river inputs of nutrient (Ingrosso et al., 2016, Grilli et al., 2020), and where primary production reaches up to 600 mg C m^{-2} (Talaber et al., 2018). On the other hand, the middle Adriatic Sea is influenced by both coastal eutrophication and circulation of water masses from the southern regions (Ninčević Gladan et al., 2010), resulting in different primary production rates between coastal and open sea. At the open-sea station Stončica (east of the island of Vis) and the coastal Kaštela Bay station, *in situ* ^{14}C primary production experiments have been carried out since 1962 and are



ongoing (Pucher-Petković 1971). $P_{Z,T}$ values at the Kaštela Bay station range between 322.4–496.6 mg C m⁻² (Pucher-Petković 1971), while at the Stončica station the values vary from 118–300 mg C m⁻² (Kovač et al., 2018), which is comparable to the values observed at Lastovo.

4.3 Biophysical coupling in the thermocline layer under ITW influence

455 In 2023, the most pronounced thermocline oscillations due to ITWs at Lastovo were observed in July and August when thermocline depths fluctuated between the 10 m to 35 m depths (Hartkamp, 2025). Furthermore, the average thermocline depth varied among summers. Gradual deepening was documented by interannual variability of the average thermocline depth: 10 m in July 2021, 20 m in July 2022 (Ljubešić et al., 2024) and 18 m in July 2023 (Hartkamp, 2025). A deeper thermocline is associated with larger amplitude ITW under resonant conditions (Mihanović et al., 2014), which explains
 460 more pronounced thermocline oscillations observed in July 2022 (Ljubešić et al., 2024) and July 2023 (Hartkamp, 2025). In this context, climate-induced changes in water column properties, such as increased sea surface temperature and prolonged stratification period (da Costa et al., 2024), could alter the timing and intensity of ITW occurrences. Specifically in the Adriatic Sea, strong rainfall and prolonged drought periods can influence stratification. For example, the RCP8.5 climate scenario indicates a 35% reduction in riverine input and a reduced stratification stability (Verri et al., 2024). Therefore, it is
 465 of high importance to understand impact of ITW on the plankton communities and their ecosystem, and how this can alter under climate change. Thus, in this section, we discuss the biophysical coupling observed in the thermocline layer during ITW events (Figs. 7–8, Table 3, Fig. S1).

4.3.1 Primary production in modulated light-nutrient environment

In June 2022, an ITW event was captured during an *in situ* primary production experiment at M1, Lastovo. $P_{Z,T}$ during this
 470 event was 97.9% higher than at the reference station P4 at Korčula (Table 3), providing initial evidence of enhanced NPP under ITW conditions. During ITW events in July 2023, $P^B_T(z)$ and $P_T(z)$ increased substantially in the thermocline layer (Fig. S1), which was reflected in a strong increase in $P_{Z,T}$ that was confined to this layer (Table 3). This pattern is consistent with oxygen-based NPP estimates from July 2022 at Lastovo, which similarly showed enhanced primary production in the thermocline layer during ITWs (Ljubešić et al., 2024). Furthermore, analysis of ocean-colour remote sensing data confirmed
 475 that ITWs contribute 1.5–3.8% to annual NPP at Lastovo (approximately 115–123 g C m⁻²), demonstrating that, although episodic and local, ITWs can provide a measurable boost to the regional productivity (Matek, 2026). Although comparable local studies are lacking, observations in other regions indicates that internal waves can enhance primary production. For example, primary production in the tropical Angolan upwelling system is strongly linked to internal waves (Körner et al., 2024), while increases of 15–37% have been reported in the northern South China Sea (Pan et al., 2012). Similarly, increased
 480 primary production during internal wave events was observed at the Nazaré Canyon (Muacho et al., 2013). Variability in $P^B_T(z)$ and $P_T(z)$ at Lastovo was largely explained by temperature, Chl *a*, nitrate and oxygen levels (Table S3). Lower $P^B_T(z)$ in the thermocline layer relative to the surface, but comparable $P_T(z)$ rates (Fig. 7), indicated that $P_T(z)$ values



in the thermocline layer can be maintained as efficiently as in the surface layer, but with reduced energy input. This suggests higher physiological efficiency of phytoplankton in the thermocline, likely associated with the greater bioavailability of nutrients essential for functioning of the photosynthetic apparatus and reduced cellular stress (Sarmiento et al., 2004; Wang et al., 2024). This can be linked to more favorable light and nutrient conditions during ITWs (Fig. 9, Fig. S1) and is further supported by enhanced bacterial abundances that recycle nitrogen and further influence an increase in nitrate concentrations (Ljubešić et al., 2024; Mucko et al., 2025).

Elevated nutrient levels in the thermocline layer during ITWs (Fig. S1) suggest advection- and convection-driven inputs from the deeper layers, consistent with other studies linking wave-induced turbulence to nutrient fluxes (Cooper 1947; Garrett and Munk 1979; Garrett 2003; Sharples et al., 2007; Villamaña et al., 2017; Li et al., 2018; Tuerena et al., 2019; Whalen et al., 2020; Dematteis et al., 2024). Sporadically elevated nutrient concentrations observed within the thermocline during the July 2022 ITW event coincided with increased oxygen-based NPP estimates (Ljubešić et al., 2024). This observation is consistent with previous findings showing that even small but repeated nutrient inputs can stimulate primary production (Spilling et al., 2023). In addition, an idealized Regional Ocean Modeling System (ROMS) coupled with a simplified NPZD ecosystem model showed that ITWs at Lastovo enhance nutrient availability and primary production in the thermocline layer up to 6.1% and 5.4%, respectively, while a diel light cycle mainly affects the spatial distribution of primary production (Jacobsen, 2024).

Internal waves also modulate the underwater light field (Holloway, 1984) and their effects are even incorporated into primary production models (Lande and Yentsch 1988; Platt and Sathyendranath 1993). Vertical displacement of phytoplankton can substantially enhance photosynthesis, with increases of up to 200% reported in light-limited systems (Evans et al., 2008). Similarly, this study observed increased light availability in the thermocline by 70 W m^{-2} during ITWs at the southern Struga cliff (Fig. 9C). Such conditions occur when ITW and light cycles are in phase (Matek et al., 2024), consistent with findings that photosynthetic enhancement is maximized when ITW crests align with the solar noon (Kamykowski, 1974). The magnitude of this effect also depends on the rate of phytoplankton photoacclimation to rapidly changing light conditions (Kamykowski 1974). This can be inferred from photosynthesis parameters derived from *in situ* primary production profiles using an inverse numerical model, provided that vertical profiles decrease with depth and concurrent optical measurements exist (Kovač et al., 2017). Accordingly, if we assume efficient photoacclimation, it is reasonable to expect that even higher NPP would be observed in areas around Lastovo where ITW crests align more closely with solar noon (e.g. eastern coast of the island), compared to the station S1 where the thermocline reached its shallowest depth later in the afternoon (around 17:00-18:00, UTC+1) (Ljubešić et al., 2024).

Nevertheless, the observed enhancement of NPP cannot be attributed exclusively to ITW dynamics, as other physical and biogeochemical processes may simultaneously regulate ecosystem productivity (Doty and Oguri 1956; De Falco et al., 2022, 2024), as corroborated by the contrasting pattern observed at S0 in June 2022. The experiment at S0, located on the opposite side of Lastovo from M1, was performed three days after the ITW event captured at M1 (Fig. 2), yet $P_{Z,T}$ was 8.9% higher than that measured at M1 (Table 3). Thus, high NPP can also occur at Lastovo in the absence of documented ITW activity.



This observation highlights the complexity of the processes regulating productivity around the islands and the importance of continuing this research.

4.3.2 Physiological and physical drivers of response by primary producers

520 Based on cell abundances in the thermocline layer (Fig. 4A, B), picophytoplankton (particularly *Synechococcus*) and nanophytoplankton (including coccolithophores, dinoflagellates, chlorophytes and cryptophytes) likely contribute most strongly to the observed primary production rates (Figs. 6–7). In oligotrophic regions of the Mediterranean Sea, picophytoplankton have been identified as the dominant contributors to primary production (Lohrenz et al., 1988, 1992). This is further supported by eDNA metabarcoding conducted at Lastovo in July 2022, which identified dominant primary
 525 producers within the pico-fraction: *Synechococcus* strain CC9902, Mamiellophyceae (green algae within Chlorophyta) and Pelagophyceae (stramenopiles) (Mucko et al., 2024; Ljubešić et al., 2024). Furthermore, primary producers in nanophytoplankton were observed: stramenopiles (*Pelagomonas*), chlorophytes (*Ostreococcus*) and Prymnesiophyceae (Mucko et al., 2024; Ljubešić et al., 2024). These observations aligned well with the pico- and nanophytoplankton structure inferred from cell abundance data (Fig. 4A, B).

530 ITW-driven modulation in the light and nutrient conditions can alter phytoplankton community structure (Ma et al., 2021; Wang et al., 2021), functionality (Ma et al., 2023; Guan et al., 2023), increases in Chl *a* (Sangrà et al., 2001), particulate organic carbon (POC) (Li et al., 2018) and bacterial activity (Chen et al., 2016). Phytoplankton responses to ITWs may be both physiological and physical, and are strongly influenced by cell size, taxonomic composition and photoacclimation capacity. Smaller cells appear more tightly coupled to the environmental variability (Fig. 4A, B) and can respond more
 535 rapidly to the thermocline oscillations than their larger counterparts. Similarly, nanophytoplankton exhibit faster responses to nutrient enrichment than microphytoplankton, whose responses may be delayed by up to 12 hours because their cell size (Ma et al., 2021; Guan et al., 2023). At the molecular level, picophytoplankton can rapidly adjust photosynthetic efficiency through transcriptional regulation of Rubisco enzyme, whereas larger eukaryotes require more time for enzymatic regulation and synthesis (John et al., 2012). In addition to nutrients, ITW-driven modulation of the underwater light field also
 540 influences further physiological adaptation. For instance, phytoplankton can modify biochemical composition of their cells in response to changes in the light spectrum (Marmelstein 1970; Wallen and Geen 1971), which may alter their nutritional quality and cause a cascade effect throughout the food web.

Vertical displacement of the thermocline increased light availability in this layer (Fig. 9). Pico- and nanophytoplankton can rapidly respond to enhanced light conditions following upward convection (Ma et al., 2021). However, not all groups
 545 respond positively; some taxa may be diluted or unable to adapt to the new environmental conditions. For example, *Synechococcus*, dinoflagellates and chlorophytes have been shown to exhibit limited response due to dilution effects, while *Prochlorococcus* may be advected but becomes outcompeted for nutrients and not adapted to higher light conditions (Ma et al., 2021). At Lastovo, changes in the vertical distribution of Chl *a* during ITW events (Fig. 6, Fig. S1) suggest that similar redistribution may have occurred. Although turbulence was not directly measured at Lastovo, we can assume variable current



550 shear associated with the observed thermocline oscillations (Ljubešić et al., 2024; Hartkamp, 2025), potentially influencing phytoplankton redistribution (Fig. S1). Increase of surface Chl *a* concentrations during ITW conditions (Fig. S1), accompanied by lower concentrations in the thermocline, suggests a redistribution of phytoplankton biomass between these layers as mixing intensified.

Although smaller fraction of phytoplankton in the thermocline appear to benefit from ITWs, it remains unclear whether this
 555 response is primarily physiological or driven by physical transport. Future studies should address the time lag in taxonomic response to changes in the light and nutrient conditions to better understand the mechanisms underlying the ITW-driven increase in NPP, as well as biophysical coupling in the stratified water column influenced by ITWs.

4.3.3 Trophic interactions in plankton

Heterotrophic bacteria exhibited the highest abundances in the thermocline layer (Fig. 4A, B), coinciding with elevated
 560 nutrient concentrations and increased oxygen-based NPP estimated by Ljubešić et al. (2024). Increased nitrite and nitrate concentrations are concurrent with enhanced remineralization processes (nitrification and aerobic ammonia oxidation) (Ljubešić et al., 2024; Mucko et al., 2025), and a greater metabolic potential of bacteria observed during ITWs (Mucko et al., 2025), further highlighting their important role in nutrient utilization and regeneration (Najdek et al., 2014). Similar responses have been observed in the South China Sea, where biomass increased by internal waves enhances bacterial
 565 remineralization, resulting in elevated nutrient levels, particularly nitrates (Chen et al., 2016). The zooplankton community at Lastovo, characterized using both morphological and molecular approaches (Ljubešić et al., 2024; Mucko et al., 2025; Pestorić et al., 2025), reflects a typical oligotrophic coastal assemblage of the southern Adriatic Sea (Milosavljević et al., 2014; Pestorić et al., 2018, 2021). It was reported that ITWs indirectly influence this community by altering phytoplankton abundance, leading to shifts in grazing pressure and feeding strategies (Ljubešić et al., 2024; Pestorić et al., 2025). For
 570 example, the abundance of dominant mesozooplankton species *Centropages typicus* increased in the thermocline layer during ITWs, coinciding with the elevated abundances of nano-scale dinoflagellates strategies (Ljubešić et al., 2024; Pestorić et al., 2025), which is consistent with its grazing preferences under turbulent conditions (Calbet et al., 2007). Similarly, microzooplankton species such as *Evadne spinifera*, *Oithona* spp. and *Paracalanus parvus parvus* were concentrated in the thermocline layer during ITWs, also likely responding to increased nanophytoplankton abundances (Pestorić et al., 2025).
 575 Furthermore, Spilling et al. (2023) confirmed a rapid shift in microzooplankton grazing preferences to nanophytoplankton following turbulence-induced nutrient influx.

In addition to nutrient-driven effects, changes in the light field during the ITW event may propagate throughout the food web. Phytoplankton can modify their biochemical composition in response to changes in light spectrum (Marmelstein 1970; Wallen and Geen 1971), potentially altering their nutritional quality and influencing zooplankton distribution and feeding
 580 behavior. This may help explain observed zooplankton aggregation in the thermocline layer during ITWs at Lastovo (Pestorić et al., 2025). Furthermore, ITWs at Lastovo can influence an increase of taxonomic diversity in plankton communities, as well as trophic network complexity (Mucko et al., 2025). Further supporting these observations, Guan et al (2023) confirmed that internal waves influence a shift in phytoplankton community from mixotrophic-dominated to



autotrophic- and heterotrophic-dominated states, thereby reducing opportunistic behavior and favoring more direct survival strategies. Trophic interactions further modulate plankton responses to internal waves. In stratified systems such as the South China Sea, distinct vertical layers exhibit different responses to internal waves, driven by interplay between bottom-up (light and nutrients conditions) and top-down (zooplankton grazing) controls (Ma et al., 2023). For example, despite increased nutrient and light availability in deeper layers, *Prochlorococcus* may decline due to inefficient nitrate uptake, while its growth is enhanced in the surface layers where it can outcompete *Synechococcus* for regenerated ammonium. In contrast, the middle layer remains relatively stable due to a balance between growth and mortality (Ma et al., 2023).

5 Conclusions

A key finding of this study is the complex interplay between ITWs, phytoplankton communities and broader food web dynamics represented by zooplankton and bacterioplankton, highlighting strong biophysical coupling within the thermocline layer at Lastovo. Primary production in this layer is predominately mediated by pico- and nanophytoplankton, which showed fast response to ITW-driven changes in the light and nutrient availability. Although advective processes redistribute biomass (Chl *a*), increased photosynthetic efficiency and primary production rates indicate an active biological response. However, it remains unclear whether this response is primarily physiological, physical, or a combination of both, and future studies should resolve taxa-specific response times to environmental forcing.

The thermocline layer is most strongly influenced by ITWs. Nitrate, phosphate and silicic acid concentrations increased during ITWs, while light availability increased by 70 W m^{-2} . Primary production is regulated by both bottom-up (light and nutrients) and top-down (zooplankton grazing) controls, alongside enhanced bacterial activity, as suggested by their increased abundances, which modulates nutrient availability. This tight coupling reflects the comparable spatio-temporal scales of ITWs and biological processes. Ecological significance of this biophysical coupling is evident in the marked increase of primary production in the thermocline layer during ITWs, which contributes to shifts in overall water column productivity under summer stratified conditions.

ITW forming at Lastovo represents a phenomenon by which a nutrient-poor, stratified system temporarily transforms into a more favorable environment for primary producers. Understanding these dynamics is crucial, since primary production remains essential for supporting and regulating our global ocean ecosystems, serving as a pillar of the marine food web and of global biogeochemical cycles.

610 Code and data availability

The data and code supporting the findings of this study will be made publicly available through the Zenodo repository upon publication of the manuscript. The repository will include the datasets, scripts, and code used for data processing and analysis.



615 Author contributions

Antonija Matek: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Hrvoje Mihanović:** Writing – review & editing, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Melissa Omand:** Writing – review & editing, Validation, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition. **Mirko Orlić:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Conceptualization. **Maja Mucko:** Writing – review & editing, Methodology, Investigation. **Branka Pestorić:** Writing – review & editing, Resources, Investigation. **Raffaella Casotti:** Writing – review & editing, Resources. **Cecilia Balestra:** Writing – review & editing. **Eric P. Achterberg:** Writing – review & editing, Resources, Formal analysis. **Hrvoje Čižmek:** Writing – review & editing, Methodology, Investigation.

625 **Barbara Čolić:** Writing – review & editing, Methodology, Investigation. **Zrinka Ljubešić:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Competing interests

The authors declare that they have no conflict of interest.

630 Acknowledgements

This work was fully funded by the Croatian Science Foundation under the ISLAND project (IP-2020-02-9524). Antonija Matek has been funded by the Croatian Science Foundation under the “Young Researchers’ Career Development Project - Training New Doctoral Students”. This paper / activity / research was supported by the European Union – NextGenerationEU through the National Recovery and Resilience Plan 2021-2026. Institutional grant of University of Zagreb Faculty of Science RC acknowledges the contribution of OBAMA-NEXT, "Observing and mapping marine ecosystems - Next generation tools" project funded by the European Union under the Horizon Europe programme (grant Agreement: 101081642). Wind data from Lastovo meteorological station in 2022 and surface irradiance and daylength data for the Lastovo region in 2023 were provided by the Croatian Meteorological and Hydrological Service (DHMZ). We thank Dr. Ivica Janeković and Gekom Ltd. for their invaluable assistance before, during, and after the experiments conducted at Lastovo Island in 2022 and 2023, and for providing the Weather Research and Forecasting (WRF) model data. We thank Prof. Zoran Pasarić for his valuable contribution to the analysis of light data. We thank Prof. Sara Rivero Calle and her PhD

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students Masud-Ul-Alam and Benjamin Lowin, from Skidaway Institute of Oceanography, University of Georgia, USA, for their valuable contribution to the field campaigns, and we extend our gratitude to the captain and crew of R/V *Baldo Kosić II* and the Marine Explorers Society 20,000 Leagues team for making this research possible.



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