Acta Adriatica 65 (2024): 205-222
https://doi.org/10.32582/aa.65.2.1

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REVIEW

Primary production research in the Adriatic Sea - a review

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Abstract: Primary production in the Adriatic Sea has been investigated for many years, however, a comprehensive systematic review of the literature is lacking. This paper aims to fill this gap by providing a thorough overview of all conducted studies, emphasising the methodologies employed, and comparing representative values. The first section introduces the history of primary production measurements and gives insights into the Adriatic basin's hydrography and its impact on primary producers and their rates of production. The second section provides an overview of productivity across the geographical regions of the Adriatic Sea. The Middle Adriatic Sea stands out as one of the rare locations in the world where *in situ* measurements of primary production have been systematically conducted since the 1960s and are ongoing. This data has only recently been synthesised and corrected for overestimates using a modelling approach. The final section is an overview of all primary production studies supported with comprehensive summarising tables. Most of the data concerns phytoplankton primary production estimated by ^{14}C method. Annual primary production in the Northern and Middle Adriatic ranges between 87.4–260.0 g C m^{-2} y^{-1}, and 70.0–177.4 g C m^{-2} y^{-1}, respectively. Southern Adriatic Sea is the least investigated, and only daily estimates are available (236–374 mg C m^{-2} d^{-1}). The purpose of this review is to highlight the significance of measuring primary production in the Adriatic Sea and the need for future research that will contribute to a more comprehensive understanding of the basin's productivity.
Keywords: primary production; Adriatic Sea; ^{14}C method; ocean colour models; satellite remote sensing; *in situ* incubation

Sažetak: ISTRAŽIVANJA PRIMARNE PROIZVODNJE U JADRANSKOM MORU – PREGLED. Primarna proizvodnja u Jadranskom moru se istražuje dugi niz godina, ali do sada nije objavljen sveobuhvatan sustavni pregled literature. Cilj ovog preglednog rada je popuniti tu prazninu dajući detaljan pregled svih provedenih studija, naglašavajući primijenjene metodologije i uspoređujući reprezentativne vrijednosti. Prvi dio predstavlja povijest mjerenja primarne proizvodnje i daje uvid u hidrografiju jadranskog bazena i njezin utjecaj na primarne proizvođače i njihove stope proizvodnje. Drugi odjeljak daje pregled produktivnosti u geografskim regijama Jadranskog mora, te se ističe srednji Jadran kao jedno od rijetkih područja u svijetu gdje se sustavno provode *in situ* mjerenja primarne proizvodnje od 1960-ih do danas. Dugoročni niz podataka je tek nedavno sintetiziran i ispravljen radi mogućnosti krivih procjena korištenjem modela. Posljednji dio sintetizira sve studije primarne proizvodnje unutar detaljnih i sažetih tablica. Većina podataka odnosi se na primarnu proizvodnju fitoplanktona koja je izmjerena upotrebom metode radioaktivnog izotopa ugljika ^{14}C. Godišnja primarna proizvodnja sjevernog i srednjeg Jadrana iznosi između 87,4–260,0 g C m^{-2} y^{-1}, odnosno 70,0–177,4 g C m^{-2} y^{-1}. Južni Jadran je najslabije istraživan, te su dostupna samo mjerenja dnevne primarne proizvodnje (236–374 mg C m^{-2} d^{-1}). Svrha ovog preglednog rada je ukazati na važnost mjerenja primarne proizvodnje u Jadranskom moru i potrebu budućih istraživanja koja će pridonijeti cjelovitijem razumijevanju ove tematike.
Ključne riječi: primarna proizvodnja; Jadransko more; ^{14}C metoda; modeli boje mora; satelitska mjerenja; *in situ* inkubacija

INTRODUCTION

Primary production review was made for the world's seas and oceans, such as the Pacific Ocean (Pennington *et al.*, 2006), and the Mediterranean Sea (Lefevre *et al.*, 1997; Magazzù and Decembrini, 1995), and there is a review on processes underlying marine primary production (Chavez *et al.*, 2011). Adriatic Sea primary production was discussed in the very early papers with a general description of the phytoplankton community and primary production (Ercegović, 1938; Buljan, 1964). There are short reviews on research done in the Middle Adriatic (Pucher-Petković, 1979; Marasović *et al.*, 1988), and Northern Adriatic (Harding *et al.*, 1999; Pugnetti *et al.*, 2006; Brush *et al.*, 2020). However, there is no systematic descriptive review of primary production research for the entire Adriatic Sea.

The first public conference on the Adriatic primary production was held in 1938 at the Institute of Oceanography in Split (at that time Yugoslavia, now Croatia), where Ante Ercegović held a public lecture on the importance of understanding primary production in the Adriatic, specifically its limiting parameters, response to the eutrophication, and its impact on fisheries (Ercegović, 1938). Later on, the article was published by Miljenko Buljan, aiming to describe zones in the Adriatic Sea based on their hydrographic and morphological properties which affect primary production (Fig. 1) (Buljan, 1964). Buljan divided the Adriatic Sea into four zones. Zone A (57% of the Adriatic surface) comprises open

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Received: 19 December 2023, accepted: 2 May 2024
ISSN: 0001-5113, eISSN: 1846-0453

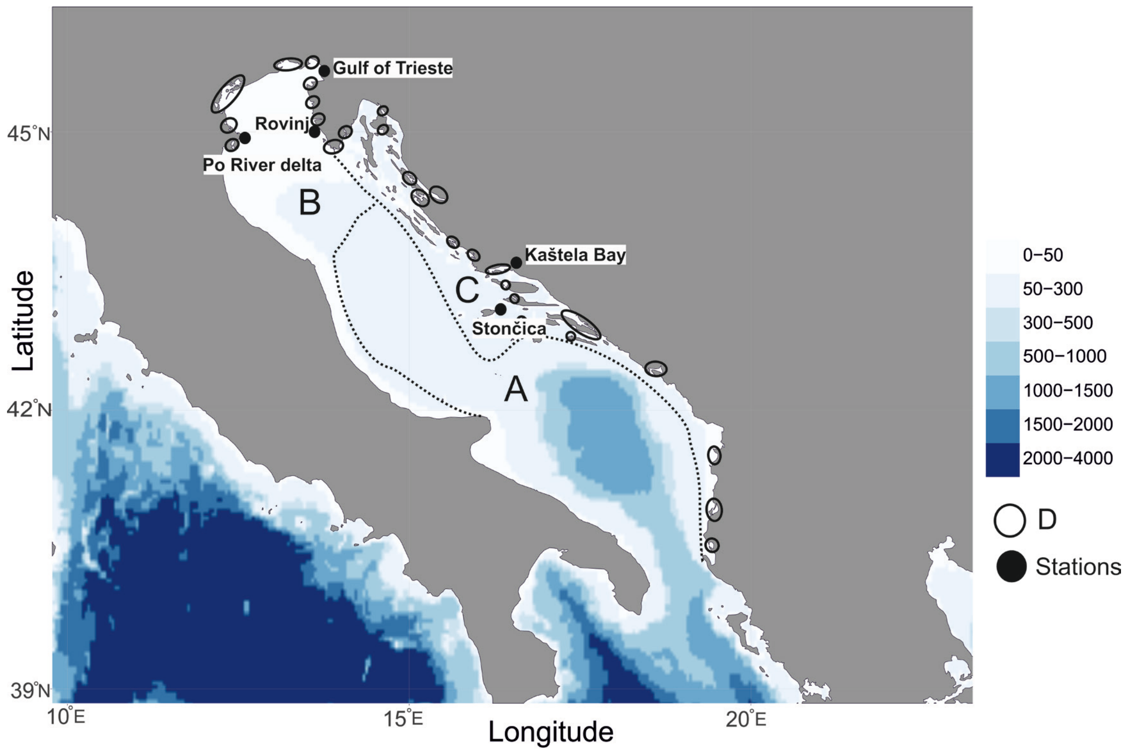

Fig. 1. Adriatic Sea bathymetry with four productivity zones and stations with most frequent primary production measurements. Zone A (57% of the Adriatic surface) comprises open deep Adriatic Sea is characterized by low productivity. Zone B (23%) is defined as the region influenced mostly by the riverine eutrophication. Zone C (18%) comprises the coastal sea up to 70 m deep that is influenced both by river discharges and circulation. Zone D (2%) is defined as a shallow coastal sea influenced by rivers and erosion from land (adapted from Buljan, 1964).

deep Adriatic Sea (Middle and Southern regions) that is characterized by low productivity. Other regions are richer in nutrients and thus more productive. Zone B (23%) is defined as the region influenced mostly by the riverine eutrophication (Northern region). Zone C (18%) comprises the coastal sea up to 70 m deep that is influenced both by river discharges and circulation, and Zone D (2%) is defined as a shallow coastal sea influenced by rivers and erosion from land (Buljan, 1964). Later on, primary production experiments started to be conducted in the Adriatic Sea, with most early publications dating from the 1960s and 1970s (Kveder *et al.*, 1967; Kveder and Kečkeš, 1969; Kveder *et al.*, 1971; Pucher-Petković, 1971; Pucher-Petković and Zore-Armanda, 1973; Pojed and Kveder, 1977). Pucher-Petković (1974) published annual gross primary production values for each zone defined by Buljan (1964) - Zone A: 55 g C m^{-2} y^{-1}, Zone B: 80 g C m^{-2} y^{-1}, Zone C: 60 g C m^{-2} y^{-1}, and Zone D: 150 g C m^{-2} y^{-1} (Buljan, 1964; Pucher-Petković, 1974). Further, the article describing the oceanographic properties of the Adriatic Sea was published, ensuring more understanding of the physical processes underlying the productivity of the Adriatic (Buljan and Zore-Armanda, 1976).

Who are the primary producers?

Primary production is a process mediated by organisms that can conduct photosynthesis and chemosynthesis, where sunlight and water are utilized to convert inorganic carbon into organic carbon molecules, and release oxygen. It is a process that regulates carbon and oxygen biogeochemical cycles. Net primary production (NPP) is equal to gross photosynthetic carbon fixation (gross primary production – GPP) minus carbon lost due to respiration. Therefore, it is the amount of carbon biomass available to the food web after the utilization in the metabolic pathways of a photosynthetic organism (Chavez *et al.*, 2011). Primary production in the oceans is constricted to the euphotic layer where there is available light irradiance. Factors limiting primary productivity can be light availability and nutrient concentrations, and they change depending on climate zone and geographical region (Kirk, 2010; Chavez *et al.*, 2011). Annual global primary production amounts to approximately 104.9 Gt C y^{-1}, of which terrestrial contribution of 56.4 Gt C y^{-1}, and oceanic production amounts to approximately 50 ± 28 Gt C y^{-1} (Longhurst *et al.*, 1995; Field *et al.*, 1998; Carr *et al.*, 2006; Fahey *et al.*, 2017).

Marine phytoplankton is a group of free-floating autotrophic prokaryotic and eukaryotic organisms that are at the basis of the pelagic food web and responsible for a large amount of carbon fixation in the planet's biosphere (Harrison, 1980; Falkowski *et al.*, 2004). Their size fractions are defined as nano, and picophytoplankton (2–10 μm, and <2 μm, respectively), and microphytoplankon (>10 μm) (Sieburth *et al.*, 1978). Marine phytobenthos is a group of autotrophic prokaryotic and eukaryotic organisms that are living on different surfaces (seabed, other organisms, etc.), and can be categorized as macrophytobenthos and microphytobenthos. They contribute to the primary production to a lesser extent than phytoplankton since they are restricted to the shallow coastal waters and to less than 30% of continental shelf waters (Meyercordt and Meyer-Reil, 1999; Goto *et al.*, 1999). In some specific continental shelfs such as Onslow Bay it was observed that microphytobenthos can contribute to primary production as significantly as phytoplankton because of physiological adaptation to light causing increase of pigments in time of shading by phytoplankton blooms and recycling of nutrients from sediments (Cahoon and Cooke, 1992). Although phytobenthos contribution to the overall ocean productivity has been deeply investigated (Cahoon and Cooke, 1992; Cahoon, 1999; Goto *et al.*, 1999; Bohórquez *et al.*, 2019), only few experiments were done in the Adriatic Sea reporting that *in situ* benthic PP ranged from 7.54 – 34.59 mg C m^{-2} h^{-1} (Cibic *et al.*, 2008), and *in vitro* benthic NPP ranged between 1.1 and 28.50 mg C m^{-2} h^{-1} (Blasutto *et al.*, 2005; Cibic *et al.*, 2022).

Adriatic basin hydrography and oceanography

The Adriatic Sea is an elongated (800 km long and 200 km wide) semi-enclosed northeastern basin connected with the Eastern Mediterranean in its southernmost part through the Otranto Strait that is 75 km wide and 780 m deep (Fig. 1). The total Adriatic Sea accounts for 139 000 km^2 of surface. The Adriatic Sea can be divided into three geographical regions based on their bathymetry – Northern, Middle, and Southern Adriatic Sea (Fig. 1). The Northern Adriatic is very shallow with an average depth between 30 and 40 m, and a maximum of around 70 m. It is a slope region from Venice-Trieste shoreline to the line connecting Ancona and Zadar on the Italian and Croatian coasts, respectively. The Middle Adriatic comprises the Middle Adriatic Pit (MAP) called Jabuka Pit (270 m) and ends with Palagruža Sill. The Southern Adriatic includes the South Adriatic Pit (1200 m) between the Palagruža and Otranto Sills (Cushman-Roisin *et al.*, 2013).

Productivity of the Adriatic Sea is limited by nutrients, specifically phosphorus which was confirmed by laboratory experiments done in the 70s and 80s (Pojed and Kveder, 1977; Chiaudani and Vighi, 1982). Orthophosphate concentrations (0.1 μmol L^{-1}) are comparable to those of the world's open sea regions (Buljan and Zore-Armanda, 1976; Marasović *et al.*, 2005). A large nutrient load with a high N:P ratio favors the environment where phosphorus is limiting primary production (Granéli *et al.*, 1999). Furthermore, the availability of nutrient forms due to water column stability and circulation dynamics also influences productivity (Cantoni *et al.*, 2003). Nutrient enrichment differs among the three geographical regions (Revelante and Gilmartin, 1977; Marasović *et al.*, 1999). The Northern Adriatic accounts for 20 000 km^2 of Adriatic Sea surface. Nutrient turnover in the coastal North Adriatic is fast, and concentrations are decreasing south towards the open sea (Campanelli *et al.*, 2011). Northern Adriatic Sea was defined as eutrophic compared to the other regions of the Adriatic (Degobbis *et al.*, 1986), since it was influenced by strong river outflow (Solidoro *et al.*, 2009), specifically Po River which discharged about 60% and 75% of phosphorus and nitrogen input, respectively (Degobbis *et al.*, 1986; Granéli *et al.*, 1999). However, recent studies show decrease of Po River discharge due to the more frequent periods of drought caused by climate change (Grilli *et al.*, 2020), causing change in nutrient ratio and favoring increase of phosphates and more oligotrophic conditions (Cozzi and Giani, 2011; Cozzi *et al.*, 2019).

Variability of primary production on a decadal scale in the Middle and Southern Adriatic Sea is influenced by the upper layer circulation pattern of the Adriatic Sea and circulation patterns of the Mediterranean Sea (Marasović *et al.*, 1995; Grbec *et al.*, 2009). Upper layer circulation in the Adriatic Sea is cyclonic, so oligotrophic and saline Eastern Adriatic Current (EAC) flows along the eastern coastline, while eutrophic and fresher Western Adriatic Current (WAC) outflows along the western coastline. Bimodal Adriatic-Ionian Oscillation (BiOS) is an internal dynamic of the Northern Ionian Gyre (NIG) that is shifting on a decadal scale, thus allowing the inflow of distinct water masses from the Mediterranean, and influencing biogeochemistry of the Southern Adriatic (Civitarese *et al.*, 2010), which may be a cause to observed decadal variations in primary production (Marasović *et al.*, 1995; Grbec *et al.*, 2009). Cyclonic NIG supports rapid advection of Levantine Intermediate Water (LIW) into the Southern Adriatic Sea which increases its salinity, temperature, and density, causing winter convection enhancement, nutricline downwelling at the border of the NIG, and primary production decrease. On the contrary, anticyclonic NIG changes the circulation dynamics by a stronger inflow of fresher and nutrient-rich Modified Atlantic Water (MAW) originating in the Western Mediterranean, causing nutricline upwelling at the NIG border, decrease of Southern Adriatic temperature, salinity, and density, and reduction of winter convection, with an effect in the increase of ecosystem productivity (Grbec *et al.*, 2009; Civitarese *et al.*, 2010). The Middle Adriatic is influenced both by incoming EAC originating from the Mediterranean Sea (Zore-Armanda, 1969) and by eutrophic water masses of WAC outflowing from the Adriatic (Marasović *et al.*, 1999), although the intrusion of Mediterranean waters from the south has proven to be more prominent variable affecting productivity than eutrophication in the north (Marasović *et al.*, 1995). Interannual variability in primary production in the Middle and Southern Adriatic has been connected to the regime shifts of water column physico-chemical parameters (Matić *et al.*, 2011).

Recent studies elucidate that atmospheric mineral dust deposition is also important environmental factor influencing primary production in the Adriatic Sea to some extent (Mifka *et al.*, 2022).

Methods, outline and purpose

Papers published between 1938 and 2022 were included in this review, and key words used in the literature search were: primary production, Adriatic Sea, ^{14}C method, ocean colour models, satellite remote sensing, and incubation. The purpose of this review is to outline the primary production studies done in each region of the Adriatic Sea and to discuss representative values in terms of the methodology used, physico-chemical parameters, circulation patterns, and climate change effects. This paper will contribute with an overview of experiments that elucidates research that is lacking, while proposing future study aiming to obtain more comprehensive knowledge of the Adriatic Sea primary production and its response to climate change.

PRODUCTIVITY OF THE ADRIATIC GEOGRAPHIC REGIONS

Northern Adriatic Sea

Northern Adriatic is highly productive (Kveder *et al.*, 1971) due to the strong influence of high nutrient enrichment by Po River (Smodlaka, 1986; Zoppini *et al.*, 1995), and minor influence by Adige (Brush *et al.*, 2020), and Isonzo Rivers (Ingrosso *et al.*, 2016). Annual primary productivity ranges from 50 g C m^{-2} y^{-1} (Istrian coast, Croatia) up to 130 g C m^{-2} y^{-1} (Po delta) (Gilmartin and Revelante, 1983). The coastal belt is highly productive with annual primary production between 200–260 g C m^{-2} y^{-1} that is decreasing towards the offshore regions (mean 120 g C m^{-2} y^{-1}) (Zoppini *et al.*, 1995). The highest values of annual productivity were measured in the central-eastern Gulf of Trieste (Fonda Umani *et al.*, 2007), the Po River plume (Pugnetti *et al.*, 2004) and the coastal station of the Senigallia-Susak transect that is crossed by the Western Adriatic Current flowing southward (Zoppini *et al.*, 1995). The seasonal variability in primary production is correlated with variations in Po River discharge, as well as with the extension of the productive layer that differs between the seasons (Pugnetti *et al.*, 2003, 2006). Northern Adriatic Sea is an effective sink for atmospheric CO_2 during the winter season of intense water column mixing that causes phytoplankon blooms (Catalano *et al.*, 2014). Furthermore, numerical studies showed the annual carbon flux is approximately 2.9 mmol m^{-2} d^{-1} over half of which is contributed by net primary production (Cossarini *et al.*, 2015; Ingrosso *et al.*, 2016).

Oceanographic research on eutrophication of the Northern Adriatic Sea started in 1966 (Kveder *et al.*, 1971), and later on productivity dynamics in response to freshwater nutrient input was frequently studied (Ivančić and Degobbis, 1987; Malej *et al.*, 1995; Giordani *et al.*, 1997; Granéli *et al.*, 1999). Degobbis *et al.* (2000) analyzed 29 years (1966–1995) database of physico-chemical parameters, phytoplankton counts, and photosynthetic activity in the Northern Adriatic to elaborate on eutrophication and river discharge variability and its influence on productivity (Degobbis *et al.*, 2000). Transparency of the Northern Adriatic water column was also observed for the period between 1911 and 1982 based on continuous Secchi disk observations. Due to eutrophication, transparency decreased over time, as well as benthic primary production and oxygen concentrations (Justić, 1988). However, more recent research contrasts these observations, showing a decadal trend of significant eutrophication decrease in the Northern Adriatic (Brush *et al.*, 2020).

Primary production monitoring was conducted from 1972 to 1975 (Smodlaka and Revelante, 1983; Smodlaka, 1986), and later on from 1980 to 1984 (Ivančić and Degobbis, 1987) and covered the entire northern Adriatic or its open waters, respectively. Micro-fraction is a major contributor to overall phytoplankton productivity (Malej *et al.*, 1995; Pugnetti *et al.*, 2006; Mangoni *et al.*, 2008; Talaber *et al.*, 2018; Mangoni *et al.*, 2020). The ratio shifts towards nano-, and picophytplankton in the stratified water column during summer months (Smodlaka, 1981; Malej *et al.*, 1995; Pugnetti *et al.*, 2003). In the period of stratification, nutrients regenerated in the deeper layer play a more crucial role in productivity, as opposed to river-sourced nutrients that are more prominent in winter and autumn months (Giordani *et al.*, 1997). Vadrucci *et al.* (2005) observed that picophytoplankton production can amount up to 44%, which is close to observed 46% for microphytoplankton, elucidating the importance of picophytoplankton in the open sea and during stratification period (Vadrucci *et al.*, 2005). Productivity of microorganisms attached to marine snow was studied as well (Kaltenbock and Herndl, 1992), and it was observed that the cyanobacteria-based marine snow contributes up to 38% to overall depth-integrated water column production (32.78 mg C m^{-2} h^{-1}) (Kaltenbock and Herndl, 1992). Microphytobenthos primary production was measured in the Northern Adriatic as well, and the first measurements were done *in situ* inside the intertidal Grado and Marano lagoons (1 - 9 mg C m^{-2} h^{-1}) (Blasutto *et al.*, 2005), after which followed *in situ* and *in vitro* measurements at the sublittoral sediments of Gulf of Trieste (7 – 35 mg C m^{-2} h^{-1}) (Cibic *et al.*, 2008; Cibic *et al.*, 2022).

Middle Adriatic Sea

This region differs from others in its extensive history of research into primary production. The Institute of Oceanography and Fisheries in Split (former Institute of Oceanography in Split, Yugoslavia) carries out highly valuable, systematic, and continuous measurements of primary production. The Middle Adriatic Sea has been monitored for primary production since April 1962 (Pucher-Petković, 1971) and measurements are done *in situ* using ^{14}C methodology at open sea station Stončica and coastal sea station Kaštela Bay (Pucher-Petković *et al.*, 1988).

This ongoing dedication has produced a globally unique time-series dataset on primary production. Numerous time-series programs were initiated worldwide in the past; however, most have ceased to exist (Kovač *et al.*, 2018). Currently, there are only a few ongoing programs, such as Bermuda Atlantic Time-Series Study (BATS) at the Bermuda station, Sargasso Sea in the North Atlantic Ocean (Lohrenz *et al.*, 1992; Bates *et al.*, 1996; Brix *et al.*, 2006), and Hawaii Ocean Time-Series (HOT) program at ALOHA station, Hawaii in North Pacific Ocean (Karl and Lukas, 1996; Karl *et al.*, 2021), both founded in 1988. Therefore, the Middle Adriatic provides a significant dataset produced by the earliest ongoing time-series program that is of high value in providing insight into multi-decadal productivity trends. For instance, recently the time-series data at Stončica station was corrected for overestimates using a non-linear production model (Kovač *et al.*, 2018). This comprehensive modeling study was able to elucidate decadal fluctuations of primary production: 1962–1979 (118 mg C m^{-2}), 1979–1997 (300 mg C m^{-2}), 1997–2008 (128 mg C m^{-2}), 2008–2013 (251 mg C m^{-2}), and 2013–2017 (154 mg C m^{-2}). Within each period there is a clear trend of primary production increase/decrease (Kovač *et al.*, 2018). The incorporation of the modeling approach increased the accuracy of this time-series data, thereby enhancing its reliability and enabling more precise comparison to the future data and monitoring of the Middle Adriatic productivity.

In general, the Middle Adriatic open sea is less productive (100-700 mg C m^{-2} d^{-1}) compared to the coastal sea (100-1500 mg C m^{-2} d^{-1}) (Marasović *et al.*, 2005). Primary production interannual variability in both coastal and open sea is observed by long-term monitoring, and research elucidates distinct drivers to that variability. At the coastal station Kaštela Bay, the period of unusual primary production increase was observed from 1970 to 1985 (150-240 mg C m^{-2}) followed by a decrease in oxygen saturation near the bottom, and water column transparency. These changes were correlated with observed eutrophication increase (Pucher-Petković, 1970; Marasović *et al.*, 1988; Pucher-Petković *et al.*, 1988; Pucher-Petković and Marasović, 1988; Zore-Armanda *et al.*, 1988). At open sea station Stončica a highly productive period with mean of 387.85 mg C m^{-2} d^{-1} was observed between 1980 and 1996 by time-series analysis (Grbec *et al.*, 2009). The analysis also elucidated two opposite trends within the period: productivity increase from 1980 to 1986, and then a decrease from 1987 to 1996 (Grbec *et al.*, 2009). The longest trend of primary production increase at Stončica was observed between 1965 to 1982 when productivity increased continuosly for about 4.8 mg C m^{-2} d^{-1} per year, with the most intense peak around 1980 (Marasović *et al.*, 1995). In contrast to the coastal Kaštela Bay, these observed decadal shifts in productivity at open sea station Stončica were not caused by eutrophication. The continouos increase in primary production correlated positively with salinity and temperature trends, therefore they were caused by shifts in Mediterranean water ingression dynamics (BiOS) (Grbec *et al.*, 2009) and North Atlantic Oscillation (NAO) (Ninčević Gladan *et al.*, 2010).

Primary production response to ocean heating due to climate change was well monitored in the Middle Adriatic. Phytoplankton size-fractionated productivity research confirmed that the open sea productivity is contributed by nano- and picophytoplankton, while microphytoplankton contributes the most to the coastal ecosystem (Ninčević and Marasović, 1998). Later on, shift from micro-scale to nano-scale phytoplankton in time of increased sea-surface temperature in the oligotrophic open sea was observed (Marasović *et al.*, 2005). Furthermore, microbial loop was investigated as it enables the transport of carbon to higher trophic levels in oligotrophic ecosystem, especially in time of stratification (Krstulović *et al.*, 1995). Krka river estuary productivity was also shortly investigated in the 1980s in order to research eutrophication caused by increased anthropogenic nutrient input (Pucher-Petković *et al.*, 1988; Gržetić *et al.*, 1991). High orthophosphate concentrations (1.7 mmol m^{-3}) contributed to the increased phytoplankton biomass and productivity that was two to three orders of magnitude higher (0.9 mg C m^{-3} h^{-1}) in comparison to values observed for the open sea (Gržetić *et al.*, 1991; Pucher-Petković *et al.*, 1988).

Southern Adriatic Sea

The research on the productivity of the Southern Adriatic basin is lagging behind the studies of Northern and Middle Adriatic. While in the Middle Adriatic there are continuous measurements of primary production, the Southern Adriatic was primarily measured for physico-chemical parameters (Marasović *et al.*, 1999). Although it is a highly oligotrophic ecosystem, there are regions where specific dynamic conditions in the water column favor high productivity (Zore-Armanda, 1984). The first record of high phytoplankton biomass was in the Southern Adriatic Pit, when unusually high Chl *a* concentrations for the open sea (>3 mg Chl *a* m^{-3}) were observed (Marasović *et al.*, 1999). The anomaly was explained by strong Adriatic ingressions since it was previously shown that, in the Middle Adriatic, interannual variability of primary production is affected by changes in circulation dynamics, specifically water exchange between Ionian and Southern Adriatic Sea (Pucher-Petković and Zore-Armanda, 1973). Later on, modeled depth-integrated water column productivity in the Southern Adriatic Pit was estimated to be between 249–374 mg C m^{-2} d^{-1}, confirming regions of high productivity in the oligotrophic South Adriatic (La Ferla *et al.*, 2005). The only published work on *in situ* ^{14}C primary production measurements in the Southern Adriatic is by Turchetto *et al.* (2000), that estimated water-column primary production of 297 mg C m^{-2} d^{-1} at the Palagruža Sill (Turchetto *et al.*, 2000). It separates the Middle Adriatic from the Southern Adriatic, and it is a region where the upwelling of deep water mass rich with nutrients increases productivity (Turchetto *et al.*, 2000).

OVERVIEW OF PUBLICATIONS

A total of 72 papers published between 1938 and 2022 were included in this review. Overview of all publications and a synthesis of primary production measurements in the Adriatic Sea are presented in Tables 1 and 2, respectively. Most publications were journal articles (N=67) followed by two review articles, two book chapters, and one conference paper (Table 1). There is no continuity in the number of publications on primary production research, and in certain periods the number of publications increased (Fig. 2). North Adriatic Sea productivity is discussed in most studies (N=46), followed by Middle Adriatic (N=21) and Southern Adriatic (N=3) (Table 1). Three papers discussed primary production on a larger spatial scale that included all regions of the Adriatic Sea (Table 1). Croatian (eastern) and Italian (western) coasts are almost equally covered (30 and 28 papers, respectively), while 12 studies included both coasts in their research (Table 1). The primary production measurements in the Adriatic Sea are mostly conducted in the framework of other research studies, such as eutrophication, biogeochemical cycles of nutrients and carbon flux (N=34), followed by research on the ecological function of phytoplankton groups (N=23), Adriatic Sea hydrography (N=22), and circulation patterns impact on productivity (N=20) (Table 1). Primary production is also studied in the contexts of monitoring the ecosystem response to the climate change effects (N=16), the food web response to the phsyico-chemical parameters (N=10), and productivity impact on fisheries (N=7) (Table 1). Long-term primary production measurements are done only in the Middle Adriatic (N=6), and they are corrected for overestimates using non-linear production model (Table 1, Table 2). There are few studies measuring productivity to correlate photosynthesis parameters (capacity and efficiency) with phytoplankton community composition, ecological function, and physico-chemical parameters (N=7). Primary production estimates by satellites and models are very recent in the literature (N=3) since they started to be implemented in the Adriatic Sea research after the 2000s (Table 1, Table 2). Most papers refer to the primary production of phytoplankton (N=61), but only few discuss the contribution of phytoplankton fractions to overall productivity and their ecological function in the phytoplankton community (Table 1, Table 2). The least frequent are the studies on the productivity of cyanobacteria (N=5) and phytobenthos (N=4) (Table 1, Table 2).

METHODOLOGIES – A COMPARISON

Primary production values depend on the chosen measurement method (^{14}C, ^{13}C, oxygen, remote-sensing satellites, models) and incubation mode (Fig. 3) because they are affected by the time of incubation, light irradiance, temperature, and the chosen sampling or optical depths. The values can be reported as a profile with depth (mg C m^{-3}) (N=37) or as depth-integrated water column production (mg C m^{-2}) (N=35) (Table 1, Table 2) that can be measured hourly (mg C m^{-3} h^{-1}) (N=40), daily (mg C m^{-2} d^{-1}) (N=25), or annually (g C m^{-2} y^{-1}) (N=13) (Table 1, Table 2). Measuring primary production using the ^{14}C method enables direct calculation of hourly primary production that will depend on the light intensity, number of sampling depths that determine the range of the euphotic zone that is covered, and incubation time. Daily and annual primary production values are estimated from hourly values, therefore they are biased by the error that can be introduced in the calculation (Balch *et al.*, 2022). In most studies, hourly primary production is measured at depth only, while daily and annual primary production values are often integrated to get water column productivity (Table 2). Therefore, it is challenging to compare productivity among different geographical regions of the Adriatic Sea if we take into account variety of applied methodologies and the reported units.

Incubation mode

Incubation ^{14}C technique by E. Steemann Nielsen (Nielsen, 1952) is a widely used method for measuring primary production in the oceans (Pugnetti *et al.*, 2006; Marra *et al.*, 2021), and it is the most frequently used method for primary production measurements in the Adriatic Sea (N=40) (Table 1). None of the research was using the stable isotope ^{13}C method, and only one study measured primary production *in vitro* based on oxygen concentrations in dark and light bottles (Buljan, 1969) (Table 1). Experiments using the ^{14}C technique are incubated *in situ* (N=40), followed by *in vitro* (N=21) and on deck (N=7) incubation, and two mesocosm experiments were conducted in the Adriatic Sea to measure phytoplankton primary production in relation to nutrients (Fuks *et al.*, 2004; Malfatti *et al.*, 2014) (Table 1).

In vitro incubation experiments in the Adriatic are mostly implemented in the laboratory under standard light (2400 lux) and temperature (20 °C), or in the incubators under constant light (70 Wm^{-2}) or light gradient (80 - 1200 μmol photon m^{-2} s^{-1}, 20 - 500 μE m^{-2} s^{-1}) and simulated sea surface temperature. On deck incubations are done in the thermostatic bath where the flow-through system maintains the sea surface temperature, and under sunlight or *in situ* light gradient that is reproduced by the nickel screens. Implementing *in situ* incubations was

Table 1. A review of 72 studies from 1938 to 2022 is summarized. The table presents reviewed categories (publications, geographical region, Adriatic coast, research topic, primary producers, measurement methods, incubation mode, primary production values and photosynthetic parameters), category elements, and the number of publications (N) belonging to each category element.

Category	Category element	N
PUBLICATIONS	Journal article	67
	Review article	2
	Book chapter	2
	Conference paper	1
GEOGRAPHICAL REGION	North Adriatic	46
	Middle Adriatic	21
	South Adriatic	3
	Adriatic Sea	3
ADRIATIC COAST	Eastern Adriatic coast (Croatia)	30
	Western Adriatic coast (Italy)	28
	Western and Eastern coast	12
RESEARCH TOPIC	Eutrophication, biogeochemical cycles, carbon flux	34
	Phytoplankton ecological function	23
	Adriatic Sea hidrography	22
	Circulation patterns	20
	Ecosystem response to climate changes	16
	Food web (Microbial loop)	10
	Photosynthetic parameters estimates	7
	Fisheries	6
	Validating models/remote sensing algorithms	3
	Primary production monitoring	3
PRIMARY PRODUCERS	Phytoplankton	61
	Nanophytoplankton	11
	Microphytoplankton	9
	Picophytoplankton	7
	Cyanobacteria	5
	Phytobenthos	4
MEASUREMENT METHODS	C^{14}	58
	Models	8
	Mesocosm experiment	2
	Oxygen concentration	1
	Remote sensing (satellites)	1
	C^{13}	0
INCUBATION MODE	*In situ*	40
	In vitro	21
	On deck	7
PRIMARY PRODUCTION VALUES	Hourly	40
	Primary production at depth	37
	Depth-integrated water column production	35
	Daily	25
	Annual	13
PHOTOSYNTHETIC PARAMETERS	Photosynthetic capacity (P_m^B) and efficiency (α_B)	8

similar among the studies. Parallel *in vitro* and *in situ* experiments have shown that *in situ* primary production rates are lower in comparison to the one measured *in vitro* (Buljan, 1969; Kečkeš *et al.*, 1969; Revelante and Kveder, 1971; Kveder and Revelante, 1973; Cibic *et al.*, 2008). For example, surface productivity of the Krka River estuary measured *in vitro* was 40% higher in comparison to values obtained *in situ* (Gržetić *et al.*,

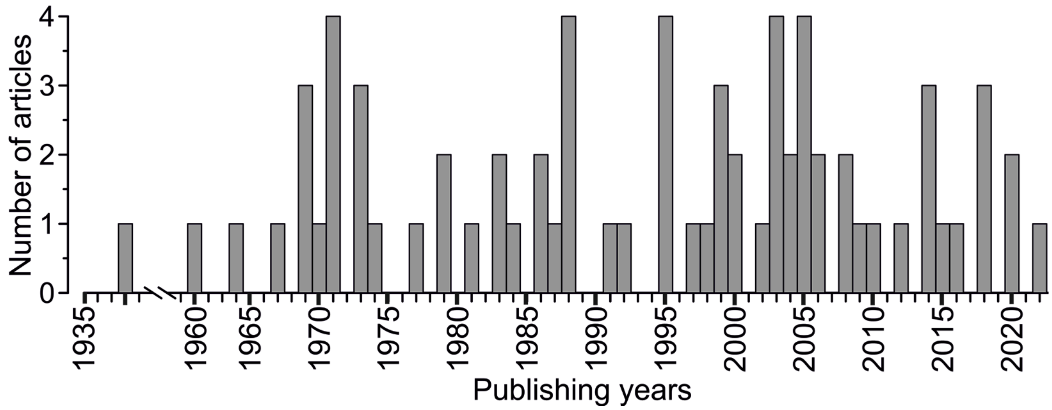

Fig. 2. Number of published articles on primary production in the Adriatic Sea from 1938 until 2022.

1991) which elucidates the bias due to the methodology being used in the experiments and the importance of considering it when discussing and comparing data from different sources.

Northern Adriatic primary production measurements are conducted *in situ*, on deck, and *in vitro*, while in the Middle and Southern Adriatic incubations are mostly performed *in situ* (Table 1, Table 2). Incubation time differs among the methods for primary production measurement. Gross primary production (GPP) and net primary production (NPP) are effectively measured during short and long ^{14}C incubations, respectively (Gazeau *et al.*, 2004; Balch *et al.*, 2022; Cibic *et al.*, 2022). Experiments in the Northern Adriatic are incubated between 0.75 and 4 hours, and average incubation time in the Middle and Southern Adriatic is 6 and 4 hours, respectively (Table 2), thus mostly calculating NPP. Certain studies lacked information on the incubation time of their experiments and the production rate (GPP or NPP). There is no standard for primary production measurements in the Adriatic Sea, specifically for incubation time that differs whether the aim is to calculate GPP or NPP. Therefore, there is a need for a standardized protocol that could be used in the future primary production measurements in the Adriatic Sea, as was done by the International Ocean Colour Coordinating Group under the NASA Plankton, Aerosol, Cloud, and ocean Ecosystem (PACE) project (Balch *et al.*, 2022).

Satellite observations and modelling studies

The advantage of remote sensing and models is in estimating primary production at much larger spatial and temporal scales in comparison to field measurements (Balch *et al.*, 2022). Therefore, satellite remote sensing allows accurate estimates of global phytoplankton primary production (Longhurst *et al.*, 1995; Field *et al.*, 1998; Carr *et al.*, 2006; Fahey *et al.*, 2017). Models can also predict the future of primary production under distinct climate change scenarios, one of which is possible water column stratification increase and net primary production decrease by 2090 (Fu *et al.*, 2016), indicating the importance of monitoring ecosystem response to climate change by having reliable measurements of primary production. Moreover, *in situ* data are very valuable since they are used in the validation of algorithms. One match-up study was done in the Adriatic Sea to validate SeaWiF measurements (Mélin *et al.*, 2003), while other ocean-colour remote sensing satellite products of the Adriatic Sea are published in a few studies (Mélin *et al.*, 2011; Cherif *et al.*, 2021; Salgado-Hernanz *et al.*, 2022). Chlorophyll *a* estimated by satellite remote sensing can be used to calculate primary production, however there is a methodological bias due to biomass not being a reliable representation of phytoplankton primary production (Vadrucci *et al.*, 2002). Recently developed models (Kovač *et al.*, 2016a; Kovač *et al.*, 2016b) effectively determine daily primary production and depth-integrated water column productivity in the Adriatic Sea, with a good example being a linear model correcting overestimates in the Middle Adriatic time series data (Kovač *et al.*, 2018).

Photosynthetic parameters

Photosynthetic parameters are a mathematical proxy of primary production that describe the productivity of the water column by defining photosynthetic capacity and efficiency (Platt *et al.*, 1983; Kovač and Sathyendranath, 2022; Balch *et al.*, 2022). Historically, these parameters were retrieved from *in vitro* or on deck incubations (Vadrucci *et al.*, 2002; Piermattei *et al.*, 2006; Talaber *et al.*, 2014; Mangoni *et al.*, 2020). The recent development of numerical (Kovač *et al.*, 2016a) and analytical (Kovač *et al.*, 2016b) models enabled the estimation of photosynthetic parameters from *in situ* measurements. Furthermore, photosynthetic parameters can be correlated with phytoplankton community structure

Table 2. Synthesis of the primary production measurements in the North, Middle and South Adriatic Sea done since 1961 with radioactive isotope ^{14}C technique by E. Steeman Nielsen. Shown are values of primary production at depth (mg C m^{-3} h^{-1}), watercolumn production (mg C m^{-2} d^{-1}), and annual watercolumn production (g C m^{-2} y^{-1}). Primary production profile - shown are range of values for measured depths or one mean value. Watercolumn production - shown are range of averaged values by season or one mean value for all seasons. Annual watercolumn production - shown are range of annual values or a mean annual value for the entire period. Furthermore, shown are photosynthetic parameters: photosynthetic capacity (PmB, [mg C (mg Chl *a*)$^{-1}$ h^{-1}]), and photosynthetic efficiency (αB, [mg C (mg Chl *a*)$^{-1}$ h^{-1} (mE m^{-2} s^{-1})$^{-1}$]), incubation method and time (h), if the net or gross primary production was measured. the period for which values were recorded, and reference to the published results. Underlined are values published in units that are non-uniform for the category: mg C m^{-3} d^{-1} (~), mg C m^{-2} h^{-1} (^), mmol C m^{-2} h^{-1} (#). Phytobenthic primary production values are marked with asterisk (*). Abbreviations: GPP- gross primary production, NPP- net primary production, SA – Southern Adriatic.

	Region	Period	Primary production at depth (mg C m^{-3} h^{-1})	Depth-integrated water column production (mg C m^{-2} d^{-1})	Annual water column production (g C m^{-2} y^{-1})	P_m^B	α_B	Method	Time (h)	References
NORTHERN ADRIATIC	Gulf of Trieste	1991		37.78^				*in vitro*		Kaltenbock and Herndl, 1992
		1989 - 1993		3.8 - 99.2^		1.8 - 13.2		*In situ*	4	Malej *et al.*, 1995
		1991 - 2001	2.7 ± 1.8	470 – 530				on deck	3	Giani *et al.*, 2003
		2003 - 2004		7.54 - 34.59^ *				*in situ*	2	Cibic *et al.*, 2008 *
		1998 - 2005		0.031 - 0.047^				*in situ*, on deck	4	Fonda Umani *et al.*, 2012
		2009 - 2010				0.60 - 4.73	0.002 - 0.025	*in vitro*, models	2	Talaber *et al.*, 2014
		2011 - 2013	0.001 - 4.06					*in situ*	2	Ingrosso *et al.*, 2016
		2010 - 2011	1 - 6.96	404 - 565	60.2 - 87.4	0.72 - 20.84		*in situ*	4	Talaber *et al.*, 2018
		2006 - 2007	7.11 ± 1.01	21.59 - 580.78				*in situ*	2	Cibic *et al.*, 2018
		2015 - 2019		17.55 - 28.50 *				*in vitro*	0.75 (GPP)	Cibic *et al.*, 2022 *
		2015 - 2019	5 - 7	11.47 - 69.30 *				*in situ*	2 (GPP)	Cibic *et al.*, 2022 *
	Po River delta	1967 - 1971			44 - 85			*in situ*		Kveder *et al.*, 1971
		1980s			130			*in situ*		Gilmartin and Revelante, 1983
		1994	0.16 - 34.4					*in situ*	4	Giordani *et al.*, 1997
		1996 - 2000	0.4 - 1.3					on deck	4	Vadrucci *et al.*, 2003
		1999 - 2001	2.3 - 7.4			3.7 ± 6.1		*in situ*	2	Pugnetti *et al.*, 2003
		1995 - 1996	30 ± 59			7.2 ± 5.8	0.05 ± 0.07	*in situ*	4	Pugnetti *et al.*, 2004
		1997				3.22 - 10.50		*in vitro*	1	Mangoni *et al.*, 2008
		1996 - 1998				2 - 20		*in vitro*	1	Mangoni *et al.*, 2020
	Po River delta - Rovinj	1967 - 1971			36 - 56			*in situ*		Kveder *et al.*, 1971
		1966 - 1995	1.23 ± 0.37			0.872 ± 0.589	0.020 ± 0.054	on deck	4	Vadrucci *et al.*, 2002
		1980s			80			*in situ*		Gilmartin and Revelante, 1983
	Western Adriatic Current	1993 - 1994	0-800					*in vitro*	1	Granéli *et al.*, 1999
		1990 - 1992		127 - 2815				on deck	4	Zoppini *et al.*, 1995
	Venice Lagoon	1958 - 1959		17 - 99				*in situ*		Vatova, 1961
		1999 - 2001				3.2 - 23		*in situ*	2	Pugnetti *et al.*, 2003
		1995 - 1996				6.6 ± 4.8	0.05 ± 0.03	*in situ*	4	Pugnetti *et al.*, 2004

	Region	Period	Primary production at depth (mg C m^{-3} h^{-1})	Depth-integrated water column production (mg C m^{-2} d^{-1})	Annual water column production (g C m^{-2} y^{-1})	P_m^B	α_B	Method	Time (h)	References
	Grado Lagoon	2002		2.8 – 9^ *				*in vitro*	2 (NPP)	Blasutto *et al.*, 2005 *
	Marano Lagoon	2002		1.1 - 3.5^ *				*in vitro*	2 (NPP)	Blasutto *et al.*, 2005 *
	Western region	1980-1984	5 - 45					*in vitro*		Ivančić and Degobbis, 1987
		1996 - 2002		453 - 511				on deck	4	La Ferla *et al.*, 2005
		1996 - 1998	4.12 ± 4.27					on deck	4	Vadrucci *et al.*, 2005
		1994 - 2002		235 - 635	80 - 150			*in situ*	2 - 4	Pugnetti *et al.*, 2006
		1996 - 1997	0-10				0.1 - 0.4	models		Piermattei *et al.*, 2006
	Western and eastern region	1966 - 1981	0.1 - 143					*in vitro*		Smodlaka, 1986
		2008		17#				*in situ*, models	4	Catalano *et al.*, 2014
		2008		210 - 366				models		Cossarini *et al.*, 2015
	Rovinj	1964 - 1966			80 - 100			*in situ*	3	Kveder and Kečkeš, 1969
		1967 - 1968		7 - 40^	75			*in situ*	3	Revelante and Kveder, 1971
		1967 - 1969		200 - 600				*in situ*	3	Kveder and Revelante, 1973
		1967 - 1971			52 - 87			*in situ*		Kveder *et al.*, 1971
		1980s			55			*in situ*		Gilmartin and Revelante, 1983
MIDDLE ADRIATIC	Kaštela Bay (coastal station)	1962 - 1968		248.6 - 438.2	103.2 -177.4			*in situ*	6	Pucher-Petković, 1970
		1962 - 1972			103.2 - 132.2			*in situ*	(GPP)	Pucher-Petković, 1971
		1962 - 1970		322.4 - 496.6				*in situ*	(GPP)	Pucher-Petković *et al.*, 1971
		1961 - 1975	20 - 140~		70 - 150			*in situ*		Gilmartin and Revelante, 1983
		1980 - 1982		7.91 - 75.42				*in situ*	6	Krstulović *et al.*, 1995
		1962 - 1996	200 - 1200~					*in situ*	6	Marasović *et al.*, 2005
	Stončica (open sea station)	1962 - 1968		76.6 - 260.4				*in situ*	6	Pucher-Petković, 1970
		1962 - 1972			44.4 - 92.2			*in situ*	(GPP)	Pucher-Petković, 1971
		1962 - 1970		106.7 - 200.9				*in situ*	(GPP)	Pucher-Petković *et al.*, 1971
		1961 - 1971	1.8	110.9 - 200.8	40 - 90			*in situ*		Pucher-Petković and Zore-Armanda, 1973
		1980 - 1982	2.96 - 11.23~					*in situ*	6	Krstulović *et al.*, 1995
		1962 - 1996		100 - 400				*in situ*	6	Marasović *et al.*, 2005
		1962 - 2017		118 - 300		5.2		models		Kovač *et al.*, 2018
	Krka River estuary	1983 - 1988	1 - 30 2 - 108					*in situ* *in vitro*		Gržetić *et al.*, 1991
SA	Palagruža Sill	1997	0.51 - 1.4	236 - 297				*in situ*	4	Turchetto *et al.*, 2000
	Southern Adriatic Pit	1996 - 2002		249 - 374				models		La Ferla *et al.*, 2005

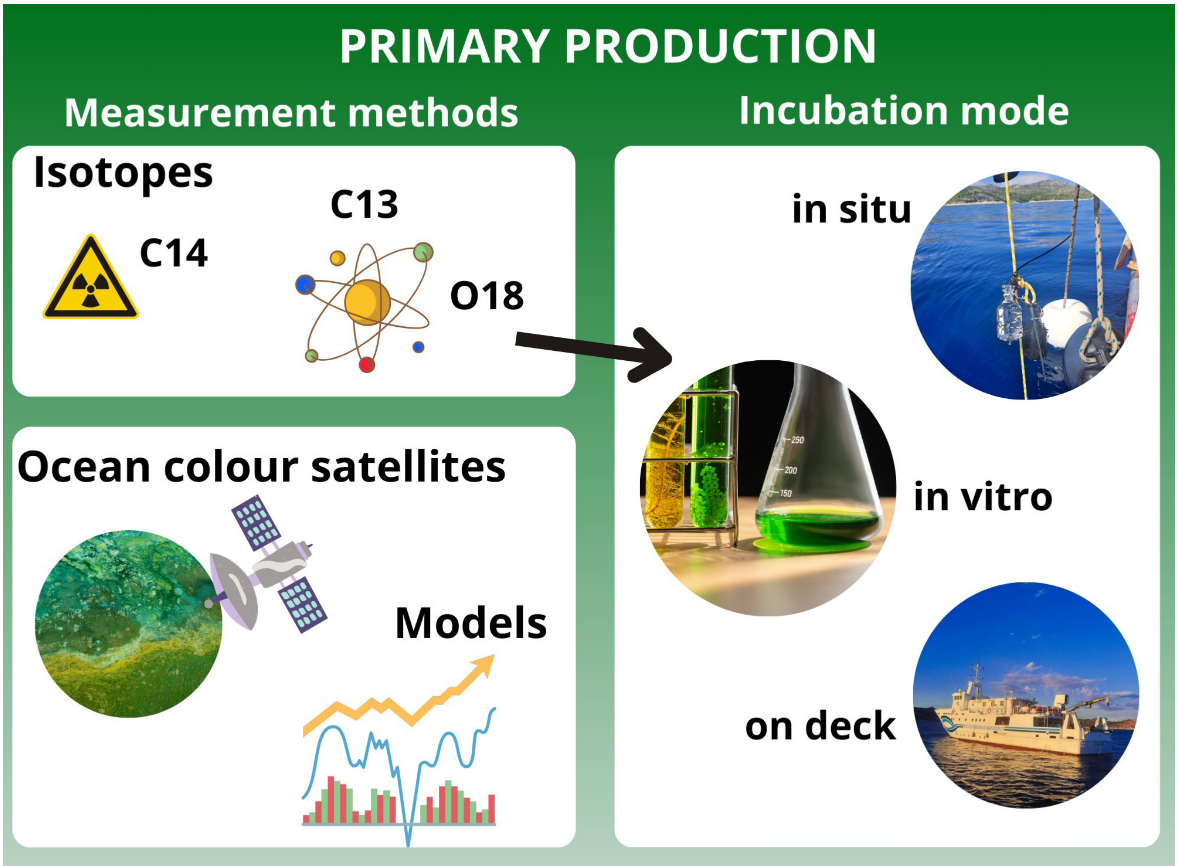

Fig. 3. General scheme illustrating the most common primary production measurement methods and incubation modes.

and environmental parameters (Talaber *et al.*, 2018; Mangoni *et al.*, 2020), ensuring an improved understanding of the primary production relationship to the environment and phytoplankton physiology and diversity. Photosynthetic parameters in the Adriatic Sea were estimated in eight studies (Table 1, Table 2) that defined phytoplankton photosynthetic rate at high light intensity (photosynthetic capacity, P_m^B) and low light intensity (photosynthetic efficiency, α_B). P_m^B values are estimated in the Northern Adriatic (0.60 and 20.84 mg C (mg Chl a)$^{-1}$ h^{-1}) and Middle Adriatic (mean 5.2 mg C (mg Chl a)$^{-1}$ h^{-1}), mostly from on deck and *in vitro* experiments, while α_B values are available for the Northern Adriatic only (0.002 and 0.4 mg C (mg Chl a)$^{-1}$ h^{-1} (µE m^{-2} s^{-1})$^{-1}$) (Table 2).

SUMMARY POINTS

- Total of 72 papers were included in this review, and most were journal articles (N=67)
- Most experiments are incubated *in situ* (N=40) using ^{14}C technique by E. Steemann Nielsen (N=58), while implementation of models (N=8) and satellite remote sensing (N=1) is in its early stages
- Northern Adriatic Sea is the subject of the most studies (N=46), especially the Gulf of Trieste, Po River delta and Rovinj area
- Middle Adriatic productivity has been systematically monitored since 1962 providing an ongoing and unique long-time series dataset on primary production comparable to the one available for ALOHA station, Hawaii
- Southern Adriatic is the least investigated region of the Adriatic Sea with only one *in situ* primary production experiment done at the open sea

CONCLUSION

Most of the published research was done in the Northern Adriatic, however the experiments were conducted sporadically in time so the largest data pool is yielded by the long-term monitoring in the Middle Adriatic. Such time-series allows us to record the variability of primary production on a decadal scale and observe changes that may be caused by climate change effects. Therefore, we want to encourage this practice in the future and highlight the importance of such datasets that need to be available and comparable to global data. In contrast, we observe a scarcity of research done in the South Adriatic Sea. Studies done so far elucidate a hot spot of productivity in certain regions such as the Palagruža Sill, and our opinion is that future primary production experiments should be implemented in the open oligotrophic South Adriatic Sea. Furthermore, it would be useful to start a monitoring program in both the southern and northern regions. It would yield a time-series data on a larger spatial scale that, in connection with the more frequent implementation of models and satellite remote sensing products, would improve how we observe changes in the Adriatic Sea ecosystem due to the effects of global shifts in the oceans and atmosphere induced by climate change.

For that to be accomplished, the development of a standardized protocol for the Adriatic Sea is crucial. For example, six decades of primary production research provided understanding that the highest productivity rates are recorded in the Northern Adriatic, especially in the Po River delta (130 g C m^{-2} y^{-1}), Rovinj (100 g C m^{-2} y^{-1}), and the Gulf of Trieste (87.4 g C m^{-2} y^{-1}). We know that the Middle Adriatic Sea is more productive in the coastal area (70–177.4 g C m^{-2} y^{-1}) in comparison to the open sea (44.4–92.2 g C m^{-2} y^{-1}), and that there are areas of high productivity in the open oligotrophic South Adriatic sea (236–374 mg C m^{-2} d^{-1}). However, the experiments were conducted without a standardized protocol, so it is challenging to compare results, discuss and draw conclusions on productivity among the regions. The synthesis of all studies that this review provided highlights the need to clarify the methods and aims of experiments, for example the productivity rate that is calculated based on the chosen incubation time, as well as the number of sampling depths.

A standardized protocol for primary production measurements in the Adriatic Sea would improve the quality of data, ensure comprehensive comparison among the regions of the Adriatic Sea and with the global datasets such as Hawaii Ocean and Bermuda Atlantic time-series. Furthermore, primary production research in the Adriatic Sea is declining, and providing such protocol could reverse this trend. To conclude, this review not only outlines the value of past studies but also highlights the need for having new revitalizing research that will incorporate both traditional and new methods, and utilize valuable time-series datasets. Given the pivotal role of primary production in the marine ecosystem as the foundation of the marine food web, the imperative is to inspire new scientific questions, hypotheses, and studies on primary production in the Adriatic Sea.

ACKNOWLEDGEMENTS

This work was funded by the Croatian Science Foundation under the project ISLAND (IP-2020-02-9524).

We acknowledge all the researchers who have contributed to the primary production study in the Adriatic Sea over the last six decades. We thank the librarians Virna Brumnić (Institute Ruđer Bošković, Rovinj) and Ingrid Čatić (Institute of Oceanography and Fisheries, Split), and the PhD students Andrea Bilajac (Institute Ruđer Bošković, Rovinj) and Nika Pasković (Institute for Coastal and Marine Research, University of Dubrovnik) for helping with literature search.

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