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Impacts of Sea Bottom Temperature on CPUE of European Lobster *Homarus gammarus* (Linnaeus, 1758; Decapoda, Nephropidae) in the Eastern Adriatic Sea

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The study describes recent decadal changes (2008–2017) in the landing biomass, fishing effort and CPUE (kg/day) data of European lobster *Homarus gammarus* in the eastern Adriatic Sea region, and relates these changes to increases of sea bottom temperatures detected at long-term *in situ* stations and modelled by an ocean numerical model (ROMS, Regional Ocean Modelling System). Modelling results were further used to quantify spatial and temporal differences of bottom temperature changes over different fishing zones. Trends of sea bottom temperature were positive and statistically significant between stations. Temporal trends of landing, effort and CPUE were also positive and significant for the northern Adriatic. Correlation analysis was used to test the relationship between winter and spring sea bottom temperatures and CPUE data of *H. gammarus*, separately for the northern and central Adriatic Sea, resulting in statistically significant correlations for both areas. Whether the increased CPUE in the northern Adriatic is due to increased abundance or catchability is discussed. The observed temperature changes likely reflect climate system changes recognised at the regional level and as such, lobster management measures will need to be revised and updated in the future.

Keywords: higher CPUE, landings, climate change, *Homarus gammarus*, Northern Adriatic Sea

INTRODUCTION

Climate change is reshaping ecosystems in ways that affect resources and ecosystem services (Nelson et al., 2013). Generally, fisheries depends first and foremost on the biomass of fishing resources, and fishing has often been the dominant driver of the status of resources. A failure to detect changes in the environment, or to act appropriately when changes are detected, can jeopardize fisheries (Holling, 2001). In term of climate change, fisheries are most often affected by rising sea temperatures and changes in ocean current systems. Cold water species are generally negatively affected by water warming, while thermophilus species benefit from it (Chaikin et al., 2021).

Climate change is already provoking changes in the spatial distribution of lobster species and therefore has the potential to alter territorial behaviour of fishermen and their landings as a consequence (Briones-Fourzán and Lozano-Álvarez, 2015). Such changes have already been reported in lobster populations worldwide, and are mainly related to sea warming (Cockcroft et al., 2008; Pecl et al., 2009; Caputi et al., 2010; Steneck and Wahle, 2013; Wahle et al., 2015; Rheuban et al., 2017; Le Bris et al., 2018). Boavida-Portugal et al. (2018) projected that clawed lobsters will contract their climatic envelope between 40 and 100% by the end of the century. Clawed lobsters of the genera *Homarus* and *Nephrops* are projected to shift their envelope to northern latitudes, likely affecting the North European, North American and Canadian fisheries, with potential detrimental effects on coastal communities (Greenan et al., 2019). Increasing temperatures and overfishing in coastal areas may result in sudden changes of environmental conditions and loss of benthic habitat (Caputi et al., 2013).

Ocean temperatures above an optimal thermal range can reduce lobster survival, growth, and reproduction as a result of stress, decreased recruitment and increased susceptibility to disease (Aiken and Waddy, 1986; ASMFC, 2015). The scale and characteristics of lobster responses to warming vary across the range of warming (Boudreau et al., 2015; Le Bris et al., 2018). For example, an overall increase of abundance was reported for of American lobster, but different trajectories were observed within the range of the species in the Gulf of Maine (Le Bris et al., 2018), with the fishery increasing dramatically in the central and northern part while it effectively collapsed at the warmer southern limit (ASMFC, 2015). Similarly, a major shift in resource availability of rock lobster *Jasus lalandii* to higher latitudes on the western coast of Africa was reported, with declined landings in lower latitudes at the end of 20th century (Cockcroft et al., 2008). A difference in the dependence on environmental variability in relation to geographic position was also determined for Scottish *H. gammarus* fisheries (Lizárraga-Cubedo et al., 2015). However, there are no published data regarding recent changes in landings and CPUE in relation to sea warming for the European lobster in southern European regions.

European lobster (*Homarus gammarus*) is a species of boreal origin inhabiting coastal shelf seas of northern Europe, with the Mediterranean Sea representing the southern limit of its distribution range (Holthius, 1991; Mercer et al., 2001). Previous studies have suggested that warming beyond the temperature optimum will lead to lower juvenile survival, lower recruitment, suboptimal growth conditions, and reduced fishery productivity in the future (Pere et al., 2019). Temperature changes might play a major role for the future southern distribution of *H. gammarus* populations, with excessively high temperatures leading to reduced population abundance at the southern boundaries (Triantafyllidis et al., 2005). In line with this, it is presumed that the coldest parts of the Mediterranean Sea (Gulf of Lyon and the northern Adriatic) could initially serve as a sanctuary for cold-temperate species (Ben Rais Lasram et al., 2010).

The European lobster fishery is one of the most valuable fisheries in northern Europe, mainly in the United Kingdom, Ireland, and northern France (Bennett and Lovewell, 1977; Bennet et al., 1993; Browne et al., 2001) with total annual landings around 5000 t in last 10 years (FAO, 2021). Beside European lobster, economically important lobster species within European water include *Palinurus elephas* and *Scyllarides latus* (Kampouris et al., 2020). The fishery is based on traps of various designs, shapes, and sizes (Cobb and Castro, 2006). Along the Mediterranean coast, *H. gammarus* is not a target species and is more often a by-catch occurring in trammel nets targeting the common spiny lobster *Palinurus elephas* (Quetglas et al., 2004) or in gillnets targeting fish (Kampouris et al., 2020) during the fishing season (Goñi and Latrouite, 2005; Pere et al., 2019). Mediterranean landings of *H. gammarus* were around 140 t for the period 2006–2015 (FAO, 2021) though this may be a general underestimation in the Mediterranean (Le Manach et al., 2011; Pere et al., 2019). Data for the Greek fleet, which reported more than 50% of Mediterranean landings in previous years, are missing for the years 2016 and later (FAO, 2021) and some data and clarifications are available (Kampouris et al., 2020). For lobster catches in Spain, there are indications of significant declines (Lloret and Riera, 2008). The lack of historical landing datasets prevents us from concluding on the reliable abundance of *H. gammarus*. However, increasing signs of possible failure in egg production and recruitment overfishing have already been reported in Irish fisheries (Tully et al., 2001) and can be worrying in the context of a lack of knowledge of the current population (stock) status of *H. gammarus* in the Mediterranean.

With regard to the current higher landings reported in some Mediterranean sub-areas, failure to recognise the impacts of sea warming on the European lobster may contribute to potential overfishing in the coming years. This fishery depends on sound management, though the size of the stock certainly depends on future temperature conditions. This study analyses recent positive changes in the reported landing biomass and catch per unit effort (CPUE) of *H. gammarus* in the official fishing zones in the Adriatic Sea and links them with positive sea bottom temperature trends at the sub-regional level. We hypothesised that a substantial increase in the winter and spring sea bottom temperatures in the period 2008–2017 is reflected in the positive trends in landings and catch per unit effort (CPUE) in the northern Adriatic. Ocean numerical model results were examined to quantify the observed spatial and temporal temperature trends. The correlations between increased abundance and the observed increased landings are discussed in detail.

MATERIAL AND METHODS

Study Area

Located in the northernmost part of the central Mediterranean, the semi-enclosed Adriatic Sea is divided into the northern, central and southern Adriatic. The Jabuka Pit depression (280 m depth) separates the northern shallow shelf (depths up to 80 m) from the deeper central Adriatic, while the northwest perimeter of the South Adriatic Pit (1200 m depth) separates the central and the southern Adriatic (**Figure 1**).

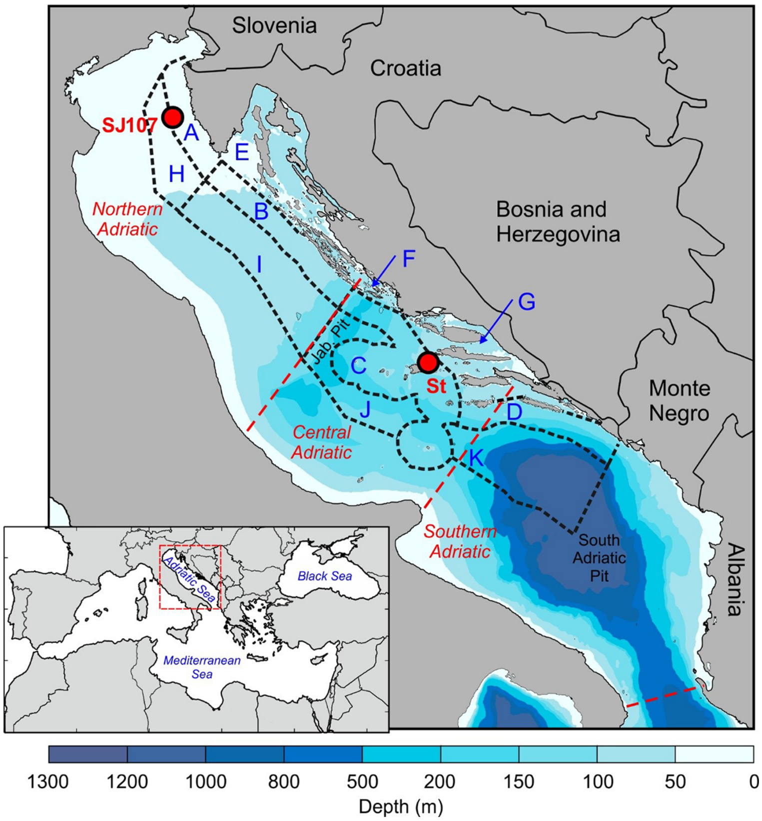

FIGURE 1 | Bathymetric map of the study area, sampling stations SJ107 and Stončica (St) with 11 fishery zones corresponding to northern, central and southern Adriatic indicated.

The most important physical parameter affecting lobster abundance, and thus landings and CPUE, is sea bottom temperature (Green et al., 2014; Zhao et al., 2019). Throughout the Adriatic, this is dominantly affected by bathymetry and seasonal changes of heat flux (Artegiani et al., 1997). Over the shallow northern Adriatic, temperatures vary from 6°C during severe winter cooling events to 20°C during periods of vertical mixing in the autumn. Deeper regions of the central Adriatic exhibit less seasonal changes with temperatures ranging from 13 to 17°C (Buljan and Zore-Armanda, 1976; Lipizer et al., 2014), and within deepest regions of southern Adriatic temperatures vary even less, from 12.4 to 13.7°C (Lipizer et al., 2014; Cardin et al., 2020).

Environmental Variables and Modelling System

Temperature data were retrieved from measurements and the numerical model Regional Ocean Modelling System (ROMS) (Shchepetkin and McWilliams, 2005; Shchepetkin and McWilliams, 2009). Temperature measurements were collected at the stations Stončica (depth: 95 m) in the central Adriatic (43° 0'0"N, 16°20'0"E) and SJ107 (depth: 35 m) in the northern Adriatic (45°2′52″N, 13°19′0″E) in the period 2008–2017 (**Figure 1**). These stations are parts of two oceanographic transects monitored for at least a half of century: Stončica by the Institute of Oceanography and Fisheries (Split) and SJ107 by Institute Ruđer Bošković (Rovinj) (Marić et al., 2012; Vilibić et al., 2012). The stations are highly representative in term of depth for the northern and central Adriatic. Also, the depths at which the measurements were performed correspond to the typical inhabitation and catch depths of the analysed lobster species in the northern (20–35 m) and central (50–100 m) Adriatic. Temperature measurements were mostly carried out once a month or once every two months. At Stončica measurements were performed in 64%, and at SJ107 in 75% of months within the study period. Measurements were taken at Stončica using CTD probes (IDRONAUT 316, SeaBird-25 and 911+) with an accuracy of ±0.003°C, and at SJ107 using protected reversing thermometers (Richter and Wiese, Berlin; precision ±0.01°C) and reversing digital thermometers (SiS RTM 4002; precision ±0.003°C) attached to Niskin bottles. For this research, we used the deepest sampling, which was usually taken 2 m above the seabed.

Daily values of the ROMS were used to reproduce temperature changes in the Adriatic Sea between 2008 and 2017. The ROMS model is a 3D hydrostatic, nonlinear, free surface, sigma coordinate, time splitting finite difference primitive equation model (Shchepetkin and McWilliams, 2005;

Shchepetkin and McWilliams, 2009). The lateral boundary conditions were taken from the AREG model of the Adriatic Forecasting System (AFS) (Oddo et al., 2006), while atmospheric forcing was prescribed *via* bulk formulation (Fairall et al., 1996), using all the required variables from the operational local area model ALADIN/HR (Tudor et al., 2013). Horizontal resolution was 2 km, with 20 sigma vertical layers in the model. River discharges were introduced to the ocean model following climatology by Vilibić et al. (2016) for all rivers except the River Po, for which real daily discharges were used. All other details about the model setup are provided by Janeković et al. (2014) and Vilibić et al. (2016). Temperatures modelled at the lowest sigma coordinate, roughly corresponding to sea bottom temperatures, were analysed in the paper.

Additionally, bottom temperature averages were calculated for each fishing zone and year/season by considering each model point within the fishing zone polygons. Trend significance of sea bottom temperature was tested by the Mann-Kendall nonparametric test.

Fisheries Data

For management purposes and data collection, the Croatian marine fishing area has been administratively divided into smaller units (11 fishing zones; OG, 2011) (**Figure 1**). All available data on *H. gammarus* landings in the Adriatic Sea for fishing zones A, B, C, D, E, F, G (coastal zones) and H, I, J, K (offshore zones) for the period 2008–2017 were obtained from the Fisheries Directorate (Croatian Ministry of Agriculture) based on fisher's logbooks (fishery dependant data). These data correspond with open season for lobsters (May–August) and the MED EU minimum legal size of 105 mm carapace length (CL) (EU Regulation 1967/2006). During the study period, insignificant landings (less than 50 kg per year) were reported in fishing zones H, I, J and K and therefore these zones were excluded from further analysis. For analysis purposes, data were standardised as the catch per unit effort (CPUE), expressed as the biomass of *H. gammarus* caught per fishing trip of a single fisher. For this study, the available data at the scale of fishing zones were aggregated to three general regions: northern, central and southern following the natural geographical division of the Adriatic Sea. Each fishing zone has boundaries expressed by geographical position. Thus, fishing zones A, B and E corresponds to the northern, zones C, F and G to the central, and zone D to the southern Adriatic. As with temperature, the trend significance in *H. gammarus* landings, fishing effort and CPUE was tested with the Mann-Kendall nonparametric test. Pearson correlation analysis was used to test the linear relationship between sea bottom temperature and CPUE (kg/day) data of *H. gammarus.*

RESULTS

Time Series of Landings and CPUE

A total of 22.83 t of *H. gammarus* was landed on the eastern Adriatic coast during the study period (data of the Fisheries Directorate for 2008–2017), distributed by region as follows: northern 13.93 t, central 8.65 t and southern Adriatic 0.25 t. Particularly, *H. gammarus* was mostly captured by pots and gillnets in the fishing zones A and E in the northern Adriatic (**Table 1**). In that area, as shown in **Figure 2A**, landings averaged over three fishing zones (A, B, E) fluctuated from 0.21 t (2008; landings = 631.5 kg; CPUE = 2.5 kg/day) to 0.75 t (2016; landings = 2244 kg; CPUE=3.41 kg/day). Landings averaged over the three fishing zones corresponding to the central Adriatic (C, G, F) ranged from 0.23 t (2010; landings = 685.7 kg; CPUE = 1.77 kg/day) to 0.37 t (2014; landings = 1112 kg; CPUE = 2.18 kg/day). In the same period, landings in the southern Adriatic (zone D) were less than 50 kg per year, namely from 14 kg (2008; 10 fishing days corresponding to CPUE of 1.4 kg/day) to 41.1 (2010; 25 fishing days and CPUE of 1.6 kg/day) and therefore the data from that zone, i.e. the southern Adriatic, were not included in the further analysis. Temporal trends (2008–2017) of *H. gammarus* landings in the Adriatic Sea indicate a statistically insignificant and weak increase in the central Adriatic (4.5 kg/year; $p > 0.05$; $R^2 = 0.008$) and a statistically significant increase in the northern Adriatic (160.9 kg/year; $p < 0.05$; $R^2 = 0.755$).

The temporal trend across the study period (2008–2017) of fishing effort (**Figure 2B**) was weakly negative and statistically insignificant (-3.1 days/year, $p > 0.05$; $R^2 = 0.021$) in the central Adriatic, while fishing effort was positive and statistically significant (40.6 days/year, $p < 0.05$; $R = 0.728$) in the northern Adriatic. As a consequence, the decennial temporal trend of *H. gammarus* of catch per unit effort followed a similar pattern as landings: the CPUE trend over time in the central Adriatic was weakly positive but statistically insignificant (0.03 kg/effort, $p > 0.05$, $R^2 = 0.307$) while CPUE was positive and statistically significant (0.09 kg/effort, $p < 0.05$, $R^2 = 0.643$) in the northern Adriatic (**Figure 2C**). The negative trend of fishing effort in the

TABLE 1 | Reported landings of European lobster, *Homarus gammarus* among seven fishing zones corresponding to the northern, central and southern Adriatic Sea across the study period (data of the Fisheries Directorate for 2008–2017).

Geographic area	Fishing zones	Total landings/zone (t)	Total landings/area (t)
Northern Adriatic	A	7.47	13.93
	B	1.14	
	E	5.31	
Central Adriatic	C	1.35	8.65
	F	2.54	
	G	4.76	
Southern Adriatic	D	0.25	0.25

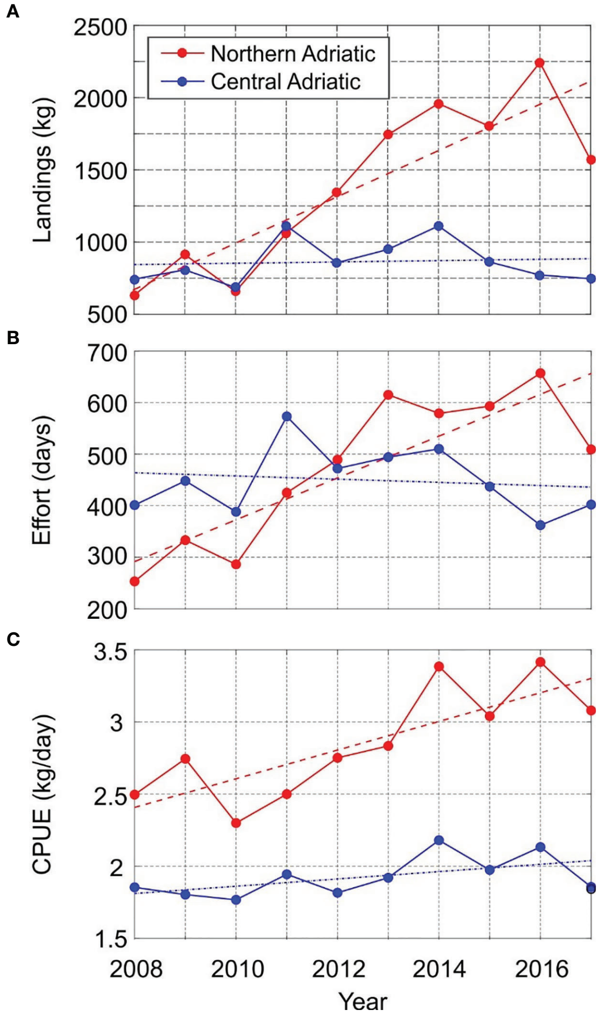

FIGURE 2 | Time series of: **(A)** landings; **(B)** effort; **(C)** CPUE. Significant ($p < 0.05$) and insignificant ($p > 0.05$) trends are plotted with dashed and dot-dash line, respectively.

central Adriatic affects the CPUE calculation in the same area and should be carefully considered.

Time Series of Bottom Temperature

Time series of the yearly averages of measured bottom temperatures at the SJ107 and Stončica stations and modelled bottom temperatures in the selected fishing zones are shown in **Figure 3**. The yearly averages of measured temperatures at SJ107 for 2012 and 2017 were not calculated, since data were lacking at SJ107 for February to June 2012, i.e. during the part of year characterised by the lowest bottom temperatures, while in 2017, measurements are lacking for September to December, i.e., the part of the year characterised by the highest bottom temperatures. Including these values would thus result in a significant overestimation (or underestimation) of the measured yearly averages for these two years.

The bottom temperature trends at both stations (0.15°C/yr, $p < 0.05$ at SJ107; 0.14°C/yr, $p < 0.05$ at Stončica) and over fishing zones were positive and statistically significant. The temperature trend is apparently governed by a pronounced jump of bottom temperatures values, starting in 2013 (**Figure 3**). This jump is evident in both the measurements and the model, in both the central and northern Adriatic, though it is more pronounced in the northern Adriatic (~1.5-2.5°C) than in the central Adriatic (~1°C). **Figure 3** clearly shows that the model is biased when it comes to reproducing absolute values of bottom sea temperature, in particularly in the shallow northern Adriatic (**Figure 3A**). Nonetheless, the reproduction of the variability of yearly (**Figures 3C, D**) and seasonal (**Figure 4**) temperature was satisfactory for both areas, and thus we chose to use the model for more detailed analysis.

Seasonal Changes of Bottom Temperature

The seasonal changes of near-bottom temperature at SJ107 (34 m) and Stončica (95 m) are shown in **Figure 4**. These changes were more pronounced in the northern Adriatic, where

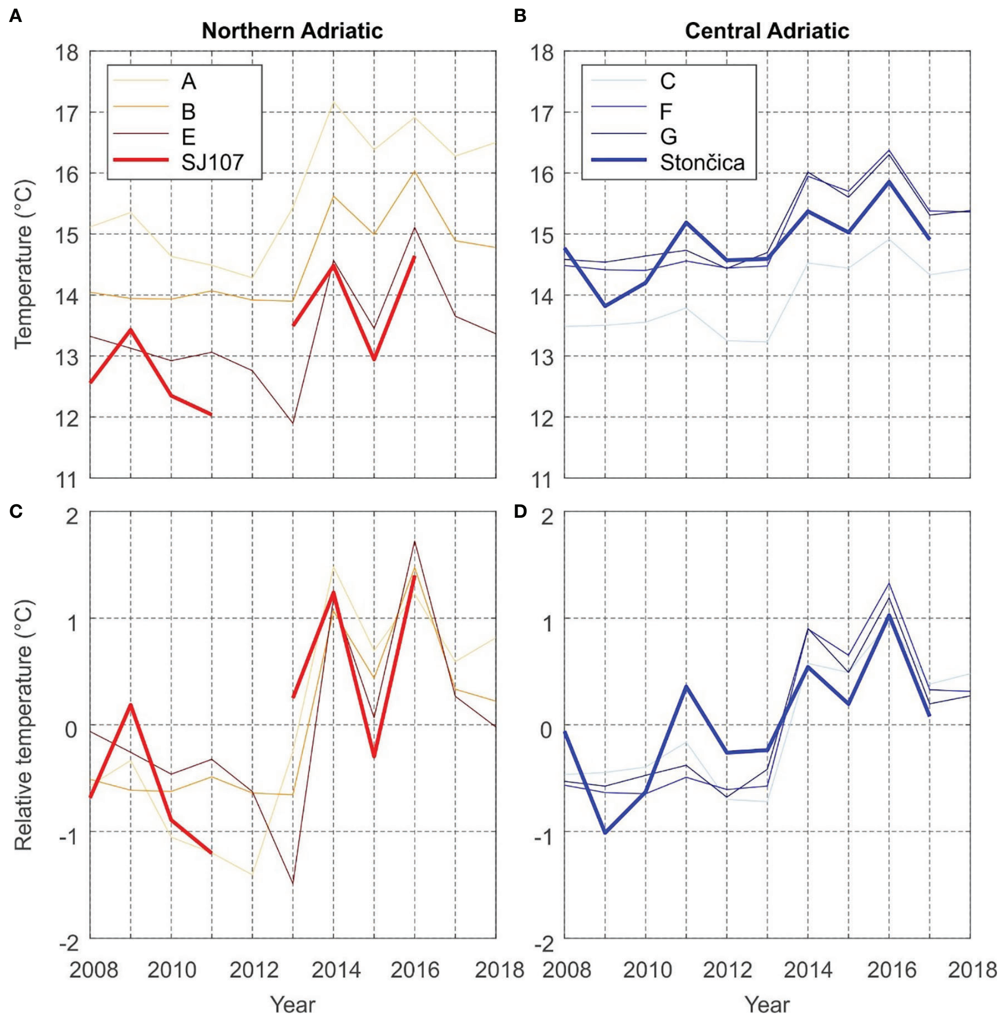

FIGURE 3 | Model to measurement comparison of annual mean value of sea bottom temperatures at: **(A)** measurement station SJ107 and the northern Adriatic fishing zones; **(B)** measurement station Stončica and the central Adriatic fishing zones. **(C, D)** same as **(A, B)** but with average values removed.

their range reaches ~7°C, than in the deeper central Adriatic (~3°C in range). The northern Adriatic is much colder during most of the year, particularly during the winter period (February-March). October is the only month in which the sea bottom temperature is higher in the deep northern Adriatic than in the deep central Adriatic.

The modelled values were overestimated at SJ107 by 0.6-0.9°C during the winter months and even more during the period of developed thermocline (May through October; up to 4.0°C). In contrast, the model slightly underestimated the bottom temperature at the Stončica station (model-to-measurements bias is up to -0.8°C in June). The offset of model values might be due to systematic offsets of values of atmosphere-ocean heat fluxes, or of lateral boundary conditions propagating from Otranto towards the central and northern Adriatic. Also, it might be due to an inadequate reproduction of vertical mixing processes. Nonetheless, it should be noted that the phase of the seasonal signal and its variability and range are well reproduced. Standard deviations of bottom temperatures are consistent between model and measurements, and are higher in the northern Adriatic (~1°C) than in the central Adriatic (~0.5°C). The model best reproduced the JFM (January-February-March) and AMJ (April-May-June) seasonal bottom temperatures. This is particularly important for this study, as JFM and AMJ were found to be the two most relevant periods in which changes can affect lobster landings and CPUE. JFM and AMJ also correspond to periods preceding and during the open fishing season.

Correlation Analysis of Modelled JFM and AMJ Temperature and European Lobster CPUE

Correlations between bottom sea temperature and CPUE (kg/day) for the fishing areas (Northern Adriatic - zones A, B and E; central Adriatic - zones C, G and F) for the period from 2008 to 2017 were found to be statistically significant both for winter (JFM) and spring (AMJ) (**Table 2**). The simultaneous time series

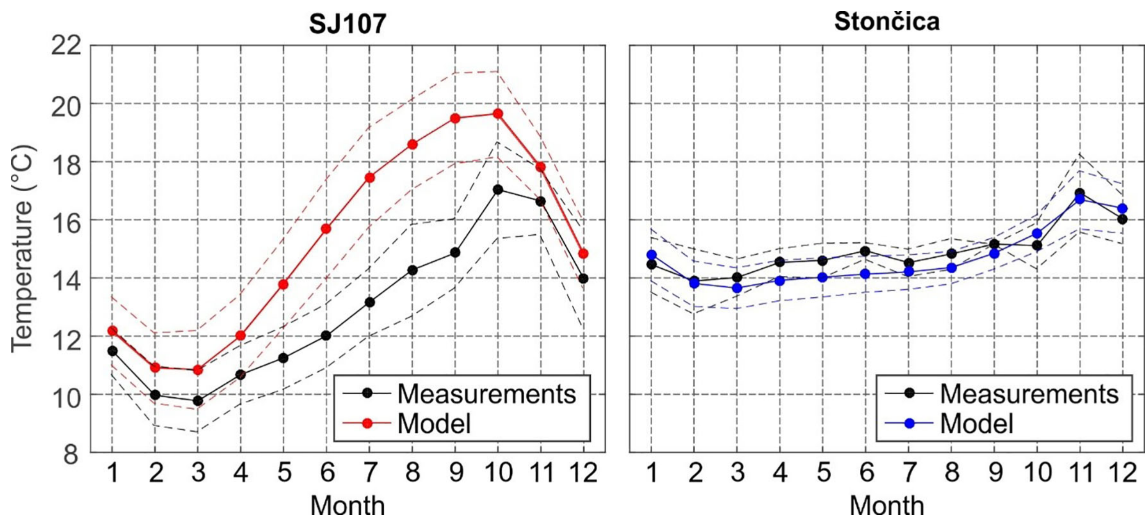

FIGURE 4 | Monthly averages (2008–2017) of measured (black) and modelled (red) near bottom temperature (full line) and corresponding standard deviation (dashed line) at (*left*) SJ107; (*right*) Stončica. For the model, temperature series were taken from the grid cell nearest to SJ107 and Stončica.

of JFM and AMJ temperatures and CPUE (kg/day) of European lobster are shown in **Figure 5** for the northern and in **Figure 6** for the central Adriatic. A high correspondence between the two variables is evident: in both areas, the CPUE values significantly increases in 2013/2014, at the same time as the bottom temperatures. Most individual peaks in CPUE also correspond with individual peaks of the temperature time series (2014 and 2016 for the northern Adriatic; 2011, 2014 and 2016 for the central Adriatic).

DISCUSSION

Changes of Sea Bottom Temperatures in the Period 2008–2017

The observed temperature changes might be the result of ongoing climate changes or just a local or regional phenomenon. Analyses of satellite-derived sea surface temperature documented the largest trend in June, with a rate of 4.3°C over 100 years over the whole Mediterranean and some 30% higher rates over the northern Adriatic (Pastor et al., 2018). This has been attributed quasi-equally to multi-decadal oscillations (like Atlantic Multidecadal Oscillation, Knight et al., 2006) and to real warming trends (Iona et al., 2018). Vilibić et al. (2019) found a substantial increase in temperature in the northern Adriatic between 1979 and 2017, particularly high on the surface and during the summer season. Modelled bottom temperatures in the present study show a substantial increase in winter (JFM) and spring (AMJ) values over the whole Adriatic between the first (2008–2012) and the last (2013–2017) five years of the simulation. These changes are clearly visible on the corresponding difference plots for JFM and AMJ (**Figure 7**). The largest increase in both seasons was found in the shallow northern Adriatic, particularly in zone A (also the zone where most lobster is caught), thereby confirming the findings of Pastor et al. (2018). The increase is less pronounced in the deeper central and southern parts of the Adriatic, as the seasonal thermocline is far shallower than the ocean depth there (Buljan and Zore-Armanda, 1976; Lipizer et al., 2014). The JFM temperature increase in zone A was between 1 and 2°C, and between 0 and 1°C over most of the central Adriatic. The AMJ temperature increases were even higher in both areas: up to 2.5°C in zone A of the northern Adriatic, and up to 1.5°C over the central Adriatic zones. Despite the observed changes, JFM temperatures remained lower in the northern than in the central Adriatic. On the other hand, the northern AMJ temperatures remained higher than central ones, with the temperature difference between the two areas increasing over time, due to the more efficient heat transfer towards the bottom in shallow waters (Artegiani et al., 1997).

TABLE 2 | Correlation indices for time series of bottom sea temperature and catch per unit effort CPUE (kg/day) of European lobster *Homarus gammarus* for the grouped fishing zones of the northern and central Adriatic in winter (JFM) and spring (AMJ) period (r-correlation coefficient; p – significance value).

Fishing area (zones)	Winter (JFM)		Spring (AMJ)	
	r	p	r	p
Northern Adriatic (A, B, E)	0.74	0.015	0.82	0.003
Central Adriatic (C, G, F)	0.84	0.003	0.79	0.006

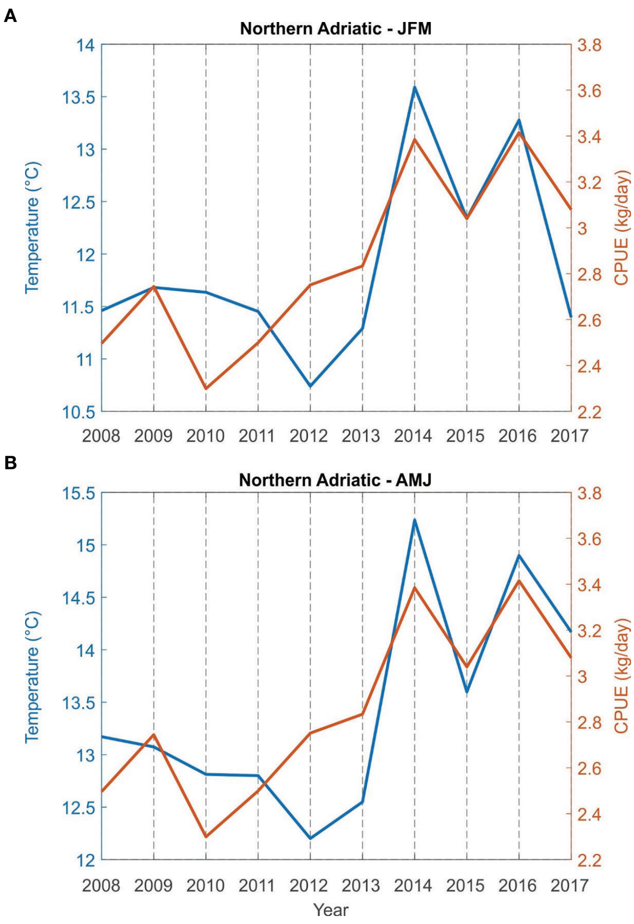

FIGURE 5 | Time series of sea bottom temperature and catch per unit effort CPUE (kg/day) of European lobster *Homarus gammarus* in winter (JFM, A) and spring (AMJ, B) for grouped fishing zones of the northern Adriatic (zones A, B and E).

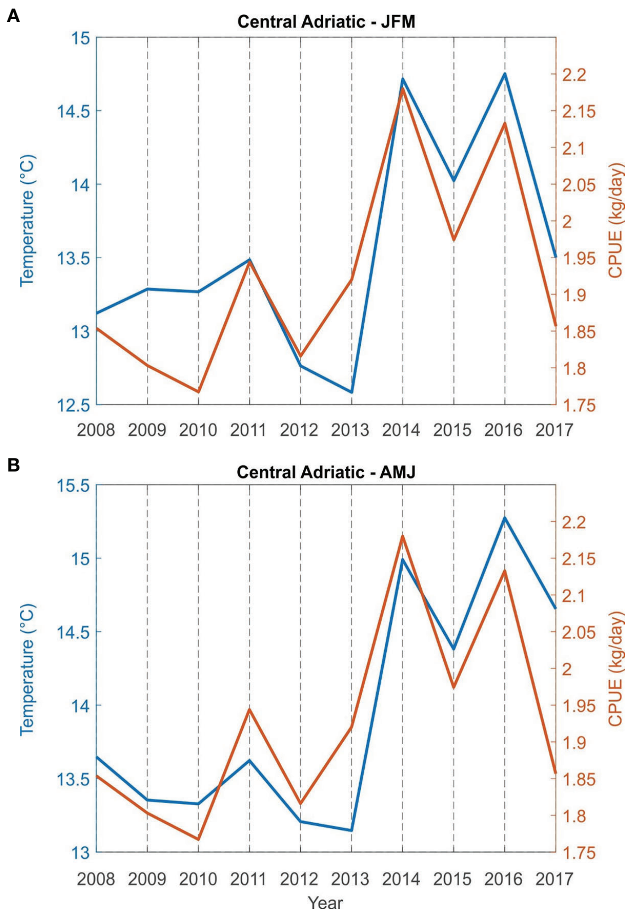

FIGURE 6 | Time series of sea bottom temperature and catch per unit effort CPUE (kg/day) of European lobster *Homarus gammarus* in winter (JFM, A) and spring (AMJ, B) for grouped fishing zones of the central Adriatic (zones C, G and F).

Increase in Lobster Landings: Higher Abundance or Increased Catchability?

The total annual European landings of *H. gammarus* over the last 10 years has been approximately 5000 tonnes (FAO, 2021). However, northern European countries have reported considerably higher landings than those in the Mediterranean basin, and a pattern of low *H. gammarus* abundance is evident throughout the Mediterranean when compared with Atlantic stocks. However, statistics of *H. gammarus* landings obtained by small-scale fisheries in general should be considered with caution across the Mediterranean, since they are difficult to evaluate and are often underestimated (Lloret et al., 2018; Pere et al., 2019). The Fisheries Department of the Croatian Ministry of Agriculture have been collecting data in a uniform manner since 2008 due to the pre-requisites of entering the EU. Thus, the ten years of data selected for the present study can be considered to have a higher degree of reliability. However, the reliability of catch statistics may be insufficient, since fishery-independent data were not available for validation of the landings and CPUE data with reference to population abundance, as suggested by Salas et al. (2007). As an example of how drastically different official statistics can be from actual ones, shows the study of Kleiven et al. (2012) where total estimated catch of European lobster was 14 times higher than officially reported. Also, CPUE data could be biased due to improvement of fishing technology, a phenomenon known as technological creep (Kleiven et al., 2022). For sure, on board surveys representing fishery-independent data together with scientific surveys will increase the reliability of catch data issue. Fluctuations in lobster abundance may occur as a consequence of the combination of environmental and fishery-related processes (Lizárraga-Cubedo et al., 2015). Since an increase in landings in the northern Adriatic was also associated with an increase in CPUE, this suggests higher abundance and/or increased catchability (Bueno-Pardo et al., 2020).

In this study, a positive and strong correlation was observed between winter (JFM) and spring (AMJ) sea bottom

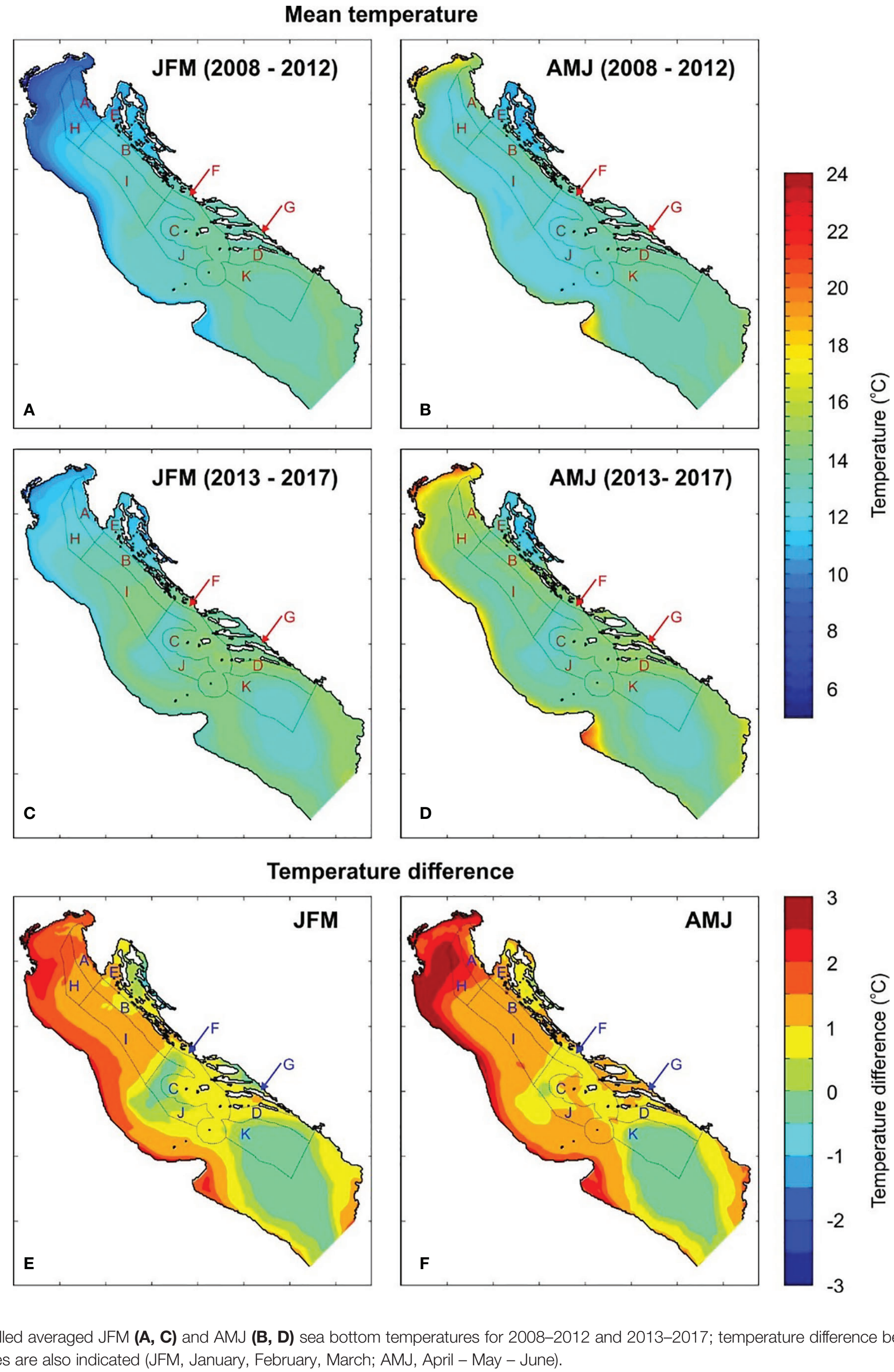

FIGURE 7 | Modelled averaged JFM **(A, C)** and AMJ **(B, D)** sea bottom temperatures for 2008–2012 and 2013–2017; temperature difference between two periods **(E, F)**. Fishery zones are also indicated (JFM, January, February, March; AMJ, April – May – June).

temperatures and CPUE. Similarly, McCleese and Wildner (1958) detected a strong correlation between long-term catch rates of the American lobster and sea surface temperature (SST) at the largest spatial scales, with lags of 0–3 years. More recently, Zhao et al. (2019) also reported that a temperature rise in Gulf of Maine led to increased catchability of American lobster over many years, with an expanded juvenile habitat in the north (Steneck and Wahle, 2013; Tanaka and Chen, 2016). These environmental changes have also been accompanied by the decline of large predators (Le Bris et al., 2018). On the contrary, warming waters have been associated with declined landings related to decreased juvenile habitat availability (Tanaka and Chen, 2015; Wahle et al., 2015) and increased prevalence of epizootic shell disease in the southern Gulf of Maine (Glenn and Pugh, 2006). Although there is no reference about the temperature range limits for European lobster in the published literature, Caputi et al. (2013) and Green et al. (2014) warn that *H. gammarus* may be sensitive to climate change, as rising temperature is the most important factor driving shifts in its distribution range, with increased abundance found at higher latitudes and decreased abundance at lower latitudes (Le Bris et al., 2018 and references therein). Sea temperature is one of the most important environmental factors affecting the fluctuations of lobster abundance, but how it contributes to total variation in the catch rate, and whether are there any temporal and spatial differences, remains unclear.

In homarid lobsters, sea temperature influences behaviour, which in turn affects their availability to fisheries (Lizárraga-Cubedo et al., 2015). Catchability is related to lobster movement and affected by numerous factors, including feeding behaviour and moulting status (Wahle et al., 2013), both of which are closely related to temperature (Green et al., 2014). Higher water temperatures affect lobster movements and catchability by encouraging increased movement, thereby increasing catchability (Smith et al., 1999; Moland et al., 2011). Rising seawater temperatures at the beginning of fishing season causes higher mobility and lobster feeding activity (Bennett and Lovewell, 1977; Lizárraga-Cubedo et al., 2015). This is followed by reduced mobility attributable to moulting activity (Miller, 1990; Sheehy et al., 1999), and then increased mobility due to higher activity observed during the post-moult period in summer. Moland et al. (2011) indicated limited movement of adult European lobsters, while American lobster exhibits higher movement and migration patterns (Estrella and Morrissey, 1997). Also, Moland et al. (2011) reported that seasonal variation in *H. gammarus* activity was correlated to water temperature, where lobster activity declined during the winter, with a minimum during February and March, and resumed again in April. This is in line with the winter (JFM) and spring (AMJ) temperatures chosen in this study, preceding and during the fishing season. Temperature is also positively correlated with growth rate among crustaceans, due to the within species thermal tolerance (Hartnoll, 2001). Higher temperature can positively stimulate growth rate by decreasing the time of the intermoult period or by increasing the moult increment (Green et al., 2014). This of course reduces the period in which lobsters are most susceptible to predatory mortality, while also increasing their fitness and the potential to affect growth rate and size at maturity.

Most crustaceans have synchronised spawning and time their reproduction based primarily on temperature (Lawrence and Soame, 2004). Harmonising hatching with food abundance increases the larval survival rate (Cushing, 1972). In this study, the reported positive trends in seawater temperature could possibly be responsible for more successful spawning and increased recruitment in the northern Adriatic, particularly due to the fact that positive trends were observed even before 2008 (Vilibić et al., 2019). The egg-bearing females of *H. gammarus* spawn in late summer (Tully et al., 2001), and egg hatching occurs in late spring to early summer (Phillips, 2013). The duration of egg development is largely influenced by temperature, with increasing temperature shortening the egg incubation process (Green et al., 2014). In the context of climate change in the North Sea, regimes with elevated temperatures (mild winters) resulted in a strong seasonal forward shift of larval hatching, while experiments showed that larval duration decreased and survival increased significantly at higher temperatures (Schmalenbach and Franke, 2010). The first few weeks post-hatching are characterised by a pelagic phase and the duration of this phase is temperature-dependent and reported to last for 14–35 days (Jørstad et al., 2001; Browne et al., 2009). Although specific observations of benthic post-hatch larvae of European lobsters in the wild are still lacking (Linnane et al., 2001), it is assumed they settle and remain cryptic in shelter-providing rocky substrata and emerge from their shelters only once they reach capapace lengths (CL) between 25 and 40 mm (Linnane et al., 2000a; Linnane et al., 2000b; Ball et al., 2001). Therefore, high temperatures in shallow coastal waters during summer in the Mediterranean could play a major role in juvenile survival and the recruitment success (Pere et al., 2019). Moreover, a recent study in the northern Adriatic reported a high number of pre-adult lobster (Pavičić et al., 2021).

Consequences for Fisheries Management in the Near Future

Regulatory measures of lobster management in Croatia include a minimum landing size, closed season and prohibition of catching berried females (OG, 2016). Currently, the fishing season is open from 5 May until 1 September. Given the possible earlier increased movement due to elevated temperature, a trend of illegal lobster catching was observed in Croatia before the open season, mainly in March and April (pers. comm). Modifications of the existing time frame of the fishing ban should be considered in the future. Also in recent years, V-notching schemes for berried females (Tully, 2001) and protected areas were implemented (Moland et al., 2021) in Europe, and the implementation of these measures should also be considered in Croatia. Recently established MPA network for European lobster in Norway provides good example of management measures (Knutsen et al 2022). After establishment of MPAs protection effects started to manifest, including effects on density, growth, demography, behaviour, and phenotypic diversity. Climate change will surely provoke changes in all fishery sectors, professional and recreational. Artisanal and industrial professional fishers may adapt to these changes mainly through the expansion of fishing grounds following the distribution of target species, which will consequently increase operation costs. The effect on the fishing community is highest when the socio-ecological system is already under pressure, such as with overfishing in the Mediterranean (Miller et al., 2010; Colloca et al., 2011; Pranovi et al., 2013) related to decreased demographic structure, limitations of geographic distribution and diversity loss (Rijnsdorp et al., 2009; Perry et al., 2010; Planque et al., 2010). It is well known that differences in lobster size at maturity, fecundity and population size structure between different areas may occur as a response to the local environmental conditions and fishing strategies (Lizárraga-Cubedo et al., 2015). Since lobster fisheries are most often regulated only through the minimum landing size (MLS) (Pere et al., 2019), fishery managers need to be sure that MLS regulation currently in force corresponds to real size at maturity, throughout the distribution range. Thus, the EU Directive recognises and prescribes different minimum landing size for *H. gammarus* for northern European countries and the Mediterranean (European Union, 2006). It is possible that this should also be considered at the subregional level, since different genetic populations have been documented in the distribution range (Triantafyllidis et al., 2005; Ellis et al., 2017), while Adriatic populations are panmictic (Pavičić et al., 2020b). It can be expected that if these warming trends continue, the differences in the main biological points between Atlantic and Mediterranean stocks will become even more pronounced. In this study, we confirm that the northern Adriatic as a particularly vulnerable area to climate change. However, it is configured as a cul-de-sac (Ben Rais Lasram et al., 2010; Pranovi et al., 2016), preventing further northward migration of temperate and boreal affinity species like *H. gammarus*. Considering its shallowness, it is questionable how these species will behave in the future. Further on, recently, the American lobster (*Homarus americanus*) was reported in Adriatic Sea (Pavičić et al., 2020a) and Aegean Sea (Kampouris et al., 2021). If American lobster establish population in the Mediterranean Sea it can negatively affect European lobster populations, since these two species compete for the same habitat and hybridization is possible (Jørstad et al., 2007). For certain, the observed changes require a deeper and more complex analysis of the lobster stocks and updating of current management measures in the Mediterranean region.

CONCLUSIONS

In summary, the present study revealed significant increase in landings and CPUE in the northern Adriatic, particularly after 2013, coinciding with significant rises in sea bottom temperature in both the northern and central Adriatic. We hypothesise that rising sea temperatures have resulted in greater lobster mobility and thus its availability to fishing, which is reflected consequently in higher landings and CPUE. It is still unknown how the increase in temperature will affect early developing stages in the coming years. With this in mind, fishery managers need to be very careful in considering the frequent requests of local fishers to open the fishing season earlier, which would impart an even higher fishing effort and pressure on the reproductive part of the lobster population.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHORS CONTRIBUTIONS

MP, SM-S, DV, and AV were involved in data collection. JŠ, IV, and IJ were involved in ROMS model setup and analysis. MP, DV, NS, JŠ, and TŠ-B analyzed the data. MP led the writing of the manuscript with contribution of JŠ and SM-S. All authors have reviewed and approved the final manuscript.

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