Short communication

The increasing temperature as driving force for spatial distribution patterns of *Parapenaeus longirostris* (Lucas 1846) in the Strait of Sicily (Central Mediterranean Sea)

Federico Quattrocchi*, Fabio Fiorentino, Valentina Lauria, Germana Garofalo

CNR-IRBIM, Institute for Marine Biological Resources and Biotechnologies, National Research Council CNR (CNR), Via Luigi Vaccara 61, 91026 Mazara del Vallo (TP), Italy

ABSTRACT

The deep-water rose shrimp *Parapenaeus longirostris* (DPS), a demersal decapod representing the most important component of crustacean landings in the Mediterranean Sea, has been suggested as a species that may exhibit temperature-driven changes in the spatio-temporal dynamics. Considering that Mediterranean waters are warming up faster than oceans, understanding the relationships of DPS populations with temperature variations and the related changes in spatial patterns is absolutely key for its management. Using a long-term dataset covering 13-years from scientific surveys (International Bottom Trawl-Surveys in the Mediterranean, MEDITS; Italian national trawl surveys, GRUND) in the Strait of Sicily (central Mediterranean Sea), the annual DPS spatial patches and the depth distribution were investigated using geostatistical and quotient analyses. The patches dimension and depth range occupation were then related to sea temperature by using linear regression analysis. Results showed that both the dimension of DPS spatial patches and the depth distribution range occupied increased concurrently with temperature. Our findings corroborate that the ongoing sea warming widen areas suitable for this species and in which it can expand its spatial distribution.

1. Introduction

Marine species distribute spatially according to specific patterns as a result of habitat and environmental preferences (e.g. Ciannelli et al., 2008; Giannoulaki et al., 2013; Romagnoni et al., 2015; Orio et al., 2019). Consequently, changes in marine environment, by influencing different mechanisms such as individual physiological and behavioural responses (e.g. changes in the aerobic scope; habitat selection and use), population dynamics (i.e. acting on growth, reproduction and mortality) or trophic interactions (e.g. Rijnsdorp et al., 2009; MacKenzie et al., 2012) determine how the abundance and distribution of a population vary over time. (e.g. Poloczanska et al., 2016; Orio et al., 2019). Thus, investigating the spatial and temporal components of species/environment relationships is essential to gain a better understanding of marine stock fluctuations (Tzanatos et al., 2014) and a greater capability of forecasting the effects of environmental changes on populations. The need for such knowledge is more obvious for commercially important species and underlies the integrated management approach to fisheries resources, which requires to adequately

consider the main biotic, abiotic and human components of ecosystems and their interactions (i.e. Ecosystem approach to fisheries; FAO, 2003); a perspective accepted and largely stressed during the last decades by numerous studies (e.g. Ciannelli et al., 2008; Planque et al., 2011; Fuentes et al., 2016; Gaines et al., 2018). Although abiotic factors affecting marine populations are numerous, temperature is considered one of the most relevant (e.g. Perry et al., 2005; Harley et al., 2006; Brander, 2013; Cheung et al., 2013; Giannoulaki et al., 2013; Lauria et al., 2015). This is because changes in sea temperature influence the spatial distribution of species both directly by affecting physiology and behaviour, and indirectly by affecting the structure and the functioning of ecosystems (e.g. Poloczanska et al., 2016). Considering that Mediterranean waters are warming up two to three times faster than the oceans (Solomon et al., 2007; Vargas-Yáñez et al., 2008; Nykjaer, 2009; Pastor et al., 2018), understanding the relationships of marine populations with temperature and the related changes in spatial patterns over time is fundamental for their sustainable management.

In the Mediterranean basin, one of the most important fishing resources is the deep-water rose shrimp *Parapenaeus longirostris* [(Lucas
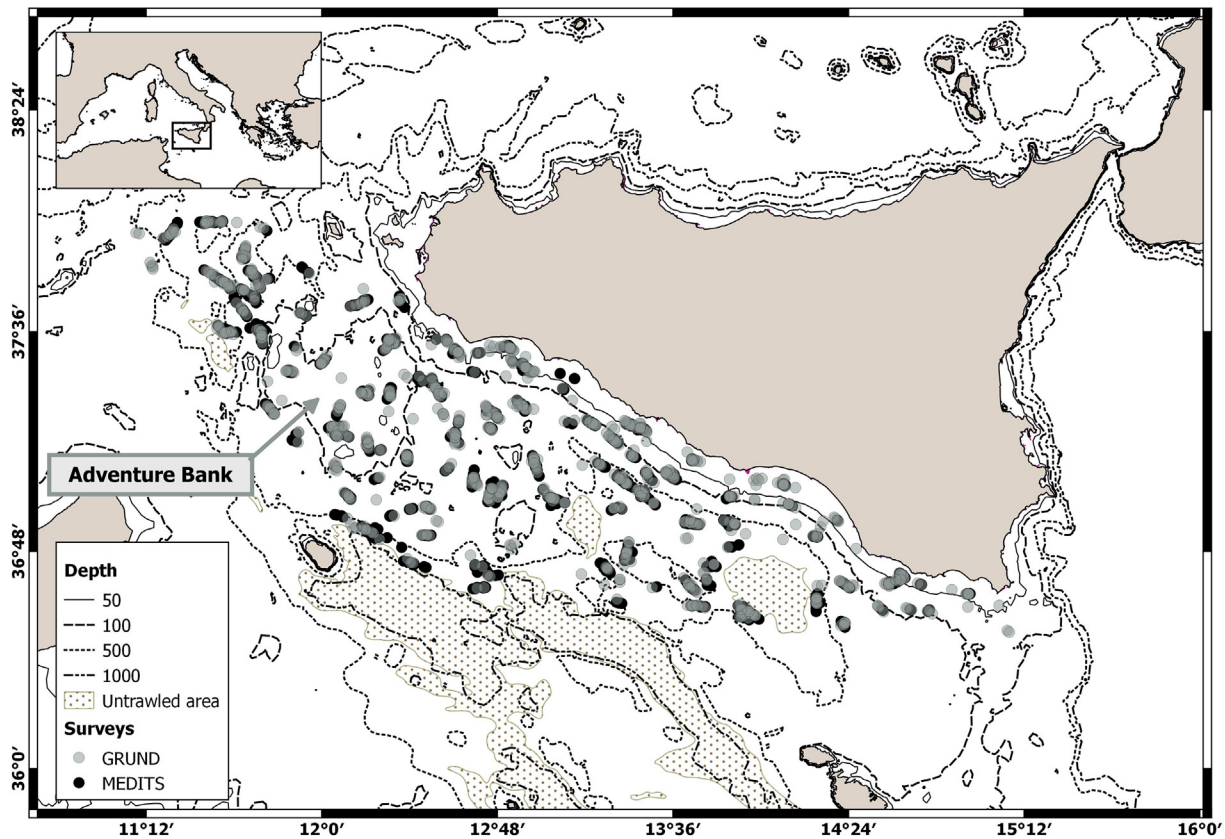

Fig. 1. Study area with the location of the sampling stations from 1994 to 2008 during autumn (Grund survey) and spring/early summer (Medits survey). Stippled areas indicate untrawlable grounds and water depths of more than 800 m.

1846), DPS],a demersal decapod shrimp which represents more than a quarter of total crustacean landings (27%; 1994–2008, FAO FishStat Plus, 2013). The DPS is a short-lived species, spawning all year-round with fast growth and high mortality rates (Abelló et al., 2002; Sobrino et al., 2005). It is distributed throughout the eastern Atlantic Ocean and the Mediterranean basin, where the highest abundance is recorded at lower latitudes, predominantly in the Strait of Sicily (central Mediterranean Sea) and the Ionian Sea (Sobrino et al., 2005). Individuals are generally found in muddy bottoms, mainly between 100 and 400 m of depth, although the bathymetric distribution is wider, ranging from 20 to 750 m (Sobrino et al., 2005; Fortibuoni et al., 2010).

This species has recently been suggested as a species that may exhibit temperature-driven changes in the spatio-temporal dynamics (e.g. Colloca et al., 2014). In the southern Adriatic Sea, for example, the highest abundance of DPS seems to be located in areas of warmer sea bottom waters (Ungaro and Gramolini, 2006). Still, in other regions of the Mediterranean Sea, positive relationships between DPS abundance and increasing of sea temperature has been shown (i.e. Ionian Sea, central-northern Tyrrhenian Sea and Ligurian Sea; [Arcuti et al., 2016; D'Onghia et al., 2012; Ligas et al., 2011; Colloca et al., 2014]). Even in Moroccan Atlantic waters, the temperature positively influences the abundance levels of the species (Benchoucha et al., 2008).

For these reasons it is reasonable to hypothesize that variations of sea temperature can influence both the spatial structure of high abundance aggregations and the depth distribution range of both DPS early and adult life stages. Considering that the Strait of Sicily hosts some of the most important DPS fishing grounds in the Mediterranean, knowing how the species is spatially structured is of crucial importance for its sustainable exploitation. Here, by using a long-term dataset (1994–2008) covering 13-years from scientific surveys in the northern sector of the Strait of Sicily (a part of the Geographical Sub Area – GSA 16; FAO, 2009) we focused on 1) characterizing the annual spatial

structure of DPS owing to spatial autocorrelation between the abundance values of the survey locations; 2) exploring depth range occupied by DPS over the period considered; and 3) investigating the effect of sea temperature on both the patterns of spatial structures and depth distribution range.

2. Materials and methods

2.1. Data sources

The study area is characterized by a narrow continental shelf in the central part with extensions off the eastern and western Sicilian coasts. Numerous oceanographic features occur in this region, including vortices, upwelling areas and fronts; the intensity and position of which are mainly driven by the variability in Atlantic Ionian Stream (AIS) meandering, the main current flowing in south east direction (Di Lorenzo et al., 2018). Persistent spawning and nursery areas of DPS have been identified along this area (Fortibuoni et al., 2010; Garofalo et al., 2011).

The abundance and spatial distribution data of DPS were obtained from fishery-independent bottom trawl surveys conducted annually from 1994 to 2008, during spring/early summer within the International Bottom Trawl-Surveys in the Mediterranean (MEDITS; Bertrand et al., 2002) and in autumn within the.

Italian national trawl surveys (GRUND-; Relini, 2000). From the original datasets, only the sampling stations located on the Sicilian shelf and slope were extracted. For each haul, DPS abundance was standardized to the haul swept area and expressed as density index (i.e. number of individuals per km², N/Km²). Due to the different catchability of the gears used in the two surveys (GOC 73 in spring/early summer and Italian commercial *tartana* in autumn) the DPS density indices from the GRUND survey were adjusted to those which would

have been obtained by the MEDITS survey by using a fishing power correction factor of 0.84, previously estimated for DPS through comparative trawling trials (Scalisi et al., 1998).

In order to guarantee a minimum of 30–50 pairs of points required for statistical consistency and representativity of the sampling space (Rossi et al., 1992) in the subsequent geostatistical analysis, it was decided to combine and analyze together the spring/early summer and autumn datasets for each year (with the exclusion of the 1999 and 2007 years in which the autumn survey was not carried out). This choice was supported by the results of Fortibuoni et al. (2010) who suggested a similar spatial pattern of DPS critical life phases (recruits and mature females) during the two seasons. In addition, nonparametric Wilcoxon rank-sum test confirmed that the abundance distribution in the two survey seasons did not differ significantly (Fig. S1). Overall, the dataset consisted of a total of 733 hauls from MEDITS surveys and 903 from GRUND surveys (Fig. 1). The total annual density index (TA) in the whole area was obtained by the ratio estimator (Cochran, 1977) as the ratio between the total abundance in the area and the total swept area, putting together the data from the two surveys.

To evaluate the temperature effects on the DPS spatial structure and depth occupation we used the monthly temperature series retrieved from Copernicus marine environment monitoring service (http://marine.copernicus.eu/). Specifically, for each year, mean monthly temperature layers with a spatial resolution of 1/16˚ x 1/16˚ (ca. $3,8 \times 3,8$ nautical miles) from spring to autumn (i.e. the whole period in which the two surveys are performed) at four different depths (surface, 250 m, 500 m and 750 m) were downloaded. The temperature obtained at different depths were then averaged over the study area by year and used as a proxy of the mean thermic profile from spring to autumn of the bathymetric range inhabited by DPS

2.2. Data analysis

To study the temporal variability and model the spatial structure of DPS population in the Strait of Sicily, we used the basic tool of geostatistical methodology -omnidirectional indicator variography- (e.g. Rivoirard, 2000). In this type of analysis, the variance of the difference between pairs of observations at sequential distance intervals (lags) across the study area is measured. For simplicity, we hereafter refer to this method as the variogram. For each haul the DPS density index was transformed into a binary variable representing two classes of values, on the basis of a predetermined threshold. This was set at value of 80% of total DPS annual abundance (c80) and computed for each year on the basis of the respective cumulative curves (Petitgas, 1998; Barra et al., 2015). The classification was done by transforming relative abundance values > c80 as 1 (presence) and 0 (absence) otherwise. The c80 does not represent a biological threshold for the DPS but it has been chosen with the aim of describing the spatial structure of the most abundant part of the shrimp population in the study area. This type of threshold, based on percentile levels of the total relative abundance, has been used in other studies and for other species in the Mediterranean (e.g. Garofalo et al., 2011; Barra et al., 2015; Criscoli et al. 2017; Milisenda et al. 2017). The empirical variogram on the presence/absence of DPS obtained using the c80 was then calculated for each year. For statistical reliability of the variogram analysis, the lag distance was set to 11.5 Km (6.2 nautical miles), which corresponds to the minimum distance including at least 35–50 pairs of points for each distance interval (Rossi et al., 1992). The empirical variograms obtained for each year were then modeled in order to estimate the standard parameters such as nugget, sill, and range. The nugget is the variability of the data (or just the effect of uncertainty) at lag distance close to 0, while the sill represents the maximum variability between pairs of observations. The range is an estimate of the maximum distance at which pairs of observations are spatially correlated, as such it represents an approximate measure of the average size of the patches (e.g. Giannoulaki et al.,

2006) which correspond, in this study, to the DPS high-abundance ones. To estimate these parameters, we selected among Gaussian, Exponential and Spherical models the one reducing the residuals sum of squares. We used the estimated ranges of each annual modeled variogram and related them to the temperature by using simple linear regression. The significance of the coefficients was tested by bootstrapping the cases with replacement ($N = 999$) and extracting the 95% intervals of these bootstrapped estimates. In order to asses the presence of a density-dependent effect on the dimension of patches, relationships of range estimates with both the total annual abundance index (TA) and c80 were tested by using linear regression models. Furthermore, to assess the association between stock density and depth preferences, we used the quotient analysis (Qi; van der Lingen et al., 2001; Bernal et al., 2007). A quotient curve is a bi-variate curve that describes the "relation shape" between relative abundance data and a given environmental variable. The first step to perform quotient analysis was to define a pertinent classification for the depth ranges (Table S1) to ensure that the occurrence of samples in each category did not exceed 20% of all data and that it remained a significant number for each category (i.e. > 5%; Bonanno et al., 2014; Drapeau, 2004). Once samples were assigned to a category, the relative "importance" or weight of each category was computed and named as % frequency of the depth class (i.e. the number of samples in the category divided by the total number of samples). Then the density value associated with each depth category was expressed as a percentage relative to the total DPS density collected during each year (abundance within the depth category divided by total abundance of DPS in each annual survey). Then the quotient values (Qi) between the relative abundance and the percentage occurrence of each category was computed as follows:

$$Qi = \frac{\%DPS \; density}{\%depth \; range}$$

Qi plotted against depth indicated preference when > 1 and avoidance when < 1. To test the significance of observed quotient values, confidence intervals for the null hypothesis of evenly distributed DPS density with respect to depth were calculated (e.g. Basilone et al., 2013; Bernal et al., 2007). The preferred depth ranges defined by the significant Qi values were extracted and divided by the whole depth range sampled each year. These proportions were then related to the temperature by using the binomial generalized linear model (binomial GLM) and owing to overdispersion, the standard errors were corrected using quasibinomial GLM (Zuur et al., 2009). Coefficients significance was then tested by bootstrap ($n = 999$).

3. Results

During our study period (1994–2008), the mean temperature along the water column from May to October increased, showing a peak of about 16.7 ˚C in 2003 and a significant positive trend of 0.034 ˚C y^{-1} (FIG. S2a).

The occurrence of DPS individuals in the study area was recorded in a depth range between 33 and 739 m. The density index showed interannual fluctuations with a significant positive trend, with the highest value of 3288 N/Km^2 observed in 2004 and the lowest value of 486 N/Km^2 in 1995 (Fig. S2b). Whithin the study area, the same fluctuation with a positive trend, is observable also when considering the proportion of the number of survey hauls showing DPS abundance above the median abundance value of the whole time period respect to the total number of annual trawl surveys (Fig. S3a). Stable high-abundance values (> 3%), with respect to the total annual abundance, were observed for each year in the north-western side excluding the 2008 and in the south-eastern side of the Adventure bank (AB, Fig. S3b). Peaks of DPS abundance (> 5%) were observed in the north western side of AB in 1994, 2000 and 2001. In the eastern part of AB, DPS abundance > 5% occurred from 1996 to 2002, and in 2006. A third stable high-abundance area was observed in the central part of the continental slope off
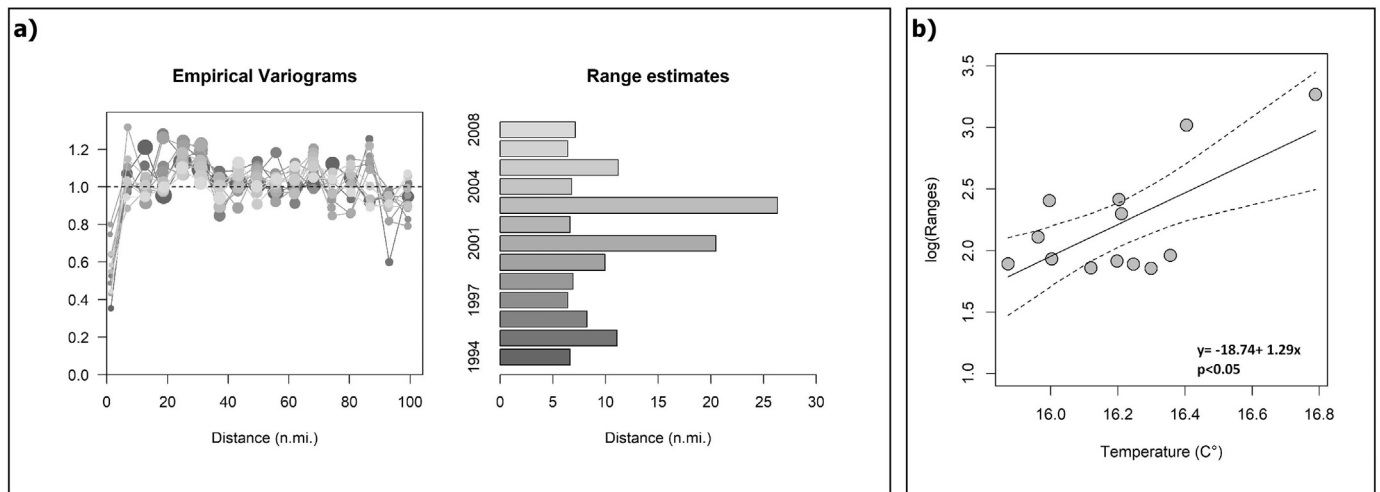
Fig. 2. a) Annual Standardized Empirical Variograms and range estimates. b) Range estimates in relation to the Temperature.

the south Sicilian coast until 2004, after that it was not longer present. Differently in the south-eastern coast of the Sicily high-abundance values of DPS were observed only in some years, specifically in 1994, 1995, 2003, 2004 and 2008 and only in the latters two years with an abundance percentage greater than 5 (Fig. S3).

The threshold to define the aggregations representing the main hauls with higher abundance of DPS (values of c80) increased indicating that this species was gradually more densely distributed over time in the considered period (Table S2).

DPS spatial structure presented interannual variability in terms of the average patch size (i.e. range; Fig. 2a). The indicator variograms showed that DPS formed the largest patches in 2003 followed by 2001, while the smallest aggregations were observed in the 1997 (Fig. 2 a). The linear model applied to relate the mean aggregation dimension and temperature resulted statistically significant, showing an increase of the range when temperature rises (Fig. 2b). Differently, there was no significant relationship between the estimated ranges in the variograms with the TA and the c80 (range = $11.9\text{--}9.5^{-08}$ x c80, $p > .05$; range = $11.9\text{--}8.1^{-08}$ x TA, p > .05).

Quotient analysis showed that DPS distribution in each year was non-randomly related to depth and that high concentration of individuals was located mainly between 100 and 230 m depth, with the exception of the years 2001, 2002 and 2006. Furthermore, during the 1995, 2003 and 2008 the preferred depth range became more widespread between 100 and 400 m of depth (Fig. 3a). The binomial GLM model corrected for overdispersion (quasi-binomial GLM) relating the depth range preference of DPS population with temperature showed a significant increase of the proportion of depth range occupied when the

temperature became higher and explained the 40% (i.e. the deviance) of the variation in depth range occupation (Fig. 3b).

4. Discussion

This study contributes to better understand the role of sea temperature on the spatial aggregation of an important commercial crustacean in the Mediterranean Sea. By using fishery-independent data from 1994 to 2008, we showed that the average dimension of the spatial aggregations as well as the depth range distribution of DPS are positively related to sea temperature in the northern part of the Strait of Sicily. Changes in environmental factors and particularly sea temperature, have been shown to play a key role on the temporal and spatial dynamics of the deep-sea living resources in the Mediterranean (Ungaro and Gramolini, 2006; Company et al., 2008; Maynou, 2008; Ligas et al., 2011b; D'Onghia et al., 2012; Colloca et al., 2014). In the Strait of Sicily, the increasing trend in water temperature (0.034 °C y^{-1}, Fig. 2) confirms the general pattern observed in the whole Mediterranean basin (ca. 0.035 °C y^{-1}; e.g. Skliris et al., 2011; Shaltout and Omstedt, 2014), which is considered one of the most important ecological phenomena occurring in the Mediterranean sea (e.g. Nykjaer, 2009; Shaltout and Omstedt, 2014). Seawater temperature rise is affecting marine populations by acting on phenological events (e.g. growing and timing of reproduction) and leading to changes at different scales of responses, from the physiological to the ecosystem ones (e.g. Rijnsdorp et al., 2009; Ottersen et al., 2010). Typically, the spatial distribution patterns of populations are recognized to be regulated by both environmental factors, which are independent from the population
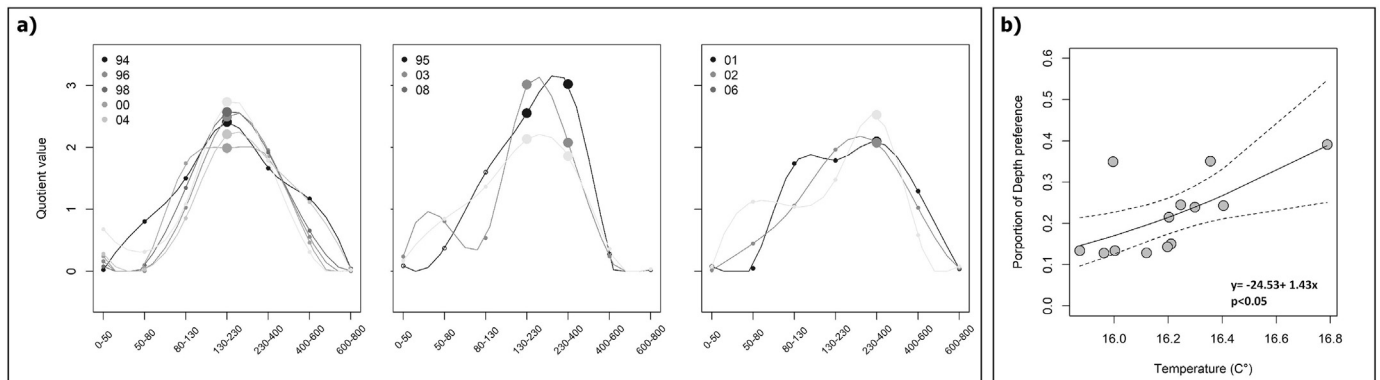

Fig. 3. a) Plots of annual quotient values grouped by years in which the significant (larger points) preferred depth ranges were similar; b) the relationship between the proportion of the preferred depth range obtained from the QI analysis and temperature.

conditions, and those strictly related to the population size (e.g. Gaston et al., 2000; Planque et al., 2011). Our results suggest that changes in annual DPS abundance during the period (1994–2008) do not have a significant role on the patches dimensions of DPS (i.e. no density dependent habitat occupation/selection responses; Gaston et al., 2000), while a marked positive effect of sea temperature was found (Fig. 2b). The annual spatial structures obtained by using variograms indicated, in fact, the existence of high-abundance DPS concentrations in certain years when suitable conditions (i.e. high temperatures) occurred. The lack of significant relationships with the DPS density could be probably related to the fact that the increase of suitable habitat makes the DPS expand without the necessity of occupying a territory up to its maximum capacity before spreading out; as often expected in the relationship between abundance and space occupancy (e.g. Gaston et al., 2000). Furthermore, the overexploitation of the demersal resources including DPS in the area (Fiorentino et al., 2013), likely can favor this phenomenon by maintaining the abundance and biomass at intermediate levels lower than the maximum capacity of its habitat. The absence of significant relationships between population abundance and spatial organization is not a new phenomenon, as this has been already reported for other marine populations (e.g. Petitgas, 1998; Anderson and Gregory 2000; Barra et al., 2015; Morfin et al., 2012).

The expansion of the autocorrelation ranges with high thermal conditions suggests, instead, the preference of DPS for warmer waters (e.g. Sobrino et al., 2005; Ligas et al., 2011; Abelló et al., 2002). Nevertheless, it is important to consider that temperature is not the only environmental driver of the spatial distribution patterns of DPS. Other factors such as the interactions between wind and current circulations (Ligas et al., 2011), high salinity (e.g. Benchoucha et al., 2008) or high primary productivity (Colloca et al., 2004) together with fishery activities (Ligas et al., 2011; Abelló et al., 2002; Sobrino et al., 2005; D'Onghia et al., 2012) have been shown to act as significant drivers for the DPS populations abundances. However, temperature seems to play a primary role on DPS abundance, for example Colloca et al. (2014) argued that higher temperature favors this species recruitment by improving the survival rates and growth processes. Furthermore, Cartes et al., (2009) reported that high temperatures can promote, together with both low rainfall and wind strength regimes, the increase of suprabenthos production, which is part of the DPS diet (Sobrino et al., 2005). Therefore, this ensemble of more suitable environmental conditions seems to enhance the DPS aggregations dimension.

Despite on average DPS was distributed from 70 to 400 m of depth which agrees with other studies (e.g. Sobrino et al., 2005; Fortibuoni et al., 2010), in the Strait of Sicily this species tend to expand its depth range occupation with the rise of temperatures. Although a significant effect of temperature is found, further highlighting its key role as ecological factor affecting the dynamics of the DPS population (e.g. Colloca et al., 2014; Ligas et al., 2011; Arcuti et al., 2016), only the 40% of the total deviance is explained by the model. This suggests that the depth range distribution, likewise to the patches dimension, is not influenced by the temperature alone. Furthermore, our results are in line with those of literature showing that marine ectotherm species can change their depth distribution range as a response to sea warming (e.g. Perry et al., 2005; Pinsky and Byler, 2015; Milazzo et al., 2016). This pattern mainly occurs where the geographical features impede the latitudinal shifts (e.g. Poloczanska et al., 2016). Where physical barriers are not so marked, as for example in the Tyrrhenian Sea, although a DPS depth range expansion has been observed, it was less conspicuous compared to the latitudinal expansion (Colloca et al., 2014; Ligas et al., 2011; Benchoucha et al., 2008). Differently, in the Strait of Sicily the increase of the DPS depth range occupied associated with the temperature rise, could have been facilitated by the presence of a natural physical features (i.e. the Sicilian coast in northern part) and a permanent current pattern flowing southward (AIS, Atlantic Ionian Stream) slowing down the northward expansion of both adults and juveniles displacement and larval dispersal.

Our study illustrates that, in the Strait of Sicily, the ongoing sea warming open suitable areas in which DPS can expand. Being the fishers' behavior based on the knowledge of how the target species are distributed, describing and characterizing their spatial structure in relation to the environmental changes may be useful for management measures. Knowing how environmental drivers, such as temperature, modulate spatial aggregation and depth range distribution of DPS, may suggest to be cautious in considering *tout court* the catch per unit effort (CPUE) in the Strait of Sicily as representative of the stock abundance. For instance, in the case of contraction of DPS' spatial aggregation structures, CPUE could be remain high while abundance declines, causing the well-known process known as "hyperstability", with the overestimation of standing stock and the underestimation of fishing mortality (Hilborn and Walters, 1992).

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2020.101871.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

References

Abelló, P., Abella, Á., Adamidou, A., Jukic-Peladic, S., Maiorano, P., Spedicato, M.T., 2002. Geographical Patterns in Abundance and Population Structure of *Nephrops norvegicus* and *Parapenaeus longirostris* (Crustacea: Decapoda) along the European Mediterranean Coasts.

Anderson, J.T., Gregory, R.S., 2000. Factors regulating survival of northern cod (NAFO 2J3KL) during their first 3 years of life. ICES Journal of Marine Science 57, 349–359.

Arcuti, S., Pollice, A., Ribecco, N., D'Onghia, G., 2016. Bayesian spatiotemporal analysis of zero-inflated biological population density data by a delta-normal spatiotemporal additive model: Bayesian analysis of zero-inflated biological data. Biom. J. 58, 372–386.

Barra, M., Petitgas, P., Bonanno, A., Somarakis, S., Woillez, M., Machias, A., Mazzola, S., et al., 2015. Interannual changes in biomass affect the spatial aggregations of anchovy and sardine as evidenced by geostatistical and spatial indicators. PLoS One 10 (8), e0135808.

Basilone, G., Bonanno, A., Patti, B., Mazzola, S., Barra, M., Cuttitta, A., McBride, R., 2013. Spawning site selection by European anchovy (*Engraulis encrasicolus*) in relation to oceanographic conditions in the Strait of Sicily. Fish. Oceanogr. 22, 309–323.

Benchoucha, S., Berraho, A., Bazairi, H., Katara, I., Benchrifi, S., Valavanis, V.D., 2008. Salinity and temperature as factors controlling the spawning and catch of *Parapenaeus longirostris* along the Moroccan Atlantic Ocean. In: Essential Fish Habitat Mapping in the Mediterranean. Springer, pp. 109–123.

Bernal, M., Stratoudakis, Y., Coombs, S., Angelico, M.M., de Lanzós, A.L., Porteiro, C., Sagarminaga, Y., et al., 2007. Sardine spawning off the European Atlantic coast: characterization of and spatio-temporal variability in spawning habitat. Prog. Oceanogr. 74, 210–227.

Bertrand, J.A., Gil De Sola, L., Papaconstantinou, C., Relini, G., Souplet, A., 2002. The general specifications of the MEDITS surveys. Sci. Mar. 66, 9–17.

Bonanno, A., Giannoulaki, M., Barra, M., Basilone, G., Machias, A., Genovese, S., Goncharov, S., et al., 2014. Habitat selection response of small pelagic fish in different environments. Two examples from the oligotrophic Mediterranean Sea. PLoS One 9 e101498.

Brander, K., 2013. Climate and current anthropogenic impacts on fisheries. Clim. Chang. 119, 9–21.

Cartes, J.E., Maynou, F., Fanelli, E., Romano, C., Mamouridis, V., Papiol, V., 2009. The distribution of megabenthic, invertebrate epifauna in the Balearic Basin (western Mediterranean) between 400 and 2300 m: Environmental gradients influencing assemblages composition and biomass trends. Journal of Sea Research 61, 244–257.

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Palomares, M.L.D., Watson, R., et al., 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nat. Clim. Chang. 3, 254–258.

Ciannelli, L., Fauchald, P., Chan, K.S., Agostini, V.N., Dingsør, G.E., 2008. Spatial fisheries ecology: recent progress and future prospects. J. Mar. Syst. 71, 223–236.

Cochran, W.G., 1977. Sampling Techniques, 3rd edn. Wiley, New York 428 pp.

Colloca, F., Carpentieri, P., Balestri, E., Ardizzone, G.D., 2004. A critical habitat for Mediterranean fish resources: shelf-break areas with Leptometra phalangium (Echinodermata: Crinoidea). Marine Biology 145, 1129–1142.

Colloca, F., Mastrantonio, G., Lasinio, G.J., Ligas, A., Sartor, P., 2014. *Parapenaeus longirostris* (Lucas, 1846) an early warning indicator species of global warming in the Central Mediterranean Sea. J. Mar. Syst. 138, 29–39.

Company, J.B., Puig, P., Sardà, F., Palanques, A., Latasa, M., Scharek, R., 2008. Climate influence on deep sea populations. PLoS One 3, e1431.

Criscoli, A., Carpentieri, P., Colloca, F., Belluscio, A., Ardizzone, G., 2017. Identification and Characterization of Nursery Areas of Red Mullet Mullus barbatus in the Central Tyrrhenian Sea. Marine and Coastal Fisheries 9, 203–215.

Di Lorenzo, M., Sinerchia, M., Colloca, F., 2018. The North sector of the Strait of Sicily: a priority area for conservation in the Mediterranean Sea. Hydrobiologia 821, 235–253.

D'Onghia, G., Giove, A., Maiorano, P., Carlucci, R., Minerva, M., Capezzuto, F., Sion, L., et al., 2012. Exploring relationships between demersal resources and environmental factors in the Ionian Sea (Central Mediterranean). J. Mar. Biol. 2012 https://doi.org/10.1155/2012/279406. Article ID 279406, 12 pages, 2012.

Drapeau, L., 2004. Introduction to the use of quotient curves for characterizing spawning habitat of small, pelagic fish. In: Report of a GLOBEC-SPACC Workshop on Characterizing and Conmparing the Spawning Habitat of Small Pelagic Fish. GLOBEC Report. Vol. 21.

FAO, 2003. The ecosystem approach to fisheries. In: FAO Technical Guidelines for Responsible Fisheries. FAO, Rome No. 4, Suppl. 2. 2003. 112 pp.

FAO, 2009. GFCM resolution RES-GFCM/33/2009/2 establishment of geographical sub-areas in the GFCM area amending the resolution GFCM/31/2007/2. In: FAO General Fisheries Commission for the Mediterranean, Report of the Thirty-Third Session. Tunis, 23–27 March 2009. GFCM Report. No. 33. Rome, Italy.

Fiorentino, F., Hamida, O. Ben Hadj, Meriem, S. Ben, Gaamour, A., Gristina, M., Jarboui, O., Knittweis, L., Rjeibi, O., Ceriola, L., 2013. Synthesis of information on some demersal crustaceans relevant for fisheries target species in the south-central Mediterranean Sea. In: GCP/RER/010/ITA/MSM-TD-32. MedSudMed Technical Documents, 32, 120 pp.

Fortibuoni, T., Bahri, T., Camilleri, M., Garofalo, G., Gristina, M., Fiorentino, F., 2010. Nursery and spawning areas of deep-water rose shrimp, *Parapenaeus longirostris* (Decapoda: Penaeidae), in the Strait of Sicily (Central Mediterranean Sea). J. Crustac. Biol. 30, 167–174.

Fuentes, M.M.P.B., Chambers, L., Chin, A., Dann, P., Dobbs, K., Marsh, H., Poloczanska, E.S., et al., 2016. Adaptive management of marine mega-fauna in a changing climate. Mitig. Adapt. Strateg. Glob. Chang. 21, 209–224.

Gaines, S.D., Costello, C., Owashi, B., Mangin, T., Bone, J., Molinos, J.G., Burden, M., et al., 2018. Improved fisheries management could offset many negative effects of climate change. Sci. Adv. 4 eaao1378.

Garofalo, G., Fortibuoni, T., Gristina, M., Sinopoli, M., Fiorentino, F., 2011. Persistence and co-occurrence of demersal nurseries in the strait of Sicily (Central Mediterranean): implications for fishery management. J. Sea Res. 66, 29–38.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M., Lawton, J.H., 2000. Abundance-occupancy relationships. J. Appl. Ecol. 37, 39–59.

Giannoulaki, M., Machias, A., Koutsikopoulos, C., Somarakis, S., 2006. The effect of coastal topography on the spatial structure of anchovy and sardine. ICES J. Mar. Sci. 63, 650–662.

Giannoulaki, M., Iglesias, M., Tugores, M.P., Bonanno, A., Patti, B., De Felice, A., Leonori, I., et al., 2013. Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages: *Habitat of anchovy in the Mediterranean*. Fish. Oceanogr. 22, 69–89.

Harley, C.D., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J., Thornber, C.S., Rodriguez, L.F., et al., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9, 228–241.

Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York.

Lauria, V., Gristina, M., Attrill, M.J., Fiorentino, F., Garofalo, G., 2015. Predictive habitat suitability models to aid conservation of elasmobranch diversity in the Central Mediterranean Sea. Sci. Rep. 5, 13245.

Ligas, A., Sartor, P., Colloca, F., 2011. Trends in population dynamics and fishery of *Parapenaeus longirostris and Nephrops norvegicus* in the Tyrrhenian Sea (NW Mediterranean): the relative importance of fishery and environmental variables: trends in P. congirostris and N. norvegicus. Mar. Ecol. 32, 25–35.

MacKenzie, B.R., Meier, H.E.M., Lindegren, M., Neuenfeldt, S., Eero, M., Blenckner, T., Tomczak, M.T., et al., 2012. Impact of climate change on fish population dynamics in the Baltic Sea: a dynamical downscaling investigation. Ambio 41, 626–636.

Maynou, F., 2008. Environmental causes of the fluctuations of red shrimp (*Aristeus antennatus*) landings in the Catalan Sea. J. Mar. Syst. 71, 294–302.

Milazzo, M., Quattrocchi, F., Azzurro, E., Palmeri, A., Chemello, R., Di Franco, A., Guidetti, P., et al., 2016. Warming-related shifts in the distribution of two competing coastal wrasses. Mar. Environ. Res. 120, 55–67.

Milisenda, G., Vitale, S., Massi, D., Enea, M., Gancitano, V., Giusto, G.B., Badalucco, C., et al., 2017. Discard composition associated with the deep water rose shrimp fisheries (Parapenaeus longirostris, Lucas 1846) in the south-central Mediterranean Sea. Mediterranean Marine Science 18, 53.

Morfin, M., Fromentin, J.-M., Jadaud, A., Bez, N., 2012. Spatio-temporal patterns of key exploited marine species in the northwestern Mediterranean Sea. PLoS One 7, e37907.

Nykjaer, L., 2009. Mediterranean Sea surface warming 1985–2006. Clim. Res. 39, 11–17.

Orio, A., Bergström, U., Florin, A.-B., Lehmann, A., Šics, I., Casini, M., 2019. Spatial contraction of demersal fish populations in a large marine ecosystem. J. Biogeogr. 46, 633–645.

Ottersen, G., Kim, S., Huse, G., Polovina, J.J., Stenseth, N.C., 2010. Major pathways by which climate may force marine fish populations. J. Mar. Syst. 79, 343–360.

Pastor, F., Valiente, J.A., Palau, J.L., 2018. Sea surface temperature in the Mediterranean: trends and spatial patterns (1982–2016). Pure Appl. Geophys. 175, 4017–4029.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912–1915.

Petitgas, P., 1998. Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves. ICES J. Ma. Sci. 55, 443–453.

Pinsky, M.L., Byler, D., 2015. Fishing, fast growth and climate variability increase the risk of collapse. Proc. R. Soc. B Biol. Sci. 282, 20151053.

Planque, B., Loots, C., Petitgas, P., Lindstrøm, U., Vaz, S., 2011. Understanding what controls the spatial distribution of fish populations using a multi-model approach: spatial distribution of fish populations. Fish. Oceanogr. 20, 1–17.

Poloczanska, E.S., Burrows, M.T., Brown, C.J., García Molinos, J., Halpern, B.S., Hoegh-Guldberg, O., Kappel, C.V., et al., 2016. Responses of marine organisms to climate change across oceans. Front. Mar. Sci. 3.

Relini, G., 2000. Demersal trawl surveys in Italian seas: a short review. In: Bertrand, J.A., Relini, G. (Eds.), Demersal Resources in the Mediterranean. Proceedings of the symposium held in Pisa, 18–21 March 1998. Ifremer, Plouzane, pp. 76–93 Actes de Colloques Vol. 26.

Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Möllmann, C., Pinnegar, J.K., 2009. Resolving the effect of climate change on fish populations. ICES J. Ma. Sci. 66 (7), 1570–1583 fsp056.

Rivoirard, J. (Ed.), 2000. Geostatistics for Estimating Fish Abundance. Blackwell Science, Oxford [England]; Malden, MA, USA 206 pp.

Romagnoni, G., Mackinson, S., Hong, J., Eikeset, A.M., 2015. The Ecospace model applied to the North Sea: evaluating spatial predictions with fish biomass and fishing effort data. Ecol. Model. 300, 50–60.

Rossi, R.E., Mulla, D.J., Journel, A.G., Franz, E.H., 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol. Monogr. 62, 277–314.

Scalisi, M., Levi, D., Fiorentini, L., Giusto, G.B., Palumbo, V., Rizzo, P., 1998. Experimental approach to intercalibrate data of trawl surveys conducted with different nets. Biol. Mar. Mediterr. 5 (2), 40–51.

Shaltout, M., Omstedt, A., 2014. Recent sea surface temperature trends and future scenarios for the Mediterranean Sea. Oceanologia 56, 411–443.

Skliris, N., Sofianos, S.S., Gkanasos, A., Axaopoulos, P., Mantziafou, A., Vervatis, V., 2011. Long-term sea surface temperature variability in the Aegean Sea. Adv. Oceanogr. Limnol. 2, 125–139.

Sobrino, I., Silva, C., Sbrana, M., Kapiris, K., 2005. A review of the biology and fisheries of the deep water rose shrimp, *Parapenaeus longirostris*, in European Atlantic and Mediterranean waters (Decapoda, Dendrobranchiata, Penaeidae). Crustaceana 78, 1153–1184.

Solomon, S., Qin, D., Manning, M., Averyt, K., Marquis, M., 2007. Climate Change 2007-the Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC. Cambridge University Press.

Tzanatos, E., Raitsos, D.E., Triantafyllou, G., Somarakis, S., Tsonis, A.A., 2014. Indications of a climate effect on Mediterranean fisheries. Clim. Chang. 122, 41–54.

Ungaro, N., Gramolini, R., 2006. Possible effect of bottom temperature on distribution of *Parapenaeus longirostris* (Lucas, 1846) in the southern Adriatic (Mediterranean Sea). Turk. J. Fish. Aquat. Sci. 6, 109–116.

van der Lingen, C.D., Hutchings, L., Merkle, D., van der Westhuizen, J.J., Nelson, J., 2001. Comparative spawning habitats of anchovy (Engraulis capensis) and sardine (Sardinops sagax) in the southern Benguela upwelling ecosystem. In: Kruse, G.H., Bez, N., Booth, T., Dorn, M., Hills, S., Lipcius, R.N. ... Witherell, D. (Eds.), Spatial Processes and Management of Marine Populations. University of Alaska Sea Grant, AK-SG -01-02, Fairbanks, USA, pp. 185–209.

Vargas-Yáñez, M., García, M.J., Salat, J., García-Martínez, M.C., Pascual, J., Moya, F., 2008. Warming trends and decadal variability in the Western Mediterranean shelf. Glob. Planet. Chang. 63, 177–184.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science & Business Media.