



The Strange Case of Tough White Seabream (*Diplodus sargus*, Teleostei: Sparidae): A First Approach to the Extent of the Phenomenon in the Mediterranean

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A worrying phenomenon has been affecting the common white seabream (Diplodus sargus) for near 40 years. Professional and recreational fishers from the Mediterranean coasts and the Atlantic coasts of Europe and Macaronesia have reported individuals of white seabream that became "like a tire" after cooking, and consequently inedible. The phenomenon was related neither to the freshness of the fish nor to the way it had been preserved or cooked. According to recreational fishers, this Abnormally Tough Specimen (ATS) phenomenon appeared singularly in time, in different places and to different extents. This singular, scattered appearance, with no area of origin from which to spread, de facto excluded any process of contagion. In order to compensate for the lack of knowledge and understanding related to this issue, we undertook a first study that aimed at addressing the extent of the white seabream anomaly in the western Mediterranean. To reach this objective, we carried out surveys on voluntary basis among fishers (both professional and recreational) and researchers throughout the western Mediterranean. Data from the surveys (n = 270) were then analyzed to evaluate the distribution of ATS and its possible relationship with human activities. Results showed that the anomaly affected the white seabream and very occasionally some other species, mainly of the same family Sparidae. In addition, the phenomenon did not occur simultaneously in the different areas surveyed over the last years and in some places it seems to have disappeared. We highlighted a possible link between ATS occurrence and the presence of human activities in adjacent areas. We hypothesized pollution – including by copper – could be a possible driver of ATS. Results suggested a tendency of ATS to cluster around fish farms and commercial and industrial ports,

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although we are aware other human factors might also influence the phenomenon. To conclude, the present study gives an overview of the importance of the white seabream anomaly in the Mediterranean and encourages further research to disentangle the exact mechanisms behind this phenomenon.

Keywords: white seabream, Diplodus sargus, Mediterranean Sea, pollution, copper, anti-fouling paint

INTRODUCTION

The common white seabream *Diplodus sargus* (Linnaeus, 1758) (F. Sparidae) is a demersal fish, living in rocky infralittoral and circalittoral habitats. It is a very common species in the western Mediterranean and in the north-eastern coast of the Atlantic Ocean, including the Macaronesian archipelagos (Pérez et al., 2007). The individuals of this species are medium-sized with a relatively long lifespan and an omnivorous benthic diet. It is an edible species with a considerable commercial interest, representing a common catch in both professional and recreational fisheries.

In recent years, this species seems to have been affected by a strange phenomenon. Professional and recreational fishers from the Mediterranean have reported the capture of white seabream that, after cooking, became "like a tire" and inedible (hereafter called ATS: Abnormally Tough Specimens). Information collected indicates that the phenomenon is related neither to the freshness of the fish nor to the way it has been conserved or cooked. Recreational fishers advocate for a number of hypotheses, including pollution, *post-mortem* stress or depletion of lipid reserves during the reproductive period.

In a previous work, we studied the muscle trace-metal loads of *D. sargus* from the Catalan coast (North-western Mediterranean, Spain). In addition to the general high levels of mercury and other potentially harmful elements (Tramati et al., 2012; Casadevall et al., 2017; Merciai et al., 2018), copper loads were especially high in specimens landed in Roses, where a port and a fish farm are located.

Aquaculture production and consequently open cage systems have increased over the past decades (FAO, 2003). Copper, zinc, and cadmium are common ingredients in fish feeds and have been used as tracers of feed pellets (Dean et al., 2007). Moreover, with the gradual elimination of triorganotin-based formulations [e.g., tributyltin (TBT)] in anti-fouling paints, copper has become the principal biocidal component of most of these paints, usually in the form of copper oxide (Cu₂O) (Yebra et al., 2004). Therefore, copper release to the environment is a characteristic that ports and farms have in common and, although the connection of the anomaly with copper is not evident, the proximity to ports and aquaculture areas could provide some clues to its origin. For this reason, the objective of this study was to investigate the spatiotemporal occurrence of the ATS phenomenon in the Western Mediterranean and the possible relationship between ATS occurrence and the presence of these facilities. To reach this goal, we first mapped the distribution of locations where ATS had been caught in the western Mediterranean, based on a voluntary survey near recreational fishers. Afterward, we analyzed the distribution of ATS observations as a function of the distance to the nearest largest (commercial) harbors and/or marine fish farms. We also considered the temporal evolution of the ATS phenomenon since its first report in the Western Mediterranean.

MATERIALS AND METHODS

Fish Forums and Data Collection

A first voluntary survey of ATS occurrence at the scale of the south French littoral was performed in 2014 by Verlaque (pers. comm.). From this first regional study, 55 answers were obtained (unpubl. results). In a second step, we posted during year 2019 the same survey, with few modifications, on a platform (SurveyMonkey) to collect answers more easily from fishers' forums and social networks. By the time we started writing up this research article, we had collected 215 positive responses that, when added to the previous 55, totalled 270 surveys, mostly answered by recreational fishers and especially by anglers. Out of these, 255 confirmed the presence of ATS. Data available from North Africa and the Atlantic were very scarce, so this work focused on data from the Mediterranean coasts of Spain, France and Italy. In addition, some locations where ATS were reported were repeated several times, and therefore considered unique. Finally, the study was centered on 96 locations for the spatial analysis of ATS occurrence. From here, therefore, ATS observations refer to these 96 locations.

The survey of recreational fishers sought information on six key topics. It included the place (or places) where ATS were caught, the year(s) and the length of the observation period, if other species with the same problem were caught and the presence of remarkable structures or elements near the fishing area (nautical port, fishing port, aquaculture facility, river, marine outfall, invasive algae, etc.). The survey (in English, French, Italian, Arabic, Spanish and Catalan) also asked about anything strange in the fish (color, behavior, parasite, etc.).

With regard to ethical issues, the work was based on observations reported from a voluntary survey. The processing of the personal data of the project informants was based on their consent, explicitly stated when sending the answers to the survey, in accordance with article 6.1 of the General Data Protection Regulation (Regulation (EU), 2016). The data from survey reports were analyzed statistically, with no links to the identifying data, and will only be processed for the time necessary to complete the ongoing project.

Our survey targeted recreational fishers because they could give us information about the capture area and the dates, and were more likely to be final consumers who would know whether or not the specimens were tough after cooking. Regarding ports, along the Mediterranean coasts of Spain, France and Italy, the location of nautical ports is so continuous that it would have masked any trend in the survey results. Thus, given the goal of the study, the selection of ports has prioritized industrial and commercial ones because of their increased port activity with ships of deeper drafts.

The geographic information structured by layers was extracted from different sources. The industrial and commercial ports' classification and location correspond to the World Port Index (pub. 150) of the National Geospatial-Intelligence Agency¹. The database containing points representing marine finfish aquaculture facilities is updated yearly by the European Marine Observation and Data Network². We supplemented this information by reviewing all the aerial orthophotos of the studied coastline and digitizing all the identified marine finfish aquaculture facilities. Industrial and commercial ports will be referred to as ports or commercial ports later in the paper; marine finfish aquaculture facilities will be referred to as farms or fish farms.

Distance and Temporal Analyses

Boxplots were useful to analyse ATS observations at atypical distance values to the nearest fish farm or commercial port. We then examined, using a dispersion plot, the interactions between distances to the nearest fish farm and to the nearest commercial port with two proposals. The first one was to determine if collinearity existed between the two-predictor variables. Indeed, we have to consider that ports and off-shore aquaculture facilities can be located close to each other. A Spearman's correlation test was performed for this purpose (considering a restrictive threshold value of 0.4; Dormann et al., 2013). The second one was to analyze whether ATS observations not explained by proximity to a fish farm could be explained by proximity to a commercial port and vice versa.

Prior to the analysis of the occurrence of ATS observations as a function of distance to nearest fish farm and to nearest commercial port, data were grouped according to 'distance classes'. The grouping distance was 2.5 km, giving a total number of 16 classes for distance to farm (maximum distance from nearest farm for ATS observation = 39.2 km) and 26 classes for distance to port (maximum distance from nearest port for ATS observation = 63.1 km). With increasing distance to the nearest farm or port, a few 2.5 km distance classes (one for distance to farm, seven for distance to port) containing no ATS observations were filled in with zero. After grouping, we analyzed the spatial distribution of the occurrence of ATS observations as a function of distance to nearest farm or port. A generalized linear model (glm) with Poisson distribution and log-link function was fit to the distance to farm data (Cameron and Trivedi, 1998; Warton et al., 2016) and a three-parameter asymptotic exponential regression model fit by non-linear least squares (nls) was fit to the distance to port data (Wooldridge, 2002; Winkelmann, 2008). The same 2.5 km distance grouping method and glm analysis (with robust parameter estimation; Cantoni and Ronchetti, 2001) were performed for a third distance factor, calculated as the

¹http://www.nga.mil

average distance for ATS observations between the nearest farm and the nearest port. The first distance class 0-2.5 km - out of the 16 from the average - with little ATS observations reported was ignored in the glm analysis (i.e., this required the farm and the port to be very close, and that the ATS fish was caught close to both, which was unlikely to happen). Finally, the effect of the two distance class factors to nearest port and to nearest farm on the occurrence of ATS observations was analyzed using generalized additive model (gam) with Poisson distribution and log-link function (Zuur et al., 2009). The gam model allows for more flexible association patterns for the response variable, ATS observation, to the predictor variables, distance to nearest farm and distance to nearest port. Grouping distance was set to 5 km before gam analysis, giving 38 classes for distance to both nearest farm and nearest port (61 classes if grouping distance of 2.5 km, so close to the number of locations where ATS fish were reported; 17 classes if grouping distance of 10 km). Model assumptions (including residual distribution, variance homoscedasticity and overdispersion) and model fit were checked with diagnostic plots and tests. Akaike information criterion and Bayesian information criterion were used to select the best fitting model (Brewer et al., 2016).

Finally, the occurrence of ATS observations over time was determined by summing the number of observations reported by fishers on a yearly basis, to see if the chronological distribution contributed with some other clues.

Data analysis and statistics were performed in RStudio version 1.1.383 (R Studio Team, 2016), using R's base functions (R Core Team, 2019) and functions of packages dplyr (Wickham et al., 2019), mgvc (Wood, 2017), nlstools (Baty et al., 2015), AER (Kleiber and Zeileis, 2008), and robustbase (Maechler et al., 2019).

RESULTS

We collected a total of 270 survey reports, taking into account the 55 of Verlaque's 2014 survey (unpubl. results) and the 215 from the present survey. From among all the responses, 255 (94.4%) were positive, which is to say that respondents indicated they had occasionally captured one or several species or individuals affected by the ATS anomaly. This confirmed the ATS anomaly is widespread. Only 15 respondents (5.6%) had never observed the phenomenon, but some indicated they had heard about it. **Figure 1** represents all sites where the presence of ATS was reported in the Mediterranean from survey reports, together with major port infrastructures and marine farms. Only 4 rivers were mentioned in the answers: Rhône, Llobregat, Ebre, and Guadalete, which are also highlighted in **Figure 1**.

Answers that were inaccurate and could not be added to the survey dataset, compared to those properly filled in reports, were discarded prior to the analysis.

ATS specimens of *D. sargus* were reported 237 times. The anomaly was observed mainly in the Mediterranean (132 reports from Spain, 61 from France, 1 from Monaco, 22 from Italy, and 1 from Tunisia), but also in the European Atlantic (3 reports from Spain and 4 from France) and in Macaronesia (5 reports). Some respondents (8) did not indicate the locality of caught

²www.emodnet-humanactivities.eu

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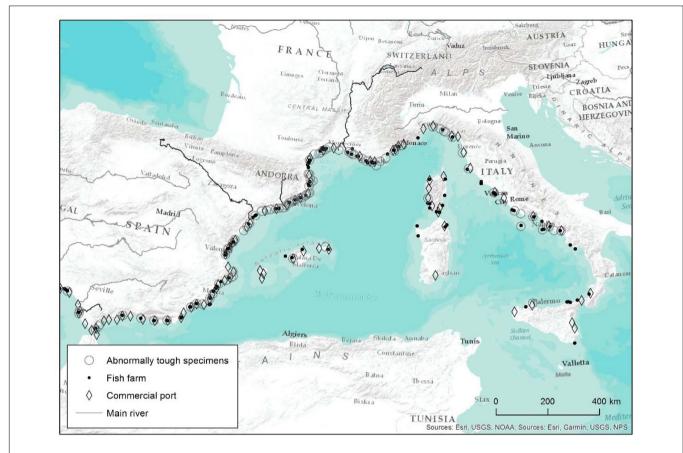


FIGURE 1 | Mediterranean locations where abnormally tough specimens of white seabream were captured according to survey data. The map includes the major port infrastructures and marine farms. The only four rivers mentioned in survey reports are also highlighted (Rhône, Llobregat, Ebre, and Guadalete).

ATS. The information collected was quite variable in the different areas (**Table 1**).

In some localities, ATS only appeared from time to time, while in others, fishers said that most specimens showed the anomaly. In addition, the presence of ATS specimens did not appeared simultaneously in the area covered by the survey, neither correlatively. Many fishers reported the anomaly from specific periods, and some noticed that, in sites where they had always fished, the problem had appeared in recent years. Fishers mentioned that the ATS phenomenon has been known for about 40 years in Catalonia (Spain), for 25–35 years in the Gulf of Lyon (Eastern Pyrenees, France), and for 30 years in Italy.

Regarding size (except in one case), all the responses referred to individuals of *D. sargus* longer than 15 cm (total length), with 81.3% of the specimens longer than 20 cm.

With respect to other affected fish, most were other species of *Diplodus*, such as *D. puntazzo* (Cetti, 1777) (6), *D. cervinus* (Lowe, 1838) (4) and *D. vulgaris* (Geoffrey Saint-Hilaire, 1817) (3). However, the anomaly was also observed in *Sparus aurata* Linnaeus, 1758 (2), *Sarpa salpa* (Linnaeus, 1758) (2), *Epinephelus* sp. (1), *Lithognatus mormyrus* (Linnaeus, 1758) (1), *Pomatomus* saltatrix (Linnaeus, 1766) (1), *Seriola dumerili* (Risso, 1810) (1), *Sciaena umbra* Linnaeus, 1758 (1), *Spondyliosoma cantharus* (Linnaeus, 1758) (1), and *Zeus faber* Linnaeus, 1758 (1). We

ignored some other responses because the common name given to caught fish by fishers could refer to two or more species.

Distance and Temporal Analyses

We finally analyzed 96 locations (i.e., 96 ATS observations; **Figure 1**), a number lower than the total surveys reporting ATS catches since some locations were repeated more than once. The furthest distance of ATS observation from a fish farm was 39.2 km, but half of the ATS observations were closer than 7.3 km, as shown on the boxplot (**Figure 2**). Two atypical values were found (38.3 and 39.2 km). However, both were quite close to a commercial port (less than 1 km to Tarragona and 5.1 km to Genova, respectively) (**Table 2**).

The furthest ATS observation from a commercial port was 63.1 km, but the median distance was only 9.7 km. The distance to the nearest commercial port showed more atypical values than the distance to the nearest fish farm; specifically, six municipalities were classified as atypical values (**Table 2**).

Atypical values ranged from 35.3 to 63.1 km. Four of them were closer to a fish farm than the median distance (7.3 km). Hence, whereas atypical values of distance to the nearest fish farm were clearly explained by their distance to a commercial port, the other way round did not apply.

Country	Region	First and last year cited	Number of answers
Mediterranea	n		
Spain	Catalonia	1980–2019	79
	Balearic Isles	2019	1
	Valencia	1990–2019	33
	Murcia	2010-2014	5
	Andalusia	2013-2019	14
France	Eastern Pyrenees	1985(–95)– 2019	10
	Aude	2014–2018	2
	Hérault	2004–2016	12
	La Camargue (Bouches-du-Rhone and Gard)	2017–2019	1
	Bouches-du-Rhone	1998–2016	17
	Var	2001–2016	13
	Alpes Maritimes	2013–2018	2
	Corsica	2005–2015	4
Monaco	Monaco	2011	1
Italy	Liguria	1989–2019	10
	Toscana	2012-2017	2
	Lazio	2009–2018	6
	Campania	2018–2019	2
	Elba	2016	1
	Sicily	Unknown	1
Tunisia	Tunisia	2018	1
Atlantic			
Spain	Asturias	2018	1
	Cantabria	2018	1
	Basque country	2018	1
France	Finisterre	2013-2018	3
	Landes	2012	1
Canary Island	s		
Spain	Canary Islands	1999–2019	5

TABLE 1 Summary of the regions grouped by country and marine area where

 fishers reported they captured anomalous white seabream, and years of the

 oldest and most recent report.

Regions are ordered from north to south and from west to east.

The interaction between both variables (distances to nearest fish farm and commercial port) was examined for ATS observations. No collinearity was observed between the two predictor variables distance to nearest farm and distance to nearest commercial port (r = 0.18; p = 0.08). The dispersion diagram (**Figure 3**) shows that ATS observations far from a fish farm tend to be close to a commercial port and vice versa. Only one point fell clearly outside of this tendency: Sabaudia (Lazio, Italy), which was classified as an atypical value regarding distance to the nearest commercial port and was located in the fourth quartile regarding distance to the nearest fish farm (but not as an atypical value).

The decrease of ATS observations with increasing distance to nearest commercial port or nearest farm was obvious when plotted according to the 2.5 km distance classes (**Figure 4**). According to model fitting and ATS caught distribution, the decrease was rapid in the first 10 km away from farms; number of

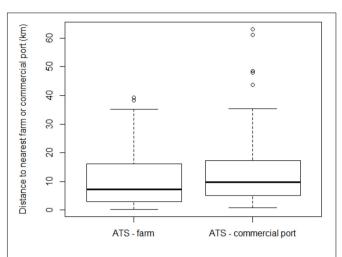


FIGURE 2 Boxplot of distance of Abnormally Tough Specimen (ATS) observations to the nearest farm or commercial port, with median, first and third quartiles (boxes), least values (dotted bars), and outliers (dots).

 TABLE 2 | Municipalities which present atypical values for distance to the nearest fish farm or commercial port.

Municipality	Distance to nearest commercial port (km)	Distance to nearest farm (km) 38.3 (Q4)	
Tarragona	0.8 (Q1)		
Genova	5.1 (Q1)	39.2 (Q4)	
Nettuno	63.1 (Q4)	2.3 (Q1)	
Ponza	61.0 (Q4)	3.7 (Q2)	
Fos-sur-Mer	43.7 (Q4)	5.3 (Q2)	
Sestri Levante	48.0 (Q4)	7.4 (Q3)	
Saint-Tropez	35.3 (Q4)	17.5 (Q4)	
Sabaudia	48.6 (Q4)	27.7 (Q4)	

Rank in distance is given between brackets.

ATS observations in that distance interval remained similar for ports. Beyond this distance of 10 km, the continuous decreases in ATS observations with the increase in distance was similar for both distance factors. The occurrence of ATS observations became zero or close to zero beyond 40 km from the nearest commercial port or farm.

The same ascertainment was made as to the number of ATS observations as a function of the average distance to the nearest farm and to the nearest commercial port. The decrease in the number of ATS observations was obvious once fishers moved away from both farms and ports. It reached zero when the average distance between the nearest farm and the nearest port was 40 km. The few ATS observations in distance class 0–2.5 km was explained by the low probability of catching an ATS at a very short distance from both a farm and a port (**Figure 5**).

The Poisson gam analyzing the occurence of ATS observations in relation to distance classes to nearest commercial port and to nearest fish farm confirmed the significant effect of the two distance factors (**Table 3**). The model explained 67.1% of deviance.

Finally, **Figure 6** illustrates the temporal evolution of ATS observations over time, since their first report. ATS observations

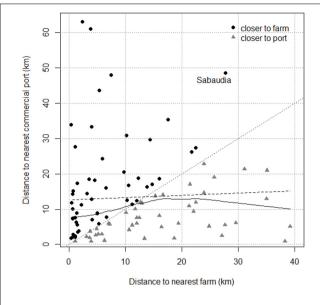


FIGURE 3 | Dispersion diagram for Abnormally Tough Specimen (ATS) observations. The dashed and full black lines are linear and smooth relationships between distance to the nearest farm and distance to the nearest commercial port, respectively. Black dots above the dotted 0–1 gray line are ATS observations closer to farms, gray triangles under are closer to commercial ports. Sabaudia ATS observation is highlighted.

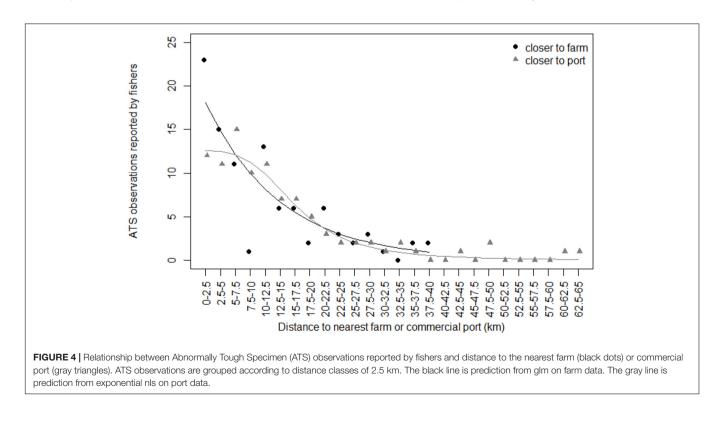
reported by fishers peaked in recent years, with a net increase since the beginning of 2000s. The increase was almost continuous since then, and showed net year-to-year variability like, e.g., between years 2003–2004, 2008–2009, or 2016–2018.

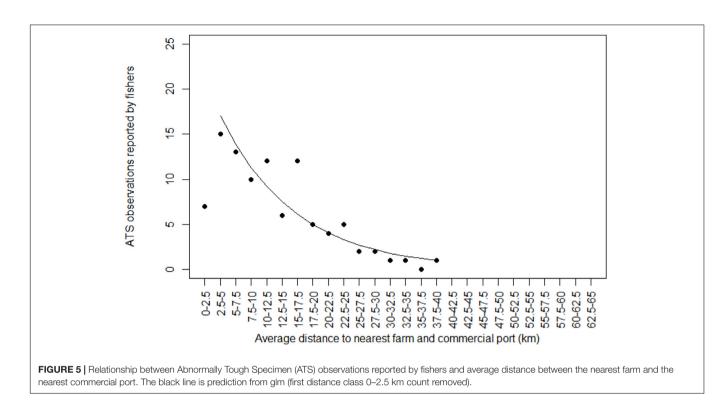
DISCUSSION

This work explores a phenomenon which has been underestimated until now and that, as evidenced by our results, is distributed at least throughout the western Mediterranean, the Atlantic coast of Europe and the Canary Islands. The first step of this survey work on ATS occurrence in the Mediterranean was performed in 2014 by Verlague (unpubl. results) along the French littoral. Data collected from his preliminary work showed that the inedible white seabream phenomenon was known and common in the western Mediterranean for at least the past 35-40 years. In 2012-2013, the anomaly was also reported on the French Atlantic coast (Landes and Finistère), and in 2018 on the Atlantic coast of Spain. The first observation we have from the Canary Islands dates from 1999. The ATS anomaly affects mainly the white seabream, but its incidence in other species has also been reported in collected survey reports, mostly after 2014. The occurrence of ATS appears to be a widespread phenomenon that deserves investigation.

For the white seabream, although the phenomenon had initially a low incidence in the Mediterranean (around 1% of caught fish in Catalonia), it reached 40–50% of individuals in the eastern Pyrenees in the last 20–30 years and 20–30% of individuals in Catalonia around 2007–2010. Elsewhere, the phenomenon has also become locally important. For example, in 2015 in Naples, 70% of the white seabream presented the anomaly, leading to a drop of about 50% of its commercial value on the local fish markets (Tundo, 2015).

Results suggest a tendency of ATS to cluster around fish farms and commercial ports. Although distance data to commercial





ports showed more atypical values than distance data to farms, nautical and fishing port breakwaters, and sometimes commercial ports are preferential recreational fishing sites. Considering this, apparent ATS clustering around ports is very likely to occur. We have also considered that ports and off-shore aquaculture facilities can be located close to each other. For this reason, we explored the collinearity between distances to ports and farms. In the literature, collinearity diagnostics relying on the determination of correlation coefficients rho often consider as threshold values 0.5–0.7 (Dormann et al., 2013). Some authors also used more restrictive values, e.g., 0.4. With a rho of 0.18, we can consider that collinearity has very limited impact in this work.

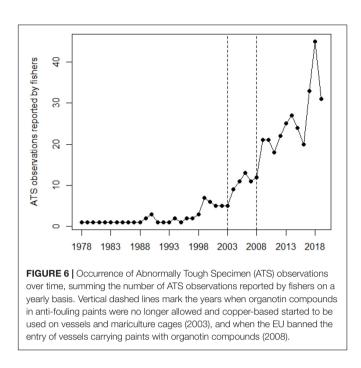
Despite white seabream exhibit high site fidelity (Abecasis et al., 2009; D'Anna et al., 2011; Belo et al., 2016) in both the reproductive and non-reproductive seasons, they have also shown the ability to cover large distances (e.g., 20 km) (D'Anna et al., 2004; Di Franco et al., 2012), proving a remarkable behavioral plasticity in habitat use (Di Lorenzo et al., 2016). Abecasis et al. (2015) observed daily displacement up to 4.97 km (which corresponds to percentile 39 of the distance to the nearest farm in our results), although trips of around 100 km have occasionally been recorded (Abecasis et al., 2009; Belo et al., 2016). It is known that marine fish farms have also an aggregation effect on wild fish populations (e.g., Valle et al., 2007; Sánchez-Jerez et al., 2011). The median distance for ATS capture sites to the nearest fish farm (7.30 km) is, therefore, of the same order of magnitude, although a little bigger than the possible daily displacement reported for that species (Abecasis et al., 2015). Most ATS observations reported in the present study referred to individuals longer than 20 cm following fishers' comments. As shown by Figueiredo et al. (2005) and Merciai et al. (2018), there is a size-related diet shift from approximately 25 cm onwards, which implies a wider home range in larger specimens that feed both in the infra- and circalittoral zones. Therefore, there is some variability in the home range, related to both the topography of the area and the size of the individuals that can explain these differences.

Searching for a common denominator for ports and fish farms, and taking into account the results of our previous work on copper concentrations in *D. sargus* (Merciai et al., 2018), we suggest antifouling paints (as a copper source) to

TABLE 3 | Results of generalized additive model.

	Parametric coefficient					
	Estimate	Std. error	z-value	p-value		
Intercept	0.6742	0.1279	5.271	<0.001		
	Approximate s	ignificance o	f smooth terms			
	Estimated df	Residual df	Chi-square value	p-value		
Distance class to nearest farm	1.290	1.522	29.77	<0.001		
Distance class to nearest port	1.057	1.111	17.66	<0.001		

Estimated regression parameters of the strictly parametric model coefficient and approximate significance of the smooth terms for the Poisson gam analyzing the occurrence of ATS observations in relation to distance classes to nearest commercial port and to nearest farm.



be a possible cause of ATS anomaly. An increase in ATS observations has apparently occurred in recent years, more obvious since around 2003. In that same year, organotin compounds were no longer allowed (Regulation (EC), 2003), and copper-based anti-fouling paints started to be used on vessels and mariculture cages. Since 2008, EU ships and other ships visiting EU ports are obliged either not to bear anti-fouling systems containing organotin compounds, or to bear a barrier coating to prevent such compounds from leaching from the underlying non-compliant antifouling system (Regulation (EC), 2008). The Regulation is further supplemented firstly by the Council Directive 76/769/EEC (European Commission, 1976) as amended that bans the marketing and use of organostannic compounds within the EU, secondly by the Comission Regulation (EC) No 536/2008 (Regulation (EC), 2008) comprising measures enabling ships flying the flag of a third State to demonstrate their compliance and procedures for control. Prior to 2003, the phenomenon of ATS was less frequent. Assuming a possible relationship between copper and ATS, the earlier cases may be related to fish farms.

Much research has been conducted on the effect of copper on aquatic organisms. Related to copper-based antifouling paints, copper oxide leaches from the boat surfaces and enters the water as free copper ion (Cu⁺), which is immediately oxidized to Cu²⁺ and forms complexes with inorganic and organic ligands (Thomas and Brooks, 2010). In aquaculture systems, copper is regularly used in the form of copper sulfate (CuSO₄) to control algal blooms and aquatic macrophyte infestations (Garcia Sampaio et al., 2008). Copper is also a common component of feed pellets used in aquaculture. Beneath aquaculture installations, waste feed originating from the cages and feces enhances the attractive effect of farms (Tuya et al., 2006), but also lead to potential organic and metal pollution of the sediment, the benthic fauna and through the food chain their predators.

It is known that copper becomes toxic to cells when its concentration surpasses certain threshold levels (Theophanides and Anastassopoulou, 2002). Baldwin et al. (2003) related copper with adverse effects such as reduced olfaction (sense of smell) that leads to reduced appetite and food intake, which, in turn, contribute to reduced growth (McIntyre et al., 2008). Gioda et al. (2007) showed that copper exposure induces lipid peroxidation in the muscle of the fish *Leporinus obtusidens* (Valenciennes, 1836). Maharajan et al. (2016) also observed that the histopathology of muscles shows progressive damage in their structure with increasing concentrations of copper. Indeed, ferrous iron (Fe²⁺) and Cu (I) promote the oxidation reaction called Fenton (Kanner, 1994) in fish muscle (Decker and Hultin, 1990).

In a recent study conducted in the Bay of Toulon (France), Bouchoucha et al. (2018) analyzed metal concentrations in juveniles of D. sargus from four sites, two representative of the different types of ports present in the bay and two representative of the other types of coastal habitats available to the juveniles of local rocky fishes. The highest muscle concentrations for copper were observed in the Saint Mandrier-sur-Mer marina, where the levels of contamination by copper in water were also the highest, and clearly higher than the concentrations found in the second port, the biggest naval port of the Mediterranean, the port of Toulon. Saint Mandrier is one of the locations where we have evidence of ATS presence, next to an area of shellfish culture and fish farming, the Lazaret and Balaguier bays [with 28 shellfish farms and 18 fish farms, according to the information available at the Direction Départementale des Territoires et de la Mer du Var (2019)].

The aforementioned evidence suggests that the exposure of fish to copper can be mediated via aquaculture farms and ports, leading to its accumulation in the flesh of fish and ATS. Copper proposed as likely responsible for ATS clearly deserves further research. In addition, many chemical substances used in aquaculture can be harmful. Aquaculture plants periodically discharges wastes from farm activities. These waste products include other trace metals, detergents, effluent from net washing, antifouling chemicals, and even chemicals such as drugs (Read and Fernandes, 2003), which also deserve to be considered.

In the present study, only two locations among all where ATS were reported were not close to either of the two facilities (farms and commercial ports), namely Saint Tropez (France) and Sabaudia (Italy) (see Table 2). Nautical ports, however, are present in both locations (see Saint Madrier example), and because white seabream are able to cover long distances (D'Anna et al., 2004; Abecasis et al., 2009; Di Franco et al., 2012; Belo et al., 2016) they could also come from areas close to other facilities. Finally, there is another possible consideration for these two specific cases. These ATS records corresponded to fish caught in winter, at the beginning of the reproductive season of D. sargus (Martínez and Villegas, 1996; Gonçalves and Erzini, 2000; Morato et al., 2003; Mouine et al., 2007). Some recreational fishers reported that white seabream are particularly tough during the reproduction period, when fish invest their fat reserves in the maturation of gonads and eggs.

Recent studies (Terlizzi et al., 2011; Felline et al., 2012; Gorbi et al., 2014) have linked a depletion of energetic reserves and a decrease in the condition factor of *D. sargus* with the uptake of lipophilic secondary metabolites of an invasive alga, *Caulerpa cylindracea* Sonder, 1845 (Bryopsidales and Chlorobionta) frequently consumed by the white seabream. This alteration represents a real threat to the health of the fish since affected individuals cannot biosynthesize essential fatty acids (Felline et al., 2014). Vitale et al. (2018) candidated caulerpin as a causal factor of the metabolic disorders observed in *D. sargus*. Caulerpin taken with diet is directly responsible of changes observed in the metabolic profile of fish flesh, including alteration of lipid metabolism, in particular with a reduction of ω 3 PUFA content (Del Coco et al., 2018).

The consumption of C. cylindracea by fish species such as Spondyliosoma cantharus, Boops boops, Sarpa salpa, and D. sargus, D. vulgaris, or Siganus luridus (Ruitton et al., 2006; Box et al., 2009; Terlizzi et al., 2011; Tomas et al., 2011; Felline et al., 2017; Vitale et al., 2018) and by sea urchins (Ruitton et al., 2006; Bulleri et al., 2011) has been extensively documented. C. cylindracea is a species of Australian origin introduced in the Mediterranean Sea and reported as a major invader since the early 1990s (Klein and Verlaque, 2008; Verlaque et al., 2015). It can modify the structure of the ecosystems it invades as well as the associated fauna and the food chain (Deudero et al., 2011; Felline et al., 2017). Another important invasive Caulerpa species in the Mediterranean Sea is C. taxifolia (M. Vahl) C. Agardh, 1817. Like its congeneric, it produces caulerpin and other similar terpenoid compounds. This species, also of Australian origin, was detected in 1984 in Monaco, from where it quickly spread in the Mediterranean (Meinesz and Hesse, 1991; Verlaque et al., 2015). A third taxon of invasive exotic Caulerpa, first detected in 2006 in Turkey, C. taxifolia var. distichophylla (Sonder) Verlaque, Huisman & Procaccini, 2013 is spreading in the central Mediterranean (Cevik et al., 2007; Verlaque et al., 2015).

The problem of ATS seems to be concentrated in very specific areas and its relationship with the introduction of invasive Caulerpa species appears unclear (Verlaque et al., 2015). For example, in Catalonia, the first known cases of ATS (1980) are prior to the (known) presence of C. cylindracea. C. taxifolia as well as its variety distichophylla have never been found in Catalonia. C. cylindracea was first observed in the south of Catalonia (Vilanova i la Geltrú) in 2009 and only recently along its northern coast (Cap de Creus and Ses Negres, unpubl. data). Along the Mediterranean coast of Spain, C. cylindracea was first sighted in the Balearic Islands in 1998 (Ballesteros et al., 1999), where there had been no cases of ATS until 2019. Besides, the algae reached the east coast of the Iberian Peninsula (Castellón) in 1999 (Aranda et al., 1999) and began to spread rapidly to the south, where it was sighted in Alicante (SE Spain) in 2000 (Aranda et al., 2003); but ATS were already reported a few years earlier. The same is true for the southwest coast of France, where the anomaly was already reported in 1985, while C. taxifolia was sighted for the first time around 1992-1994 in the port of St. Cyprien (Boudouresque et al., 1992), the only known locality colonized by that species, while C. cylindracea has not been observed in the region. In addition, no invasive Caulerpa

species are present in the Atlantic coastal regions of France and continental Spain where ATS have been reported. In brief, although (a) the first reports of an invasive species can occur sometimes after the species' settlement, and (b) a synergetic effect between caulerpin and other toxicity sources cannot be excluded, a clear relationship cannot be established between ATS and *Caulerpa* species invasions. This hypothetical caulerpin relationship with the ATS anomaly in *D. sargus*, like the exposure to copper requires more investigation, including experimental works under control conditions.

Although D. sargus seems to be the species most affected by the ATS phenomenon, other species have been reported in the present survey. They are mostly species of the same F. Sparidae that share habitat and therefore can be subjected to the same stressors and physiological anomalies. The higher propensity of D. sargus to be affected by the anomaly compared to other species sharing the same habitat may depend on its feeding habits. The diet of D. sargus is based on algae and hard-shelled benthic invertebrates widely acknowledged to accumulate trace metals (Sala and Ballesteros, 1997; Linde et al., 2004; Merciai et al., 2018), including those living close to structures treated with antifouling chemicals and affected by copper-enriched feed pellets. It is known that D. sargus can use their strong teeth to crush hard-shelled prey (Vandewalle et al., 1995). Linde et al. (2004) suggested that larger, rounded, protruding and robust incisors of D. sargus would be preferentially useful to pick tough invertebrates adhered to the substrate. By feeding on prey including directly on facility treated surfaces, it could incorporate more easily toxic components of anti-fouling paints than other species sharing the same environment, or even fish in aquaculture cages. Overfed, 'fat' farmed fish may be less affected by the anomaly as they never deplete their fat reserves, unlike wild fish. If environmental factors affecting fish result in a progressive loss of their lipid reserves, D. sargus with different degrees of affection should be observed within a same population, implying the existence of specimens hardly recognizable as ATS, which would not be detected through a superficial examination.

According to fishers, the ATS phenomenon appeared singularly in time in different places. This scattered, diffuse appearance, with no area of origin to spread from, de facto excluded any process of contagion. We disregarded too the hypothesis of a stress-induced ATS syndrome driven by (a) the noise from boats and nautical activities peaking in the 0-10 m depth zone, the main feeding zone of the white seabream, or (b) by the stress due to catch and landing. The reason to exclude those explanations is that fishers reported to have caught both ordinary specimens and ATS in the same outing, with the same gear. The stress is expected to be the same for all caught fish, making this hypothesis implausible. Nor would it explain why one fish species is more affected than others, be the reason an environmental issue or a fishing gear. Furthermore, in the survey, we asked about the presence of remarkable features near the fishing area (e.g., nautical port, fishing port, aquaculture facility, river, marine outfall, and invasive algae). Water courses and marine outfalls are important pollution sources to the coastal marine environment, but very few fishers reported their presence close to the locations of ATS captures. On the other hand, many nautical-recreational ports were reported, whose pollution in some periods of the year may exceed that of industrial or fishing ports. Nevertheless, all these potential impacts on ATS occurrence will have to be investigated in future studies.

The fact that 20% of the entire Mediterranean basin and 60– 99% of the territorial waters of EU member states are heavily affected by intense human impacts occurring in all ecoregions and territorial waters (Micheli et al., 2013) suggests pollution as one of the global threats that could explain the scattered appearance of the phenomenon. Results show that the ATS occurrence is a general phenomenon along all the western Mediterranean coasts. The drivers of the ATS anomaly could be multiple and synergistic; therefore, potential explanations to the phenomenon need to be investigated in the next field surveys of the ATS anomaly.

Being aware of the spread of the ATS phenomenon will be necessary to perform quantitative and qualitative analyses of its environmental drivers, general physiological conditions of fish, flesh biochemistry and degree of flesh alteration in both ATS and unaffected fish, to better understand it. The dietborne uptake of copper and other pollutants may be investigated, e.g., the role of metal bioaccumulator preys like sea urchins. This work, therefore, opens up numerous research possibilities in order to understand, next, the causes of the ATS anomaly.

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DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

MC, CR-P, and RM designed the new survey, distributed it, analyzed the results, and prepared this article. ER, JT, and JR helped in the collection of data, evaluation of results, and the revision of the manuscript. MV made the first survey and the first assessment of the case and helped in the revision of the manuscript. CM, JP, and JR performed the spatial analysis and also helped in the revision of the manuscript.

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