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The declining availability of wild mussel seed for aquaculture in a coastal upwelling system

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A general decline in foundation species at the rocky intertidal has been observed during the last decades all around the world and primarily related to climate change. In agreement with that trend, the mussel aquaculture sector in Galicia (NW Spain), the main production area in Europe, has warned over the last years about a decline in the availability of wild mussel seed from the rocky coast. Here we compile for the first time, mussel seed collection reports by mussel farmers in Galicia for the period 2006–2021. We employed that dataset as a proxy of mussel recruitment evolution in the rocky shore for the last 16 years. Temporal analysis of our data confirmed the reported decline (-148 t yr-1), particularly pronounced from 2012 onwards. The data base also allowed us to analyze inter-annual variability according to both, climatic variations and management scenarios. Since cultivated mussels conform a meta-population with wild mussels from the rocky shore, alterations on the market preferences towards smaller individuals at harvest, could also contribute to a reduction in reproductive output. Our results show a decrease in life-time egg production under certain scenarios. Nonetheless, coastal upwelling seems to be the largest factor conditioning recruitment abundance, explaining as much as 60% of the variability observed. Decline on recruitment abundance was highly modulated by the observed increment in frequency of intense upwelling events, exceeding 500 m3 km-1 s-1 between July and November. Meridional winds also determined the spatial recruitment patterns, pointing to the large role of wind forcing on mussel larval dispersal. Our results highlights how alterations on upwelling regimes related to climate change can interact with mussel population dynamics and also condition aquaculture sustainability and food security.

KEYWORDS

mussel aquaculture, mussel seed availability, recruitment time series, upwelling, reproductive output, management, climate change

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1 Introduction

Marine aquaculture is expected to provide a large part of the 60% increase in food production necessary to feed the world population by 2050 (Science Advice for Policy by European Academies, 2017). To ensure the growth of sustainable aquaculture, the increase should focus particularly on offshore aquaculture and the production of filter feeders (+100 Mt) (Science Advice for Policy by European Academies, 2017). Among these, the cultivation of bivalves has a minimal environmental footprint with lower CO_2 emissions per gram of edible protein than any marine animal production (Froehlich et al., 2018; Kim and Kim, 2020; Gephart et al., 2021) and it provides important benthic and coastal ecosystem functions (Wilberg et al., 2011; Froján et al., 2016). Considering these factors, bivalve farming is an attractive alternative for the future expansion of sustainable seafood (Smaal et al., 2019; Costello et al., 2020; Gentry et al., 2020) and a substitute for the stagnant global fisheries production (Science Advice for Policy by European Academies, 2017).

The production of mussels which are the main aquaculture species in Europe, has reported a significant decreasing trend over the past two decades, mainly in northern countries (Avdelas et al., 2021). This decline has not yet been reported in Spanish mussel production, which is the first European producer with 90% of its production coming from Galicia (NW Spain; Labarta and Fernández-Reiriz, 2019). Nonetheless, forecasts from the Spanish Ministry of Agriculture, Fisheries and Food do point to a future stagnation by 2027 (SGP-MAPA, 2022).

The decline in European mussel cultivation has been attributed to several factors, including diseases, harmful algal blooms, and the impacts of climate change, as highlighted by previous studies (Álvarez-Salgado et al., 2009; Rodrigues et al., 2015; Fuentes-Santos et al. 2021; Outeiro et al., 2018). Another critical factor often cited for the decline in mussel production is the low and unpredictable availability of mussel seed (Filgueira et al., 2007; Avdelas et al., 2021). The dependence of current aquaculture on wild mussel seed stocks, which exhibit significant interannual fluctuation, compromises the sustainability of production in Northern European countries (Avdelas et al., 2021). Population dynamics shifts and mussel seed scarcity have been linked to global change (Handisyde et al., 2017; Petraitis and Dudgeon, 2020; Baden et al., 2021). Global change encompasses not only seawater warming but also a series of cascading effects across different temporal and spatial scales, potentially impacting the replenishment of natural populations (Scheffers et al., 2016).

The supply of mussel seed has not been considered a limiting factor for mussel (*Mytilus galloprovincialis*) cultivation on the Galician coast until recently. The main source of mussel seed comes from exposed intertidal rocky shores (Mariño et al., 1982; Pérez-Camacho et al., 1991), and it is tightly linked to the spawning of cultivated mussels, which concentrate the largest adult populations in Galicia (Fernández-Pulpeiro et al., 2002; Fernández-Pulpeiro and Aldariz, 2003). However, mussel farmers in the region have increasingly perceived a decrease in mussel seed availability from the rocky shore during the latter years of 2010s. This concern, communicated through the media, highlighted the lack of adequate spat stock monitoring programs to assess spatio-temporal variability in annual mussel seed availability and underscored the need for more flexible management strategies for its collection. Nonetheless, mussel farmers are required to officially report their annual mussel seed collections (tonnes and origin of the seed outplanted on their rafts), which they do with considerable variation in the frequency and detail on the information provided. However, these reports are the sole source of information on the mussel seed stock status in Galicia, and constitute a very valuable long-term time-series of mussel recruitment data. This data has not been systematically analyzed yet to link environmental factors with mussel seed spatio-temporal variability.

In addition to the possible impact of the changing environment, the recent scarcity of mussel seed in Galicia could also be related to the lower production of larger individuals, which may affect the reproductive efficiency of populations and lead to recruitment failures. The progressive preference for smaller individuals in the fresh mussel market has steadily increased over the last two decades, accounting for more than 60% of production in 2015 (Labarta and Fernández-Reiriz, 2019). This shift in production, driven by consumer preferences, also offers significant economic benefits for mussel growers by reducing culture cycles and losses, occasionally massive, attributed to dislodgement events during cultivation (Pérez-Camacho et al., 2013; Babarro et al., 2020). The shortening of cultivation timing could limit or reduce the number of spawning opportunities and optimal periods for reproduction before adult harvesting. In addition, adult size exponentially determines the number of gametes that can be produced which is proportional to spawner size (Oliveira et al., 2021) and could also determine its viability (Sukhotin and Flyachinskaya, 2009). Nonetheless, the analysis of the impact of harvesting progressively smaller mussels on the potential reproductive output of their populations and, consequently, the processes of fertilization and viability of larvae has not been investigated in detail for mussel culture in Galicia.

Therefore, our goal is to investigate the impact of both, environmental variability and shifts in the cultivation standards over the past two decades. We aim to understand their links to the interannual variability observed in mussel seed collection, using this as a proxy to assess the status and replenishment of natural mussel populations. With this purpose, we have analyzed, for the first time, the mussel seed collection reports from mussel farmers, compiling a 16-year time series of mussel seed recruitment. This information provides an updated assessment of the amount of mussel seed used in Galician mussel farming to sustain the current production levels and allows to identify the main environmental factors that explain its interannual variability. In addition, the spawning stock was also estimated to infer the impact of reducing the amount of large reproducers on the availability of mussel seed along the rocky shore. This approach deepens our understanding of how management practices and climatic alterations contribute to the scarcity of mussel seed. This will help to develop dynamic management measures that balance profitability with the long-term sustainability of mussel aquaculture, paying special attention to the interaction between climatic conditions and the maintenance of the natural stocks.

2 Materials and methods

2.1 About mussel production and the study area

Mussel aquaculture in Spain is primarily concentrated in rias, coastal bays of tectonic origin, located on the Galician coast (NW of the Iberian Peninsula; Figure 1). Among these embayments, the four rias located in the southern part of the Galician coast, named the "*Rías Baixas*", stand out for their high mussel production. The high productivity of these rias is largely influenced by upwelling regimes and river discharges (Álvarez-Salgado et al., 2000; Figueiras et al., 2002).

The coast of Galicia represents the northern limit of the Canary Current Eastern Boundary Upwelling Ecosystems (Arístegui et al., 2009; Chavez and Messié, 2009). On the west coast of Galicia, due to coastal upwelling dynamics, the northerly wind component drives the surface waters offshore, inducing the rise of deeper, cooler, and nutrient-rich subsurface waters close to the coast. Southerly winds have the opposite effect, they induce coastal downwelling that piles up warmer, nutrient-poor surface waters near the coastline. Throughout the seasonal cycle, northerly winds and coastal upwelling dominate from April to September while southerly winds and downwelling prevail during fall and winter (Pardo et al., 2011). The primary production associated with the coastal upwelling of nutrient-rich waters (Pauly and Christensen, 1995) makes the Galician coast (Arístegui et al., 2009; Santos et al., 2011) one of the most productive regions in the oceans and ideal for the aquaculture of marine bivalves (Kämpf and Chapman, 2016; FAO, 2018; Varela et al., 2018).

Mussel aquaculture in the Galician coast is carried out in 3387 floating rafts, which are rectangular wooden grids with a maximum surface area of 550 m2 and a maximum lateral length of 27 meters. 500 ropes of 12 meters length are hung from each raft (Decree 174/2002 amending Decree 406/1996). The ria named "*Ría de Arousa"* is the largest of the *Rías Baixas* covering an area of 245 km2 and hosting 2319 mussel rafts, 68% of total rafts in Galicia, distributed in several polygons (Figure 1). Other rias such as the "*Ría de Vigo"* and "*Ría de Pontevedra"* are also important areas of mussel production accounting for 14% and 10% of total rafts, respectively.

Mussel cultivation begins with the outplanting of mussel seed obtained from the intertidal rocky shore or from subtidal suspended collectors (Figueira et al., 2007). At the end of the last century, approximately 65% of the producers used exclusively seed from the rocky shore, while 10% employed only seed from collector ropes and the rest combined the two seed sources (Mariño et al., 1982; Pérez-Camacho et al., 1991). Thus, the intertidal rocky shore is the main source of seed for mussel aquaculture in Galicia (Cáceres-Martínez et al., 1993; Molares and Fuentes, 1995; Brea Bermejo, 2009). The extraction of this wild seed is permitted from December to April, when mussel farmers are allowed to collect a maximum of 3500 kg of mussel seed per raft through manual scraping of wild seed on rocks, following the regulations set by the Regional Administration (DOG N° 228 Order of 26th October, 2000).

Although mussel larvae can be found throughout the year at these latitudes, the reproductive cycle of mussels is characterized by a main peak of spawning during spring followed by a minor peak during the autumn (Villalba, 1995; Philippart et al., 2012; Philippart et al., 2014). The pelagic life of mussel larvae has an average duration of 4 weeks. After that time, they would search for a settlement substrate to metamorphose on the rocky shore (Seed, 1969; Aguirre, 1979; Widdows, 1991; Cáceres-Martínez and Figueras, 1998). Therefore, mussel seed harvested from the rocky shore during winter and early spring corresponds mainly to the autumn spawning peak, while the offspring of the main spring spawning peak is collected in the collector ropes of the rafts.

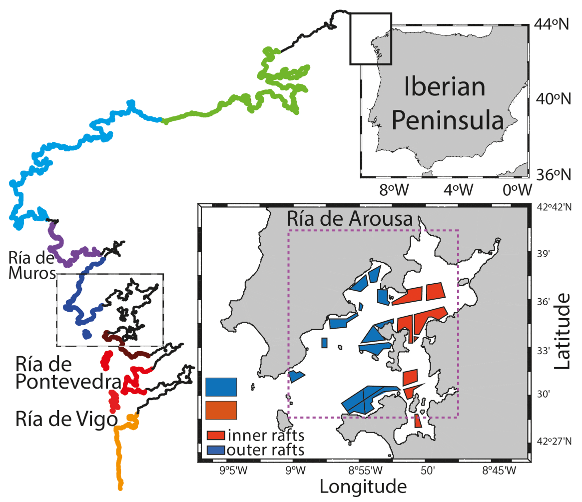

FIGURE 1
Map of the Galician coast with the coastal sectors for mussel seed collection (see Figure 8) and map of the Ría de Arousa, including the outer and inner mussel farming areas, and the window used for obtaining satellite measurements of temperature and chlorophyll.

2.2 Mussel seed collection time-series

Mussel seed collection reports were provided by mussel producers belonging to 6 associations of the *Ría de Arousa*, integrated into the OPMEGA organization (Organización de Productores de Mexillón de Galicia). These reports offer information on the amount of mussel seed harvested for each date, detailing the location of extraction and the raft of destination of the mussel seed. For this study, reports covering the period from the 2005–2006 to the 2021–2022 campaign (December to April) were used. Hereafter, these consecutive campaigns will be referenced by their closing year, thus referring to a study period from 2006 to 2022.

In total, 17363 records on mussel seed collections have been gathered over the entire study period. Inputs reporting the maximum authorized amount of mussel seed (3500 kg) on a single date have been excluded from the original database (totaling 261 entries) because of their lack of reliability. Accepted records were then grouped by destination raft for each campaign, resulting in a final database of 3720 annual reports of wild mussel seed harvested for individual rafts (Table 1). To account for the

TABLE 1 Annual summary of the reports in the database including: number of mussel rafts, percentage of the total mussel rafts in the area, average quantity and standard deviation of mussel seed collected for each raft in the outer and inner areas of the Ría de Arousa.

YEAR	outer region of Ría de Arousa				inner region of Ría de Arousa				Galician coast	
	n° bat	% bats	mean seed kg bat^{-1}	std seed kg bat^{-1}	n° bat	% bats	mean seed kg bat^{-1}	std seed kg bat^{-1}	Mussel seed t	std seed t
2006	102	8	2750	499	196	18	3002	298	8770	784
2007	102	8	2972	342	201	19	3078	292	9222	553
2008	45	4	2663	474	11	1	2596	477	8014	942
2009	110	9	2875	508	192	18	2891	603	8788	1134
2010	123	10	3067	427	213	20	3137	352	9456	739
2011	107	8	2969	505	194	18	3110	431	9266	926
2012	113	9	3016	542	202	19	3264	364	9574	906
2013	38	3	3054	547	24	2	3057	592	9313	1161
2014	64	5	2675	641	48	4	2635	644	8092	1325
2015	32	3	2986	805	46	4	2900	640	8969	1511
2016	105	8	2475	826	217	20	3041	562	8414	1463
2017	94	7	2102	750	182	17	2732	682	7376	1490
2018	107	8	2552	880	198	18	2929	757	8358	1720
2019	105	8	2496	788	175	16	2748	627	7995	1477
2020	58	5	2100	725	49	5	2116	630	6425	1405
2021	74	6	1997	794	66	6	2135	802	6299	1672
2022	61	5	2590	463	66	6	2031	830	7035	1398

Total quantity of mussel seed estimated for the mussel rafts in Galicia including the standard deviation calculated as the linear combination of the data obtained on mussel seed used in the outer and inner rafts of Ría de Arousa.

oceanographic heterogeneity of the *Ría de Arousa* (Alvarez-Salgado et al., 1996; Rosón, 1997), and differences in mussel productivity along the Ría (Pérez-Camacho et al., 2014; Babarro et al., 2018, Babarro et al., 2020; Padin et al., 2021), rafts were split into two distinct regions: an outer zone with 1262 rafts under greater oceanic influence and an inner, less productive, sheltered zone with 1057 rafts with higher river influence (Ulla and Umia rivers). This division ensured the availability of mussel seed collection reports from each raft group in every seed collection campaign (Table 1).

The quantity of mussel seed collected annually from the reports of the *Ría de Arousa* was extrapolated to the total number of mussel rafts in Galicia, classified equally as outer and inner rafts, resulting in 1849 and 1538, respectively. A total of 339 rafts were excluded from the outer rafts group to account for the 10% of producers which exclusively employ seed from collector ropes, which are usually located in the outer areas of the embayments (Mariño et al., 1982; Pérez-Camacho et al., 1991). Therefore, the average values for the inner and outer rafts of the *Ría de Arousa* were extrapolated to a total of 1510 outer and 1538 inner rafts to estimate the total amount of wild mussel seed used by the aquaculture sector in Galicia.

The geographical location of the wild seed collection sites was mainly provided with colloquial names (headlands, nearby beaches, islands, coastal stones, close-by towns…) without including geographical coordinates. The spat collection area used by the mussel farmers of the *Ría de Arousa* extends along the entire Atlantic coast of Galicia, covering more than 300 km. This coast was divided into 7 continuous segments of outer rocky shore areas (Figure 1). The quantities of mussel seed declared in each report were allocated among the corresponding sectors.

The average distance (km) from the headquarters of each association, that provided their mussel collection reports, to the center of each of the mussel seed collection sector was calculated using Google Maps. Generalized additive models (GAM), as implemented in the mgcv library of R 3.6.2 (R Core Team, 2018), were used to investigate the relationship between the amount of mussel seed collected at each sector and the distance by road between the association and the center of each segment. Model validation included the verification of homogeneity, normality, and independence assumptions (Zuur et al., 2009).

2.3 Estimation of egg life-time production under cultivation

Mussel production data are available at www.pescadegalicia.gal disaggregated by market destination in fresh and processed production. While mussels for the processing industry (canned, frozen, etc.) lack the information about specific size at harvest, mussels for fresh consumption are classified into three size categories according to the number of mussels per kg: small mussels (35 - 70 pieces kg^{-1}), medium (24 - 35 pieces kg^{-1}) and large (<24 pieces kg^{-1}). Using the relationship between weight (W) and antero-posterior shell length (L) ($L(mm)=23.398\ W(g)^{0.3377}$; r2 = 0.9811), obtained from monitoring of mussel growth in the *Ría de Arousa* during several cultivation cycles (unpublished data), the mean extrapolated shell length for each size category was 62.83 mm, 76.14 mm and 85.27 mm for small, medium and large mussels, respectively. Subsequently, these lengths were used to estimate the potential egg production of each individual during the spring spawning according to the formula:log (N° Eggs $mussel^{-1}$) = -1.43 + 2.99 logL (mm), R2 = 0.51 extracted from Oliveira et al. (2021) as the average of the northernmost populations evaluated, which are the most similar to the Galician coast. Autumn spawning capability was calculated with the same relationship, but dividing the result by 2 to account for the reduction of intensity of the autumn spawning peak with regard to the spring one (Philippart et al., 2012).

Following these assumptions, the potential egg production during each of the spawning peaks was estimated for an average production of 140K tonnes of mussels declared for fresh consumption during the 2006–2022 period. Since we assume mussel rafts are mainly seeded during winter, mussels are considered immature during their first spring under cultivation. Therefore, small mussels at harvest (8–10 months old) were considered to have only one spawning opportunity during the autumn peak (Aguirre, 1979), while medium (14–16 months old) and large sized mussels at harvest (17–19 months old) would contribute to both spawning peaks, first autumn and second spring under cultivation.

In order to estimate errors, the error propagation equation was applied (Bevington and Robinson, 2003) to each calculation step or transformation. The error for percentages of size category were estimated using the 25% of the standard deviation (6.25% of the variance) of the original time series and a 6.25% of the time covariance with the total fresh mussel production as initial errors. For the initial error of the number of mussel pieces per kilogram and size category a 25% of the size range for each category was used. Finally, for both sets of coefficients in the weight-length and length-egg potential equations a 1% of the absolute values of the coefficients was used to estimate their initial standard deviation.

2.4 Environmental conditions

The upwelling index at the geographical coordinates 42°N 10°W representing the region of interest, was obtained for the period between 2005 and 2021 from the Instituto Español de Oceanografías (http://www.indicedeafloramiento.ieo.es). This index is computed following Lavín et al. (1991) and based on 6-hourly geostrophic winds obtained from the Atmospheric Prediction System (NOGAPS) model, maintained by the Fleet Numerical Meteorology and Oceanography Center (FNMOC). This upwelling index has been previously identified as suitable for describing the oceanographic variability in the *Rías Baixas* (Gonzalez-Nuevo et al., 2014).

Chlorophyll-a concentration (Chl-a) and sea surface temperature (SST) were obtained from L4 satellite products with a spatial resolution of 0.05°. Whereas Chl-a was obtained from the Atlantic Ocean Color (GlobColour) Bio-Geo-Chemical product, SST was extracted from the European North West Shelf/Iberia Biscay Irish Seas product, both available at the Copernicus Marine Service (https://data.marine.copernicus.eu/). L4 products were selected because they are produced using a consolidated and consistent input dataset and have sufficient temporal coverage. The Chl-a and SST daily mean were estimated for the *Ría de Arousa* area, between 42.66°N - 42.46°N and 9°W - 8.78°W (Figure 1).

Daily discharge data for the main rivers flowing in the *Ría de Arousa* (Ulla and Umia) were obtained through the Spanish regional organization Augas de Galicia (https://augasdegalicia.xunta.gal/). Further information about gauging stations and the methodology can be obtained in Otero et al. (2010).

On one hand, temporal trends in environmental variables were explored with the Mann-Kendall test and Sen's slope computed using the *pyMannKendall* library (Hussain and Mahmud, 2019). A variant of this test, the Correlated Seasonal Mann-Kendall test (Hipel and McLeod, 1994), was performed when seasonality and autocorrelation were present in the time series. On the other hand, Rodionov (2004) methodology was applied to detect level shift, based on a sequential t-test analysis on the time series. Statistically significant deviations from the mean value were calculated with a software provided by NOAA (http://www.beringclimate.noaa.gov/regimes/index.html). A 10-year cut-off length and a Huber parameter of 1 were set (deYoung et al., 2004). Pre-whitening was performed before shift analysis to prevent autocorrelation (Rodionov, 2004). It is important to note that shifts detected close to the tails of the time series must be interpreted with caution under this methodology. A 0.05 significance level was set in both analyses.

In addition, oceanographic conditions during the larval phase prior to recruitment on the rocky shore were summarized for each of the years where mussel seed collection reports were available. Taking into account the seasonal presence of mussel larvae (Philippart et al., 2012), an average pelagic larval duration of 30–40 days (Cáceres-Martínez and Figueras, 1998) and post-settlement growth rates of around 0.23 mm day^{-1} for early recruits (Peteiro et al., 2007), it can take 4 to 6 months from the time of spawning to reach an appropriate size for mussel seed collection (< 2 cm). Therefore, the seed collected between December and April was considered as planktonic between July and November. SST, Chla-a and river flow between July and November were characterized from their median values for each year. The upwelling index between July and November of each year was summarized as the sum of the daily values of the upwelling index greater than 500 $m^3\ km^{-1}\ s^{-1}$. This value nearly coincides with the median of positive daily values of the upwelling index (493 $m^3\ km^{-1}\ s^{-1}$) during the period 2005–2021 and has been previously described as a threshold for detrimental effects on mussel settlement at certain locations (Peteiro et al., 2011) and the value at which the upwelling index induces the greatest change in the water column temperature (Otero et al., 2023). Simple linear regressions were employed to test for relationships between the interannual variability of the total amount of coastal wild spat collected for seeding in rafts and the oceanographic conditions observed during the larval phase prior to recruitment on the rocky shore.

Finally, the sum of the meridional wind component from July to November each year was calculated to explore correlations (Pearson's Correlation Coefficients) between the prevalent wind direction along-shore of each year and the amount of mussel spat collected at each of the 7 continuous segments of rocky coast designated.

3 Results

3.1 Environmental variability

The upwelling index computed in the outer waters of the *Rías Baixas*, SST and Chl-a estimations from satellite sensors and the fluvial discharge of the Umia and Ulla rivers were analyzed for the period 2005–2021. Monthly climatology values showed a marked seasonal pattern of these variables (Figure 2).

The upwelling index showed positive mean values between March and September with a maximum in August of 647 ± 761 m^3 km^{-1} s^{-1} when northerly winds dominated (Figure 2A). In contrast, the autumn and winter seasons were characterized by negative values, especially in December with -454 ± 1027 m^3 km^{-1} s^{-1} under the dominance of southerly winds. The variability of the upwelling index throughout the seasonal cycle was generally lower during the months with positive coastal upwelling (Figure 2A).

The daily SST of the *Ría de Arousa* was 15.05 ± 1.87°C with a total range between 10.67°C and 20.27°C (Figure 2B). The monthly mean temperature was highest in July with 17.2 ± 0.8°C while the coldest waters of 12.7 ± 0.5°C were observed in February. Chl-a concentration (Figure 2C), which had a mean value of 7.24 ± 6.90 mg m^{-3}, showed the highest values during the upwelling season, with a peak of 9.6 ± 6.6 mg m^{-3} in August. In contrast, lower and less variable Chl-a was recorded during the autumn and winter, with a minimum mean value of 3.2 ± 1.9 mg m^{-3} in January. The joint discharge of the Umia and Ulla rivers (Figure 2D) showed a strong seasonal cycle with higher values from November to February, a period characterized by southerly winds and wet weather conditions, and a maximum of fluvial discharges in December.

Monthly mean variability 2005–2021 is shown (Figure 3) along with the 12-month moving average showing positive (red) and negative (blue) periods with respect to a zero baseline in the upwelling and to the mean in the Chl-a and SST series. The upwelling index alternated between positive and negative interannual anomalies shorter than 2 years between 2005 and 2015, with a clear predominance of positive anomalies in 2016–2021 (Figure 3A). In addition to a marked seasonal variability, the surface temperature in the Ría de Arousa also showed a succession of warm and cold interannual intervals throughout the study period (Figure 3B). These periods were mainly modulated by an inverse

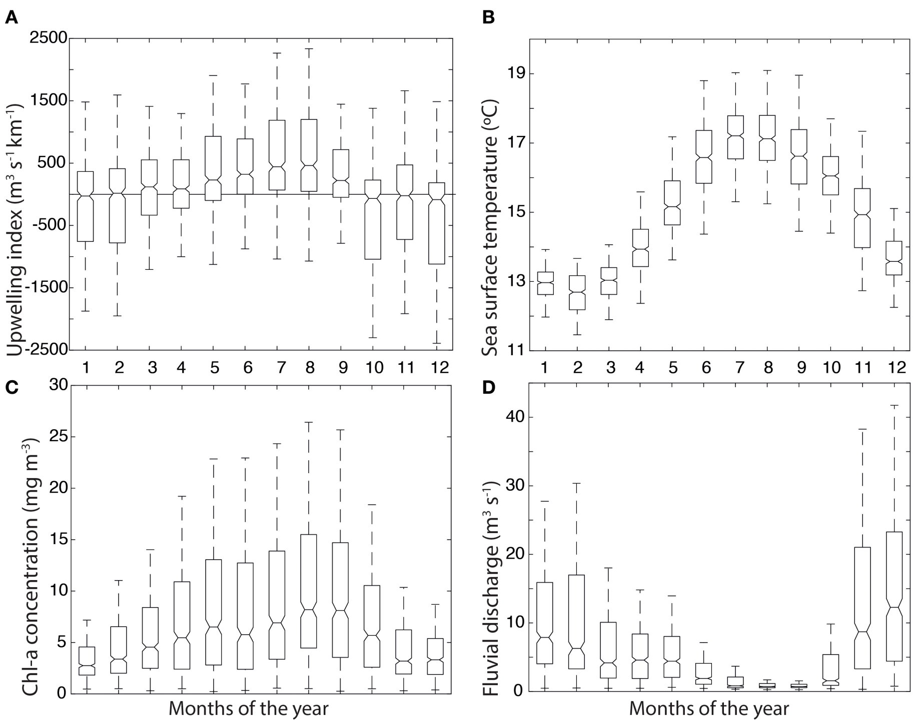

FIGURE 2
Boxplot of the seasonal variability of the **(A)** upwelling index, **(B)** sea surface temperature, **(C)** chlorophyll concentration, and **(D)** river discharge of Umia-Ulla rivers in the Ría de Arousa.

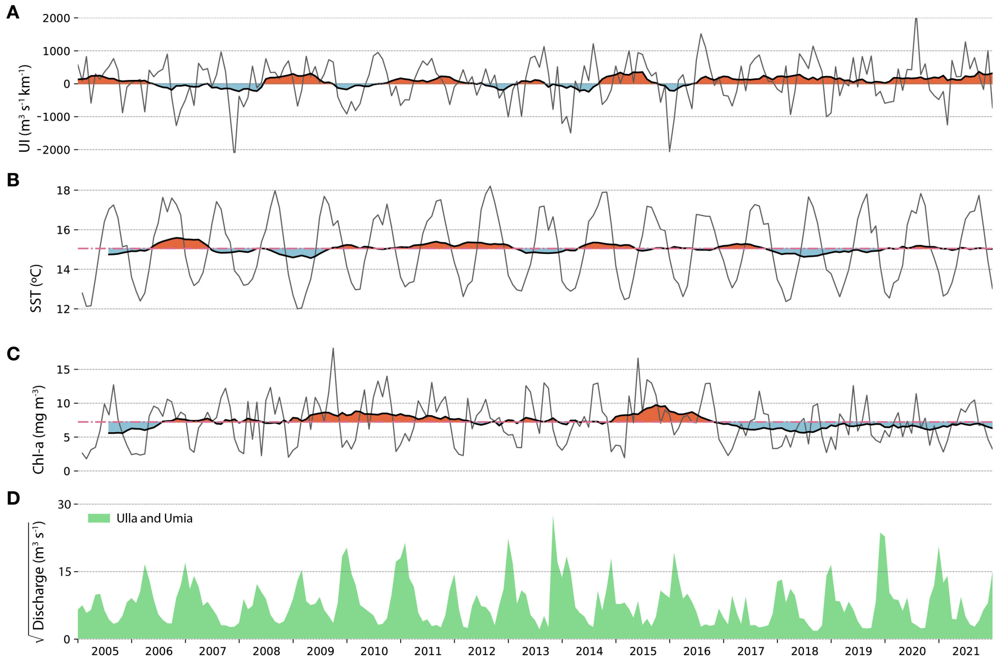

FIGURE 3
Monthly mean time series of **(A)** upwelling index, **(B)** chlorophyll concentration and **(C)** sea surface temperature in the Ría de Arousa and **(D)** the square root of the discharge of Umia-Ulla rivers instead of its mean monthly value in order to allow graphical visualization of maximum and minimum values. Red (blue) areas highlight positive (negative) anomalies from the mean in the Chl-a and SST, and from a zero-based line in the upwelling index. The black line is the 12-month average running mean of the time series.

relationship with the interannual anomalies of the upwelling index. Periods of cool surface waters were coincident with positive upwelling index anomalies (2008–2009) while warm waters were observed during periods of particularly negative upwelling index (2006–2007). Nevertheless, the impact of upwelling did not seem to be as evident in the interannual temperature anomalies during other periods.

Chl-a showed two clear phases throughout the study with a period between 2006 and 2015 dominated by positive anomalies and a final period with negative anomalies between 2016 and 2021 (Figure 3C).

None of these parameters showed a significant interannual trend in the period 2005–2021. Neither did the upwelling index and Chl-a, despite showing a significant shift in 2016.

3.2 Mussel seed collection temporal trends

A total of 3720 annual quantities of mussel seed collection from individual rafts were analyzed for the 17 years period (Table 1; Figure 4), with a large variability on the number of rafts recorded per year, which ranged from 56 to 336 for 2008 and 2018, respectively (Table 1). This information represented 7 ± 2% and 12 ± 7% (mean ± std) of the total number of 1262 outer and 1057 inner rafts in the *Ría de Arousa*, respectively. The average amount of mussel seed collected for the outer rafts (2679 ± 712 kg raft^{-1}, n=1440) was significantly lower (two-sample z-test: $p<0.05$) than the average amount destined for the inner rafts (2917 ± 619 kg raft^{-1}, n=2280) (Figure 4A). Despite this difference, the interannual variability is similar in the two groups with an initial increasing trend in mussel seed collection until 2012–2013 when maximum wild seed collection of 3264 kg raft^{-1} and 3054 kg raft^{-1} were observed for the inner and outer region, respectively (Figure 4B; Table 1). From these maximum values, mussel seed collection decreased until 2022 at a rate of -78 ± 31 kg raft^{-1} yr^{-1} in the outer rafts and -107 ± 22 kg raft^{-1} yr^{-1} in the inner rafts. This decreasing trend is also observed in a group of 12 singular rafts (10 outer and 2 inner) that provided data for the entire period 2006–2022. These rafts analyzed separately and standardized (Figure 4C), reinforce the decreasing trend of wild seed collected between 2013 and 2021 (Figure 4B).

The average amount of seed collected estimated for the total number of rafts on the Galician coast for the period 2006–2022 is 8316 ± 1027 tonnes (Figure 4D) with a maximum value of 9575 tonnes in 2012 and a minimum harvest of 6300 tonnes in 2021. A decreasing trend of -148 ± 36 t yr^{-1} (p-value<0.01, r^2 = 0.53) characterized mussel seed availability on the Galician coast for the period 2006–2022 (Figure 4D; Table 1). This interannual decline was particularly pronounced from 2012 onwards with a rate of -288 ± 55 t yr^{-1} (p-value<0.01, r^2 = 0.75).

With regard to the influence of oceanographic conditions during the larval phase on the interannual variability observed on the total amount of coastal wild spat collected for seeding in rafts only the sum of upwelling index values greater than 500 m^3 km^{-1} s^{-1}

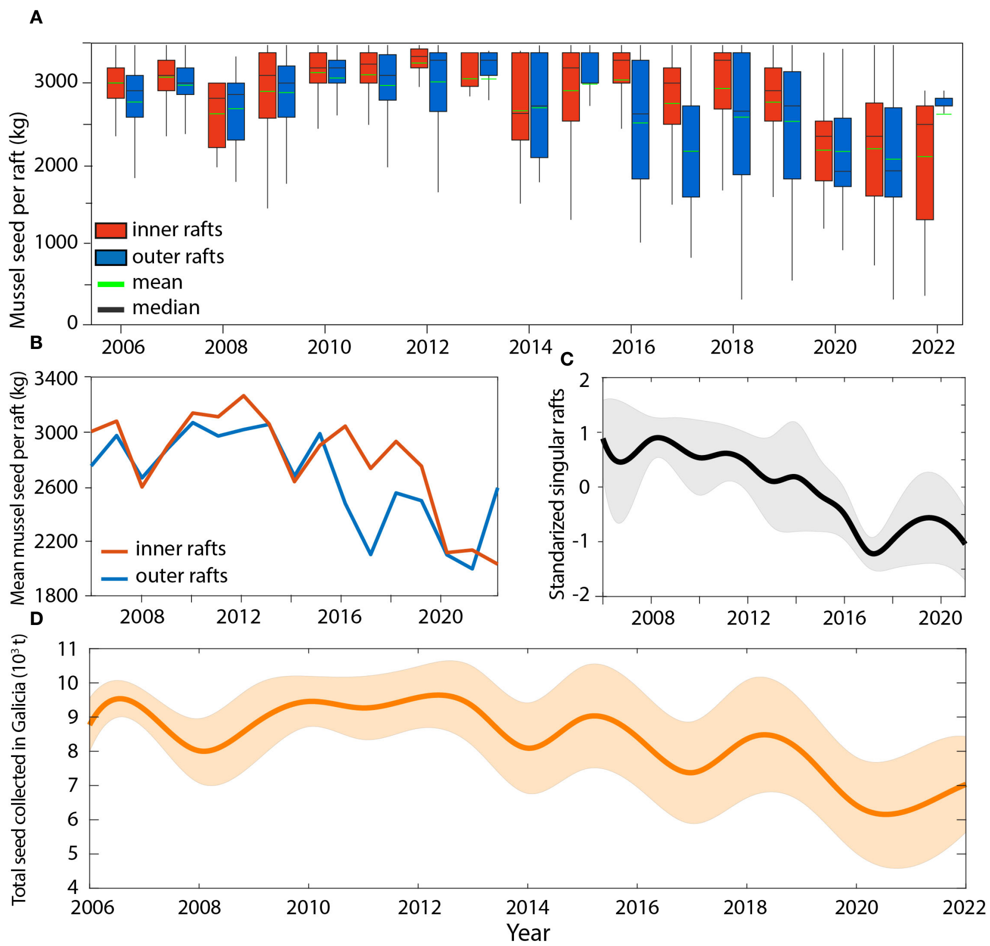

FIGURE 4
(A) Boxplot of the mussel seed quantity allocated to the inner and outer mussel farming areas of the Ría de Arousa. **(B)** Time series of the average mussel seed used in both outer and inner mussel rafts. **(C)** Time series of the mussel seed used in 12 rafts with data available for all years between 2006 and 2022. Values are normalized by dividing the difference between the reported quantities of wild seed and the mean value of mussel seed collected for each raft by the standard deviation. **(D)** Evolution of the total mussel seed quantity collected for all mussel rafts in Galicia based on Ría de Arousa data for all mussel rafts in Galicia.

and the median of the Chl-a concentration were significant (Figure 5).

The sum of upwelling index values greater than 500 m^3 km^{-1} s^{-1} showed a significant negative correlation with the averaged amount of mussel seed collected (Figure 5A). The amount of intense events explained as much as 60% of the interannual variability observed on mussel seed collection along the Galician coast (r^2 = 0.60; Figure 5B) In addition, the number of days with intense upwelling events showed an interannual increasing rate of 1.0 ± 0.4 days per year (r^2 = 0.25; $p<0.05$) ranging from 38 to 70 days for the period between July and November between 2006 and 2022, and an average value of 51 days.

In contrast, the median of the Chl-a concentrations in the *Ría de Arousa* (Figure 5A) showed a positive relationship with the amount of mussel seed collected, explaining 26% of the interannual variability observed (r^2 = 0.26; Figure 5C). On the other hand, SST and river discharge did not show significant correlations with the amount of mussel seed collected.

3.3 Mussel seed collection spatial trends

Mussel seed destined for the mussel raft cultivation in the *Ría de Arousa* was collected at more than 150 locations along ~300 km of the Atlantic coast of Galicia (Figure 1). Preferential sites for mussel seed collection of each association is mainly determined by distance (Figure 6A), with most of the seed collected within 50 km from the headquarters of the association and only 10% collected farther than 150 km. Accordingly, mussel farmers whose associations are located on the north shore of the *Ría de Arousa* were preferentially collecting seed from the northern sectors, while the opposite happened with the associations located on the south shore, which travelled preferentially to the southern locations. To analyze spatial variability of mussel seed availability during the study period without bias related to the distance to the association headquarters, only years with reports of associations from both shores of the *Ría de Arousa* were considered. The reported annual quantities of wild seed were weighted to equal the total amount of

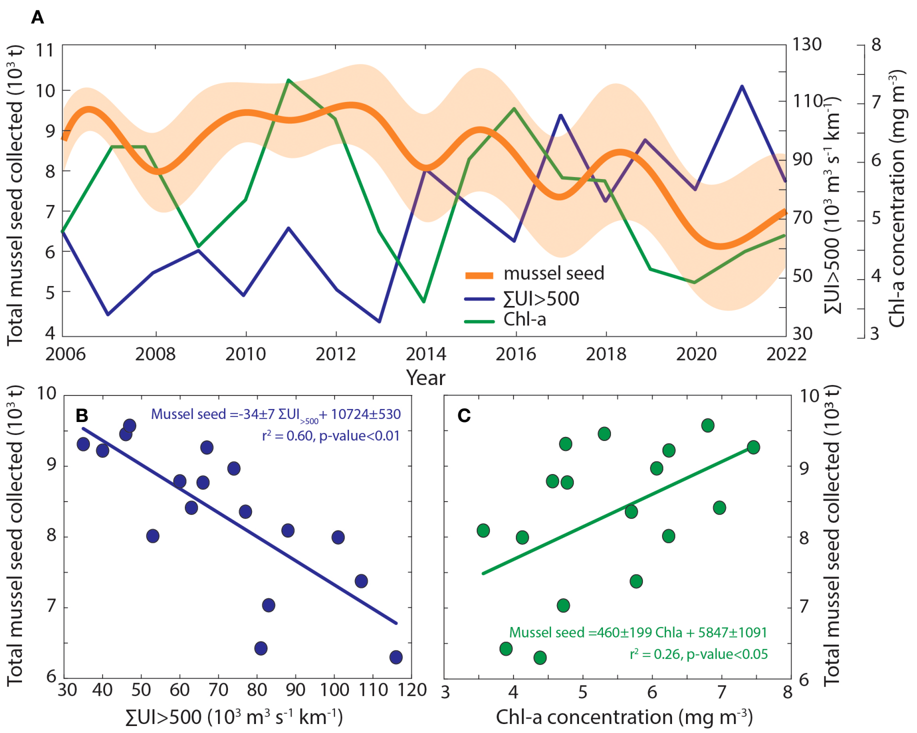

FIGURE 5
(A) Time series of the estimated mussel seed quantity for all mussel rafts in Galicia and the mean values of chlorophyll concentration and the sum of the upwelling index with values above 500 m^3 km^{-1} s^{-1} between July and November. **(B)** Linear relationship between the total mussel seed quantity and the sum of the upwelling index with values above 500 m^3 km^{-1} s^{-1} and **(C)** chlorophyll concentration.

mussel collected from each shore before calculating the percentage of seed supplied from each segment of the Galician coast to the mussel rafts in the *Ría de Arousa* (Figure 6B).

The rocky shore immediately north (North_1) and south (South_1) of the *Ría de Arousa* were the preferred harvesting areas contributing 36 ± 22% and 27 ± 15% of the total mussel seeds respectively. The third most common origin was the southern shore of the *Ría de Pontevedra* (South_2) with 25 ± 11% while the southernmost area of the Galician coast (South_3) contributed only 2 ± 3% to the total seed collected. The areas to the north (North_2, North_3 and North_4) contributed 6 ± 3%, 2 ± 2% and 2 ± 3% of the total amount collected by mussel farmers of the *Ría de Arousa*, respectively. It is also worth noting that regular visits to the most distant locations (North 4 and South 3) only started to be visited regularly for mussel seed collection from 2013.

The amount of mussel seed collected within each coastal sector exhibited pronounced interannual variability. The collection of mussel seed between 2010 and 2014 was primarily conducted along the northern shoreline of *Ría de Arousa* (North_1), surpassing 60% in 2013 and 2014. Although with a lower contribution to the total amount of mussel seed collected, North_2 and North_3 sectors showed high positive correlation coefficients with the North_1 segment (r= 0.89 and r=0.65, respectively; Table 2). In contrast, the northernmost and more distant sector (North_4) exhibited a significant inverse correlation with regard to the rest of sectors to the north of *Ría de Arousa* (Table 2).

In the period 2016–2020, the main sector for harvesting wild seed shifted to the southern segments of *Ría de Arousa*. This transition was notably pronounced in 2016 when the southern shore of the *Ría de Arousa* (South_1) supplied a maximum value of 55% of the total mussel seed, while the northern shore (North_1) contributed only by 1% (Figure 6B). Even the sector encompassing the southern coast of *Ría de Pontevedra* and the northern region of *Ría de Vigo* (South_2) emerged as the preferred region for seed collection in the year 2020. During the latest campaign, 2022, the coastal segment that contributed the highest percentage was once again North_1 sector, although the quantities of wild seed harvested from the north and south of *Ría de Arousa* were similar. In general, there is an inverse relationship between the amount of mussel seed collected from the north and south sectors (Table 2). However, while the northern areas demonstrated some consistency in their interannual variability, the three southern segments of the *Ría de Arousa*, which represent the margins of important mussel production areas such as the *Ría de Arousa*, *Ría de Pontevedra* and the *Ría de Vigo* did not exhibit statistically significant correlations between them. An unexpected finding was the significant positive correlation (r=0.78) between the northern (North_4) and southern (South_3) sectors, located at the furthest points from *Ría de Arousa*.

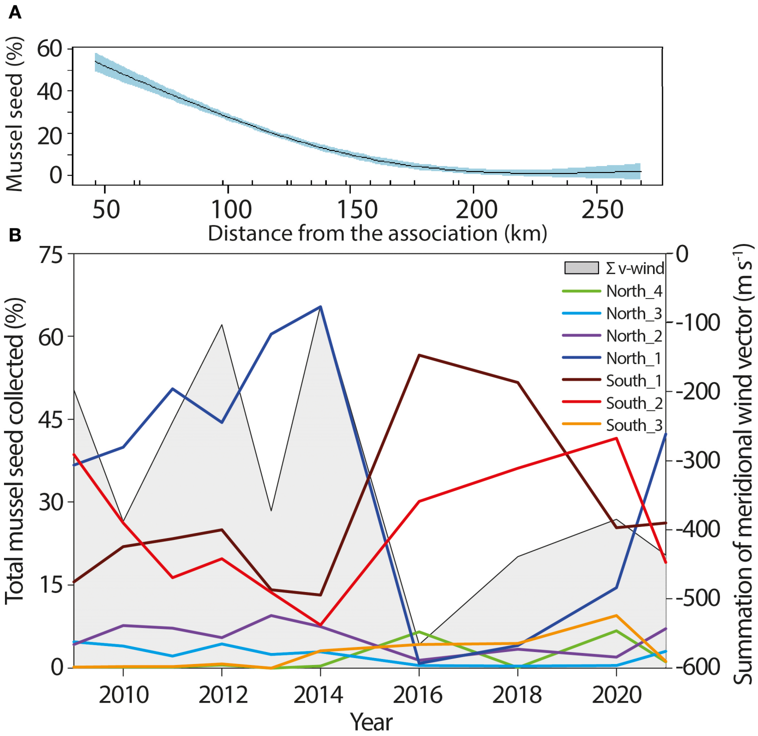

FIGURE 6
(A) Dependence of the percentage of mussel seed collected and the road distance from the mussel farmers' association to the collection site. **(B)** Time series of the percentages of mussel seed collected in the coastal sectors described in Figure 1 and the sum of the meridional wind stress between July and November, where the lower negative values of Σv-winds indicate lower prevalence of northerly winds, since positive values of v indicate wind is coming from the South while negative values of v indicate wind is coming from the North.

The two distinct periods evidenced by contrasting mussel preference collecting zones also exhibited a clear disparity in the prevailing meridional wind patterns. These patterns were determined by calculating the sum of the meridional wind component from July to November each year. The preference of areas north of the *Ría de Arousa* as the main seed source during the period 2010–2014 was observed under a greater dominance of southerly winds (Figure 6). Conversely, a shift towards a dominance of northerly winds in the period from 2016 to 2020 placed the harvesting areas to the south of *Ría de Arousa*. The correlation coefficient between the southern wind component and the main mussel harvesting areas on both, the southern (South_1) and northern (North_1) shores of *Ría de Arousa* exhibited identical magnitudes (|r|=0.68) but opposite signs, with a negative relationship for the southern shore and a positive one for the northern shore (Table 2). In addition to these areas, a statistically significant correlation with wind patterns was only observed in the sector North_3. This segment, which does not have any major estuaries, is located in the westernmost corner of the Galician coast just north of the mussel production areas. The positive correlation between southerly wind and wild seed collected in this area was 0.63 despite having an exclusively natural mussel population.

TABLE 2 Correlation matrix with the significant coefficients between the percentages of wild mussel seed collected in each of the coastal sectors between 2006–2022 and the sum of the meridional wind component (∑V) between July and November.

	South_3	South_2	South_1	North_1	North_2	North_3
South_3						
South_2						
South_1						
North_1	-0.62	-0.81	-0.87			
North_2	-0.71	-0.80	-0.69	0.89		
North_3	-0.75		-0.68	0.65		
North_4	0.78			-0.65	-0.75	-0.63
Σ v			-0.68	0.68		0.63

3.4 Mussel production management trends

The mussel aquaculture production in Galicia for the period 2006–2022 (Figure 7A; Table 3) was mostly dedicated to fresh consumption (53%), while 47% went to the processed industry for canned, frozen or other derivative products.

The total mussel aquaculture production exhibited in general terms a significantly positive trend (3703 ± 1135 t yr^{-1}; $r^2 = 0.40$) for the studied period when the peak of production of 2006 is excluded (an outstanding production year of 290K tonnes dedicated towards industry (65.5%).

In addition to the increase in total mussel production, a progressive shift towards small commercial sizes was also observed (Figure 7B). The fraction of production dedicated to small mussels (45–70 pieces kg^{-1}) increased at a rate of 3660 t yr^{-1}, going from 50% to almost 70% of the fresh production during the study period. Accordingly, large mussels (<24 pieces kg^{-1}) decreased their contribution to the fresh production at a rate of -543 t yr^{-1}, dropping from 25% to 10% of the production during the study period. Medium-sized mussels kept more or less the same percentage of the fresh production (24%), with a slight decreasing rate of -0.2% yr^{-1}. This shift in market preferences towards smaller individuals is even more evident when the percentage of mussel production in tonnes is transformed to the number of mussels of each size (Figure 7C).

The impact of this change in the number of individuals of each size was analyzed in terms of their potential egg production (Figure 8). For this purpose, egg production was estimated for a stable production of 140K tonnes with the variability of the observed mussel size fraction. The mean egg production in autumn in both situations was 36 10^{12} eggs with a significant increasing interannual trend of 0.07 ± 0.01 10^{12} eggs yr^{-1}. When including spring in this analysis to calculate lifetime egg production of the cultivated population, the mean potential production would almost doubled (61 10^{12} eggs), but a decreasing trend of -0.60 ± 0.09 10^{12} eggs yr^{-1} arise, since the fraction of small mussels would be harvested before their reach their second spring and the contribution of big mussels have continuously decreased over the last decade (Figure 8).

4 Discussion

This analysis is based on the first compilation of reports on the quantities of mussel seed collected and declared by mussel farmers in the *Ría de Arousa* for the period 2006–2022. This large amount of unpublished information constitutes the only time series record of mussel seed availability along the Galician coast. Despite certain methodological limitations, this information allows for the first time to study the effect of changes in aquaculture management and environmental variability on the regulation of mussel settlement.

This 17-year time series has revealed the progressive decline in the amount of wild mussel seed collected (Figure 4) on the Galician coast since 2012. This decline is more pronounced in the inner rafts (-107 ± 22 kg $year^{-1}$ $raft^{-1}$) than in the outer ones (-78 ± 31 kg $year^{-1}$ $raft^{-1}$) which on average use a 9% more mussel spat from the rocky shore for seeding their ropes (2917 ± 619 kg $raft^{-1}$ and 2679 ± 712 kg $raft^{-1}$ for the inner and outer rafts respectively). The lower dependency on wild seed in the rafts located in the outer estuarine zones would be associated with the higher efficiency of suspended collector ropes for seed capture at the most exposed locations (Pérez-Camacho et al., 1991; Peteiro et al., 2007; Peteiro et al., 2011).

The extrapolation of these data to the entire Galician production, resulted in an annual quantity of wild seeds collected of 8316 tonnes on average, with a range that oscillates between 9575 and 6300 tonnes estimated for 2012 and 2021, respectively. These quantities of wild mussel seed are higher than the 7500 tonnes

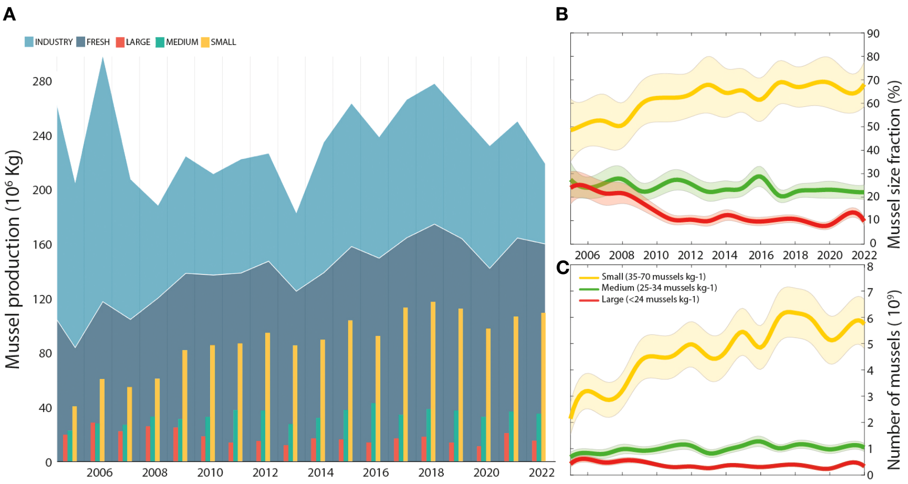

FIGURE 7
(A) Mussel production destined for the industry and for fresh consumption from 2006 to 2022, indicating the proportion of mussel sizes. **(B)** Evolution of the number of individuals produced for fresh consumption in each size class of mussels: small, medium, and large. **(C)** Number of individuals produced for fresh consumption in each mussel size class: small, medium and large.

TABLE 3 Annual summary of mussel production collected by www.pescadegalicia.com for industry and for fresh consumption.

year	total	industry	fresh		Small (35–70 ind kg^{-1})				Medium (25–34 ind kg^{-1})				Large (<24 ind kg^{-1})			
							individuals				individuals				individuals	
	10^3t	10^3t	10^3 t	ind 10^6	10^3t	%t	10^6	%	10^3t	%t	10^6	%	10^3t	%t	10^6	%
2005	205.2	121.2	84.1	3238	40.8	49	2141	66	23.1	27	693	21	20.2	24	404	12
2006	298.9	180.9	118.0	4622	60.9	52	3196	69	28.3	24	850	18	28.8	24	575	12
2007	208.2	103.3	104.9	4154	54.9	52	2881	69	27.4	26	821	20	22.6	22	452	11
2008	188.8	68.2	120.6	4732	61.1	51	3208	68	33.4	28	1001	21	26.2	22	523	11
2009	225.1	86.2	138.9	5756	81.9	59	4302	75	31.6	23	947	16	25.3	18	507	9
2010	212.0	74.4	137.6	5867	85.7	62	4497	77	33.1	24	994	17	18.8	14	376	6
2011	222.9	83.8	139.1	5984	86.8	62	4557	76	38.0	27	1141	19	14.3	10	286	5
2012	227.2	79.4	147.8	6412	94.7	64	4974	78	37.7	25	1131	18	15.4	10	308	5
2013	183.2	57.4	125.7	5568	85.4	68	4482	80	28.0	22	839	15	12.4	10	248	4
2014	235.5	96.0	139.4	6031	89.8	64	4714	78	32.4	23	972	16	17.2	12	344	6
2015	264.1	105.4	158.7	6926	103.7	65	5446	79	38.2	24	1146	17	16.7	11	335	5
2016	239.3	89.2	150.1	6436	92.4	62	4849	75	43.2	29	1297	20	14.5	10	290	4
2017	266.9	101.8	165.1	7331	113.3	69	5949	81	34.6	21	1038	14	17.2	10	345	5
2018	278.7	103.6	175.1	7710	117.5	67	6168	80	38.9	22	1168	15	18.7	11	374	5
2019	255.5	91.2	164.3	7314	112.3	68	5897	81	37.7	23	1131	15	14.3	9	286	4
2020	232.8	90.3	142.5	6360	97.9	69	5137	81	33.0	23	991	16	11.6	8	232	4
2021	250.9	85.9	165.0	7137	106.6	65	5597	78	37.2	23	1117	16	21.1	13	423	6
2022	238.2	59.1	160.6	7121	109.4	68	5742	81	35.5	22	1065	15	15.7	10	314	4

The quantity of mussels destined for fresh consumption is disaggregated by mussel size classes (small, medium and large) indicating their weight percentage, the number of individuals considering a usual market classification of individuals per kilogram and the percentage that the individuals of each class represent of the total production of mussels destined for fresh consumption.

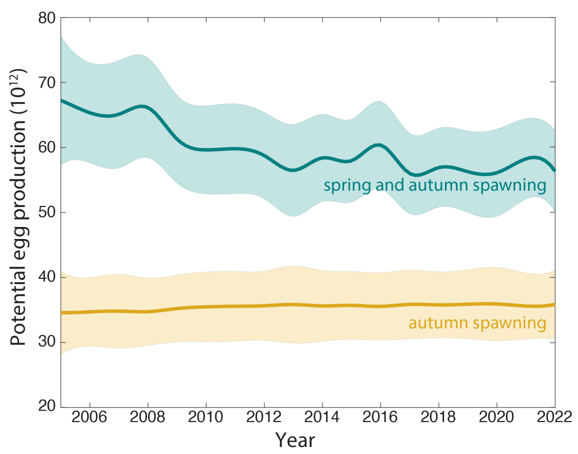

FIGURE 8
Time series of the estimated potential egg production of an average production of 140K tonnes but with the observed interannual variability of each size category in autumn (yellow lines) and in spring and autumn (blue lines) using the relationship between mussel size and number of eggs described by Oliveira et al. (2021).

(Camacho et al., 1995) and 6540 tonnes (Cáceres-Martínez and Figueras, 2007) estimated at the end of the 20th century as the amount of mussel seed necessary to maintain mussel cultivation. Considering that 10% of the rafts use exclusively collector seed and 25% combine both sources (Mariño et al., 1982; Pérez-Camacho et al., 1991), the contribution of collector ropes to the total seed would be approximately 22.5%. Assuming these percentages, the wild seed contribution from the rocky shore would have been around 5440 tonnes according to these previous studies (Camacho et al., 1995; Cáceres-Martínez and Figueras, 2007) and would have increased by 53% to our average estimate of 8316 tonnes. Furthermore, our calculations, which would represent 77.5% of the mussel seed destined for cultivation, would also raise the total seed required to an average of 10730 tonnes.

The entire time series of wild seed destined for the total number of mussel rafts in Galicia estimated from mussel farmers' reports exhibited an annual reduction of 148 ± 36 t yr^{-1} which reached 288 ± 55 t yr^{-1} from 2012 onwards. This decline follows the reduction in recruitment and stability observed in natural mussel populations across different coasts of the Atlantic and Pacific Oceans which have been mainly attributed to environmental changes and overexploitation (Sorte et al., 2017; Commito et al., 2019; Petraitis and Dudgeon, 2020; Avdelas et al., 2021). The variable explaining the larger amount of this variability (60%) was the intensity of upwelling between July and November, specifically the recurrence of intense upwelling events (>500 m^3 km^{-1} s^{-1}), which have a detrimental effect on the abundance of mussel seed. Similar results have been reported before in the NW Pacific Coast (Menge et al., 2022), and also at the Galician rías, where the adaptation of mussel larvae to the characteristic intermittence of upwelling has been highlighted (Peteiro et al., 2011). Prevailing northerly winds, favorable to nearshore upwelling, may be behind the offshore transport of larvae during the pelagic phase of the mussel and can also prevent the accumulation of phytoplankton. Recently, a study by Otero et al. (2023) has determined that upwelling index values around 500 m^3 km^{-1} s^{-1} would be a threshold for the activation of temperature changes in the water column of rías, and presumably, the limit for most noticeable effects on actual upwelling conditions. Our data also showed an increase in the number of days with an upwelling index above this threshold value over the period 2006–2022. Although many larval behaviors have evolved to avoid offshore wastage in upwelling systems (Shanks and Brink, 2005; Queiroga et al., 2007), several studies agree on reporting lower recruitment rates in areas with persistent downwelling or upwelling conditions (Navarrete et al., 2005; Broitman et al., 2008; Dudas et al., 2009; Menge et al., 2003; Smith et al., 2009). Intermittent upwelling, and the reversal currents associated with that process, might play a major role in regulating larval behavior and transport, as has been described before (Guisande et al., 2001; Otero et al., 2008, Otero et al., 2009; Peteiro et al., 2011; Pfaff et al., 2011; Bashevkin et al., 2020). Our results would confirm the importance of the frequency and variability of wind-driven currents as a key factor in recruitment success for autumn mussel spawning on the Galician coast (Pérez-Camacho and Román-Cabello, 1979; Mariño et al., 1982; Cáceres-Martínez et al., 1993; Villalba, 1995).

As stated above, the system has an evident response to regional winds, modulated in their persistence and duration by the atmospheric variability of the North Atlantic (Fraga, 1981; Blanton et al., 1984). Climate indices such as the North Atlantic Oscillation (NAO; Hurrell, 1995) and the East Atlantic (EA; Barnston and Livezey, 1987) capture the variability of recurrent spatial patterns at the basin level. The coupled patterns of the NAO and EA enhance upwelling, especially in winter (Dickson et al., 1988; deCastro et al., 2008). The decrease in seed availability began in 2012, coinciding precisely with significant changes in NAO and EA, which experienced a positive shift in their mean values (see Figure 5 in Otero et al., 2023) that contributed to the expansion of the subpolar gyre (de Jong and de Steur, 2016; Josey et al., 2018) and consequently, a freshening of the surface waters in the eastern subpolar North Atlantic basin (Holliday et al., 2020). Although it is difficult to establish a cause-effect relationship due to the different scales involved, it is not negligible that abrupt atmospheric, thermohaline, and seed availability changes coincide in time. In contrast to NAO, EA and seed variables showed a significant correlation between winter EA values and subsequent seed reports (r=0.44; p=0.01). Understanding system variability through these indices could potentially contribute to predicting the recruitment success of wild seeds on the coast.

In addition to the influence on larval transport processes, the wind pattern also affects temperature and food availability in the area. In this respect, increasing temperature has a complex effect on the mussel population, since it increases growth but could also have a detrimental effect on condition index and reproductive output when certain thresholds are surpassed (Franz et al., 2019; Menge et al., 2022), although its effect is largely modulated by food availability. Our results did not show a significant effect of temperature on mussel seed abundance, but we do detect a positive effect of Chl-a, which explains 25% of the variability observed. Chlorophyll concentration has a well-established effect on larval production and settlement of mussel recruits (Suárez et al., 2005; Broitman et al., 2008; Peteiro et al., 2010, Peteiro et al., 2011; Fuentes-Santos et al., 2014; Fuentes-Santos and Labarta, 2015; Fuentes-Santos et al., 2016), and is a proxy for food availability that would affect both, the physiological condition of the spawning mussels and larval development.

The inverse correlation between Chl-a and the annual cumulative sum of the upwelling index exceeding 500 m^3 km^{-1} s^{-1} (p-value=0.11) seems contradictory to the expected direct response of phytoplankton biomass to increased nutrient inputs resulting from enhanced upwelling (Gregg et al., 2005). However, the growth of phytoplankton is favored by the succession of upwelling and downwelling events (Figueiras et al., 2002). The intense and/or persistent upwelling events could hinder from assimilating the nutrient injection due to the reduction of the retention time of the water within the estuary (Gilcoto et al., 2007; Largier, 2020) and the flushing of phytoplankton biomass offshore (Álvarez-Salgado et al., 2008). In this sense, increasing intensity of upwelling has also been related to a reduction of the impact of harmful algal blooms in the Rías Baixas (Álvarez-Salgado et al., 2008). Although coastal upwelling has a direct positive effect on productivity and consequently on mussel growth (Pérez-Camacho et al., 1991; Figueiras et al., 2002) and condition index (Blanton et al., 1987; Figueiras et al., 2002), maintaining its characteristic intermittent nature is key to ensure population equilibrium, particularly to ensure recruitment and replenishment of natural populations (Peteiro et al., 2011).

Our results suggest an important role of upwelling intensity in the offshore advection of larvae and its distribution along the coast as has been reported before (McQuaid and Phillips, 2000; Ruiz-Villarreal et al., 2008; Pineda et al., 2010; Peteiro et al., 2011; Reis, 2015; Nolasco et al., 2018; Demmer et al., 2022). The selection of wild seed collection sites has a strong dependence on the meridional component of the wind between July and November. According to the correlations observed between the preferential areas for mussel collection and the meridional wind component, the prevalence of upwelling favorable winds observed between 2016 and 2020 favored the settlement on the southern areas of the Galician coast, while downwelling favorable winds registered from 2010 to 2014 favored larval transport towards the north. The role of wind in controlling the connectivity of mussel populations has been reported before as a key element regulating meta-population persistence (Peteiro et al., 2011; Gomes et al., 2016; Franz et al., 2019; Bashevkin et al., 2020;

Demmer et al., 2022). Since most of the mussel rafts are concentrated in *Ría de Arousa*, this is a key "source" sub-population for the Galician coast (Reis, 2015), and predominant winds will highly determine the role and relevance of different "sink" sub-populations and regions along the coast. Some exercises on meta-population modelling to understand key processes for mussels populations persistence (Carson et al., 2011) have highlighted the relevance of self-recruitment at the main source subpopulation as a key factor to ensure meta-population growth.

The distribution of wild seed collection sites also shows how mussel farmers started to travel longer distances since 2014 (North 4 and South 3; Figure 6), indicating an increase in the effort needed to obtain the required mussel spat for seeding their rafts. The observed decline in mussel seed availability also encompasses the general trend of declining natural mussel populations observed along the Atlantic and Pacific coasts (Sorte et al., 2017; Commito et al., 2019; Franz et al., 2019; Petraitis and Dudgeon, 2020; Avdelas et al., 2021; Baden et al., 2021; Menge et al., 2022). Certain studies document as much as a 60% reduction in mussel populations during the last 40 years (Sorte et al., 2017), motivated by mass mortality events but also by continuous declines in mussel recruitment (*M. edulis*) estimated at 15.7% less recruitment per year by Petraitis and Dudgeon (2020) in the western North Atlantic. Over-exploitation and climate change are the most often reported causes of this decline (Baden et al., 2021; Menge et al., 2022).

The management shifts of the aquaculture sector towards the harvest of smaller individuals due to market preferences and larger proficiency, could partly motivate the high demand for wild mussel seed and even be responsible for the reduction of this availability. Intuitively, a shorter cultivation period would require a higher supply of seed to maintain mussel production as observed when comparing the current wild seed supply estimated in this study (8316 tonnes) with that reported at the end of the 20th century (Pérez-Camacho et al., 1995; Cáceres-Martínez and Figueras, 2007). However, this increased use of seed did not translate into increased production. Our results show a lack of correlation between wild seed availability and total mussel production in the same year and a negative relationship with the following year's production (p-value<0.05, $r^2 = 0.30$).

This unexpected no-correlation between wild seed availability and mussel production could be related to numerous and complex factors. Among them, coastal upwelling emerges as a significant and oppositely controlling forcing between seed availability and mussel production. As described in this research, intense coastal upwelling events increase the probability of offspring loss due to offshore transport of mussel larval stages. Conversely, coastal upwelling was directly related to mussel growth (Pérez-Camacho et al., 1991; Figueiras et al., 2002), condition index (Blanton et al., 1987; Figueiras et al., 2002) and even the reduction of production closures due to harmful algal blooms (Álvarez-Salgado et al., 2008). Upwelling has been even suggested as a resilience mechanism against stressful conditions because of the supply of food, which might help to maintain the known efficiency of mussel farming in Galicia (Pérez-Camacho and Labarta, 2004; Kamermans and Capelle, 2019) even in a context of generalized production recession in Europe (Avdelas et al., 2021). The ability of coastal upwelling to act as a counterbalance between larval recruitment success and adult mussel physiological conditions may be related to its intensity and seasonality, which may also determine the net impact on primary production and transport processes.

Other factors that could explain the null impact of the quantity of seed collected in the coast and mussel production would be specific aspects of the mussel culture process in rafts. The most obvious explanation would be a much larger contribution of seeds from the collector ropes than suggested previously, which would compensate for the observed decline in wild seeds. However, no information is available on this seed contribution to the rafts. Another explanation could be that the use of the wild seed in the rafts above the threshold of seeded individuals would have a negative effect on production. In fact, the number of mussel seeds is indeterminate as the amount of wild seed collected is reported in kilograms. The high size heterogeneity of this resource, which also incorporates small mussel seeds (<1 mm), could account for a considerable number of individuals. In addition, the need for completely covering the ropes with mussel seed to avoid epifauna fixation makes it infeasible to manage the density or number of wild seed sown during the onset of cultivation. In this situation, shelf-thinning due to interspecific competition for food and space determines the number of mussels that will initiate the subsequent fattening process (Camacho et al., 1995).

The reduction of the traditional 18-month cultivation cycle to less than 12 months can also have a significant effect on the availability of mussel seeds in the rocky shore by reducing the spawning opportunities for adult mussels before harvest. In particular, the production of smaller mussels, mainly seeded in rafts during the winter-spring and harvested in late winter-early spring, would only participate in the fall spawning, as they would be immature during their first spring (Villalba, 1995) and harvested before the next one. When considering a stable mussel production dedicated to the fresh market and only altering the proportion of individuals of each size according to the progression over the last 16 years, a detrimental effect on the total reproductive output is observed only when both reproductive peaks are taken into account. The greater number of smaller individuals would compensate for the loss of spawning potential of larger individuals during the fall peak, but during spring, this potential is reduced. It should be noted that these estimates do not take into account the possible loss of fecundity due to the reduction in egg diameter, which depends on the size of the broodstock (Dare et al., 2004). The large sensitivity of population dynamics to changes in adult fecundity has been previously pointed out, signaling reproductive output as the most relevant factor controlling meta-population persistence, above survival and growth of juvenile stages or even population connectivity (Carson et al., 2011). Specific studies evaluating the reproductive performance of the adult population and its viability under different production scenarios (% of production of different sizes) are lacking to determine the actual impact of changes in the mussel farming strategy in Galicia on the availability of mussel seed.

In this scenario of climate change, the intensification of coastal upwelling is the most accepted hypothesis (Bakun, 1990) and forecasted by future climate projections (Rykaczewski et al., 2015; Cordeiro Pires et al., 2016; Álvarez et al., 2017; Soares et al., 2017; Sousa et al., 2017; Sousa et al., 2020). These climate models indicate that the increase in coastal upwelling will be particularly significant between May and October (Rykaczewski et al., 2015; Álvarez et al., 2017; Sousa et al., 2017; Sousa et al., 2020), which practically coincides with the pelagic phase considered in this study for the mussel seed collected from the rocky shore. This seasonal intensification would project more adverse conditions in the future for mussel larval recruitment success (Bashevkin et al., 2020), exacerbating wild mussel seed supply problems. However, these projections are still not confirmed by trends observed along the Galician coast to date (Álvarez-Salgado et al., 2008; Pérez et al., 2010; Pardo et al., 2011; Barton et al., 2013; Sydeman et al., 2014), where some data indicates even a decrease on the average intensity and duration of northerly winds during the upwelling season (Álvarez-Salgado et al., 2008).

In parallel to the possible increase in coastal upwelling and nutrient input into surface waters, global warming would promote stratification of the water column limiting fertilization (Sousa et al., 2020). The reduction in nutrient injection and possible decrease in phytoplankton abundance (Behrenfeld et al., 2006; Li and Harrison, 2008; Richardson, 2008; Sommer and Lengfellner, 2008; Morán et al., 2010) would have a direct negative impact on mussel production (Des et al., 2020). In addition to affecting mussel growth, suboptimal dietary conditions would also compromise the physiological condition of mussels, influencing their response to other environmental stressors, such as ocean acidification (Lassoued et al., 2019; Bashevkin et al., 2020; Lassoued et al., 2021), which is particularly pronounced in coastal waters off the Galician coast (Padin et al., 2020).

These environmental perturbations related to global change would also have an impact on reproductive seasonality (Edwards and Richardson, 2004; Philippart et al., 2012, Philippart et al., 2014) and larval survival (Poloczanska et al., 2013). However, it is important to note that climate projections are particularly inaccurate in coastal areas (Sarà et al., 2018; Stavrakidis-Zachou et al., 2018; Falconer et al., 2020). Therefore, incorporating these climate models as tools to improve the management and sustainability of mussel production requires better climate projections (Ahmed et al., 2019).

The sustainability and resilience of mussel aquaculture must be based on a thorough understanding of the environmental and management factors that regulate natural and cultured populations and their complex interactions. Understanding the processes underlying the variability of mussel seed availability is crucial not only to secure the future of the mussel aquaculture sector, but also to ensure the stability of wild populations. This is particularly significant in the context of global change, where cascading effects on marine ecosystems significantly impact mollusk aquaculture (Handisyde et al., 2017) due to their high sensitivity to environmental conditions (FAO, 2018). Our results highlight how such knowledge needs to be supported by long-term monitoring systems, ensuring the availability of time series long enough to detect the effect of environmental and management changes on aquaculture systems and their impact on natural populations.

5 Conclusions

Mussel seed collection reports from mussel producers in the *Ría de Arousa* are a useful source of information to know the availability of mussel seed, inter-annual variability and identification of the forcings that determine its highly variable stock on the rocky coast. The present analysis showed a decline in the availability of wild seed on the coast over the period 2006–2021. Extrapolation of these results to the total number of mussel rafts in Galicia would estimate the average annual quantity of seed collected to be 8316 tonnes within a range of 9575 tonnes in 2012 and 6300 tonnes in 2021. The entire time series of mussel seeds collected for initiating cultivation across all Galician rafts exhibited a reduction of 148 ± 36 t yr^{-1} which was particularly marked from 2012 onwards (288 ± 55 t yr^{-1}). These values update the estimates made in the 20th century for the supply of wild seed from the coast at 5440 tonnes (Camacho et al., 1995; Cáceres-Martínez and Figueras, 2007).

The decreasing availability of mussel seed was related to wind and chlorophyll concentration during the larval stage of recruits collected between December and April. The sum of coastal upwelling episodes greater than 500 m^3 km^{-1} s^{-1} explained 60% of the observed interannual variability of collected wild seed. The meridional component of the wind also determined the settlement pattern and dispersal of mussel seed along the coastline on both sides of the *Ría de Arousa*, the main source of mussel larvae as it accumulates 68% of the mussel rafts on the Galician coast. Chlorophyll also showed a significant correlation with seed availability explaining a 25%. These changes appear to be associated with larger-scale alterations observed in the Atlantic Ocean that could significantly link wild seed recruitment success to basin-scale climate indices.

The results reported here corresponded to a period with a marked shift in the farming strategy of the sector with regard to the increased production of small-sized mussels to meet market demand and improve profitability. As a consequence, the number of individuals farmed increased by 75% for the period 2006–2021 at the same time as the growing period was reduced. These changes in culture practices may also affect the reproductive potential of mussels as it limits spawning opportunities and the number of gametes which is proportional to the size of broodstock. This potential impact was analyzed based on a mean production value including the inter-annual variability of sizes observed over the period. Such simplistic approximation showed that the reproductive potential would remain stable in the autumn spawning due to the increase in the number of spawners while the sum of spring and autumn spawning would show a significant decrease in reproductive potential linked to reduced optimal reproductive time opportunities.

This first analysis of mussel seed harvesting reports highlights the importance of large monitoring time series for understanding the processes that determine the prosperity or decline of exploited wild seed stocks. Improving the quality and reliability of this information is therefore a necessity for the optimal management of this resource in the near future. The participation of observers to control the quantity of seed collected, the identification of collection areas by geographical coordinates and the digitalization of this information are aspects that need to be implemented in the compilation of these reports. In addition, *in situ* monitoring of environmental conditions jointly with the wild seed stock and size distribution during collection could allow a more rational establishment of both the collection period and areas, as well as a more precise estimation of the number of individuals used during the seeding process in the rafts. The contribution of collectors should also be included in such reports. Environmental conditions and changes in the availability of wild seed reported here may suggest that the contribution of mussel from the latter collector source is higher than previously considered (22.5%) and most likely would have considerable temporal and spatial variability to be determined in detail. Our data would indicate that throughout the study period the contribution of the collector ropes together with other factors of the cultivation process would contribute to compensate for the lack of seed from the rocky shore.

This knowledge would also represent an advance in addressing the impact of climatic changes on mussel seed availability, as well as how changes in mussel aquaculture management may interact with those that directly or indirectly drive changes in the replenishment and growth of natural mussel populations.

Data availability statement

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

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

XP: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. JB: Conceptualization, Formal analysis, Funding acquisition, Investigation, Supervision, Validation, Writing – original draft, Writing – review & editing. PO: Conceptualization, Data curation, Formal analysis, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. MG: Funding acquisition, Supervision, Validation, Writing – original draft, Writing – review & editing. TR: Data curation, Writing – review & editing. LS: Data curation, Writing – review & editing. AV: Data curation, Funding acquisition, Writing – original draft, Writing – review & editing. LP: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note

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