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Management and ecology of the wedge clam (*Donax trunculus*) in the NW Mediterranean Sea: The case of Ebro Delta (NE Spain)

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A B S T R A C T

The wedge clam (*Donax trunculus*) is one of the most prized clam species fished in the EU. Clam fisheries have experienced a dramatic decline during the last decades on Spanish coasts resulting in the progressive closure of fishing grounds. The Ebro Delta (NW Mediterranean Sea) is one of the few areas of the Spanish coast where there is still some fishing activity. In this context, the main objectives of this study were: to provide novel data on the ecology of this species and to analyse the management of *D. trunculus* fisheries in the Ebro Delta. The results showed a depth segregation phenomenon and suggested that *D. trunculus* performs two migrations during its benthic life cycle, i.e., (1) the settlement of planktonic larvae occurs more intensely in the deepest part of its bathymetric distribution, where the survival was more intense. As clams progressively increase in size, they move to shallower areas; (2) adults tend to move back to the deepest part of their bathymetric distribution as they increase in size. The management of *D. trunculus* has improved significantly in the last decade. However, some issues are still unsolved (e.g., fishing gear limits are unclear; population boundaries do not coincide with political boundaries). Moreover, the shallower areas where juveniles are located concentrate the highest fishing pressure over the stock.

1. Introduction

Clams are among the most valued commercially exploited bivalve species in the European Union: the total fishery production is 0.18 million tonnes per year, representing about 30% of EU bivalve fishery production (Eurostat, 2020). Among the clams caught in the EU, the wedge clam (*Donax trunculus*) is one of the most prized species. It is a commercially important species in France (Atlantic coast), Portugal, Spain, Bulgaria and Italy. But also, for other countries *i.e.*, Turkey, Egypt, Algeria, and Morocco.

Bivalves of the genus *Donax* are an important component of the shallow-bottoms macrofauna of exposed sandy beaches in temperate and tropical waters worldwide (Ansell, 1983). These bivalves are suspension-feeders on phytoplankton and suspended particulate organic matter (Wade, 1967; McLachlan and Lewin, 1981). They are particularly well adapted to the surf zones of the beaches, reaching high densities in areas where food is abundant (McLachlan and Young, 1982; McLachlan et al., 2018). The surf zones are characterized by sediment instability and a strong hydro-dynamism, which favours the presence of suspended particles and impedes rapid sedimentation of the organic matter (Zeichen et al., 2002). *D. trunculus* is an Atlantic-Mediterranean warm-temperate species inhabiting the Mediterranean and the Black Seas (Bayed and Guillou, 1985), and the Atlantic coast from the north Atlantic of France to Senegal (Tebble, 1966). Its distribution is limited to moderately exposed beaches of well-graded fine sands (Mazé and Laborda, 1988) at depths ranging between 0 and 6 m along the Atlantic coast and between 0 and 2 m depth in the Mediterranean and the Black Seas (Salas, 1987; Gaspar et al., 2002a); (La Valle et al., 2011). It is a fast-growing species with relatively short lifespan (Zeichen et al., 2002), making its population sizes very dependent on the success of spawning and recruitment. This bivalve shows an intraspecific segregation between juvenile and adult specimens (Gaspar et al., 2002a; Zeichen et al., 2002). In several areas, such as the Atlantic coast of France and Spain, Portugal, and Southern Adriatic coast, juveniles are commonly located in shallower areas, whereas the oldest specimens are found at greater depths (Ansell and Lagardère, 1980; Mazé and Laborda, 1988; (Gaspar et al., 2002a; Zeichen et al., 2002)). It has been suggested that this distribution is the result of current and hydrodynamic influences (Gaspar et al., 2002a), as well as to avoid intraspecific competition (Ansell and Lagardère, 1980). However, along the Moroccan Atlantic coast, the adults occupy shallower depths while the juveniles are in greater depth (Bayed and Guillou, 1985). There, the higher temperature in the

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shallower areas is a limiting factor for the settlement of juveniles. *D. trunculus* has recently been proposed as an interesting species as a bioindicator of the presence of microplastics (Ben-Haddad et al., 2022) and as a sentinel species for the presence of chemical contaminants in coastal areas (Tlili and Mouneyrac, 2019).

Clam fisheries, including wedge clam fisheries, are small-scale fisheries in Spain. These fisheries make an important contribution to the local economies, providing employment to many fishers, and contributing to the development, tourism and food supply, as well as poverty alleviation of local economies and societies (Béné, 2003; Jentoft and Eide, 2011; Harper et al., 2020). Small-scale clam fisheries also contribute to gender equality and women's employment. Clam gathering is frequently carried out by women worldwide. This is particularly important on the Atlantic coast of Spain, where only in Galicia 3724 fishers are working on intertidal shellfisheries (mainly women) (Pita et al., 2019; Villasante et al., 2021). However, small-scale fisheries worldwide are facing major challenges (declining fisheries resources, competition with large-scale fisheries, increased exposure to competition from global and corporate markets and anticipated effects of climate change) that affect their sustainability and viability (Chuenpagdee, 2011; Jentoft and Chuenpagdee, 2018). In the Spanish Mediterranean, clam fisheries have experienced a dramatic decline over the last decades, resulting in job loss for hundreds of small-scale fishers (Baeta et al., 2021b). The decline in landings caused the progressive closure of fishing grounds by the local authorities: the first was Murcia in 1998, the Balearic Islands in 2003, and Valencia in 2017. The clam fisheries have been closed in several areas of Catalonia (Rosas Bay, L'Estartit, North Barcelona and South Barcelona). However, in the Ebro Delta an important clam fishery is still present (Baeta et al., 2018).

Clam fisheries are generally data-poor, and their management success requires case-specific solutions (Ostrom et al., 2007; Baeta et al., 2021b). Management measures to the decline of clam fisheries in the Spanish Mediterranean have typically included at first, as an emergency solution, a drastic reduction of fishing effort or the introduction of catch quotas. As this action has rarely produced positive effects, the next step has usually been the closure of fishing activity. However, it seems that fishery closures have not always helped the recovery of stocks. For example, Baeta et al. (2021a) evaluated the effect of fishing closure on the smooth clam (*Callista chione*) bed after 5 years without fishing activity in Catalonia (NE Spain). These authors observed that the stock was in worse condition than when the closure was lifted (smaller individuals with fewer densities, etc.). Similar results were obtained by Escrivá et al. (2021) on the wedge clam (*D. trunculus*) after 2 years without fishing activity in Valencia (W Mediterranean Sea).

In this context, the main objectives of this study were: (1) to evaluate the management of *D. trunculus* in the Ebro Delta (NW Mediterranean Sea) as an illustrative example of its fisheries along the coast of Spain; and (2) to provide novel data on the ecology of this species that may contribute to its better management.

2. Materials and methods

2.1. Study area

The study site is located on the coast of the Ebro Delta (NW Mediterranean), in the northeastern part of the Spanish coastline, between 40° 48′N and 40° 32′N and 0° 45′E and 0° 38′E (Fig. 1). The Ebro Delta is an alluvial plain of about 35,000 ha, mainly devoted to intensive agricultural activities, highlighting the rice cultivation. Its coastline extends approximately 50 km and is surrounded by a wide continental shelf, with high biological productivity as a result of the nutrients provided by the Ebro River and the mixing effect of the Liguro-Provençal-Catalan current on the continental slope (Salat, 1996). This area sustains one of the most important commercial fisheries in the Western Mediterranean (Irazola et al., 1996). The main fishing ports in the study area are Sant Carles de la Ràpita, Alcanar, Deltebre and l′ Ampolla.

2.2. Fishing gears

Throughout history, clams, like other bivalves (*i.e.*, mussels, cockles, and oysters) that inhabit intertidal and shallow areas of the rocky and sandy subtidal, have been harvested from nearly every accessible beach and estuary along the Mediterranean coast of Spain, where they have been exploited for centuries. Clam landings were low and to supply local markets until the mid-XX Century. They were harvested using ancient and artisanal gears *i.e.*, (1) manual handling (2) small sailing or rowing boats towing a unique clam dredge around large cities such as Barcelona. The first records of the wedge clam fisheries are from the late XVII Century on the Mediterranean coast of Spain. Fishers gathered the wedge clam using hand-operated dredges (Sañez Reguart, 1795). The introduction of mechanized clam dredges to collect the wedge clam probably did not happen until the 1980s. Currently, both fishing gears coexist in the Ebro Delta area. Hand-operated dredges operate from the mainland to depths of 1.2 m. In a hand-operated dredge fishery, each shell fisher tows a single dredge (frame mouth width 70 cm; height 16 cm; depth 40 cm) (Fig. 2), along the bottom of the sea. The dredges are rigged with metal teeth (approx. 50 teeth of 13 cm) along the lower leading edge. The mesh size of the dredges at the top, end and both sides is constant 9 × 9 mm and 7 mm × 10 cm at the bottom of the box. The duration of a tow is between 10 to 20 min. The average number of tows per fishers per day is 12.

Mechanized clam dredges operate between depths of 1 and 2.5 m. In the mechanized clam dredge fishery, each boat typically (10 m in length: 100 HP) tows three or four clam dredges (frame mouth width 70 cm; height 53 cm; depth 120 cm) along the bottom of the sea, lasting 30 min at a towing speed of 3 to 6 kn. The average number of tows per boat per day is 20 in summer and 15 in winter. The dredges are rigged with metal teeth (approx. 20–30 teeth of 10–20 cm) along the lower leading edge. The mesh size is constant 11 × 17 mm (since 2020).

2.3. Data sources

The evolution of the total annual landings, the proportion of the total landings by fishing gear and the number of fishers and boats by year from 2000 to 2022 was obtained from the General Fisheries Directorate (GFD) of the "Departament d'Agricultura, Ramaderia, Pesca i Alimentació" (Catalan Government). The catch per unit effort (CPUE), number of fishing trips was obtained from the same source. Data of the mechanized clam dredge fishery was available from 2000 to 2022, whereas in the case of the hand-operated fishery data was available only from 2007 to 2022.

2.4. Sampling methods

D. trunculus has a bimodal recruitment in the Mediterranean Sea populations, one in summer and the other in winter (Ramón et al., 1995). Samplings were carried out to match the first recruitment period, May, June, July and August 2021. Four areas (Z1, Z2, Z3 and Z4) were defined inside the clam fishing bed (Fig. 1). Each area had a length of 50 m parallel to the coastline. In each area, two equidistant transects perpendicular to the coastline were defined, with three sampling stations at 0.2, 0.5 and 0.7 m, while only one transect was defined in the middle of the area with

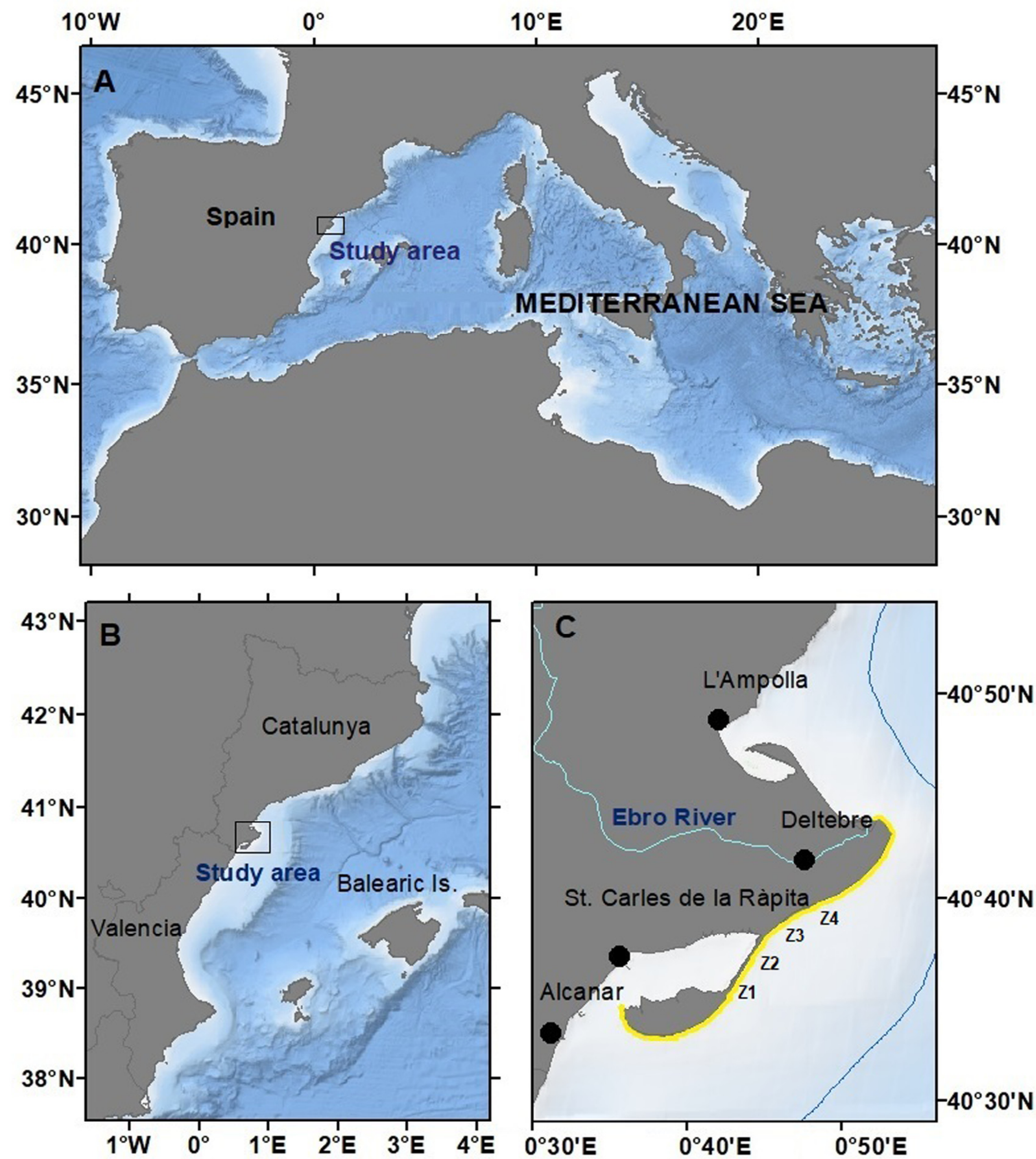

Fig. 1. (**A**) Location of the study area in the Mediterranean Sea. (**B**) Location of the study area on the Mediterranean coast of Spain. (**C**) Map of the study area in the Ebro Delta. Black dots indicate the wedge clam fishing ports; the yellow area indicates the wedge clam bed. Z1, Z2, Z3 and Z4 indicate the areas where the experiment was done. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

three sampling stations at 1, 1.5 and 2 m depth (Table 1). The shallowest sampling stations (0.2, 0.5 and 0.7 m) were sampled using a hand-operated dredge (only one) (Fig. 2). At each station, a tow of 25 m long was done parallel to the coastline. Three replicates were done at each station each month. The deepest stations were sampled using mechanized clam dredges (aboard a wedge clam fishing boat). Two commercial clam dredges equipped with a mesh of 11 × 17 mm were used to sample at each boat station. A tow of 50 m in length parallel to the coastline was done at each station for 20 min at a towing speed of 1–1.2 knots (a tow of 25 m was not possible to perform). Three replicates were done at each boat station each month. The geographical position of each tow was recorded using GPS. Specimens of *D. trunculus* collected in each sample and replicate were transported independently in a cooler with ice (4 °C) to the laboratory. All individuals of *D. trunculus* were counted and measured with a digital caliper (precision of 0.1 cm). Additionally, a Van Veen grab, covering an area of 0.1 m^2, was used at each station in all the samplings (each month) to collect sediment from the clam bed. Three replicates were performed at each station each month to study the recruitment and population bathymetric distribution. The sediments were filtered with a mesh size of 500μ, then all the recruits of each sample were preserved with ethanol. Furthermore, recruits of *D. trunculus* were identified under stereomicroscope and measured using the software cellSense Standard 1.6 and the camera Olympus SC30. An additional sample was obtained in each station each month to study the granulometry of the sediment. Sediment samples were processed according to a standard dry-sieving procedure (Wentworth, 1922) for grain size distribution analysis and classified following the ISO 14688-1 international grain size scale. The grain size distribution was summarized by an identification of a characteristic grain diameter, and in our case we chose the median (d50).

To study the differences in length-frequency distributions of the population of *D. trunculus* gathered by each fishing gear two

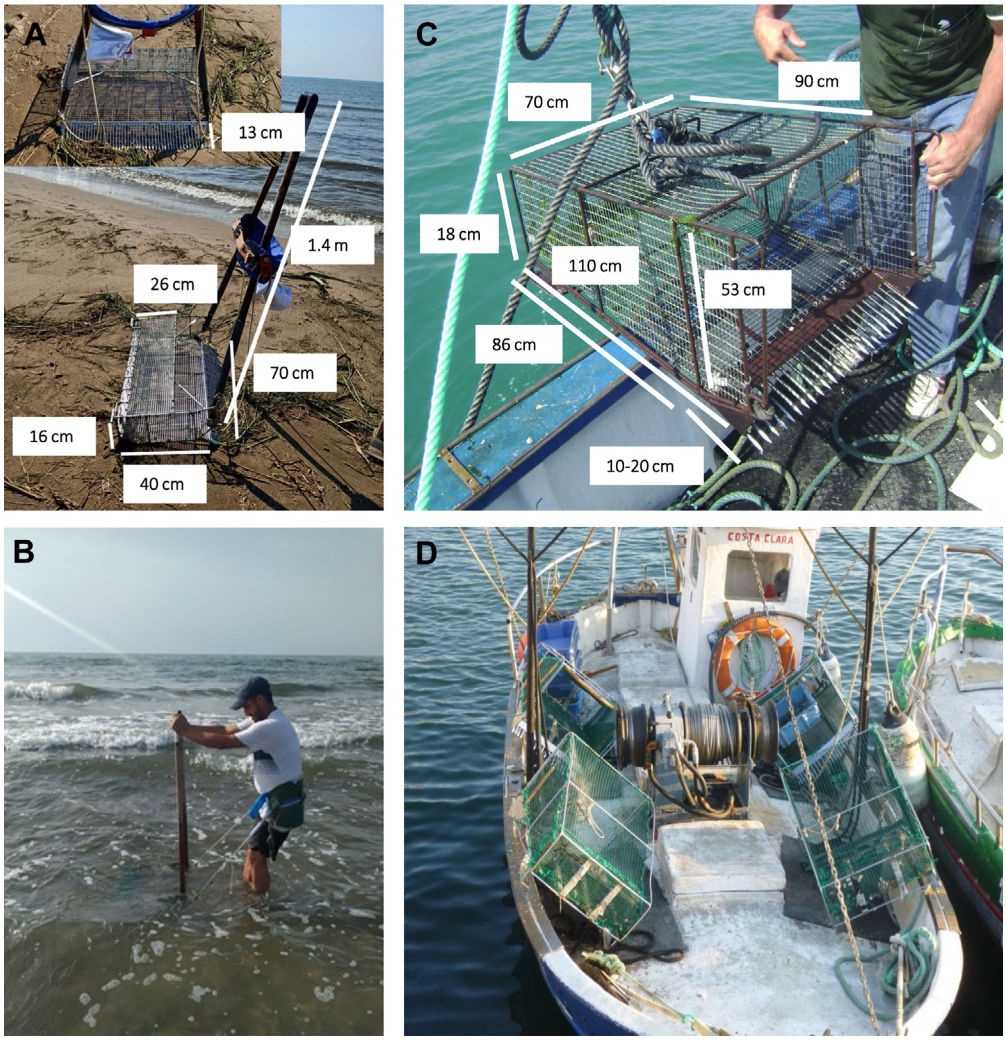

Fig. 2. **(A)** Hand-operated dredge dimensions; **(B)** Fishing operation; **(C)** Mechanized clam dredges; **(D)** A typical boat of the mechanized clam fleet in Catalonia.

Table 1
Experimental design and sampling. Four areas were defined (Z1, Z2, Z3 and Z4). Each area has a length of 50 m parallel to the coastline. Each area had two transects (T1, T2) at 0.2, 0.5 and 0.7 m depth, while one at 1, 1.5 and 2 m depth. The fishing gear used for sampling was a hand-operated dredge at 0.2, 0.5 and 0.7 m; while a mechanized clam dredge at 1, 1.5 and 2 m depth. Three replicates were performed at each station.

Fishing gear	Depth (m)	Z1		Z2		Z3		Z4	
		T1	T2	T1	T2	T1	T2	T1	T2
Hand-operated dredge	0.2	3	3	3	3	3	3	3	3
Hand-operated dredge	0.5	3	3	3	3	3	3	3	3
Hand-operated dredge	0.7	3	3	3	3	3	3	3	3
Mechanized clam dredge	1.0	3		3		3		3	
Mechanized clam dredge	1.5	3		3		3		3	
Mechanized clam dredge	2.0	3		3		3		3	

groups were considered: the specimens collected with a hand-operated dredge at 0.2, 0.5 and 0.7 m depth; and specimens collected with mechanized clam dredges at 1, 1.5 and 2 m depth. First, a nonparametric Kruskal–Wallis H test was used to compare the medians of both groups. Second, a Kolmogorov–Smirnov goodness-of-fit test (K–S) was applied for the two sampled groups to identify the differences between the population structure between both groups. The size and density of individuals (individuals m^{-2}) were compared for each sampled depth (0.2, 0.5, 0.7, 1, 1.5 and 2 m), also with the nonparametric Kruskal–Wallis H test. A nonparametric Kruskal–Wallis H test was also used to compare the medians of the grain size by depth (0.2, 0.5, 0.7, 1, 1.5 and 2 m)

2.5. Legal framework and management

The competencies in the governance and management of some coastal fisheries, including clam fisheries, were transferred in the mid-1980s to the regional authorities (Comunidades Autónomas) in Spain. From the mid-1980s, each local authority had its own governance system. In the case of the Ebro Delta area, the local authority is the Catalan Regional Government (Generalitat de Catalunya).

From 1984–2014, the Catalan Regional Government progressively implemented the legislation associated with the management of wedge clam fisheries. The following rules regulated the wedge clam fisheries in the Ebro Delta during this period: (1) The

Decree 9/1987, of 15 January, on the breeding and collection of seafood, defined the users of the clam fishing areas in Catalonia (including the Ebro Delta). It specified that to gather the wedge clam users must have (a) one of two types of fishing licenses: Type 1: to gather clams with a vessel (off 1.2 m) and Type 2: to gather clams without a vessel (from the shoreline to 1.2 m); (b) being part of a Fishers Guild, Cooperative or Organization of fishery producers. (2) The order of 9 June 1993 established the limits of the clam fishing areas in Catalonia. There were 5 in the case of the Ebro Delta (CAT1-01, CAT1-02, CAT1-03, CAT1-04 and CAT1-05). All these clam fishing areas targeted the wedge clam species. (3) The Order of June 13, 1994, defined: (a) a minimum legal size of 27.2 mm (total length); (b) limits on engine power per vessel (200 cv); (c) a mesh size for both fishing gears (mechanized clam dredges and hand-operated dredges) of 15 × 15 mm. However, this was exclusively for the side of dredges, but not for the base or bottom of both fishing gears. This means that there was not a clearly defined rule for the dredges mesh size; (d) before being sold, the clams must be screened by a machine and, if they are smaller than the minimum legal size, they must be returned to the sea; (e) the regulation of working hours for each fishing modality was delegated to the most important Fishers Guild in the area (Sant Carles de la Ràpita). Fishers of each fishing modality (mechanized clam dredges and hand-operated dredges) decided in regular meetings (one or two per year) the working hours per day, usually based on the prize of clams in the market. For example, fishing time for mechanized clam fleet was from 9:00 to 11:30 and for hand-operated dredges from 10:00 to 14:30 (in the 1980's and 1990's).

The Council Regulation EC 1967/2006 concerning management measures for the sustainable exploitation of fishery resources in the Mediterranean Sea established the need to approve management plans for fisheries conducted in territorial waters. In compliance with this regulation, on January 21, 2014, Catalonia drafted a new management plan for mechanized dredgers, which was approved by the European Commission. This management plan did not include hand-operated dredgers, as this fishing gear is excluded from the scope of Regulation (EC) 1967/2006. It is revised every three years by the European Commission. The management plan for mechanized dredges is based on co-management and defined by: (a) resource boundaries (fishing areas) and fishing gear technical specifications; (b) regulations on appropriation and provision rules and local conditions for this fishing gear (specific catch limits, a minimum legal size (TL: 25 mm), reduction of fishing effort, including the number of vessels and engine power, and fishing measures to maintain the biomass level of exploited populations within safe biological limits); (c) collective-choice arrangements (i.e., legitimate users can participate in the development and modification of their operational rules) involving clam fishers, scientists, NGOs and administrators; (d) monitoring the status of all fishing grounds; and (e) graduated sanctions for users who violate the operational rules.

Additionally, in 2019 the Catalan Regional Government defined a specific management plan for the hand-operated dredges exclusively for the Ebro Delta area. This management plan was also based on co-management and is exclusively revised by the Catalan administration (not the European Commission). This management plan defined: (a) the resource boundaries (fishing areas) and the fishing gear technical specifications; (b) regulations on the rules of appropriation and provision and local conditions for this fishing gear. For example it defined: a maximum number of fishing licenses (81); fishing time per day (2 h and a half); a minimum legal size (width: 7 mm) (c) collective-choice arrangements (i.e., legitimate users can participate in the development and modification of their operational rules) involving clam fishers, scientists, NGOs and administrators; (d) monitoring the status of all fishing grounds; and (e) graduated sanctions for users who violate the operational rules. Moreover, these management plans are updated almost yearly, adapting to new realities.

The management of the wedge clam in the Ebro Delta area has improved significantly in the last decades, however, some issues are still unsolved: (1) Two different fleets/users coexist targeting the same species and the same fishing stock. This implies that the same fishing resource has two different legitimate users that are using different fishing gears, have different fishing licenses and are under different management plans. These users have no boundaries between them neither supra-governance nor management. (2) The minimum legal size of the wedge clam was 27.2 mm (TL) in 1994 for both fishing gears. It was reduced to 25 mm (TL) for mechanized clam dredges in 2014 and to 7 mm (width) for hand-operated dredges. In fact, the TL-width relationship was evaluated in the area and 7 mm equals to a TL of 21.86 mm. It implies that the minimum legal size has been progressively decreasing over time and that there are two different minimum legal sizes for the same stock of the same species in the same place. In addition, the wedge clam is sold in the same fish market. (3) Monitoring the status of fishing grounds. The wedge clam is a fast-growing species and requires continuous and accurate monitoring throughout the year of all the fishing grounds which is very expensive. On the one hand, the low registered landings of this species, particularly in the fishing modality of mechanized dredges, often make it difficult for the administration to invest economic resources in monitoring them, which implies biased information on the real state of the fishing grounds. On the other hand, currently, the monitoring of the hand-operated dredges is weak (systematic and methodical sampling is lacking). The data is not subject to the supervision of the European Commission as are the mechanized clam dredges, they are only supervised by the Catalan Regional Administration.

3. Results

3.1. Evolution of the wedge clam fishery in the ebro delta

Total annual landings of *D. trunculus* in the Ebro Delta showed a well-defined decreasing trend from 2006 (201 tonnes) to 2020 (0.19 tonnes) (Fig. 3). Most of the landings (>60% between 2000–2020) were gathered by hand-operated dredges (Fig. 4). The proportion of landings gathered by hand-operated dredges has progressively increased over time. The number of fishers dedicated to gathering the wedge clam has declined since the mid-1990's. The mechanized clam dredge fleet comprised 20–30 fishing vessels in the 1970-1990's, 15 in the 2000s and 2 by 2020. In the past, these boats targeted exclusively in clams (mainly *D. trunculus* but also *Chamelea gallina*. Currently 7 vessels have the license to target clams in the Ebro Delta, but only 3 occasionally target *D. trunculus*. These vessels mainly target other species. They use passive-attractive gears (*e.g.*, traps and clay pots) to fish for common octopus (*Octopus vulgaris*) and bottom-set stationary gears (*e.g.*, gillnets, trammel nets, longlines) to target fish (*e.g.*, *Sparus aurata* and crabs (*Callinectes sapidus*). Regarding the number of licensed fishers that can target the wedge clam using hand-operated dredges, it was around 200 in the mid-1990s. In the last 15 years, the number of licenses have been 81, but the number of active fishers was only 60 from 2007 to 2016 and strongly declined since 2018, and in 2020 less than 20 were active. The CPUE of the mechanized clam dredge fishery has shown a decreasing trend over the last 22 years (Fig. 5). It was 267 kg boat^{-1} and day^{-1} in 2000 while only 3.5 in 2019; although it seems that it has been increasing again since 2019. The CPUE of the hand-operated dredge fishery has also shown a negative trend from 14 kg. fisher^{-1} and day^{-1} in 2000, whereas 6 in 2022.

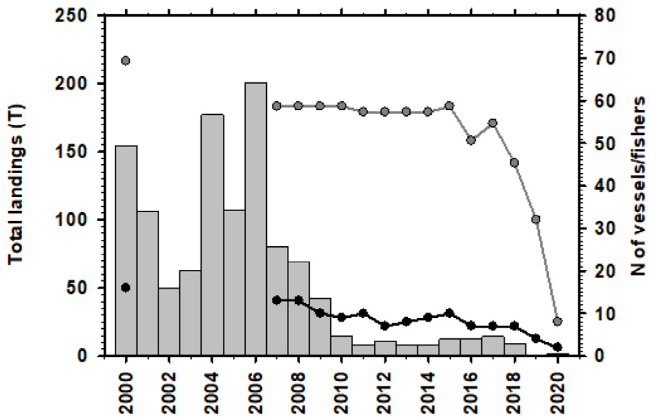

Fig. 3. Total landings of wedge clam in the Ebro Delta from 2000 to 2020. The grey dots indicate the number of hand-operated dredgers per year, whereas the black dots indicate the number of fishing vessels using mechanized clam dredges per year.

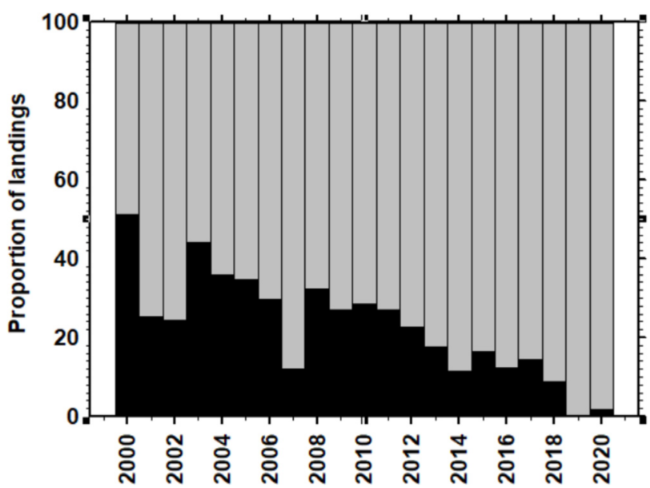

Fig. 4. Evolution of the annual proportion of the total landings by fishing gear in the Delta Ebro area throughout the period 2000–2020, where black indicates mechanized clam dredge and grey, hand-operated dredges.

3.2. Fraction of the population gathered by each fishing gear

The individuals of *D. trunculus* gathered in the study by hand-operated dredges between 0.2 to 0.7 m depth showed smaller total length (mean size: 24.41 mm) (H = 662.67; dF = 5 $P < 0.005$) compared to those gathered by mechanized clam dredges between 1 to 2.5 m depth (mean size: 26.61 mm) (Fig. 6). The K-S test revealed highly significant differences in the length frequency distributions between individuals gathered by each fishing gear (K-S = 29.81; $P < 0.001$). 66.16% of the individuals gathered by hand-operated dredges were <25 mm, while only the 34.75% gathered by mechanized clam dredges.

The median size of the individuals gathered by hand-operated dredges from 0.2 to 0.7 m tended to increase with depth (H = 19.58; dF = 2; $P < 0.001$) (Fig. 7). The median size was 24 mm at 0.2 m and 25 mm at 0.7 m. No significant differences were detected in those gathered by mechanized clam dredges from 1 to 2 m. The minimum size obtained in hand-operated dredges was 12.7 mm and the maximum was 32.2 mm, while in mechanized clam dredges, it was 16 mm and 35.2 mm respectively. The density of the commercial catch (Fig. 8A) decreased with depth (H = 152.41; dF = 5; $P < 0.001$); from 0.2 m (7.12 ind m^{-2} SE ± 0.50) to 1 (1.97 ind m^{-2} SE ± 0.18) and then it increased slightly at 1.5 and 2 m depth (2.55 ind m^{-2} SE ± 0.22 and 2.52 ind m^{-2} SE ± 0.19) respectively.

3.3. Recruitment, population distribution and granulometry

The non-parametric Kruskal–Wallis One-Way Analysis of variance showed that median values among recruits collected by depth (0.2; 0.5; 0.7; 1; 1.5 and 2 m) were significantly different (H = 1115.75; dF= 5; $P < 0.001$). It decreased progressively with depth from 1.78 mm (0.2 m) to 0.99 mm (2 m) (Fig. 9). The minimum size of the recruits also decreased with depth from 0.77 mm (0.2 m) to 0.50 mm (2 m). No significant differences were observed by depth and month. Regarding recruit density (Fig. 10), it increased exponentially with depth (H = 173.50; dF = 5; $P < 0.001$); from 0.2 m (38.30 ind m^{-2} SE ± 6.26) to 1.5 m (369.96 ind m^{-2} SE ± 28.00) and 2 m (368.34 ind m^{-2} SE ± 26.15). No significant differences were observed by depth and month except at 2 m depth ($P < 0.005$), where the density was higher in May and June than in July and August.

Considering all the specimens of *D. trunculus* captured in each station by the Van Veen dredges (Fig. 11A), results showed that the mean size decreased progressively with depth from 2.93 mm (0.2 m) to 1.07 (2 m). The maximum size of the specimens captured was between 28 and 29 mm except at 0.7–1 m depth that was between 23 to 24 mm. The minimum size tended to decrease with depth, from 0.77 mm (0.2 m) to 0.44 mm (2 m). The median superficial particle diameter (d50) decreased with depth in the study area (H = 34.08; dF = 5; $P < 0.001$) (Fig. 11B). It was 270.55 μm at 0.2 m, while it was 211.35 μm at 2 m.

4. Discussion

The beaches of the Ebro Delta are dissipative (Mendoza and Jiménez, 2009). These types of beaches have typically smooth coastal profiles, wide surf zones and they are composed of firm fine-grained sand and the waves dissipate their energy as they break passing over bars in the surf zone (Thornton and Guza, 1983). Ansell (1983) observed that *Donax* species are found more abundantly in eutrophic areas with high plankton productivity. On dissipative beaches, the detritus, phytoplankton and zooplankton are concentrated in the surf zone than in offshore areas due to the recirculation formed by rip currents (Fujimura et al., 2014; Morgan et al., 2017). Therefore, food availability may explain why adults are more abundant in the shallower areas (0.2 to 0.7 m) than offshore areas (1 to 2 m). The food for suspension feeders is more abundant in shallower areas. The predation is another key factor controlling patterns of distribution and abundance (Beal et al., 2001). During samplings wasthe presence of several species that potentially may prey on *D. trunculus* was reported sea stars: *Astropecten jonstoni* and *Astropecten irregularis*; gastropods mollusks: *Neverita josephinia* and *Naticarius hebraeus*; decapod crustaceans: *Portumnus latipes*; *Callinectes sapidus*, *Liocarcinus depurator* and *Liocarcinus vernalis*; and fishes as *Sparus aurata*, *Lithognathus mormyrus*. These predators are more abundant as depth increases. Accordingly, predation may also explain why adults and juveniles of *D. trunculus* densities are higher in shallower areas, to avoid predation. However, it does not explain why small recruits are more abundant in deeper areas. Moreover, La Valle et al. (2011) mentioned that sediment grain size is a key factor controlling the distribution of *D. trunculus*. Our results showed that the sediment tends to be finer, as depth increases in Ebro Delta. Small recruits perhaps can find better refuge to avoid predators than adults in finer sediments.

Focusing on the life cycle of the wedge clam, results suggested that *D. trunculus* in the NW Mediterranean Sea exhibited a depth segregation phenomenon as previously studies observed both

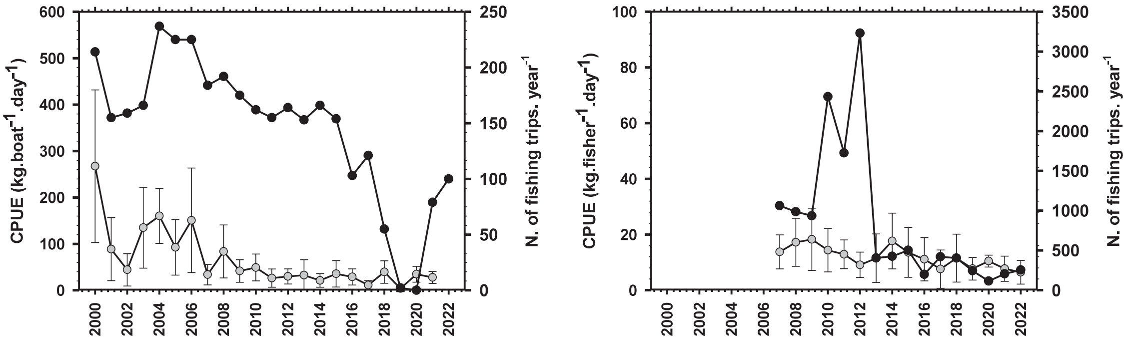

Fig. 5. Evolution of the catch per unit effort and the number of fishing trips per year by fishing gear (2000–2022). **(A)** Grey dots indicate the catch per unit effort (CPUE, mean kg boat^{-1} and day^{-1}) and whiskers indicate ± Standard deviation. Black dots indicate the evolution of the total number of fishing trips by year of the mechanized clam dredge fleet. **(B)** Grey dots indicate the catch per unit effort (CPUE, mean kg fisher^{-1} and day^{-1}) and whiskers indicate ± Standard deviation. Black dots indicate the evolution of the total number of fishing trips by year of the hand-operated fishers.

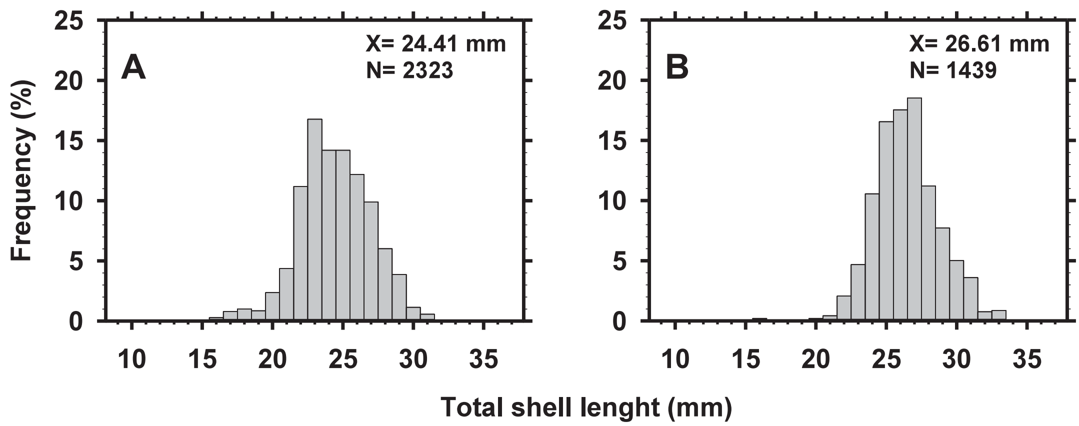

Fig. 6. Length frequency distribution of *Donax trunculus* by fishing gear. **(A):** Hand-operated dredges (0.2 to 0.7 m); **(B):** mechanized clam dredges (1 to 2.5 m).

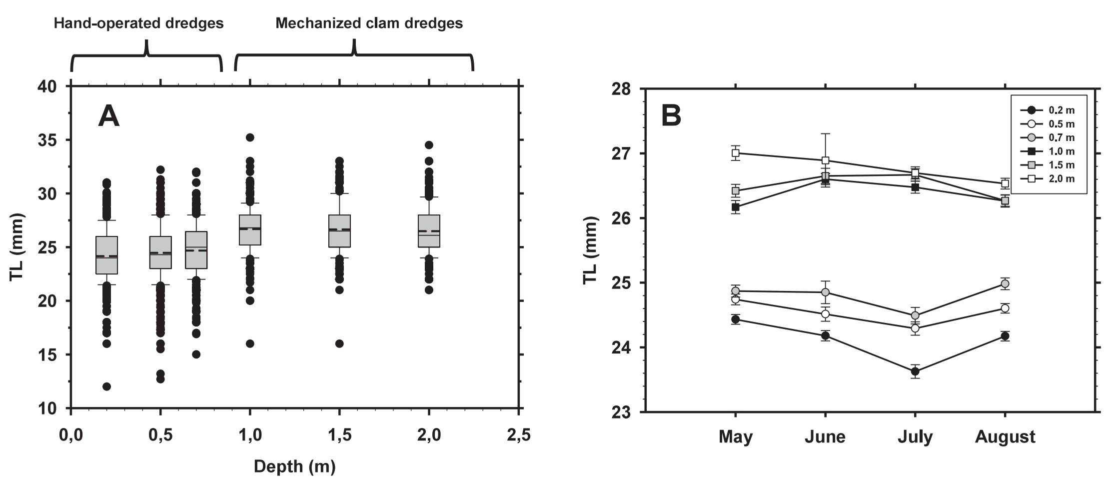

Fig. 7. **(A).** Bathymetric distribution of the wedge clam (TL: total length) by depth (0.2; 0.5; 0.7; 1, 1.5 and 2 m); and fishing gear (hand-operated dredges and mechanized dredges). The boundary of the box closest to zero indicates the 25th percentile, continuous line within the box marks the median, dashed line within the box marks the mean and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles. Black dots indicate outlying points. **(B)** Bathymetric distribution of the wedge clam (TL: total length) by depth and month.

in the Mediterranean and the Atlantic (Gaspar et al., 2002a); (Escrivá et al., 2021). In addition, although our results must be interpreted with caution because the sampling was limited to only four months, they suggested that *D. trunculus* perform two migrations during its benthic life cycle (Fig. 12): (1) The first one: the settlement of planktonic larvae occurs more intensely at the deepest part of their bathymetrical distribution (1.5 to 2 m depth), where the survival is higher. As they progressively increase in size, they appear to move to shallower areas (from 1.5–2 to 0.2 m). There, they remain until they achieve a mean size of 24 mm. (2) The second one: as adults increase in size, they tend to move back to the deepest part of its bathymetrical distribution (from 0.2 to 1–2.0 m). Results about the mean size of adults and juveniles' bathymetrical distribution can be strongly influenced by the different selectivity of the fishing gears. However, this second migration agrees with previous findings in the

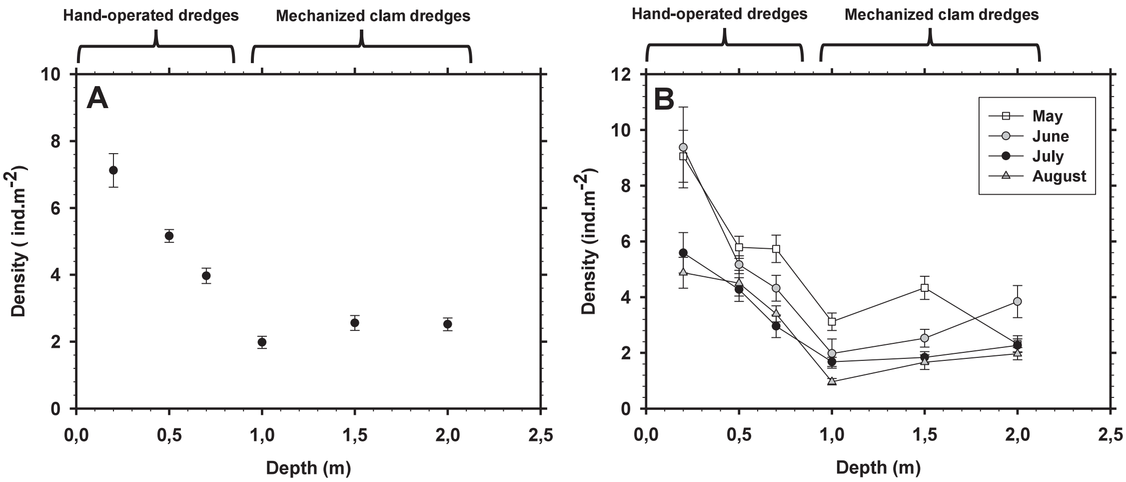

Fig. 8. **(A)** Density of wedge clam commercial catches (individuals m^{-2}) by depth (0.2; 0.5; 0.7; 1, 1.5 and 2 m). Black dots indicate the mean size per depth and whiskers indicate ± Standard Error. (**B)** Density of wedge clam commercial catches density (individuals m^{-2}) by depth (0.2; 0.5; 0.7; 1, 1.5 and 2 m) and month (2021).

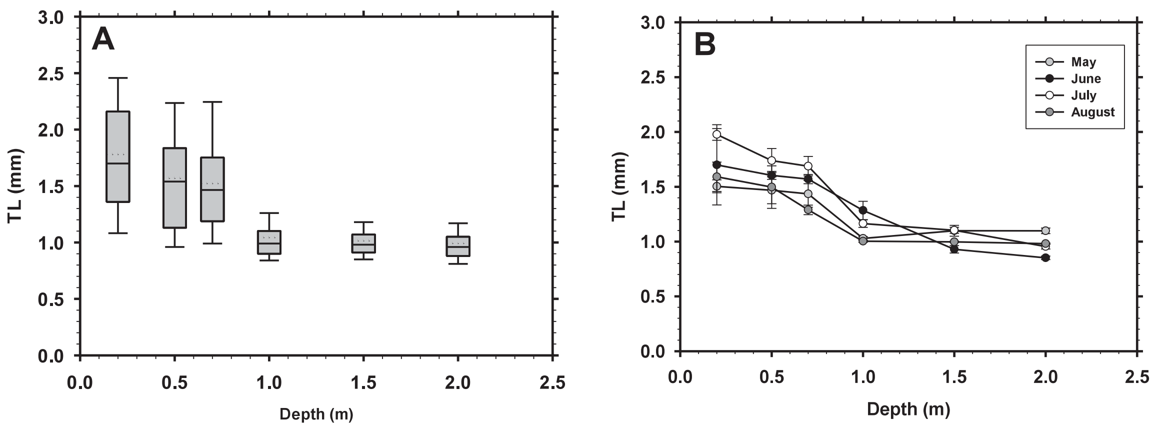

Fig. 9. (A): Size distribution of wedge clam recruits (TL: total length) by depth (0.2; 0.5; 0.7; 1, 1.5 and 2 m). The boundary of the box closest to zero indicates the 25th percentile, continuous line within the box marks the median, dashed line within the box marks the mean and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles. (**B):** Size distribution of wedge clam recruits (TL: total length) by depth (0.2; 0.5; 0.7; 1, 1.5 and 2 m) and month. Whiskers (error bars) above and below the box indicate the Standard Error.

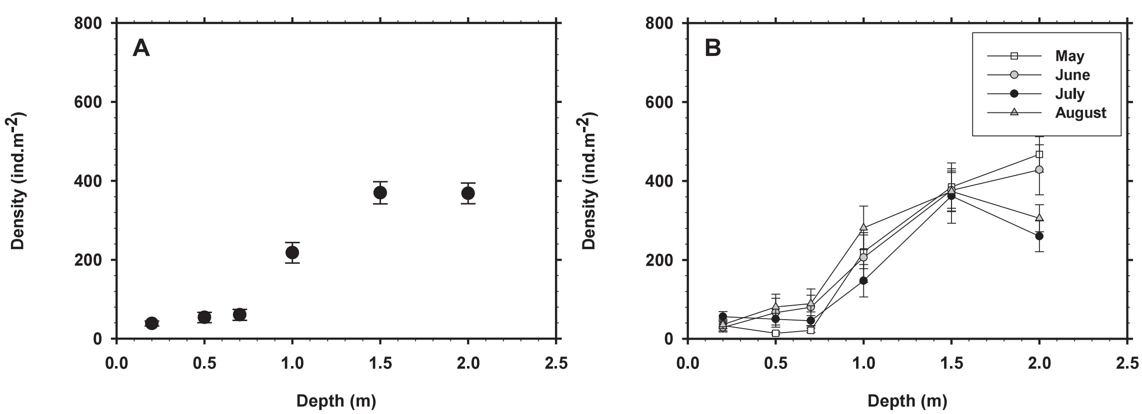

Fig. 10. **(A):** Wedge clam recruit density (individuals m^{-2}) by depth (0.2; 0.5; 0.7; 1, 1.5 and 2 m). Black dots indicate the mean size by depth and whiskers indicate ± Standard Error. (**B):** Wedge clam recruit density (individuals m^{-2}) by depth (0.2; 0.5; 0.7; 1, 1.5 and 2 m) and month (2021), whiskers indicate ± Standard Error.

Atlantic Sea (Guillou and Le Moal, 1978; Ansell and Lagardère, 1980; Guillou and Bayed, 1991; Gaspar et al., 2002b), Adriatic Sea and South Adriatic Coast (Italy) (Zeichen et al., 2002). Ansell et al. (1980) suggested that this behaviour is to avoid food competition and population density. However, they differ from the results obtained by Mouëza and Chessel (1976) in Algeria. These authors found that all sizes of *D. trunculus* displayed a similar vertical distribution by depth. However, they differ from what was reported by Bayed and Guillou (1985), along the Moroccan Atlantic, where coastal juveniles occupy the greatest depths, and adults the shallower areas. This second migration of the larger individuals to deeper areas could also maximize reproductive

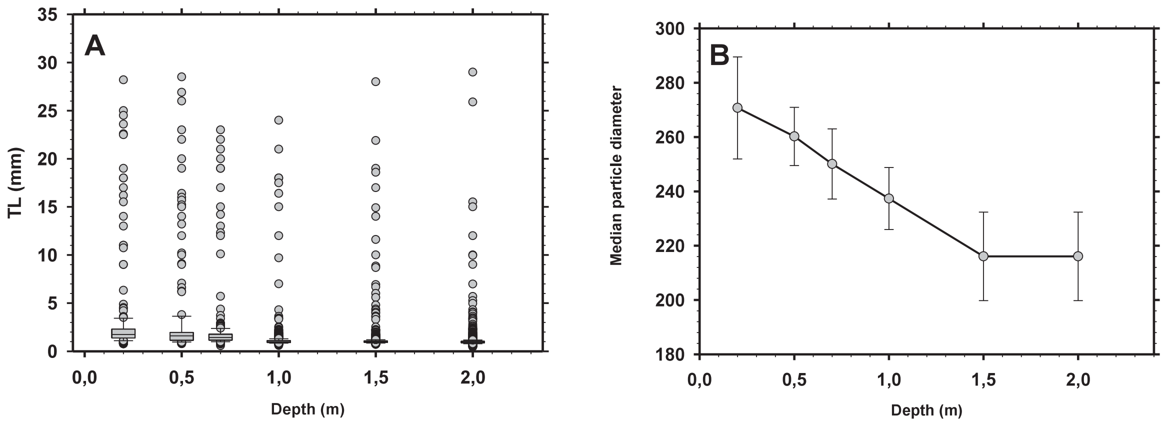

Fig. 11. **(A):** Size distribution of wedge clam (TL: total length) by depth (0.2; 0.5; 0.7; 1, 1.5 and 2 m). The boundary of the box closest to zero indicates the 25th percentile, continuous line within the box marks the median, dashed line within the box marks the mean and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles. Grey dots indicate outer points. **(B):** Median superficial particle diameter (d50) μm by depth for the study area, whiskers indicate ± Standard deviation.

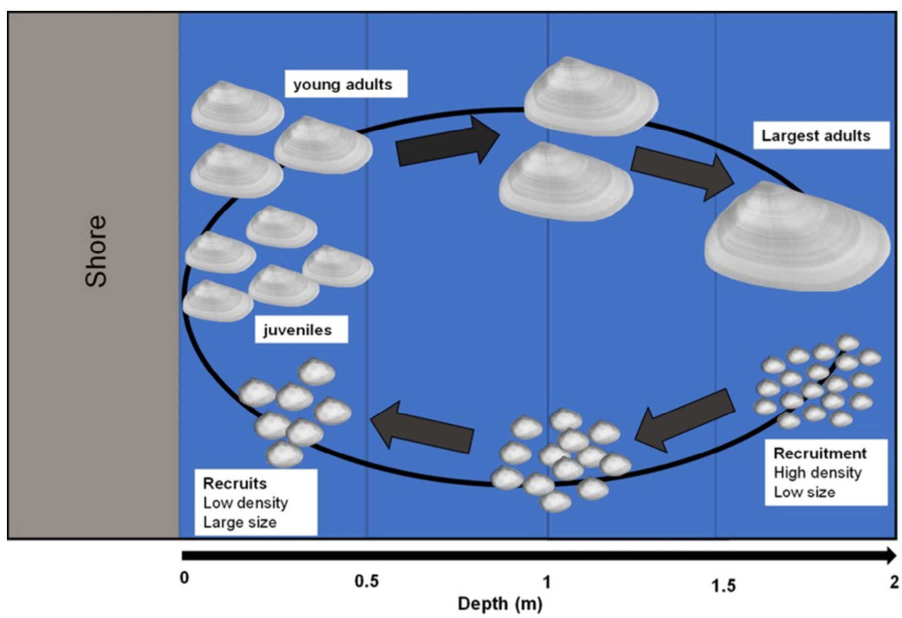

Fig. 12. Scheme of the suggested benthic part of *D. trunculus* life cycle in the Ebro Delta according to our results.

success and avoid conspecific predation on gametes. In deeper areas, the hydrodynamics is soft and more favourable. Therefore: (1) the risk of gametes and pelagic larvae being dragged towards the shore and dying is smaller and (2) the risk of being ingested by conspecifics in shallower areas where they are more abundant is lower.

The settlement magnitude of littoral invertebrate populations is affected by many factors, *i.e.*, (1) pelagic larvae mortality during dispersal, oceanographic conditions such as winds, currents, temperature, salinity and other environmental forces; (2) delivery from nearshore waters to the substrate (*e.g.*, nearshore hydrodynamics); (3) larval adherence to the surface, depending on the characteristics of the physical environment (*e.g.*, grain size); (4) intraspecific relationships between adults and pelagic larvae at the settlement time, which can increase it at low densities or decrease it in high densities (Defeo, 1996; Schoeman and Richardson, 2002). Therefore: (1) the risk of pelagic larvae of small benthic recruits being dragged towards the shore and dying is smaller; and (2) the risk of the pelagic larvae being ingested by conspecifics in shallower areas where they are more abundant is lower. However once pelagic larvae have settled as a small benthic recruit, as they grow, they migrate to shallower areas where food is more abundant, and predation is lower. Hydrodynamic processes (*e.g.*, advection of surface gravity waves and turbulent mixing in the bottom boundary layer) influence the settlement of invertebrate larvae to the bottom substrate (Pineda et al., 2010). Crimaldi et al. (2002) showed that hydrodynamics imposes a negative effect on the pelagic clam larvae settlement. The Baltic tellin *Macoma balth*ica (Linnaeus, 1758), for example, settles in the low intertidal in the Wadden Sea due to hydrodynamics but then migrates to the upper intertidal (Beukema et al., 1993; Hiddink and Wolff, 2002). The predation by suspension-feeding bivalves on their own larvae has been described for many species (Tamburri and Zimmer-Faust, 1996; Lehane and Davenport, 2004), but its significance in regulating recruitment in the field is difficult to document. Several authors reported that larval recruitment is inversely related to adult bivalve density suggesting an adult predation on larvae (André and Rosenberg, 1991). For example, Lima et al. (2000) observed that high adult densities of *Amarilladesma mactroides* seem to reduce the recruitment through the passive filtration of the larvae. The predation of bivalves on their own larvae has been observed. These type of predation on their own pelagic larvae potentially mediates population structure through settlement inhibition (Pineda et al., 2010).

Small-scale fisheries constitute complex socio-ecological systems, where economic, cultural, historical and political aspects interact with the biophysical component of the system, with interdependent feedback relationships (McLachlan et al., 2018). In these multidimensional systems, any intervention, small or large, may change the structure and functioning of the system (Jentoft and Chuenpagdee, 2018). In fact, this complexity makes these systems difficult to manage. Focusing on the wedge clam fisheries, their management is affected, among others, by the following factors: (1) These species inhabit shallow waters, and they are easily accessible, and relatively simple to harvest (Defeo, 2003). The fishing pressure from illegal and recreational fishers is difficult to control and quantify. (2) Wedge clam populations have a naturally high variation in interannual densities (Delgado et al., 2017). Environmental factors (e.g., rain, chlorophyll-a, wind and SST, salinity) play an important role in both the biomass and location of the wedge clam beds (de Almeida et al., 2021) and the survival and recruitment success (Reyes-Martínez et al., 2020) (3) The congruence between appropriation and provision regulations and local conditions is difficult to achieve, because the wedge clam is a very fast-growing species (Ramón et al., 1995). This fact implies that a continuous monitoring of the fishing grounds is strongly required to manage this resource. It requires a strong investment by the authorities that are usually not willing to make it due to the low economic return it generates. As a result, biological data on the wedge clam fishing grounds are scarce. (4) The disparity of criteria in the management and governance framework both at the regional and local levels of the wedge clam fisheries in the Mediterranean coast of Spain generates confusion. For example, two different fleets/users coexist targeting the same species and the same fishing stock in the same geographic area, but they have different Management Plans (the first controlled by the Catalan Regional Government and the European Commission, and the second only by the Catalan Regional Government). This duality in the governance and management of the wedge clam in the Ebro Delta area generates misgovernance. In this context, a unique management is required. Another good example is the Minimum Legal Size (MLS) which is not uniform in Spain. It is 25 mmm for the mechanized clam dredge fleet, while it is 21.86 mm for the hand-operated fishers in Catalonia. However, it is 25 mm in Andalusia (S Spain), 25 mm in Valencia (W Spain) and 35 mm in Galicia (NE Spain). (5) Additionally, environmental, genetic and anthropogenic factors (e.g., fishing pressure) can affect the gametogenesis in marine species (Tobin and Wright, 2011). Moreover, the biological features of some species can vary (e.g., length at first maturity) to adapt to commercial exploitation and environmental changes (Domínguez-Petit et al., 2008; Hunter et al., 2015). For example, Galimany et al. (2015) reported a decrease in the L50 for an overexploited clam population (*Callista chione*) on the Catalan coast.

Management responses to reconcile declining fisheries frequently include the closure of specific areas (Barnes and Sidhu, 2013). These areas are implemented for conservation and fisheries benefits, but the effects of such initiatives are often not tested (Balcells Surroca et al., 2016; Gray, 2016). Fishery closures were recently implemented as a tool for the recovery of clam stocks in the Mediterranean coast of Spain (*e.g.*, Valencia and Catalonia) (Baeta et al., 2018). Below a threshold population size, the population growth slows down as population abundance declines, preventing the recovery of the stock (Stephens and Sutherland, 1999). Considering the results obtained, we suggest that spatial and temporal fishing closures located in shallower areas (0.2 to 0.7 m) where juveniles are concentrated may improve landings of the wedge clam in the Ebro Delta. Moreover, this area has concentrated the highest fishing pressure over the stock. A management plan for the Ebro Delta should include both fishing gears targeting *D. trunculus* (*i.e.*, hand-operated dredges and mechanized clam dredges). Both target the same population but in different bathymetrical range.

Understanding the ecology of marine commercially exploited species is essential to sustainable fisheries management. This is particularly important in species that has experienced critical declines in their populations (e.g., clam species in Mediterranean coast of Spain) and its crucial to achieve their recovery. A holistic approach has been done in the present study to provide tools for the authorities that allow improving the management of the clam *D. trunculus* in Ebro Delta area. The causes of the dramatic decline in wedge clam in the Mediterranean coast of Spain remain unknown. However, the conservation of the remaining resources, a sustainable management and the recovery of their populations must be a priority to preserve them for future generations and to maintain healthy coastal ecosystems.

CRediT authorship contribution statement

Marc Baeta: Conceptualization, Sampling, Methodology, Writing – original draft, Visualization, Writing – review & editing. **Marco Antonio Solís:** Sampling & review. **Silvia Frias-Vidal:** Sampling, Visualization, Writing – review & editing. **Laura Claramonte:** Sampling & review. **Manuel Ballesteros:** Review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Marc Baeta reports financial support was provided by Generalitat de Catalunya Departament d'Agricultura Ramaderia Pesca i Alimentacio. Marc Baeta reports financial support was provided by European Maritime and Fisheries Fund.

Data availability

Data will be made available on request.

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