#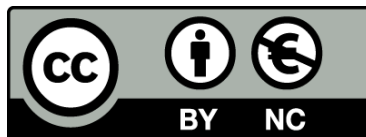 Ecology of some keystone invertebrates inhabiting shallow soft bottom communities of the Maresme coast (NW Mediterranean Sea)

Marc Baeta Alacio

Ecology of some keystone invertebrates inhabiting shallow soft bottom communities of the Maresme coast (NW Mediterranean Sea)

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PhD Thesis, 2015

Ecology of some keystone invertebrates inhabiting shallow soft bottom communities of the Maresme coast (NW Mediterranean Sea)

Ecología de algunos invertebrados clave que habitan en comunidades de fondos blandos someros de la costa del Maresme (noroeste del Mar Mediterráneo)

Marc Baeta Alacio

Memoria presentada por Marc Baeta Alacio para optar al grado de doctor por la Universitat de Barcelona

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A la Carlota, a l'Oriol, al Fonoll i als meus pares.

"Estamos tan cerca del límite, que puede que despertemos un día para darnos cuenta que ya no queda nada por salvar".

Maneka Gandhi

Research framework

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"You've heard the old law of physics that a bumble bee can't fly. Every aerodynamic principle says that its wing span is too short to support its massive body in flight. But a bumble bee doesn't know that. It never took physics. It just flies around all over the place and that's what you have to do." (Dr. Julian Earls, NASA).

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INDEX

1. ABSTRACT

Bivalves living in large aggregations of individuals (reefs or beds), such as mussels, clams, cockles and some high trophic predators such as sea stars, play an essential ecological role in the structure, integrity, stability, and diversity of the biological communities; being usually considered as keystone species. Their disappearance or decline could lead to disproportionate effects in their communities, even affecting the survival of other species. Although keystone species are crucial for maintaining the Earth biodiversity, often their study has not taken enough attention. The main aim of this Doctoral Thesis was to study the ecology of some keystone invertebrates inhabiting shallow soft bottom communities of the Maresme coast (Northwestern Mediterranean Sea). The results enhance the knowledge of the smooth clam (*Callista chione*) and also of its potential predators, several species of sea stars (*Astropecten* spp.) co-occurring in the area. But at the same time, our findings help to understand their trophic interactions, the status of their populations and propose guidelines for their conservation. Maresme coast is close to Barcelona and it has concentrated historically a high anthropogenic pressure that has altered and modified its environment. Our results have showed the critical status of the smooth clam bed as a consequence of the combination of different human coastal uses: sand dredging and clam fisheries. These anthropogenic pressures have also led to significant changes in *Astropecten* populations. *A. aranciacus* has been shown to be the most vulnerable, and consequently the most affected, to the extent that its population suffers an important and worrying decline. Moreover, *A. aranciacus* reproductive cycle, growth and depth segregation between size classes along the continental shelf have been described for the first time. Our results have documented *Astropecten* species niche segregation, which allow them to co-occur within a biological community scale, without compete for the same available recourses. Sea stars showed a partitioning of the prey (species) and microhabitats in the Maresme coast. This Doctoral Thesis aims to provide a valuable background to improve the conservation of these keystone invertebrates, as well as to promote the sustainable exploitation of shellfish.

Los bivalvos que viven en grandes agregaciones de individuos, como por ejemplo algunas especies de mejillones, almejas y berberechos; y algunos predadores que ocupan elevados niveles tróficos como por ejemplo las estrellas de mar juegan un papel crucial en la estructura, integridad, estabilidad y diversidad de la comunidades biológicas, siendo habitualmente considerados como especies clave. Su desaparición o declive puede conducir a efectos desproporcionados sobre el conjunto de sus comunidades, incluso afectando la supervivencia de otras especies. Aunque las especies clave son esenciales para mantener la biodiversidad en el planeta Tierra, a menudo no se ha prestado suficiente atención a su estudio. El principal objetivo de esta Tesis Doctoral fue el estudio de la ecología de algunas especies clave que habitan los fondos blandos y someros de la costa del Maresme (noroeste del Mar Mediterráneo). Los resultados obtenidos mejoran de forma significativa el conocimiento sobre la concha fina (*Callista chione)* y sus depredadores potenciales, distintas species de estrellas de mar del género *Astropecten* que cohabitan en la zona. Al mismo tiempo ayudan a entender sus relaciones tróficas, el estado de sus poblaciones y se proponen pautas para mejorar su conservación. La costa del Maresme se halla cerca de la ciudad Barcelona, y por ello ha concentrado históricamente una elevada presión antropogénica que ha modificado y alterado su medio ambiente. Los resultados de esta Tesis Doctoral muestran como el estado crítico de la población de concha fina (*C. chione*) es consecuencia de la

combinación de distintas presiones antrópogenicas: dragados de arenas y pesquerías de moluscos bivalvos. También se ha observado que estas mismas presiones han producido cambios significativos en las poblaciones de estrellas de mar *Astropecten*. *A. aranciacus* ha resultado ser la estrella más vulnerable a dichas presiones y en consecuencia ha sido la más afectada, viéndose su población disminuir a un rito preocupante. Además, se ha descrito por primera vez la reproducción, el crecimiento y la segregación batimétrica por tallas de *A. aranciacus*. Los resultados documentados también muestran que las distintas especies de *Astropecten* pueden cohabitar por la segregación de sus nichos ecológicos permitíendoles no competir por los recursos disponibles (presas y hábitat). Esta Tesis Doctoral pretende proporcionar un trasfondo valioso para mejorar la conservación de estas especies clave, así como promover la explotación sostenible de los moluscos bivalvos.

Els bivalves que viuen en grans agregacions d'individus, com ara algunes espècies de musclos, cloïsses i escopinyes; i alguns predadors que ocupen elevats nivells tròfics com ara les estrelles de mar juguen un paper fonamental en l'estructura, integritat, estabilitat i diversitat de les comunitats biològiques, sent habitualment considerats com espècies clau. La seva desaparició o declivi pot conduir a efectes desproporcionats sobre el conjunt de les comunitats on habiten, fins i tot afectant la supervivència d'altres espècies. Tot i que les espècies clau són essencials per mantenir la biodiversitat al planeta Terra, sovint no s'ha prestat prou atenció al seu estudi. El principal objectiu d'aquesta Tesi Doctoral ha estat l'estudi de l'ecologia d'algunes d'aquestes espècies clau que habiten els fons tous poc profunds de la costa del Maresme (nord-oest del Mar Mediterrani). Els resultats obtinguts milloren de manera significativa el coneixement de la població de petxinot de sang (*Callista chione*) i dels seus potencials depredadors, diferents espècies d'estrelles de mar (*Astropecten* spp.) que cohabiten a la zona. Al mateix temps ajuden a entendre les seves relacions tròfiques, l'estat de les seves poblacions i es proposen pautes per a la seva conservació. La costa del Maresme és molt propera a la ciutat Barcelona, i per això ha concentrat històricament una elevada pressió antropogènica que ha modificat i alterat el seu medi ambient. Els resultats d'aquesta Tesi Doctoral mostren com l'estat crític de la població de petxinot de sang (*C. chione*) és conseqüència de la combinació de diferents pressions antropogèniques: dragatges de sorres i la pesca de bivalves amb dragues. També s'ha observat que aquestes mateixes pressions han produït canvis significatius en les poblacions d'estrelles de mar *Astropecten*. *A. aranciacus* ha resultat ser l'estrella més vulnerable a aquestes pressions i en conseqüència ha estat la més afectada, veient-se la seva població disminuir a un ritme preocupant. A més, s'ha descrit per primera vegada la reproducció, el creixement i la segregació batimètrica per mida de *A aranciacus*. Els resultats obtinguts també mostren que les diferents espècies de *Astropecten* poden cohabitar per la segregació dels seus nínxols ecològics permeten-los no competir pels recursos disponibles (preses i hàbitat). Aquesta Tesi Doctoral pretén proporcionar un rerefons valuós per a millorar la conservació d'aquestes espècies clau*,* així com promoure l'explotació sostenible dels mol·luscs bivalves.

2. GENERAL INTRODUCTION

The concept of keystone species has been widely employed in community ecology and conservation biology (Simberloff 1998) since it was firstly coined by Paine in 1966. Keystone species are those considered exceptional, relative to the rest of the community, in maintaining their organization and diversity (Paine 1969; Mills *et al.* 1993). Bivalves living in large aggregations of individuals (reefs or beds) such as mussels, clams, cockles and some high trophic predators such as sea stars have been widely considered as keystone species (Paine 1969; Dame 1996). Unfortunately, some of these species have been relatively poor studied, even though the essential role that they play in marine ecosystems.

The world's biodiversity is diminishing quickly due to human activities (Jenkins *et al.* 2003). Several studies suggested that a sixth mass extinction may be under way (Barnosky *et al.* 2011). Over the last years, conservation experts have focused on identifying areas of prime importance as one of the keys to preserve species, genes and ecosystems, and their work resulted in the identification of 25 biodiversity hotspots, being the Mediterranean Basin one of them (Myers *et al.* 2000; Shi *et al.* 2005). The conservation status of all species inhabiting the Mediterranean Sea is difficult to determine because there are more than 17000 species occurring (Coll *et al.* 2010). On one hand, scientists historically have focused on the knowledge of commercially exploited species with an associated important economic value, and over these species those that may have a major impact on the human economy (e.g. toxic phytoplankton, virus, bacteria and jellyfish). On the other hand, conservationists have barely focused on rare, endemic, large, attractive and flagship species such as seagrass, marine turtles, sharks, sea birds and marine mammals. Unfortunately species not included in any of these groups have been usually less studied, even though they sometimes play a crucial role in ecosystems (keystone species).

This Doctoral Thesis has contributed to enhance the knowledge of the biology and the ecology of some of these keystone species; the smooth clam *Callista chione* and sea stars of genus *Astropecten*. Smooth clam is currently one of few bivalve species of commercial importance in the Mediterranean Sea, which historically has constituted a clam bed in the Maresme coast and sustained an important clam dredge fishery. In the same area several *Astropecten* sea star species appeared regularly as a smooth clam fishery by-catch. These sea stars are voracious predators at or near the top of the coastal food chain and play an essential role in soft bottom ecosystems, where they can strongly influence commercial shellfish beds; unfortunately most of their ecology was unknown. Moreover, this Doctoral Thesis has contributed to improve the knowledge about status of their populations, and has defined management strategies for the clam bed restoration. These measures would benefit the entire coastal ecosystem, including those species occupying upper trophic levels, such as sea stars of the genus *Astropecten*.

2.1. *Mediterranean Sea*

The term Mediterranean derives from the Latin word "*Mediterraneus*", meaning "between lands" as it is located between the continents of Africa, Asia and Europe. The Mediterranean Sea covers an area of approximately 2.5 million km^2, with an average depth of about 1500 m (the deepest recorded point is 5267 m in the Calypso Deep, at the Ionian Sea), a total volume of 3.7 million km^3; and a renewal period of 80 years

(Ambroggi 1977; Vanney and Gennesseaux 1985). The coastline extends for 46000 km. It is the largest semi-enclosed sea in the world (Tyler 2003), being connected to the Atlantic Ocean through the Strait of Gibraltar at the east (with a mean depth of 300 m and a width of 14 km); to the Black Sea through the Strait of Dardanelles at northwest (mean depth of 50 m and a width of between 1.6-6.5 km); and to the Red Sea through the artificial Suez Canal at southeast (length of 193.30 km, mean depth of 24 m and wide of 205 m). It is divided into two main basins: the eastern and the western depressions of respectively 0.85 million km² and 1.65 million km², connected through the Strait of Sicily (wide of 145 km and mean depth of 90 m).

The Mediterranean Sea is now known to have a complex thermohaline. Wind and water flux is driven in a multi-scale circulation with an important local variability (Robinson *et al.* 1991). The evaporation greatly exceeds the total of precipitation and river runoff (Hopkins 1985). Furthermore, the water exchange within the Strait of Gibraltar strongly influences the general circulation of the entire sea (Huertas *et al.* 2012). There is an inflow of surface Atlantic water from the Strait of Gibraltar that spreads throughout the whole basin flowing from the west to the east and becoming progressively denser. The return of Mediterranean waters to the Atlantic Ocean occurs through deep waters flowing from the east to the west (Astraldi *et al.* 2002). It also has some upwelling areas with high productivity, achieving the highest levels along the coastline, especially near the major estuaries (Salat *et al.* 1978; Malak *et al.* 2011). These areas contribute to provide a vertical recycling of nutrients and other dissolved substances (Margalef 1978). Notwithstanding, it is an oligotrophic sea, with low primary production in comparison with other oceans and seas, and the nutrient concentration decreases from west to east, being the eastern basin one of the poorest marine areas of the Earth (Danovaro *et al.* 2010). The other main physical features that characterize the Mediterranean Sea are a high and relative constant temperature below 200 m depth (12.5-14.5ºC), a high salinity (38.0-39.5‰) and high oxygen values (4.5-5 ml/l), reaching saturated levels at the surface layer (Hopkins 1985).

The Mediterranean Basin constitutes one of the 25 biodiversity centers (hotspots) that are recognized on a planetary scale, featuring exceptional concentrations of endemic species and experiencing exceptional loss of habitats (Myers *et al.* 2000). Estimates of Mediterranean marine species, taken from compilations of previous works, show approximately 17000 species occurring in the Mediterranean Sea. This corresponds to 4-18% (according to taxonomic group) of the world's known marine species in only 0.82% of the world surface area (Bianchi and Morri 2000). However anthropogenic impacts such as coastal infrastructures, dam construction, overpopulation, tourism, land-based pollution, erosion, droughts, alien species and overexploitation of fauna and flora are all driving the decline of this biodiversity. Among all menaces, Costello *et al.* (2010) identified that overfishing, habitat loss and pollution are the greatest threats. Anthropogenic threats to marine diversity are several and extend from coastal regions to the open seas in the Mediterranean Sea, but they are more intense in the coastal regions (Coll *et al.* 2010).

2.2. *Coastal regions*

There is no consensus of what constitutes a coastal region, although most definitions are based on an area within 60 to 200 kilometers from the intertidal zone out to the continental shelf break (Creel 2003). These areas have a high primary and secondary

productivity, supporting a great abundance and diversity of fauna and flora (Beck *et al.* 2001), being the most ecologically and socio-economically vital on the planet. They provide over US$14 trillion worth of ecosystem goods (e.g. food and raw materials) and services (e.g. disturbance regulation and nutrient cycling) per year (Costanza *et al.* 1997). Moreover, coastal regions play an important role for many fish and invertebrate species, which may utilize these areas during one or several parts of their life cycle. Some species live permanently in these coastal regions, whereas other species may be present as juveniles, migrate seasonally or pass through on their way between marine and fresh waters (Elliott and Dewailly 1995). Additionally, these areas are generally considered to be important nurseries, environments where recruits experience enhanced survival and growth. These habitats may provide refugee from predation and a rich production of food (Rozas and Odum 1988).

Coastal regions are highly variable systems, where changes in the water circulation patterns and fluctuations of land influences (e.g. rivers, sewage flow) induce high temporal variability on scales ranging from hours to seasons. This variability may be reflected in the dynamics of populations, particularly planktonic ones, thriving in coastal systems. Such variability may hide the underlying seasonal patterns of organism abundance and biomass (Calbet *et al.* 2001).

The coastal strip (200 kilometers inland from the coastline) is the most densely populated area of the world and many of the largest cities are located there; even though, this fringe is only the 10% of the Earth's surface (UNFPA 2007). Today, $3.5 \cdot 10^9$ people, about half of the world's population, live there and an increase of more than 75% of the total population is expected to live within this area by 2025 (EEA 2006). This high concentration of people has produced many economic benefits, including improved transportation links, industrial and urban development, revenue from tourism, and food production (Creel 2003). Notwithstanding, the pressure derived from these activities has severely impacted these areas (Burke *et al.* 2001), resulting in habitats that are no longer adequate to fulfill nursery, feeding, or reproductive functions (Seitz *et al.* 2013). As a consequence, marine species composition, distribution and abundance have been strongly altered throughout the last decades and species occupying higher trophic levels have been particularly affected (Menge *et al.* 1994; Jackson *et al.* 2001; Hutchings and Baum 2005).

2.3. *Maresme coast (NW Mediterranean Sea)*

All the samples used in this Doctoral Thesis were collected in the Maresme coast (Catalonia, NW Mediterranean Sea). The region of Maresme is located at northeast of Barcelona city, inside of its metropolitan area, being one of the heavily populated and industrialized zones of Spain. It has a coastline of 51 km long between the Tordera River Delta (northeast) to the Tiana seasonal stream (southwest), which displays a NE-SW trend, and has been structurally controlled by the Pyrenean fault complex since the Oligocene (Ercilla *et al.* 2010) (Fig. 1).

Maresme coast has a straight and wave dominated coastline with reflective and coarse sandy beaches originated from the erosion of degraded granite from the nearby mountains carried by short rivers, such as the Tordera, and seasonal stream "*rieres*". The coastal area is affected by a low-energy wave climate, with mean wave heights of 1 m and a mean period of about 4 s. The most important storms are those from the east,

which have a typical duration of few days and are often associated with the above cyclonic activity in the Western Mediterranean (Ojeda and Guillén 2006). Storm conditions are recorded essentially from October to December, which affect the seafloor down to a water depth of 20 m (Ercilla *et al.* 2010).

The continental shelf has a mean width of 21 km, a gradient among 0.01-10º and its shallow seabed consists of coarse to medium-sand bottoms and mud or/and sandy bottoms occur offshore (Díaz and Maldonado 1990). Furthermore, it has a narrow infralittoral plain between 0-30 m that displays parallel to the coastline. This coastal fringe has historically concentrated the high anthropogenic pressures and its environment has been modified. For example, human actions related to dredging operations (beach nourishment and infilling of the harbor entrance) have impacted on the sedimentary system (Ercilla *et al.* 2010).
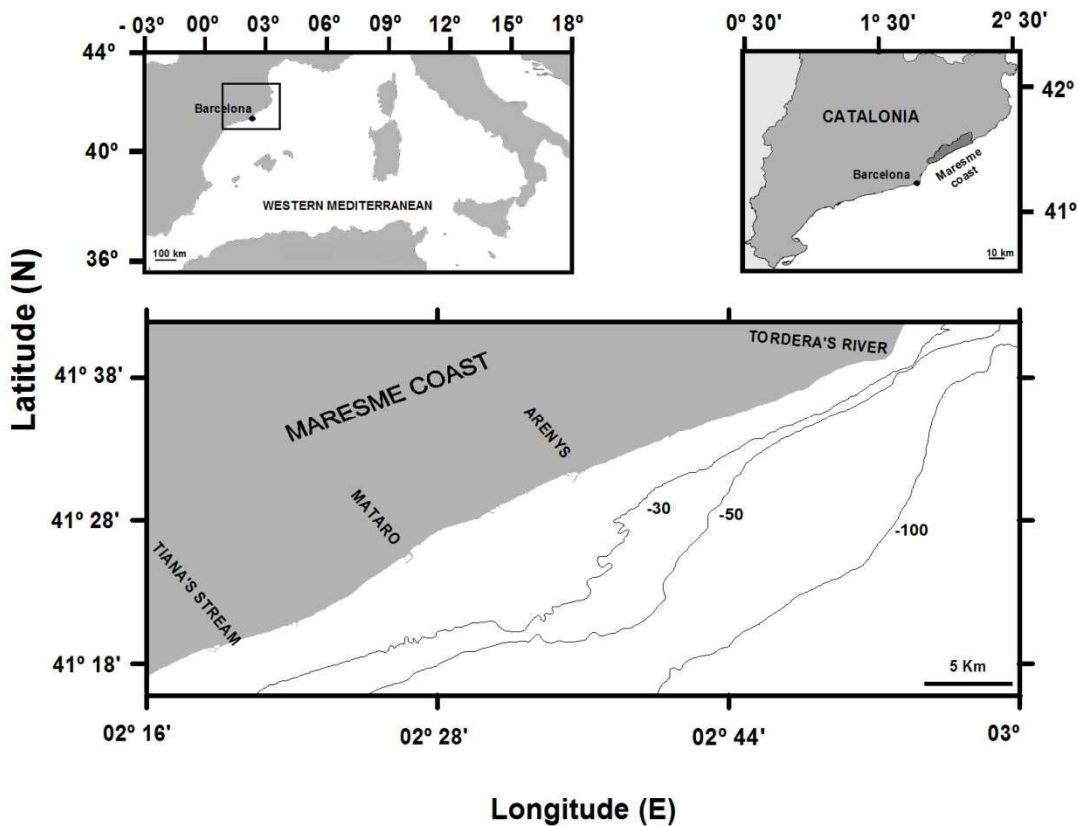
Figure 1. Study area (Maresme coast) location

2.4. *Largest habitats on Earth: marine soft bottoms*

Marine soft bottoms comprise one of the largest and oldest habitats in the world (Gray 2002). Sediments have a reputation for being flat and brown, and are certainly less glamorous than the colorful rocky pinnacles, seamounts and coral reefs that attract mass media attention. However, soft bottoms host a diverse array of organisms and play a pivotal role in marine ecosystem functioning (Lohrer and Hancock 2004). Therefore, organisms residing in marine sediments constitute the largest faunal assemblage on Earth coverage (Snelgrove 1998). Their activity impacts global carbon, nitrogen and

sulfur cycling, transport, burial and metabolism of pollutants, secondary production (including commercial species), and transport of sediments (Snelgrove 1998; Díaz-Castañeda and Harris 2004). This biogenic influence is generally minimal where, for instance, tidal currents or wave surge have an overriding impact. Notwithstanding, where physical processes are less rigorous or are infrequent, biologically induced modifications to the sediment-water interface assume increasing importance and the structure of the benthic community becomes defined in part by the dynamic inter-relationships between the sedimentary requirements of one species and the hydrodynamics of near-bottom flow (Probert 1984). The correlation of groups of soft-bottom animals and certain types of sediment and depth zones, was first described by Petersen (1914). A correspondence between sediment types and major benthic communities for Mediterranean Sea has long been recognized; it was described from a qualitative and quantitative point of view by Pérès and Picard (1964); Picard (1965); Pérès (1982).

Grain size is the most fundamental physical property of sediment. The granulometric nature of sea soft sediments ranges from clays ($\phi \leq 0.002$ mm) to large boulders ($\phi > 630$ mm), following the grain size International scale ISO 14688-1. Muds and clays are prevailing in most of the seabed corresponding to deep areas, while sands are predominant in the continental shelf. Coarse sand bottoms (0.63-2.0 mm) are relatively scarce in the Western Mediterranean, appearing only in areas where granitic or volcanic intrusions occur among the mainly calcareous sedimentary rocks (e.g. limestone). Along the Mediterranean shores of the Iberian Peninsula, coarse sandy beaches are found only in a relatively small region at the north of Barcelona (Maresme and Costa Brava) and in the Alboran Sea (Mediterranean coast of Andalusia) (Pubill *et al.* 2011). Gravel and coarse sandy bottoms are mostly populated by filter feeders and fine sandy bottoms are predominantly composed of deposit feeders; while muddy substrates are mainly inhabited by deposit and detritus feeders (Dobson and Frid 2008).

Soft bottoms and associated benthic communities of coastal shelf areas are subject to many forms of natural disturbance, which vary in the extent of their influence from a few meters to hectares. As a consequence, life histories of benthic organisms are closely linked to the regime of local prevalent natural disturbances. Often, there exists a threshold scale and frequency of these events at which long-lasting ecological effects may occur. However, anthropogenic ones may exceed this threshold (Kaiser and Spencer 1996). Within disturbances, there is a consensus that fishing; in particular bottom trawling and dredging, are the most severe anthropogenic impacts on marine environments, being the main responsible of soft bottoms deterioration on the continental shelf (Dayton *et al.* 1995; Jennings and Kaiser 1998; Thrush and Dayton 2002). It is well known that these fisheries severely damage the epi- and infaunal communities inhabiting intertidal and subtidal sediments, because they not only remove the target species but also impact on associated flora and fauna (Piersma *et al.* 2001). Usually greatest impacts affect to slow-growth, low recruitment and long-life species. In general, these fishing techniques have a limited impact in shallow areas where species conforming communities are well adapted to environmental disturbances (e.g. waves and tides) (Gaspar *et al.* 2001). Species inhabiting these areas are characterized by fast-growing and short lives. Even though, impact is more intense in deeper areas; where storms and strong waves influence are less important or imperceptible (Watling and Norse 1998; Gaspar *et al.* 2001).

Figure 2. Coarse sandy bottoms (Source: http://www.noaa.gov/)

Last decades the demand for marine sand for coastal development and coastal protection has increased throughout the world (van Dalfsen *et al.* 2000). In the European Union, marine sand has emerged as a strategic mineral resource. This is due to an increasing general demand and to stricter regulations on the exploitation of land-won aggregates. Annually, approx. 40 million m^3 of marine sand are extracted, alone, from the North European inner continental shelf (<60 m) (Bonne 2010). An important human population growth and an intensive tourist development have led to the artificialisation of large extensions of the Mediterranean coast of Spain. Piers, jetties, breakwaters, ports, artificial beaches and boardwalks have modified the natural dynamics of the sediments. It has resulted in a severe erosion all along the Mediterranean coast and has led to an increased need for material for beach recharge (van Dalfsen *et al.* 2000). Marine sand extraction could be a source of sand for construction and industrial uses, although in the Mediterranean coast of Spain is mainly used for beach replenishment to combat coastal erosion and in lesser extent for harbor maintenance (ICES 2006). The extraction of sand may interfere with the sand balance of the coast and influence the ecological functions of the seabed (De Groot and Forster 1979; van Dalfsen *et al.* 2000). Several studies have analyzed the effect of dredging on benthic communities (Newell *et al.* 1998; Sardá *et al.* 2000; Bolam *et al.* 2006) and it is known that the degree and duration of change in sediment composition caused by sand extraction has large implications for the recovery of the benthic fauna (van Dalfsen *et al.* 2000). When an area is depopulated by sand extraction, recolonization largely depends on the settlement of larvae and immigration of mobile species. Newell *et al.* (1998) suggested that long-life and slow-growing species may take several years before larval recruitment occurs, and subsequent growth of the juveniles allow restoration of the original community composition and biomass.

2.5. *Species coexistence*

The term species coexistence is defined as two or more species being found in the same place at the same time. In some sense, all the species on the Earth coexist, because they

are found in one place (the Earth) and at same time (now) (Holt 2001). For this reason, coexistence may depend on the scale of the space considered (Hanski 1983) and the persistence over time (Holt 2001). Therefore, hereafter when referring to species coexistence, it is understood within a biological community scale. Biological communities characteristically are assemblages of organisms whose composition and aspect are determined by the properties of the environment and by the interactions of the organisms to each other (Krebs 2009). These interactions can occur directly (e.g. via interference competition, predation, parasitism, commensalism and mutualism) or indirectly (via altering biotic conditions, resource competition and apparent competition) (Siepielski and McPeek 2010). This Doctoral Thesis has focused its attention in the study of two of these interactions: resources competition (among sea stars) and predation (sea stars over clams). Interspecific competition, has long been thought to be one of the most important processes determining the structure of natural communities (Cody 1975); whereas predation was relegated to play a secondary role (Chase *et al.* 2002). Notwithstanding, recent studies have assigned both interactions an equal relevance in structuring and promoting communities diversity (Chesson and Kuang 2008).

Resource competition is the interaction in which two (or more) species exert negative influences upon each other through resource exploitation. First theoretical models stated that two species competing for the same resource cannot coexist at constant population values if other ecological factors remain constant. One of the two competitors always overcame the other, leading to either the extinction or the migration of the competitor (Gause 1934). Notwithstanding, later MacArthur (1972) showed that the stable coexistence actually requires species to differ in their niches. Ecological niches are all relationships that each organism or population has with its environment and with other organisms and populations in its environment. In addition, species may interact directly via predation. Predation occur when a member of one species, predator (organism that is hunting), feds on its prey (organism that is consumed). Predators may or may not kill their prey prior to feeding on them, but the act of predation often results in the death of its prey and the eventual absorption of the prey's tissue through consumption (Begon *et al.* 1996; Krebs 2009). The presence of species inhabiting together under competitive and predator-prey interactions within natural communities indicates that these species have accommodated themselves to each other's presence, and have evolved ways to survive despite the pressures. In other words, they have coevolved. Therefore, both interactions play an essential role in generating biological diversity.

2.6. *The concept of keystone species*

The concept of keystone was first coined for top predators in marine rocky benthic communities by Paine (1966); since then, many ecologists and conservationists have focused their attention on it. Paine (1966) noted that the experimental removal of the top predator (a sea star, *Pisaster ochraceus*) from a section of shore resulted with the reduction of original diversity in intertidal rocky ecosystems on the coast of Washington. Subsequently Paine (1969) showed that the top predator (the gastropod *Charonia* spp.), which feeds on the coral predator sea star *Acanthaster planci,* prevents the over-consumption of coral on some parts of the Great Barrier Reef. He defined keystone species as a species whose presence, activity and abundance are crucial in the integrity, stability, organization and diversity of the community, whereas variations in the abundance of other predators would not produce any impact comparable to that

produced variations in keystone species. Then, the term has been generalized and applied to many species at various trophic levels (Mills *et al.* 1993). Of the current various definitions of keystone species that have been attempted, perhaps the most useful is that given by Jones *et al.* (1994): "those whose removal from the community would precipitate a further reduction in species diversity or produce significant changes in the community structure and dynamics".

Keystone species are usually noticed when they are removed or they disappear from an ecosystem, resulting in dramatic changes to the rest of the community. Identifying keystone species is difficult, but essential to understanding how their lost will affect ecosystems (Power *et al.* 1996) and can be a helpful tool for their management and conservation. It is expected that all species of a given ecosystem rank in a *continuum* of levels of "*keystoneness*", with only some designated to be keystone species (Libralato *et al.* 2006). Unfortunately, attempts to develop a set of species traits that would *a priori* determine keystone interactions have thus far proved elusive (Menge *et al.* 1994; Payton *et al.* 2002).

The keystone species role can arise in several different ways. This Doctoral Thesis has focused its attention in two types of organism on the basis of their functional role as keystones: (I) predators and (II) habitat modifiers and/or engineers:

I. *Predator keystone species:* It is the classical definition coined by Paine (1966). There is only one predator in a community that alone determines most of the patterns of prey community: structure, distribution, abundance, size composition and diversity (Menge *et al.* 1994). Keystone species can be top predators, although commonly they are nothing but simply predators. Top predators are thus without any natural predators and occupying the highest trophic level at their food chain. Some examples of top predators keystone species are: gray wolves (*Canis lupus*) in National Parks and isolated islands (Berger and Smith 2005) and jaguar (*Panthera onca*) in Mesoamerica on terrestrial environments (Swank and Teer 1989) and the nile crocodile (*Crocodylus niloticus*) in Olifants River, South Africa (Joubert 2007) on aquatic continental environments. Even though, most widely recognized keystone predators are sea otters (*Enhydra lutris*) in North West America (Estes *et al.* 1978) and several species of sea stars in rocky intertidal and subtidal habitats (Paine 1969).

Since Paine (1969), increasing numbers of studies on asteroids role in organizing benthic marine communities have been published. They summarized that sea stars are among the most important predators in benthic marine communities, exerting a strong influence on the structure and function of the community they prey on, promoting its heterogeneity and diversity in the community (Jangoux 1982; Menge 1982). Sea stars have been observed worldwide inhabiting different habitats from rocky to soft bottoms, from intertidal to deep areas and from Tropical to Arctic seas (Menge *et al.* 1994; Navarrete and Menge 1996; McClintock *et al.* 2008).

II. *Habitat modifiers and/or engineers:* "The activities of many species greatly affect habitat features without necessarily having direct trophic effects on other species. If the modified habitat affects the survival of many other species, the modifying species has been considered a keystone species" (Mills *et al.* 1993).

prairie dogs (*Cynomys* spp.) in prairie systems of the United States, rabbits (*Oryctolagus cuniculus*) in Southwestern Europe, plateau pikas (*Ochotona curzoniae*) on the Tibetan plateau and beavers (*Castor canadensis*) in North America stream system are the most famous examples of keystone species of this subgroup (Mills *et al.* 1993; Kotliar *et al.* 1999; Smith and Foggin 1999; Delibes-Mateos *et al.* 2011). It has been argued that these species increase species richness (vertebrates, invertebrates and plants), but additionally they play an important role as ecosystem service. Their activities increase habitat for other species, enhance water infiltration, minimize erosion and improve nutrient cycling. Furthermore they are active dispersal of seeds and improve seed germination rate and success, and at last they stabilized vegetative community (Delibes-Mateos *et al.* 2011).

A good example of keystone habitat modifiers and/or engineers in marine ecosystems are large concentrations of bivalves (e.g. oyster reefs, clam beds, scallop beds and cockle beds) (Dame 1996). It has long been recognized that large concentrations of bivalves can play an important structural role in coastal waters, providing habitats and refuges for characteristic assemblages of organisms (including vertebrates, invertebrates and algae) (Wells 1961; Hall-Spencer and Moore 2000). For instance, eastern oysters (*Crassostrea virginica*) can create large reefs in temperate estuaries of the eastern coast of North America. Lenihan and Peterson (1998) showed that fishing pressure over oysters in Neuse River estuary (North Caroline) caused an important increase of bioturbation and habitat degradation; extending bottom-water hypoxia/anoxia throughout the estuary. The consequence was massive oyster mortality, and then a significant reduction in other species abundance and distribution.

There is an increasing consensus that it is necessary to identify at least the keystone species in each habitat and carry out detailed biological and ecological research to understand these organisms. Then they should be protected, and even enhanced, to maintain ecosystems biodiversity and equilibrium.

Large concentrations of bivalves have been widely considered keystone species in marine ecosystems (Dame 1996). As habitat modifiers and/ or engineers, because they structure provided by shells and by byssal threads in soft sediments serve to ameliorate environmental extremes, deposit organic matter, fertilize sediments and promote growth of marine plants (Coleman and Williams ; Reusch *et al.* 1994). In addition, they provide habitats and refuges for characteristic assemblages of organisms (including vertebrates, invertebrates and algae) (Wells 1961; Hall-Spencer and Moore 2000). But sometimes also as predator keystone species: in bivalve dominated systems they directly control phytoplankton and zooplankton through top-down forces, and they also compete with herbivorous zooplankton for phytoplankton (Dame 1996; Davenport *et al.* 2000; Prins and Escaravage 2005). The smooth clam population from the Maresme coast can be considered as a keystone species. Its role as habitat modifier is clear; Pubill *et al.* (2011) observed that *C. chione* was a dominant species in "*coarse sand shallow assemblage*" and "*coarse sand deep assemblage*" in Maresme coast, where these assemblages are characteristics. Due to their burrowing activity and its large size, these species can increase sediment water and oxygen content and enhance exchange with the overlying water column, thereby affecting nutrient cycling. Moreover, the sediment is full of old dead shells serving to dwell and refuge for many other benthic invertebrates, promoting

biodiversity. However, its role as a predator keystone species should be analyzed in the future because no information on filtration rates exists to estimate how their feeding activity affects the water column. Anyway, it is not difficult to assume that being the most prominent suspension-feeding bivalve species inhabiting the soft bottoms of the Maresme coast, its role in the benthic pelagic coupling must not be negligible.

Sea stars are important predators in many intertidal and subtidal ecosystems, and they have been widely considered as keystone species in marine ecosystems (Lawrence 2013). In fact, the term keystone species was first applied by Paine (1966) in reference to an intertidal sea star, *Pisaster ochraceus,* common on the rocky shores of the Pacific coast of America. He argued*: "prey species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are keystone of community's structure, and the integrity of the community and its unaltered persistence through time… are determined by their activities and abundances"* (Paine 1969). Later Mills *et al*. (1993) categorized keystone species into five types and considered sea stars as predator keystone species, i.e., species that control (by predation) the density of other ecologically significant species. Baeta and Ramón (2013) observed that *A. aranciacus* feed preferably on *C. chione* in the shallow coast of Maresme, although it was not the most abundant bivalve species in the environment. These authors reported that each sea star ingested large amounts of smooth clam recruits, suggesting that may control their populations. The importance of the smooth clam bed on the Maresme coast would justify considering *A. aranciacus* as a predator keystone species.

2.7. *Bivalve beds and fisheries*

Some species of bivalves are found in nature in high densities. They can create biogenic structures such as oysters' reefs, and dense concentrations of benthic species such as clam, mussel and scallop beds in soft and hard bottoms. These high densities of bivalves commonly inhabit shallow coastal and estuarine soft bottoms, where often they play an essential role for the functioning of the entire ecosystem. They increase the complexity and heterogeneity of substrates where they live (Commito and Rusignuolo 2000). For example, the horse mussel (*Modiolus modiolus*) forms dense beds in shallow cobble sublitoral areas of Southern Irish Sea. They can build up as biogenic reefs through the accumulation of shell and faecal deposits that can create, in some specific cases, suitable conditions for infauna more typical of inshore muddy sands enriched by organic matter (Rees *et al*. 2008). Clam beds also influence the biogeochemistry of sediments and control the water column phytoplankton dynamics (Dame 1996). Newell (1988) argued that american oyster was the responsible of controlling phytoplankton dynamics, turbidity and anoxia problems in Chesapeake Bay (the largest estuarine water body in the United States). Kemp and Boynton (1984) showed that the decline of the oysters caused an important increase of the zooplankton (an oyster competitor), that allowed consequently the development of the pelagic web with its now common predators, jellyfish and ctenophores. At the same time, increased the ungrazed phytoplankton sinking to the bottom and favored anoxic conditions at sea bed.

It is thought that hominids began consuming bivalves around the Mediterranean Sea at Lower Paleolithic. During the Middle Paleolithic and the early Upper Paleolithic, humans (*Homo neanderthalensis* and *Homo sapiens*) fed on them at many sites across the Mediterranean, although the scale of this exploitation is still unclear (Colonese *et al.*

2011). Notwithstanding, bivalve exploitation apparently increased in the Late Glacial and Early Holocene, when humans collected them in relatively large quantities and from all available ecosystems (Colonese *et al.* 2011). For example, archeologists have discovered strong evidences of shellfish harvesting at Neanderthal sites in Gibraltar (Wennersten 1981).

It is well known that bivalves exploitation and consumption was very popular in the Classical Greece (V and IV BC), as it was recorded by several authors such as Aristotle, Hippocrates, Xenocrates, Galen, Dioscorides and Athenaeus (Voultsiadou *et al.* 2009). Throughout ancient Roman Empire the consumption and exploitation of bivalves was also widespread. Oysters were undoubtedly the most appreciated in gastronomy. They were considered delicacies and served as appetizers and dainties at banquets (Walker 1997). Since the 5th century BC, Romans cultured oysters, which were carefully tended and protected, and began importing wild ones from the North Sea because the local supply could not met demand (Lotze 2010).

Figure 3. Hawk's Point, Oysterville, Washington 1932 (Source: http://www.willabay.com/).

There are written evidences of an important bivalve fishing industry through the middle ages since the 10th century at Southern Europe (e.g. Spain, France and Italy) and since the 12th and 13th century at Northern Europe (e.g. Holland) (Lotze *et al.* 2011). The production was low, collected with artisanal gears (i.e. manual handling and some dredges) and mainly destined to local and regional markets. But at the 19th century, their demand increased and an export market was developed throughout Europe. Since then, it has expanded to its present scale (MacKenzie *et al.* 1997b). Bivalve fisheries have been important to coastal human communities, often providing employment in the harvesting and processing of shellfish. Before the 1940's, harvesting was mainly concentrated in bays and estuaries, but afterwards it began expanding onto the continental shelves (Burrell 1997).

Bivalves have a high value as food for human beings and over generations individuals often have developed special strategies and fishing gears to collect them (Rothschild *et*

al. 1994). Throughout history, mollusks have been harvested from nearly every accessible estuary and bay of Europe and North America (MacKenzie *et al.* 1997a), where they have been exploited for centuries, although it was not until mid 1800's and early 1900's when the first problems were detected in wild exploited populations, which led to the collapse of most wild flat oyster (*Ostrea edulis*) beds (Hofrichter 2002). For example, United Kingdom initiated an expansion in oyster dredging on the onset of industrialization in the early 19th century, which turned it into the largest fishery half a century later, employing about 120000 people (Edwards 1997; Gardner and Elliott 2001). Seven hundred million oysters were consumed in London alone in 1864, but the UK catch fell to 40 million in 1920 and to 3 million in the 1960's (Cole 1951). Since then, the industry has never recovered fully (Edwards 1997; Kamphausen 2012).

Similar tendency was observed with the eastern oyster (*Crassostrea virginica*) along the eastern coast of North America. Baltimore began a small fishing industry at the early 18th century. The landings increased progressively until oyster canning turned as one of the most profitable industries at the end of 18th century, when oyster production reached 9-10 millions of bushels and at least 3000 people were employed as oyster shuckers. Landings began to diminish after 19th century, being 3 million of bushels in 1901 and 0.5 million of bushels in mid-1930's (MacKenzie *et al.* 1997b). Goulletquer and Héral (1997) observed in several places of the Atlantic coast of France, such as Cancale, that fishing effort on oyster beds increased by a factor of 13 from 1857 to 1872, reducing drastically its populations. The same negative tendency was observed in other commercially exploited species along the western coast of America in olympia oyster (*Ostrea conchaphila*) in California (early 19th century) and pearl oyster (*Pinctada mazatlanica*) in Panama (mid-19th century) (Shaw 1997; Villaraz and Gomez 1997). The introduction of imported allochtoon species, such as the portuguese oyster (*Crassostrea angulata*) in 1868 and the pacific oyster (*Crassostrea gigas)* in 1972, and the development of aquaculture techniques, fullfilled the demand of oysters (MacKenzie *et al.* 1997c).

Clams and scallops exploitation was intensified in the 20th century (Lotze *et al.* 2011). Since then, wild populations have declined and some of them have collapsed. These decline has been reported worldwide even though the underlying processes are not yet fully understood (Tezuka *et al.* 2012). It has been associated with loss, disturbance and/or destruction of habitat, hypoxia and anoxia episodes, harmful algal blooms, diseases, increase of predation, marine ecosystems imbalance and presence of high levels of pollution. But in nearly all the cases, bivalve population was additionally subjected to an important fishing pressure (Bricelj and Lonsdale 1997; Lenihan and Peterson 1998; Canestri-Trotti *et al.* 2000; Ford 2001; Walton *et al.* 2002; Hawes *et al.* 2011). For that reason, I suggest that the commercial exploitation of clam beds is probably a key factor in bivalve fisheries collapse; sometimes, as a direct cause by overfishing and sometimes, as an indirect cause of stressing populations and being more vulnerable to other perturbations.

Since the first episodes of bivalve fisheries collapse, the interest for their management and for their fisheries regulation has increased worldwide, although usually with uncertain results. Currently, on a worldwide analysis, several studies give information on the status of the bivalve stocks in the United States (Peterson 2002; Kraeuter *et al.* 2005; Peterson *et al.* 2008), South America (Defeo *et al.* 1992; Mendoza and Marcano 2000; Orensanz *et al.* 2005; Morsan 2007), Asia (Kripa and Appukuttan 2003; Toba

2004), and Oceania (Peterson *et al.* 1994; Hawes *et al.* 2011), but information on bivalve stocks in Europe is scarce.

Focusing on the situation in the Mediterranean Sea, landings began to diminish around the 80's and the early 90's especially in Europe (excluding the Black Sea). In Greece for example, this negative tendency was observed in most of the commercially exploited species (*Donax trunculus*, *Venus verrucosa*, *Ostrea edulis*, *Mytilus galloprovincialis,* etc.) (Koutsoubas *et al.* 2007). Another examples can be found in *Chamelea gallina* in Venice Lagoon (Italy) (Romanelli *et al.* (2009) and *D. trunculus* and *C. gallina* in Spain. In Catalonia, (Northeast of Spain) total bivalve landings were about 1300 t·y^{-1} from 1991 to 1995; they reached about 500 t·y^{-1} from 1996 to 2000; and rarely exceed 200 t·y^{-1} from 2001-2012 (Baeta *et al.* 2014) (Fig. 4).
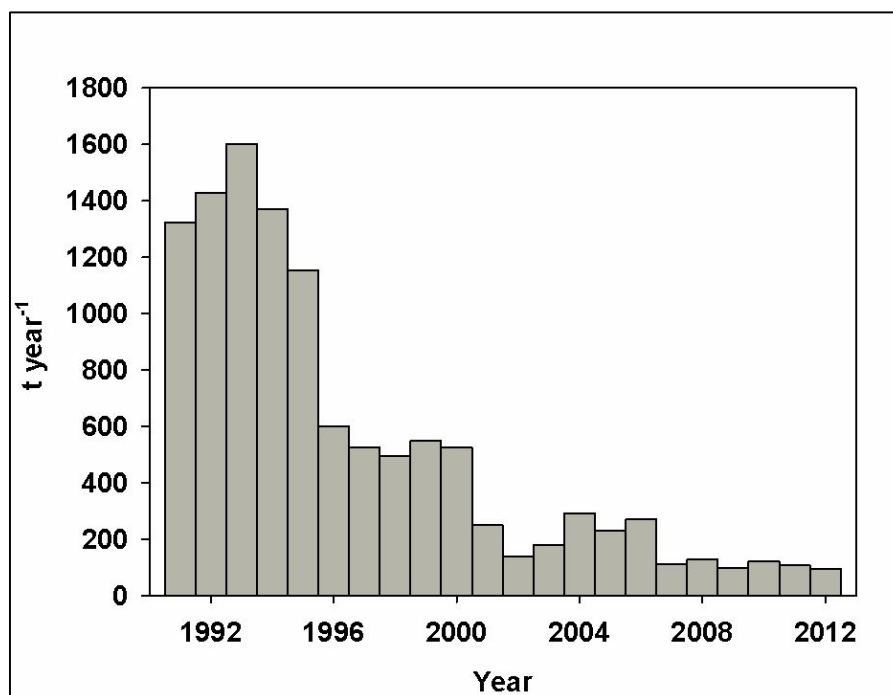
Figure 4. Total bivalve landings in Catalonia (NW Mediterranean Sea) (includes only natural clam beds, not aquaculture production) (Baeta *et al.* 2014).

Probably one of the species that has suffered a major drop in catches throughout the Mediterranean Sea is the striped venus (*C. gallina*). This venerid inhabits in fine well-sorted coastal areas in Mediterranean and Black Sea (Pérès and Picard 1964). It is targeted by a large fleet operating hydraulic dredges and "*rapido*" beam trawls at 3-12 m depths in Adriatic Sea and Black Sea (Romanelli *et al.* 2009; Dalgıç and Ceylan 2012); mechanic and manual dredges in the Mediterranean coast of Spain; and mechanic and hydraulic dredges in the Atlantic coast of Spain. Landing of *C. gallina* had an important economic role in the Mediterranean coast of Spain among the 70's and the 80's, and is still having an important economic role in the Central and Northern Adriatic coasts of Italy (Morello *et al.* 2005; Moschino and Marin 2006). Striped venus landings decline has been particularly acute in the western and central Mediterranean Basin. Its decrease was first detected in the 80's at the Adriatic Sea and in the 90's along the Mediterranean coast of Spain and Morocco. Romanelli *et al.* (2009) estimated

that in the Italian coast of the Adriatic Sea landings were among 80000-100000 t·y^{-1} in the 80's, but decreased to 21125 t·y^{-1} in 2005. Throughout the Mediterranean coast of Spain the situation is not better: Andalusia landings reached 552 t·y^{-1} in 1990, but did not exceed 15 t·y^{-1} in 2011 (http://www.juntadeandalucia.es/); Murcia and the Balearic Islands closed its fisheries in 1997 and 2003 respectively, after several years of significant and extended landing declines (pers. communication Consejería de Agricultura y Agua, Region de Murcia and pers. communication Conselleria d'Agricultura i Pesca, Illes Balears). Along the Valencian coast important beds of *C. gallina* were recorded, especially in Castelló, Gandia and Cullera. Unfortunately, at the latter two locations they have almost disappeared (Ramón 1993; Ramón *et al.* 2005). Landings of striped venus reached 340 t·y^{-1} in Gandia and 351 t·y^{-1} in Cullera in 1994, whereas they were 48 t·y^{-1} and 24 t·y^{-1}, respectively, in 2005 (pers. Communication Conselleria de Agricultura Pesca y Alimentación, Generalitat Valenciana). The fishery was also closed in Morocco in the 90's (pers. communication Ministère de la Pêche et des Ressources Halieutiques). This negative tendency has not been detected in the Eastern Mediterranean and Black Sea fisheries, probably because its commercial exploitation with hydraulic dredges began later. For instance, the striped venus exploitation started in 1986 in Turkey (Marmara and Black Sea) and since then, landings have been increasing progressively: 4169 t·y^{-1} (1988), 12700 t·y^{-1} (1990), 30000 t·y^{-1} (1991), 41000 t·y^{-1} (1994) and 61225 t·y^{-1} (2012) (Alpbaz and Temelli 1997; Deval 2001; Turkish Statistical Institute 2012).
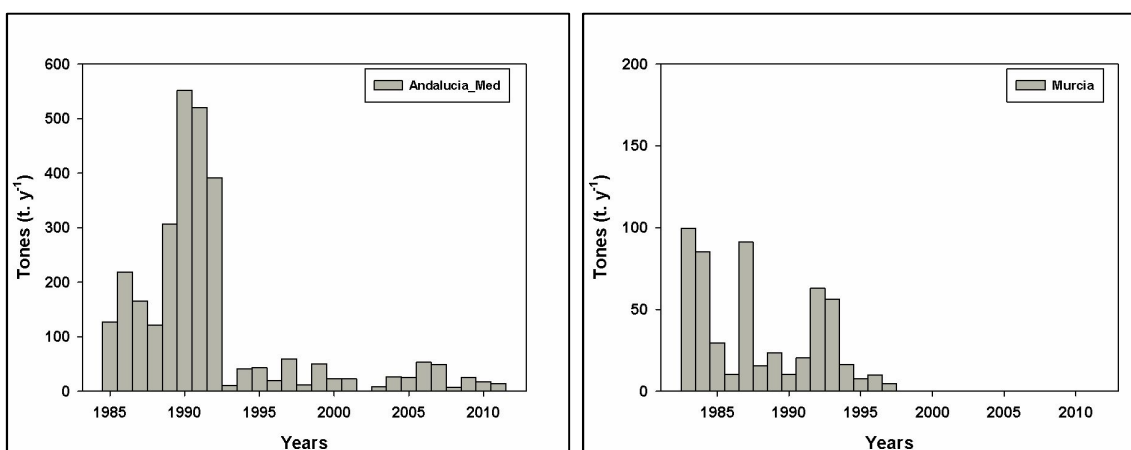
Figures 5 and 6. Striped venus landings in the Mediterranean coast of Andalusia (left) and in Murcia (right).

Commercial exploitation of bivalves has a great impact on long-life and slow-growth species. Unexploited long-life soft bottom bivalve populations are worldwide composed by large size, old individuals with slow growth at high densities. Wolff (2005) compared the same bed of the bloody cockle *Anadara senilis* in Banc d'Aguin (Mauritania), first unexploited (1986-1987) and years after being exploited (2001-2002). This author observed that the initial population was dominated by 10 to 20 years old individuals, whereas after exploitation, it was composed by individuals between 0-5 years old. A similar negative tendency was observed in Malaga (Spain), where the average length of the smooth clam (*C. chione*) population decreased from 70 mm in 1979-1981 (Cano 1981) to 54 mm in 2000 (Tirado *et al.* 2002) as a result of fishing pressure.

The consequences of clam bed decline or collapse have important effects on the local economy associated to its fishery, but also on coastal and estuarine ecosystems. Notwithstanding, these processes have been poorly studied and there are few examples available in the literature. One of them is the case of the common cockle (*Cerastoderma edule*) in the Dutch Wadden Sea and in the Wash (Eastern England) in the 1990's, where mass mortalities of this coastal bivalve produced high mortality and emigration rates in specialized shellfish predators such as oystercatchers (*Haematopus ostralegus*) (Beukema and Cadée 1996; Atkinson *et al.* 2003).

2.8. *Trophic cascading effects: top-down and bottom-up interactions*

The dichotomy between top-down and bottom-up forces acting on populations and communities has informed and motivated research in ecology over its entire history. The correlation of food availability and predation is essential in driving abundance and distribution of marine organisms (Power *et al.* 1996). On one hand, a top-down cascade occurs when the food chain is disrupted by the removal of a top predator, or a third or fourth level consumer. On the other hand, a bottom-up cascade occurs when a primary producer, or primary consumer is removed or there is a reduction of population size. Leopold and Schwartz (1949) are generally credited with first describing the mechanism of a trophic cascade, based on their observations of overgrazing of mountain slopes by deer after human extermination of wolves. The difficulty with bottom-up and top-down forces is that they both can be strong at the same time and that their relative roles are not easily inferred from field patterns (Scheffer *et al.* 2005).

The impact of individual species loss can cascade through food webs, secondarily affecting species further up or down the food chain (Byrnes *et al.* 2006). These cascades have been found in a variety of ecosystems (Borer *et al.* 2006) and tend to be stronger if larger species from higher trophic levels are lost. Thus, the interaction of altered top-down forcing, driven by the loss of large top predators, and bottom-up forces, driven by species occupying low trophic levels, may play an important role in determining community structure and dynamics (Jochum *et al.* 2012). In order to predict future shifts in food webs, it is critical to get a better understanding of the cascading top-down and bottom-up role in ecosystems (Heithaus *et al.* 2008).

Sea stars have been largely recognized as predators at or near the top of food webs (Dame 1996). Variations of their populations can, therefore, have cascading influences on ecosystems (Steneck 1998). Sea stars can control the recruitment, abundance and distribution of their prey in a local scale (<1 km) (Hart 2006). Sometimes their aggregations may even decimate their primary source of food (Brewer and Konar 2005). Predation is often the most important cause of mortality in bivalve populations (Dame 1996; Nakaoka 1996; van der Veer *et al.* 1998; Salas *et al.* 2001). For example, the sea star *Asterias rubens* controls the abundance and distribution of mussels in both intertidal and subtidal areas of the Wadden Sea (Saier 2001). The population size of the commercially exploited sea scallop *Placopecten magellanicus* is greatly limited by sea stars and crabs preying on its juveniles in Atlantic Canada and the Northeastern United States (Naidu *et al.* 1989). Sea scallop recruitment in the Mid-Atlantic Bight is significantly related to depth and to the abundances of *Astropecten americanus* and *Asterias* spp. (Hart 2006). *Spisula subtruncata* was almost eliminated as a result of *A.*

irregularis predation in Danish waters (Muus 1966). Moreover, the negative effect of some sea stars has also been documented in aquaculture activities. For instance, in Japan an outbreak of *Asterias amurensis* produced serious damage to natural and cultured bivalve beds (Nojima *et al.* 1986). In addition, when an ecosystem is dominated by a large population of bivalves, their reduction or demise can lead to dramatic changes to water column food webs. Therefore, they can also strongly influence the ecosystem by top-down forces (Newell 1988; Dame 1996). However, in a larger scale (>1 km), bottom-up forces may control the system (Seitz 2011) and the availability of prey can control their natural predators (i.e. behavior, development and abundance) (Barahona and Navarrete 2010). Seitz *et al.* (2003) showed that the blue crab (*Callinectes sapidus*) is controlled by the availability of its primary prey, the baltic clam (*Macoma balthica*) in the York River (Chesapeake Bay).

2.9. *Doctoral Thesis framework*

Over the last decades, a significant decline of coastal bivalve beds has been reported in the Mediterranean coast of Spain (Ramón *et al.* 2005; Baeta *et al.* 2014). The Maresme coast (Catalonia, NW Mediterranean Sea) has been one of the main shellfish areas where an artisanal clam fishery was maintained until recently, with the smooth clam (*C. chione*) as the main target species. Notwithstanding, the catches of *C. chione* have been dropping since 1997 and, as a consequence, the local administration commissioned a study of the smooth clam beds status in 2004, which results prompted the bed closure for commercial exploitation from March 2008 until April 2009 and an annual closing season in March and April for the following four years. The fishery was reopened after April 2009 but most of the fishermen had to fold out due to the scarcity of the resource and the majority of the catches did not reach the minimum legal size. The main aim of this Doctoral Thesis was to study the ecology of some keystone invertebrates inhabiting shallow soft bottom communities of the Maresme coast (Mediterranean Sea). This includes analyzing the smooth clam population and sea stars species of the genus *Astropecten*, common inhabitants in this ecosystem.

The bivalve *C. chione* is a shallow-burrowing suspension-feeding organism (Charles *et al.* 1999) inhabiting clean sandy shallow grounds in coastal waters at depths down to 180 m, being more abundant between 5 to 30 m depth. It is a long-life bivalve that can live over 40 years (Forster 1981). The species inhabits in the Mediterranean Sea and the Eastern Atlantic from British Isles to Morocco, including the Canary Islands and Azores (Tebble 1966). The smooth clam is a target-species for bivalve fisheries and it has economic importance in the Mediterranean coast of Spain (mainly Maresme coast and Malaga coast), Portugal, Italy, France, Croatia, Greece, Turkey and Morocco. *C. chione* is usually fished with different modalities of clam dredges and, in some places it is also collected by divers (Gaspar *et al.* 2001; Metaxatos 2004; Pubill *et al.* 2011).

Figures 7: Smooth clam dredge catch in Maresme coast in December 2004.

Five sea star species of the genus *Astropecten* (*A. aranciacus; A. irregularis pentacanthus*; *A. platyacanthus*; *A. jonstoni* and *A. spinulosus*) inhabit the shallow soft-bottoms of the Maresme coast and are captured as a by-catch of the smooth clam fishery. The status of their populations and their role in the *C. chione* clam bed through trophic interactions (e.g. predator-prey and competition) has been also analyzed in this Doctoral Thesis. *Astropecten* is one of the genus with more species among sea stars and its members are worldwide distributed, inhabiting soft-bottom ecosystems from polar to tropical seas and from intertidal areas to deep sea (Zulliger and Lessios 2010). This genus includes six species in the Mediterranean Sea: *A. aranciacus* (Linnaeus 1758); *A. bispinosus* (Otto 1823); *A. irregularis pentacanthus* (Pennant 1777); *A. platyacanthus* (Philippi 1837); *A. jonstoni* (Delle Chiaje 1827); and *A. spinulosus* (Philippi 1837); being the last three endemic of the Mediterranean Sea. *Astropecten* spp. are voracious predators mainly feeding on mollusks (gastropods and bivalves). These carnivores swallow whole preys and have intra-oral digestion (Christensen 1970). Despite being first described as non-selective feeders (Wells *et al.* 1961), it has been observed some feeding selection and specialization (Baeta and Ramón 2013). They have chemoreceptive abilities to distinguish prey quality, choosing preferentially those with higher nutrient composition and providing more energy (Beddingfield and McClintock 1993). Sea stars as species occupying high trophic level can be particularly affected by the decline in their prey populations, but at the same time their population outbreak could lead their prey species to a critical situation. Therefore it is crucial to know which is role of the sea stars and their population dynamics for the suitable management of the smooth clam bed.

3. AIMS AND OBJECTIVES

The overall aim of this Doctoral Thesis is to improve the knowledge in the ecology of the smooth clam (*C. chione*) and their predators, sympatric sea stars of the genus *Astropecten* inhabiting the coastal soft bottoms of the Maresme coast, Catalonia, (NW Mediterranean Sea), but at the same time to analyze their trophic relationships, and understand how these species are vulnerable to human pressures.

The following specific objectives that were addressed are:

I.   To characterize the smooth clam bed inhabiting the Maresme coast, describing growth, population structure and spatio-temporal distribution patterns.

II.   To analyze the potential causes of the smooth clam population decline and the consequent collapse of the fishery.

III.   To assess the trophic relationships of three sympatric *Astropecten* species, based on feeding strategy, diet overlap, ontogenetic changes in the preys consumed (species and sizes) and prey selection. A special emphasis on predation over *C. chione* was devoted.

IV.   To provide new insights into medium-term asteroidean population dynamics by examining spatio-temporal changes in five sea star species of the genus *Astropecten* inhabiting the Maresme coast, focusing on *Astropecten* spp. population composition, abundance, spatial distribution and size structure.

V.   To analyze factors affecting *Astropecten* spp. distribution in the study area.

VI.   To improve the knowledge in the ecology of *A. aranciacus*; describing for the first time its reproductive cycle, growth and distribution.

4. SUMMARY OF RESULTS AND GENERAL DISCUSSION

4.1. *Smooth clam bed in Maresme coast*

This Doctoral Thesis showed the decrease in density and biomass of the *C. chione* bed between 2004 and 2010. The highest density values found for each year were 1.65 ind.m^{-2} at 10 m depth and 0.52 ind.m^{-2} at 15 m depth in 2004 and 2010, respectively. Results showed a change in the structure of the population, with a decrease in the mean and modal length over time in the studied area. The frequency of individuals longer than 40 mm was 15% in 2004 and 9% in 2010, whereas the percentage of individuals smaller than 24 mm was 18% in 2004 and up to 37% in 2010. The population modal value was 26 mm in 2004 and 22 mm in 2010. *C. chione* was found inhabiting sediments with D50 values ranging from 0.2 to 0.9 mm, corresponding to medium and coarse sands.

Landings were under 110 t year^{-1} between 1980 and 1994, peaked to a maximum of 290 t year^{-1} in 1997, and finally decreased progressively to reach 80 tons in 2005. This negative tendency culminated with the collapse of the bivalve fishery at the end of 2005. Later, after the biological closure in 2010, 90% of the population was composed of individuals smaller than 45 mm long, which according to our growth estimations, corresponds to ages below 4 years. Moreover our results showed the presence of only 2% of individuals over the minimum commercial legal size (60 mm length). The smooth clam population structure in Maresme coast was very young compared with other populations in the Mediterranean Sea, for which ages between 5 and 15 years have been reported (Leontarakis and Richardson 2005; Ezgeta-Balić *et al.* 2011).

Our results showed that the smooth clam is a slow growing bivalve. Individuals reach the legal commercial size of 60 mm length, when they are 5–6 years old. Information on growth of this species differs among geographical areas and locations, giving different estimations of parameters of the von Bertalanffy growth function. Its lifespan has been estimated between 12 and 20 years (Hall *et al.* 1974; Strada and Zocco 1985; Keller *et al.* 2002; Metaxatos 2004; Leontarakis and Richardson 2005; Moura *et al.* 2009; Ezgeta-Balić *et al.* 2011). Our estimated VBGF values were in the range of the previously published data, although the methodologies used were different. The previous studies used surface growth ring and/or internal shell micro-growth line readings; in contrast, our methods were based on field observations (monthly samples and mark/recapture experiments). Slow-growing species are highly vulnerable to disturbances prolonged in time.

Our results showed a significant change in the sediment particles size between 2004 and 2010, when fine sand and mud portions clearly increased in the southwestern area of the clam bed. The increase in fine sand and mud may make this area inhabitable for *C. chione* because, as observed in our study, it prefers medium and coarse sand. Persistent sand dredging operations since 1987 have gradually reduced the distribution area of the smooth clam to the northeastern part of the clam bed. Consequently, fishing activity had concentrated on a smaller area, thus increasing the fishing effort in the northern part. Therefore, the results clearly suggested that the decline of *C. chione* bed was mainly caused by the interaction of two coastal uses: sand dredging and clam fisheries.

4.2. Challenges for the smooth clam bed future

Based on this Doctoral Thesis, some management guidelines were proposed for the restoration of the smooth clam bed in the Maresme coast. The following management guidelines were suggested: (1) banning artisanal clam dredging until the population has recovered; (2) implementing other alternatives to beach nourishment to mitigate coastal erosion. If no alternatives to beach nourishment are found, sand dredging should be restricted to the southern area and preferably to depths at which there are no vulnerable species; (3) establish and develop a management plan for recovering clam bed, which has to be led by scientists, funded by the public administrations (i.e. Catalan and Spanish Governments) and should involve all local stakeholders (e.g. municipalities, counties, clam fishermen, fishermen associations). This plan should include measures that have been successful in other areas, such as the establishment of a sanctuary of large individuals; the restocking of the clam bed with juveniles provided by aquaculture techniques, performing information campaigns and research over the effect of the smooth clam decline in the whole ecosystem.

4.3. How can sympatric Astropecten species coexist in Maresme coast?

Within the framework of niche theory, the coexistence of species playing identical ecological role and occupying an equal niche within the same ecological community cannot co-occur. These species are linked to the principle of competitive exclusion concerning the inability of ecological equivalents to coexist stably (Gause 1934). Sympatric species (i.e. existing in the same geographic area and thus regularly encounter one another) coexistence requires niche differences (i.e. trophic, spatial or temporal segregation to avoid competitive exclusion) (Hutchinson 1957). When sympatric species overlap in the use of a shared resource along one dimension, they must differ along another resource to coexist (MacArthur 1958). Therefore, it is intriguing to find closely related and ecologically similar species living in sympatry, as the struggle for existence should be greater (Gavrilchuk *et al.* 2014). The study and the comparison of the ecological niches of these potentially interacting species is fundamental to evaluate underlying mechanisms of coexistence, and to eventually predict consequences of ecosystem change on animal communities (Chase and Leibold 2003).

The coexistence of several *Astropecten* species in the same area is not an unusual event and it has been described worldwide e.g. Venezuela (Bitter 2000), Brasil (Ventura 1999), Japan (Nojima 1984), Australia (Lemmens *et al.* 1995) and Mediterranean Sea (Ribi and Jost 1978). Notwithstanding, the mechanism to understand how these sympatric species can coexist has been poorly analyzed. Some factors such as partition of prey by species or size has often been suggested to be a mechanism for reducing competition between coexisting sea star species (Menge and Menge 1974; Schoener and Schoener 1982). In the shallow bottoms here studied, the diet composition of coexisting asteroids was significantly different between species, showing little food overlap. Our results showed that food competition between *Astropecten* sea stars was avoided by partition of prey resources. The bivalves *Glycymeris glycymeris* and *C. chione*, together with the gastropod *Cyclope neritea*, predominated in the stomachs of *A. aranciacus*. The bivalves *Goodallia triangularis* and *C. chione* were abundant in *A. platyacanthus* stomachs, while the gastropods *C. neritea* and *Nassarius pygmaeus* were common in the diet of *A. irregularis pentacanthus*. The clear preference of *A. irregularis pentacanthus*

for gastropods over bivalves indicated that it did not compete with the other two sea star species for food species. The only exceptional value reflecting high diet overlap was observed between *A. aranciacus* and *A. platyacanthus* in winter.

Partitioning of habitats has been theoretically considered and empirically found to be the most common mechanism of sympatric species niche separation (MacArthur and Wilson 1967) and habitat differences are often cited as being the responsible for multispecies coexistence (Schoener 1974). In accordance with this, our results showed *Astropecten* sea stars habitat partitioning. Each species occupied different microhabitats to avoid interspecific competition. *A. aranciacus* preferred the presence of *C. chione*, low concentrations of organic matter, coarse grain, and higher depths at the northeast of the studied area. *A. irregularis pentacanthus* selected areas with finer sediments and high percentages of organic matter, at higher depth. Finally, *A. platyacanthus* chose areas with low concentrations of organic matter at higher depth, but with coarse sand at the southwest of the studied area.

Other mechanisms have been described for reducing interspecic competition in sea stars; for instance, to have different daily activity patterns. Ribi and Jost (1978) showed that *Astropecten aranciacus*, *A. bispinosus* and *A. jonstoni* have different peaks of daily activity, but this kind of information does not exist for other Astropectinids such as *A. platyacanthus* and *A. irregularis pentacanthus*.

This Doctoral Thesis results showed that *Astropecten* species did not compete for the available resources in the Maresme coast. Despite their similarity in external morphology and relatively close phylogenetic relatedness (Zulliger *et al.* 2009) we found major differences in diet and habitat use between this sympatric sea stars, supporting the idea that competition does not occur between them because each species has specialized in the use of available resources. Moreover, when two species overlap in the use of one resource they diverge in the use of others. Dieckmann and Doebeli (1999) observed that this sympatric specialization has often been the origin of many new species.

Intraspecific differences in prey sizes of dietary compositions were also detected, suggesting that competition could not occur in the selection of prey items. This behavior could be a strategy to avoid intraspecific competition, because it indicates that although they fed in the same prey items, prey sizes varied as sea stars grew.

4.4.   *Responses of Astropecten* **spp.** *to changes in habitat*

This Doctoral Thesis has analyzed medium-term (between 2004-2006 and 2010-2011) asteroidean population dynamics in an area that has suffered habitat (sediment grain size) and prey abundance shifts as a result of human pressures (sand extractions for beach nourishment and overfishing). Our results showed that *Astropecten* species have been affected by these human pressures, revealing changes in composition, abundance, spatial distribution and population structure. *A. aranciacus*, showed a density and distribution reduction, population mean size increase, recruitment failure and diet change. *A. irregularis pentacanthus* decreased its spatial distribution concentrating in smaller areas, but the density remained similar. *A. platyacanthus,* not observed in 2004-2006, became abundant in 2010-2011. *A. jonstoni* and *A. spinulosus* were scarce in 2004-2006 but both were not observed six years later. *A. aranciacus* has observed as the

most vulnerable sea star to habitat and prey abundance shifts. *A. aranciacus* has been described as an important predator for other astropectinids (e. g. *A. jonstoni* and *A. bispinousus*) in the northwestern Mediterranean Sea (Ferlin-Lubini and Ribi 1978; Pabst and Vicentini 1978; Schmid and Schaerer 1981) suggesting that it occupy a higher trophic level in the food chain of shallow bottoms. Human pressures has led many marine predators that occupy high trophic levels to a severe decline worldwide in the last few decades at a worrying rate (Heithaus *et al.* 2008). Understanding how species are vulnerable to human pressure is an essential prerequisite for designing effective conservation strategies (Pinsky *et al.* 2011).

4.5. *Astropecten aranciacus distribution, growth and reproduction*

The results indicated that *A. aranciacus* individuals smaller of 80 mm were abundant in shallow waters (5-30 m depth) whereas large individuals (>130 mm) were observed mostly offshore (50-150 m depth). The use of different gears to sample both bathymetric ranges in this study may have caused bias collecting small sizes offshore, but no bias for bigger sizes in shallow waters could happen. Therefore, in case of bigger individuals of *A. aranciacus* inhabiting from 5 to 30 m, they would have been collected in our sampling. Burla *et al.* (1972) studied the activity pattern of *A. aranciacus* by scuba diving in Sardinia (Italy) and found only small specimens. These authors suggested that adults and juveniles may dwell in different parts of the ecological zone occupied by the species, the fully-grown specimens invading the deeper waters. Our study is the first that had sampled most of the bathymetrical distribution range of this species, allowing us to confirm a bathymetrical segregation by size in *A. aranciacus.* Size depth trends were also reported for the asteroid *Protoreaster nodosus*, whose large specimens inhabits between 0 and 33 m depth whereas small specimens were exclusively found in shallower habitats (< 5m) (Bos *et al.* 2008). Young sea stars might prefer shallow areas, where food and shelters to avoid predation are usually more abundant (Manzur *et al.* 2010).

Despite growth has been extensively analyzed in echinoderms by Jangoux and Lawrence (1982), there is some controversy regarding sea stars, because environmental factors, *i.e.* temperature, salinity and quality and quantity of food, can influence growth rates (Feder and Christensen 1966). In addition, one of the most familiar features of sea stars functional morphology and physiology is their remarkable facility for regeneration (Emson and Wilkie 1980), which can lead to some erroneous results. For these reasons, growth parameter estimations are only valid for a specific environment (Jangoux and Lawrence 1982) in our case, Maresme coast (NW Mediterranean Sea).

The *A. aranciacus* population studied exhibited a seasonal pattern of growth, being higher from June to October in the nearshore cohorts. Growth period was wider offshore (February-October) although the growth rate was lower (about half) in comparison with nearshore values. Seasonal variation in growth has been described in other *Astropecten* species, that usually showed a decrease in growth rate associated with gonad maturation (Nojima 1982; Ventura 1999; Freeman *et al.* 2001), but it was not observed in *A. aranciacus*. Growth rate seems to be related to sea water temperature in *A. aranciacus*. Higher growth was recorded nearshore when sea water temperature was above 21ºC (between June to October). Moreover, sea water temperature increased slightly from February to December offshore, in coincidence with the period of higher growth rate. Ventura (2013) reported that the decrease in *A. brasiliensis* and *A.*

cingulatus growth rate coincided with the seasonal upwelling period in Brazil, suggesting that it could be related to sea water temperature decline. Other factors like the amount and quality of available food can also affect growth, as observed by Guillou and Guillaumin (1984) in *Asterias rubens*.

The *A. aranciacus* population here studied seems to have variable reproductive and recruitment success. Recruits were detected on February 2010 and April 2012 nearshore, but they were not detected on 2011. The absence or low rate of recruitment throughout a period of time is not rare in echinoderms, and it has been attributed to hydrological processes and predation upon embryos and larvae (Thorson 1946; Freeman *et al.* 2001). Therefore, even if the reproductive cycle is annual, recruitment may not be successful every year.

In general the reproductive cycles of sea stars are correlated with a combination of endogenous (*i.e.* hormones) and exogenous factors (*i.e.* temperature, photoperiod, food availability, lunar cycle, tidal flux and light intensity) (Mercier and Hamel 2009). However, the direct influence of each factor remain poorly understood (Mercier and Hamel 2009). In *Astropecten* species, breeding season commonly coincides with the increase of water temperatures on temperate areas (Grant and Tyler 1986; Marion *et al.* 1998; Freeman *et al.* 2001). For instance, Freeman *et al.* (2001) reported that the spawning periods for *A. irregularis* coincided with the rise from 8ºC to 15ºC in seawater temperatures (North Wales). Our results showed the same pattern, because *A. aranciacus* spawning season was in spring, when the sea water temperatures begun to increase in the Mediterranean. Our findings also showed that spawning occurred during the minimum day length period of the year. This inverse relationship found between GI and photoperiod has not been described previously in the genus *Astropecten*, and it is rare in sea stars although it is common in other echinoderms (Mercier and Hamel 2009). We also observed that *A. aranciacus* GI was related to the highest chlorophyll-a concentration in the water, which was originated by the spring phytoplankton bloom typical from the Mediterranean Sea. The correlation between phytoplankton concentration and GI has been previously described in other echinoderms, but it is rare in sea stars (Mercier and Hamel 2009). The majority of the species of the genus *Astropecten* have planktonic larvae (bipinnaria). Bipinnaria larva nourish essentially on detritus, bacteria, phytoplankton (mainly small diatoms and small flagellates) and small zooplankton (Ayukai 1993). The synchronism between the gonadal development of *A. aranciacus* and the phytoplankton bloom could be a strategy to guaranty higher survival of early developmental stages.

An inverse correlation between GI and PCI has been usually described in most sea stars, suggesting the transference of nutrients from the pyloric caeca to the gonads during gametogenesis (Lawrence and Lane 1982). Nevertheless, this interaction has not been observed in those species inhabiting areas with stable environmental conditions (Benítez-Villalobos and Martínez-García 2012). This relationship was not observed in the studied *A. aranciacus* population despite inhabiting in a seasonally changing environment, in accordance with the results obtained by Ventura *et al.* (1998) in *A. cingulatus*. Individuals of *A. aranciacus* collected in the offshore zone of the study area had large amount of preys in the stomach throughout the year. Most of these prey items were the venerid *Timoclea ovata* (>55%, abundance in 224 sea stars analyzed) and each sea star stomach contains a mean of 49 *T. ovata* items of a mean size of 5.77 mm (SD = 5.52, N=9682) (*unpublished data*). Then, food does not seems to be a limiting factor in

the Maresme coast, suggesting that sea stars do not need to storage large amount of nutrients in pyloric caecum, because nutrients can be easily obtained from the environment throughout all year. This may be the reason why an inverse correlation between GI and PCI was not observed in *A. aranciacus*.

4.6. *Summary*

In summary, keystone species strongly influence biodiversity because they play an elemental role in structuring and maintaining the integrity of ecosystems. Their decline and loss can result in more species becoming endangered, compromising the conservation of biodiversity. Therefore, efforts to manage and protect keystone species can help stabilize the entire biological community and preserve biodiversity. Notwithstanding, to be properly managed and protected, status of their populations, biology and ecology should be previously known. This Doctoral Thesis conducted an effort towards enhance the knowledge of some of these species: smooth clam and *Astropecten* spp., providing novel scientific information of their population status, biology and ecology. It is relevant to note that before this dissertation previous information on these species was insufficient in the case of the smooth clam and non-existent in the case of *Astropecten* sea stars.

5. CONCLUSIONS

This Doctoral Thesis has contributed to expand the knowledge of some keystone invertebrates inhabiting shallow soft bottom communities by studying an exploited smooth clam bed in Catalonia (NW Mediterranean Sea) and different ecological interactions between clams and sea stars (predator-prey interactions) and among sea stars (coexistence and competition). Human pressures that have led smooth clam bed to the collapse (sand dredges and overfishing), and how this decline has affected the upper trophic levels in the soft bottom ecosystem, have been analyzed. Growth and reproduction of *A. aranciacus* has been described for the first time. Finally, some measures for the clam bed restoration have been proposed, that would benefit the entire coastal ecosystem, including those species occupying upper trophic levels, such us sea stars of the genus *Astropecten*.

Based on the research developed in this Doctoral Thesis, it is concluded the following:

I. A significant decrease in density and biomass of the smooth clam in the Maresme coast has been observed through the last years. This decline has been particularly intense among the period studied 2004-2010, leading its commercial fishery to the collapse. The measures applied by local administration to reverse this trend have arrived too late and have been ineffective to recover the clam bed.

II. The main causes that have led the clam bed to the collapse were a combination of different human coastal uses: sand dredging and clam fisheries. Persistent sand dredging operations since 1987 have gradually pushed the smooth clam to the northeastern part of the initial distribution of the bed. Consequently, fishing activity had concentrated in this smaller area, thus increasing the fishing effort. This situation has led the clam bed to a critical status and its fishery to collapse.

III. Most of smooth clams in the Maresme coast population were very young compared to other areas in the Mediterranean Sea. Only 2% of individuals detected were over the legal commercial size in 2010. Moreover, the modal size value diminished from 26 mm in 2004 to 22 mm in 2010. Both are strong indicators of the critical situation of the population.

IV. Smooth clam has an asymptotic growth, reaching the legal commercial size of 60 mm long between 5-6 years old in the studied area, confirming that smooth clam is a slow-growing species.

V. A management plan is needed for the restoration of the clam bed. Clam beds play an essential role for the health and the structure of the ecosystems where they inhabit. Its current status may have unpredictable effects for the whole ecosystem and other fisheries. We suggest the following management guidelines: (1) banning artisanal clam dredging until the population has recovered; and (2) implementing other alternatives to beach nourishment to mitigate coastal erosion. If no alternatives to beach nourishment are found, sand dredging should be restricted to the southern area and preferably to depths at which there are no vulnerable species.

VI. Spatio-temporal changes of *Astropecten* populations to changes in habitat (sediment grain size decrease) and prey abundance (*C. chione* decline) were described for the first time to be caused by shallow coastal area uses, i.e. overfishing and beach nourishment. According to these results, it is of prime importance to analyze several trophic levels of the food web to better understand community changes in ecosystems suffering from biotic and/or abiotic disturbances.

VII. *Astropecten* species are assumed to be generalist predators, but our results showed that they have some degree of prey selection, i.e. *A. aranciacus* selected the bivalves *G. glycymeris* and *C. chione*, together with the gastropod *C. neritea*; *A. platyacanthus* the bivalves *G. triangularis* and *C. chione;* and *A. irregularis pentacanthus* the gastropods *C. neritea* and *N. pygmaeus.*

VIII. *Astropecten* species co-occur within a biological community scale, but not compete in the Maresme coast. They presented niche segregation showing a partitioning of the resources and occupying different microhabitats. For this reason *Astropecten* usually exhibited a patchy distribution.

IX. *A. aranciacus* showed depth segregation between size classes along the continental shelf. The size frequency distribution showed the predominance of smaller individuals (<40 mm major radius length) in shallow areas (<30 m depth) and the prevalence of larger individuals (>140 mm major radius length) at greater depths (50-150 m depth).

X. *A. aranciacus* showed a seasonal growth. Moreover growth rate seems to be related with the seasonal increase of the sea water temperature.

XI. *A. aranciacus* male-female ratio was almost 1:1 throughout the year. It reached sexual maturity at 112 mm major radius length. The gametogenic cycle was classified into five gonadal stages. Histology and organ indexes revealed an annual well-defined reproductive cycle, with a maturation peak occurring between February and April, coinciding with the spring phytoplankton bloom, the increase of sea water temperatures and a short day photoperiod. Notwithstanding *A. aranciacus* recruitment may not be successful every year.

XII. *A. aranciacus* did not show an inverse relationship between gonad index and pyloric caeca index, suggesting the transference of nutrients from the pyloric caeca to the gonads during gametogenesis does not occur.

XIII. An important decline in *A. aranciacus* population has been detected in the study area, as well as in other areas of the Mediterranean Sea; suggesting this may be a widesread trend.

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7. PUBLICATIONS

Dr. Montserrat Ramón, Director of this Doctoral Thesis "Ecology of some keystone invertebrates inhabiting shallow soft bottom communities of the Maresme coast (NW Mediterranean Sea)" certifies that the following peer-reviewed scientific publications have been published or are in the ordinary process to be published in the specified scientific journals. All scientific journals have been categorized and ranked by the Institute for Scientific Information (ISI) and its Impact Factor has been assigned according to the Journal Citation Reports (JCR).

Barcelona 13/02/2015   **Fd:** Dra. Montserrat Ramón

7.1. Decline of a *Callista chione* (Bivalvia: Veneridae) bed in the Maresme coast (northwestern Mediterranean Sea).

Abstract

Bivalves are considered key species in many marine communities and the decline of their populations usually causes changes in the structure of the ecosystems. The aim of the present study was to investigate changes in the spatial distribution and population structure of an exploited shellfish bed of *Callista chione* at a location of the northwestern Mediterranean Sea and analyze its potential causes. To this end field surveys for the years 2004 and 2010 covering the whole distribution area of the species were performed and all historical data on commercial landings, clam biomass and density, and locations and volume of dredged sand for beach nourishment were compiled. Results showed that the distribution had been hugely reduced, showing a sharp decline in density and biomass and a decrease in the mean population size in 2010. Our results confirm that the species is a slow-growing bivalve that is highly vulnerable to disturbances prolonged in time. Persistent sand dredging operations since 1987 have gradually reduced the distribution area of the smooth clam to the northeastern part of the clam bed. Consequently, fishing activity has concentrated on a smaller area, thus increasing the fishing effort in the northern part. Therefore, the results clearly suggest that the decline of *C. chione* bed was mainly caused by the interaction of two coastal uses: sand dredging and clam fisheries. Based on this study, some management guidelines are proposed.

Figures 8 and **9:** Photographs of the smooth clam growth experiment.

Resumen

Los bivalvos son considerados como especies clave en muchas comunidades bentónicas marinas y el declive de sus poblaciones a menudo provoca cambios en la estructura de los ecosistemas. El objetivo del presente estudio fue investigar los cambios en la distribución espacial y la estructura de la población del banco de concha fina *Callista chione*, que se explota comercialmente en noroeste de del Mar Mediterráneo, así como averiguar sus potenciales causas. Para lograr dicho objetivo se efectuaron varios muestreos en los años 2004 y 2010 cubriendo todo el área de distribución del banco natural; se analizaron los datos históricos de capturas comerciales, de biomasa y densidad y se recopiló información sobre la localización y el volumen de arena dragados para la restauración de las playas de la zona metropolitana de Barcelona (especialmente las playas de la ciudad y de la costa sur del Maresme). Los resultados mostraron que la distribución de *C. chione* se redujo drásticamente entre ambos períodos de estudio, mostrando una severa disminución en la densidad, biomasa y talla media de los ejemplares. Nuestros resultados confirmaron que este bivalvo se caracteriza por tener un crecimiento lento, lo que la hace enormemente vulnerable a perturbaciones prolongadas en el tiempo. Los dragados persistentes que se realizaron en la zona para la extracción de arenas desde 1987 fueron reduciendo paulatinamente la zona de distribución de este bivalvo, quedando restringida a la zona noroeste de su area natural de distribución. Esta situación comportó que la actividad pesquera se concentrara en una zona más pequeña, incrementándose así el esfuerzo pesquero en la zona noroeste, donde el banco no se había visto afectado por los dragados. Por lo tanto, los resultados de este estudio indican que el declive de la población del bivalvo *C. chione* fue causado por la interacción de dos actividades antropogénicas costeras: los dragados de arena y la pesca con rastros. Basándose en este estudio se proponen distintas medidas de gestión.

Participación de los distintos autores

Todos los coautores participaron en la elaboración y corrección del manuscrito

Trabajo del doctorando

El doctorando ha participado en el diseño experimental de los muestreos, la recogida y posterior análisis de las muestras en el laboratorio, así como en el análisis de los datos y la posterior redacción y corrección del manuscrito.

Decline of a *Callista chione* (Bivalvia: Veneridae) bed in the Maresme coast (northwestern Mediterranean Sea)

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ARTICLE INFO

ABSTRACT

Bivalves are considered key species in many marine communities and the decline of their populations usually causes changes in the structure of the ecosystems.

The aim of the present study was to investigate changes in the spatial distribution and population structure of an exploited shellfish bed of *Callista chione* at a location of the northwestern Mediterranean Sea and analyse its potential causes. To this end field surveys for the years 2004 and 2010 covering the whole distribution area of the species were performed and all historical data on commercial landings, clam biomass and density, and locations and volume of dredged sand for beach nourishment were compiled. Results showed that the distribution had been hugely reduced, showing a sharp decline in density and biomass and a decrease in the mean population size in 2010. Our results confirm that the species is a slow-growing bivalve that is highly vulnerable to disturbances prolonged in time. Persistent sand dredging operations since 1987 have gradually reduced the distribution area of the smooth clam to the northeastern part of the clam bed. Consequently, fishing activity has concentrated on a smaller area, thus increasing the fishing effort in the northern part. Therefore, the results clearly suggest that the decline of *C. chione* bed was mainly caused by the interaction of two coastal uses: sand dredging and clam fisheries. Based on this study, some management guidelines are proposed.

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1. Introduction

Bivalves can play essential ecological roles in ecosystem functioning through their impact on benthic-pelagic coupling (Dame, 1996), nutrient regeneration (Sandwell et al., 2009) and facilitation of surrounding communities (Norkko et al., 2006). They are also an important resource that has historically been subjected to great fishing pressure as they are a cheap and nutritious source of protein. Bivalve fisheries are an important part of the economy and culture of many coastal communities, and human activities have led exploited bivalves to decline sharply, especially in recent decades. This decline has been associated with loss, disturbance and/or destruction of habitat, hypoxia and anoxia episodes, harmful algal blooms, disease, increase in predation, marine ecosystems imbalance, overfishing, and high levels of pollution (Bricelj and Lonsdale, 1997; Canestri-Trotti et al., 2000; Ford, 2001; Hawes

et al., 2011; Lenihan and Peterson, 1998; MacKenzie et al., 1985; Paul and Feder, 1975; Rothschild et al., 1994; Shivji et al., 1983; Walton et al., 2002). Several studies have provided information on the status of the bivalve stocks in the United States, South America, Asia and Oceania (e.g. Hawes et al., 2011; Kripa and Appukuttan, 2003; Peterson et al., 2008, among many others), but information on bivalve stocks in Europe is scarce. A combination of intensive fishery and failing recruitment over several years caused a great decrease in intertidal mussel and cockle beds in the Dutch Wadden Sea (Beukema and Cadée, 1996; Beukema and Dekker, 2005; Dankers and Zuidema, 1995). The Manila clam stocks in Arcachon Bay (France) have decreased since 2003 as a result of poor recruitment, slow growth, and high fishing effort (Dang et al., 2010). The decrease in *Chamelea gallina* clam landings in the Adriatic Sea since the early 1980s has been correlated with the progressive reduction of freshwater flow, as well as of its phosphate content (Romanelli et al., 2009).

Since the early 1980s, the decline of bivalve beds has also been severe on the Mediterranean coast of Spain (Ramón et al., 2005). For example, in Malaga (SE Spain), the average length of the *Callista chione* population decreased from 70 mm in 1979–1981 (Cano, 1981)

to 54 mm in 2000 as a result of fishing pressure (Tirado et al., 2002). Despite this alarming situation, neither the authorities nor scientific studies have analysed the causes of the problem. The sandy Maresme coast (Catalonia, northwestern Mediterranean Sea) is one of the main shellfish areas where an artisanal clam fishery has been maintained until recently, with the smooth clam as the target species. It has been a regulated fishery since 1988 with regard to the fishing zone, fishing licenses, the number and power of vessels, gear dimensions and number, minimum legal size of clams, schedules and landing quota. A commercial fishery targets the entire distribution range of the species in the area, between 5 and 30 m depth. The fleet was composed of 11 boats in 2004. The catches of *C. chione* have been dropping since 1997 and, as a consequence, the local authorities commissioned a study of the status of smooth clam beds in 2004, resulting in the closure of the bed for commercial exploitation from March 2008 to April 2009 and an annual closed season in March and April for the following four years. The fishery was reopened in April 2009 but most of the fishermen had to abandon it due to the scarcity of the resource. Most of the catches did not reach the minimum legal size and the shellfish fleet in Arenys de Mar harbour fell to two fishing boats in 2012.

The venerid bivalve *C. chione* (smooth clam) is a shallow-burrowing, suspension-feeding organism (Charles et al., 1999) inhabiting clean sandy shallow grounds in coastal waters at depths ranging from 1 to 180 m, though it is more abundant between 5 and 30 m depth on the Catalan coast. It is a long-life bivalve that can live over 40 years (Forster, 1981). It inhabits the Mediterranean Sea and the eastern Atlantic from the British Isles to Morocco, including the Canary Islands and Azores (Tebble, 1966). *C. chione* is a target-species for bivalve fisheries and it has economic importance on the Mediterranean coast of Spain, Portugal, Italy, France, Croatia, Greece, Turkey and Morocco. It is usually fished with different types of clam dredges and, in some places, it is also collected by divers (Ezgeta-Balić et al., 2011; Gaspar et al., 2001; Metaxatos, 2004; Pubill et al., 2011).

An efficient clam bed management should be based on a good knowledge of the biology of the target species, of the available resource (through stock evaluation), and of the impacts affecting the shellfish bed (fishing pressure and other disturbances). Knowledge of the biology of *C. chione* is still scarce and no stock evaluations have been made in Spain. No information on the existence of annual stock evaluations in other countries has been found. Studies on smooth clam growth and age are based on growth rings (Ezgeta-Balić et al., 2011; Leontarakis and Richardson, 2005; Metaxatos, 2004; Moura et al., 2009) and results vary according to the area, even among locations within the same area, making it difficult to extrapolate the results to other sites. Information on its reproduction is limited to the studies of Tirado et al. (2002) and Moura et al. (2008), both of which found three spawning peaks although the last peak differed slightly in time. Size at first maturity of this species in the Mediterranean is unknown, but it has been estimated at 50.81 mm on the south-western coast of Portugal (Moura et al., 2008). To our knowledge, there are no available data on recruitment and mortality of the species.

The main goal of this study was to investigate changes in the spatial distribution pattern and the population structure of *C. chione* in two sampling periods (the years 2004 and 2010) in order to analyse potential causes for the decline and collapse of the fishery on the Maresme coast. To accomplish this goal, we performed intensive samplings along the whole smooth clam bed distribution area, and searched for historical information (fishery statistics records, clam biomass and density, locations and volume of dredged sand). In addition, a mark-recapture experiment to estimate *C. chione* growth was performed. The information reported in this article can be used to plan actions for recovering the *C. chione*

bed on the Maresme coast and some management guidelines are also suggested.

2. Materials and methods

2.1. Smooth clam sampling

Specimens were collected on the Maresme coast (Catalonia, NW Mediterranean Sea), a narrow and shallow area approximately 51 km long parallel to the coastline, between the Tordera River and the Tiana seasonal stream (Fig. 1). The area is characterized by an infra-littoral plain of soft bottoms dominated by reflective beaches of coarse granitic sand.

Several daily surveys were performed during two periods, from 23 November to 16 December 2004, and from 1 May to 15 May 2010. Samples were collected on board the F/V *Nautes* (10 m in length; 100 HP), involved in the fishery of *C. chione*. The study area, which coincides with the commercial fishing area, was subdivided into 17 transects perpendicular to the coastline, with a distance of 3 km between each other. They were consecutively numbered from northeast to southwest (T1—T17) (Fig. 1). Five stations corresponding to depths of 5, 10, 15, 20 and 25 m were sampled in each transect whenever possible (avoiding the existence of sea grass, rocky outcrops and submarine outfalls). Two clam dredges (frame mouth width 70 cm; height 53 cm; depth 120 cm) were used for sampling (Pubill et al., 2011), each one provided with a different mesh size: a commercial mesh size of 24×24 mm, and an experimental mesh size of 12×12 mm used to collect juveniles. Both dredges were used simultaneously in each tow, which lasted 30 min at a towing speed of 1—1.2 kn; the geographical position was recorded using GPS; the transect length ranged between 925 and 1 110 m. All of the smooth clam specimens collected were transported to the Institut de Ciències del Mar (CSIC) laboratory, where they were counted, weighed and measured (maximum length to the nearest 0.1 mm using digital vernier calliper).

Analysis of covariance (ANCOVA) was used to test for an effect of both year and transect on three clam parameters: density (ind. m^{-2}), biomass (g m^{-2}) calculated using the fresh total weight of the bivalve, and modal value of the size—frequency distribution. Transect T17 was eliminated from the analyses because it was not sampled in 2004. The median of the particle size (D50) distribution was used as a covariate in the statistical analysis. When ANCOVA tests detected significant differences between groups, pairwise multiple comparisons were made using Tukey post hoc tests (Zar, 1999).

The geographic distribution of the smooth clam biomass (g) was examined using the Kriging interpolation algorithm (SURFER 8® Golden Software, Colorado). Data from 2004 to 2010 samplings, obtained with the clam dredge with a mesh size of 12×12 mm, were used to generate a $2\,000 \times 2\,000$ m grid for both time periods.

2.2. Sediment sampling

A Van Veen grab covering an area of 0.1 m^2 was used at each station in all the surveys to collect sediment from the clam bed. Sediment samples were processed according to a standard dry-sieving procedure (Wentworth, 1972) 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 choose the median (D50).

2.3. Historical catches analysis

A compilation of all existing data on commercial and experimental catches of the smooth shell clam in the study area was
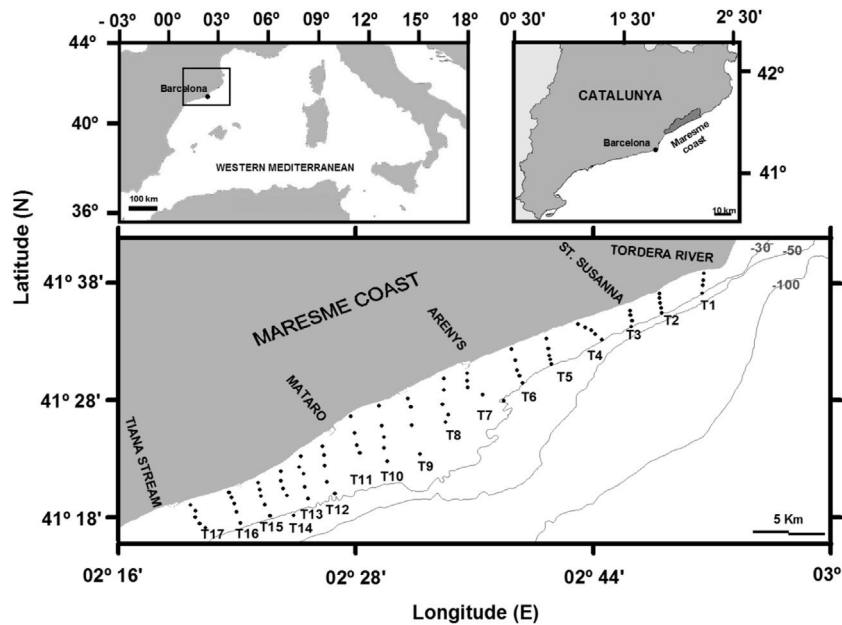
Fig. 1. Study area in the northwestern Mediterranean Sea showing the distribution of sampling stations (points), transects (T), and isobaths (30, 50 and 100 m).

performed to study trends. Three different sources of data provided by the Catalan government and local fishermen's associations were obtained: (1) commercial data on annual landings of total bivalve species in Catalonia from 1980 to 2012, including the Maresme coast; (2) commercial data on annual landings of smooth clams on the Maresme coast from 1980 to 2012; and (3) detailed data relative to experimental catches performed in January and February 1984, including location, landings, gear used and tow duration. From this last batch of data we selected those allowing comparisons of *C. chione* density and biomass with the ones obtained in our sampling, i.e. the ones collected at 10 m depth with the mesh size of 24 × 24 mm. In addition, experimental hauls were performed to compare the size class composition of catches obtained with the commercial mesh size of 24 × 24 mm used by fishermen to target *C. chione* before the bed was closed to commercial exploitation, and a clam dredge with a mesh size of 29 × 29 mm used to target *C. chione* after the area was reopened to fishing. Two hauls of the same duration were performed using both dredges simultaneously, at 3 different depths (5, 10 and 20 m) in December 2006. Once on board, the catch from each dredge was placed in a labelled plastic bag and the smooth clams were measured and weighed in the laboratory.

A Kolmogorov–Smirnov test was used to study whether there were differences in the length–frequency distributions of the catches between the two clam dredges. A Kruskal–Wallis test was used to test for differences within the median shell length values captured by each clam dredge.

2.4. Growth study

Two methods were used to estimate the growth parameters of the von Bertalanffy growth function (VBGF).

2.4.1. Modal class progression analysis

The first method is based on modal class progression analysis, which infers growth from the apparent shift of the modes in a time series of length frequencies. The methodology of length–frequency analysis is based on the assumption that size composition reflects a stable balance between recruitment, growth and survival. Total

Fig. 2. *Callista chione* mark-recapture experiment: (a) Specimen showing the numbered tag (scale bar 1 cm); (b) Experimental cage at recovery.

Table 1
Callista chione density (ind. m^{-2}) by depth (5, 10, 15, 20 and 25 m), sampling period (2004 and 2010) and transect (T1—T17), obtained using the clam dredge provided with 12 × 12 mm mesh size. Lines represent no available data.
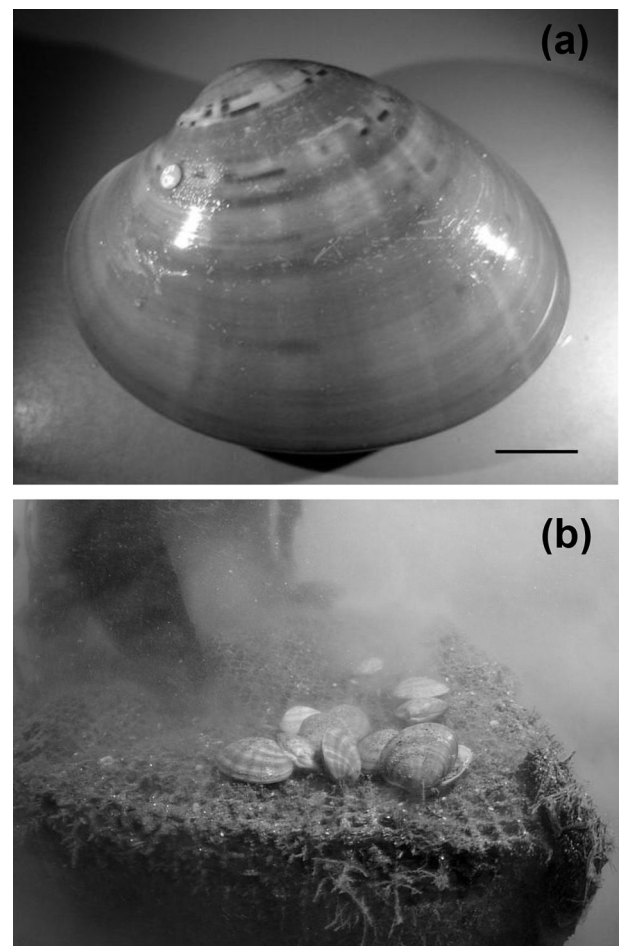
	5		10		15		20		25	
	2004	2010	2004	2010	2004	2010	2004	2010	2004	2010
T1	0.30	0.00	0.29	0.09	–	0.12	–	–	0.00	–
T2	2.76	0.10	5.85	1.10	–	0.39	0.33	1.50	0.01	0.21
T3	2.28	0.03	2.55	0.68	–	0.36	2.12	1.28	–	–
T4	0.37	0.07	1.53	1.10	–	1.06	0.98	0.15	0.00	0.35
T5	0.40	0.16	1.98	0.73	–	0.49	1.39	0.19	0.22	0.01
T6	1.51	0.52	1.54	0.07	–	0.22	1.50	0.28	0.76	0.35
T7	0.86	0.06	4.76	0.53	–	1.31	1.06	0.35	0.55	0.35
T8	2.05	0.94	0.92	0.80	–	0.62	0.64	0.11	–	0.04
T9	0.33	0.03	1.57	0.14	–	–	–	–	0.00	0.00
T10	0.89	0.36	0.99	0.31	–	0.25	0.00	0.00	–	0.03
T11	0.42	0.94	0.49	0.07	–	0.10	0.00	0.06	–	–
T12	0.82	0.00	0.72	0.02	–	0.86	0.02	0.28	–	0.15
T13	0.05	0.01	0.56	0.12	–	0.30	0.44	0.15	–	0.21
T14	–	0.04	0.00	–	–	0.53	0.14	0.99	–	0.60
T15	0.01	0.01	1.56	0.11	–	1.38	0.08	0.16	–	0.02
T16	0.17	0.00	1.14	0.19	–	0.13	0.03	0.14	–	0.05
T17	–	0.00	–	0.20	–	0.81	–	0.19	–	0.10

length of all smooth clams collected with two dredges carrying 12 × 12 mm mesh size was measured monthly between February 2005 and February 2006 (900—2000 clams per month) in transects T3 and T5, which were chosen randomly. Length—frequency distribution, grouped in 1-mm size classes, was decomposed into its components to identify cohorts using Bhattacharya's method (Bhattacharya, 1967), included in the FiSAT II software (Gayanilo et al., 2005). The parameters of the VBGF ($L_t = L_\infty(1 - e^{-k(t-t_0)})$) were estimated by nonlinear regression using the FiSAT II software package, where, from left to right, L_t is the predicted length at time t (mm), L_∞ is the asymptotic length (mm), k is the growth constant (year^{-1}), t is the age (year) of the clam, and t_0 is the age at which $L_t = 0$ (Gulland, 1983).

2.4.2. Mark-recapture experiment

The second method for estimating the growth parameters of the VBGF was based on mark-recapture data. A total of one hundred *C. chione* with shell lengths between 20 and 80 mm were collected in May 2005 in transects T3 and T5 at 20 m depth and transported

to the laboratory. Specimens were marked with numbered and coloured plastic tags on both valves. The tags were attached to the shell surface with cyanoacrylate glue and covered with nail polish to prevent abrasion (Fig. 2a). When dried, they were kept overnight in sea water aquaria and returned to the sea the following day. Just before the release, the bivalves were distributed in 10 cages containing 10 individuals each, at similar densities and size—frequency composition to average values in the natural bed. Cages were deployed by divers at the same sites and depth where clams were collected (Fig. 2b). Each cage consisted of a metal structure (50 × 50 × 20 cm) covered with a plastic mesh (mesh size 0.75 × 0.75 cm), buried 2 cm in the sediment and anchored with 20 cm iron bars. All experimental cages containing the tagged animals were recovered one year later (May 2006). At both marking and recapture, specimens were measured for shell length with a digital calliper (precision of 0.01 mm) and weighed for total weight on a top-loading digital scale (precision of 0.01 g).

We followed the Fabens method (1965) to estimate the L_∞ and k parameters of the VBGF from growth increment data. The parameters were estimated by fitting a rearranged function of the VBGF to the data on shell increment using FiSAT software (Gayanilo et al., 1996), $L_2 = L_1 + (L_\infty - L_1)*(1 - e^{(-k(t_2-t_1))})$, where L_1 is shell length at marking, L_2 is shell length at recovery, and t_1 and t_2 are the corresponding dates. The theoretical age at shell length zero (t_0) cannot be obtained from growth increment data (without specific size-at-age information). For the purposes of this study t_0 was assumed to correspond to the shell length of the smallest smooth clam found in infaunal samples in the area, which was 3.46 mm.

3. Results

3.1. Distribution, abundance, and population structure

Smooth clam density decreased considerably between 2004 and 2010 at 5 and 10 m depth in most transects (Table 1) and density decreased at half of the sampled stations at 20 m depth. No comparisons can be made at 15 m and 25 m depth because information is lacking. No clams were present at twelve of the stations, six in each year.

As shown in Table 2, the highest density values in 2004 were found in T2 and T3 (above 2.20 ind. m^{-2}), whereas density for all transects from T9 to T16 was under 0.64 ind. m^{-2}. In 2010 the

Table 2
Characteristics of the *Callista chione* population by year (2004 and 2010) and transect (T1—T17). *N*, total number of individuals collected; *W*, total weight (g); L_M, mean length (mm); L_{Mod}, mode length (mm); mean density in number (ind. m^{-2}); mean biomass (g m^{-2}); and D50, median particle size (mm).

T	2004							2010						
	N	W	L_M	L_{Mod}	Ind. m^{-2}	g m^{-2}	D50	N	W	L_M	L_{Mod}	Ind. m^{-2}	g m^{-2}	D50
T1	122	1 444	33.71	36	0.20	2.35	0.30	25	172	28.52	26	0.05	0.38	0.40
T2	1 714	16 994	29.78	27	2.24	22.30	0.43	597	3 241	27.58	22	0.66	3.58	0.51
T3	1 371	13 930	30.66	30	2.32	23.72	0.68	387	2 519	27.57	25	0.47	2.92	0.64
T4	609	8 028	30.36	27	0.72	12.80	0.89	552	4 740	26.23	22	0.55	4.19	0.75
T5	807	8 462	31.40	26	1.00	10.79	0.73	197	1 435	28.39	26	0.32	2.44	0.82
T6	818	7 660	30.34	26	1.33	12.78	0.58	281	1 782	27.62	26	0.29	1.83	0.53
T7	1 628	14 518	31.30	26	1.81	15.99	0.58	364	2 631	27.74	24	0.52	3.69	0.54
T8	830	7 152	29.51	30	1.20	10.40	0.35	689	3 484	25.02	21	0.50	2.50	0.64
T9	460	4 192	29.28	26	0.63	8.64	0.42	34	486	34.00	31	0.06	0.62	0.38
T10	394	5 575	30.37	27	0.63	13.27	0.68	262	1 991	27.75	24	0.19	1.51	0.82
T11	186	3 152	35.83	34	0.30	7.55	0.36	254	1 284	25.62	21	0.29	1.53	0.84
T12	345	3 869	30.68	30	0.52	5.85	0.52	166	1 811	32.32	23	0.26	2.65	0.47
T13	245	3 926	37.49	34	0.35	5.71	0.60	149	1 340	29.24	25	0.16	1.44	0.37
T14	30	340	33.67	27	0.07	1.62	0.36	260	1 812	27.72	25	0.54	2.96	0.28
T15	387	3 051	29.35	27	0.55	4.35	0.49	241	1 837	29.55	24	0.34	2.33	0.20
T16	334	5 755	31.95	26	0.45	7.70	0.57	206	1 759	30.34	27	0.26	2.31	0.44
T17	–	–	–	–	–	–	–	52	481	32.55	37	0.10	0.89	0.25
All	10 280	108 048	31.03	26	0.84	9.75	0.50	4 716	32 804	27.57	21	0.33	2.22	0.52

Table 3
Characteristics of the *Callista chione* population by year (2004 and 2010) and depth (5, 10, 15, 20 and 25 m). N, total number of individuals collected; W, total weight (g); L_M, mean length (mm); L_{Mod}, mode length (mm); mean density in number (ind. m^{-2}); mean biomass (g m^{-2}); and D50, median particle size (mm).

Depth	2004							2010						
	N	W	L_M	L_{Mod}	Ind. m^{-2}	g m^{-2}	D50	N	W	L_M	L_{Mod}	Ind. m^{-2}	g m^{-2}	D50
5	2 698	29 195	31.06	29	0.88	9.55	0.52	701	4 067	25.37	21	0.19	1.46	0.68
10	5 563	53 930	30.33	26	1.65	16.99	0.84	1 266	9 242	26.23	21	0.39	2.81	0.46
15	–	–	–	–	–	–	–	1 302	9 194	28.56	24	0.52	3.96	0.57
20	1 851	22 627	32.42	25	0.62	7.68	0.50	1 012	7 026	28.86	22	0.39	2.62	0.63
25	168	2 296	32.56	24	0.22	3.00	0.84	435	3 275	29.13	26	0.15	1.41	0.56
All	10 208	108 048	31.03	26	0.84	9.75	0.50	4 716	32 804	27.57	21	0.33	2.22	0.52

highest density values ranged between 0.52 and 0.66 ind. m^{-2} and were located in T2, T4, T7 and T14. Annual mean values of 0.84 and 0.33 ind. m^{-2} for density and 9.75 and 2.22 g m^{-2} for biomass were obtained in 2004 and 2010, respectively. The highest mean transect biomasses were found in T2 and T3 (above 22.0 g m^{-2}) in 2004 sampling and in T4 and T7 (above 3.6 g m^{-2}) in 2010 sampling.

A pattern of higher densities at intermediate depths can be observed (Table 3). The highest density values found for each year were 1.65 ind. m^{-2} at 10 m depth and 0.52 ind. m^{-2} at 15 m depth in 2004 and 2010, respectively. Results showed a change in the structure of the population, with a decrease in the mean and modal length over time in most transects (Table 2) and at most depths (Table 3). The frequency of individuals longer than 40 mm was 15% in 2004 and 9% in 2010, whereas the percentage of individuals smaller than 24 mm was 18% in 2004 and up to 37% in 2010 (Fig. 3). The modal value was 26 mm in 2004 and 22 mm in 2010.

C. chione was found inhabiting sediments with D50 (median particle size) values ranging from 0.2 to 0.9 mm, corresponding to medium and coarse sand (Tables 2 and 3). The smooth clam bed exhibited a quasi-continuous distribution between transects T2 and T12, with patchy areas of higher biomass in the northeastern locations (T2 and T3) in 2004 (Fig. 4). On the other hand, clams were scarce in the southwestern area (between transects T12 and T16). Six years later, in 2010, clam distribution was limited to some patches located in transects T3, T4, T7 and T12.

Smooth clam densities differed significantly according to both year (ANCOVA $F_{(1,94)}$ = 16.7, $p < 0.0001$) and transect (ANCOVA, $F_{(15,94)}$ = 13.7, $p < 0.005$). Densities were higher in 2004 than in 2010 (Tukey's HSD, $p = 0.0001$). Accordingly, smooth clam biomass differed significantly between years (ANCOVA, $F_{(1,94)}$ = 2.43, $p < 0.00001$; Tukey HSD, $p = 0.0001$) and transects (ANCOVA, $F_{(15,94)}$ = 2.41, $p = 0.005$; Tukey HSD, $p = 0.09$ between T1–T2 and T1–T3). No significant differences were found in smooth clam modal value according to year (ANCOVA, $F_{(1,68)}$ = 0.67, $p = 0.42$) or transect (ANCOVA, $F_{(15,68)}$ = 1.69, $p = 0.07$).

3.2. Sediment changes

The Maresme coastline was dominated by coarse sand (2.0–0.63 mm in T3, T4, T5 and T10) and medium sand (0.63–0.2 mm in T1–T2, T7–T8 and T11–T17) in 2004 (Fig. 5). However, changes in granulometry occurred between the two periods of study. The distribution of the median grain size (D50) revealed that the sediments became finer everywhere in 2010, with the appearance of a larger area of fine sand (0.2–0.063 mm), even with silt (0.063–0.0063 mm), mainly between T12 (south of Mataró) and T17 (Tiana stream).

3.3. Commercial catch analysis

Three different periods can be distinguished in total annual bivalve landings in Catalonia: from 1991 to 1995 the captures were

about 1300 t year^{-1}; from 1996 to 2000 they were about 500 t year^{-1}; and from 2001 to 2012 they rarely exceeded 200 t year^{-1} (Fig. 6a). On the Maresme coast, smooth clam landings were under 110 t year^{-1} between 1980 and 1994, increased to a maximum of 290 t year^{-1} in 1997, and finally decreased progressively to reach 80 tons in 2005 (Fig. 6b). This negative tendency culminated with the collapse of the bivalve fishery at the end of 2005.

The evolution of the density and biomass of the population distributed at 10 m depth in three time periods (1984, 2004 and 2010) spanning 26 years showed that the highest changes throughout the clam distribution area (from T1 to T16) were found between the last two periods, 2004 and 2010 (Table 4). For example, transect T4 had a density of 0.75 and 0.65 ind. m^{-2} in 1984 and 2004, respectively but only 0.11 ind. m^{-2} in 2010. Biomass showed a gradual downward trend from 1984 to 2010 although the
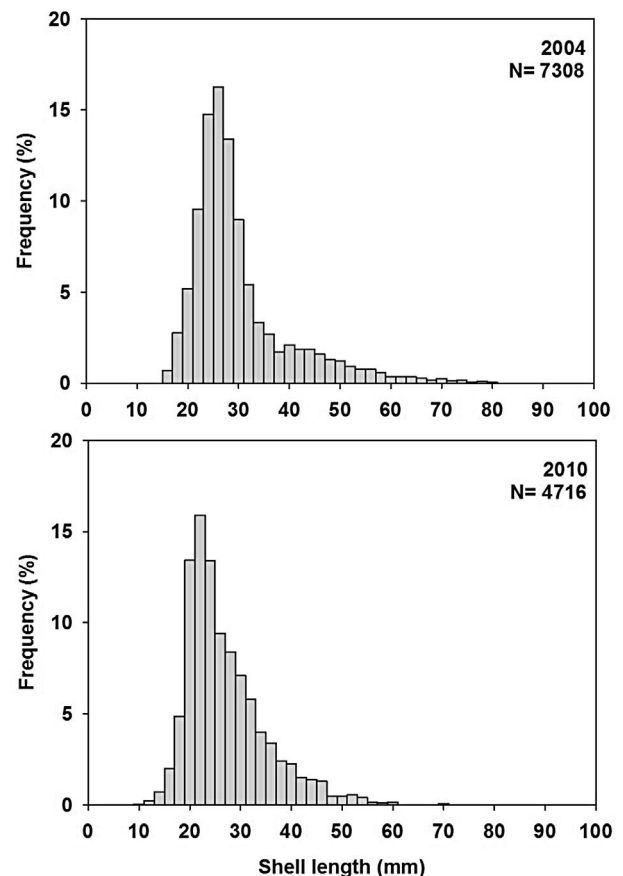

Fig. 3. Length–frequency distributions of *Callista chione* in the two sampling periods obtained using the clam dredge provided with 12 × 12 mm mesh size.
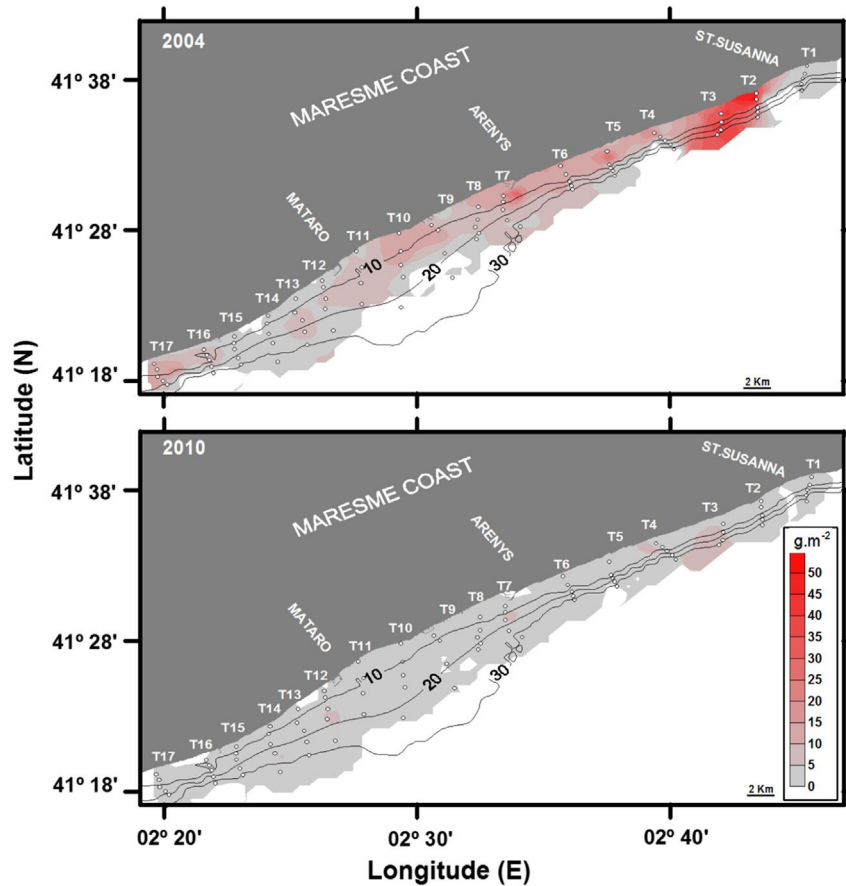
Fig. 4. *Callista chione* spatial distribution and abundance (g m^{-2}) in two different sampling periods (2004 and 2010) in the study area, obtained using the clam dredge provided with a 12 × 12 mm mesh size.

decline was sharper between 2004 and 2010. Following the same example of transect T4, biomass had a maximum value of 27.15 g m^{-2} in 1984, decreased to 14.74 g m^{-2} in 2004, and reached a minimum of 4.69 g m^{-2} in 2010.

3.4. Fraction of the population fished by mesh size

The length composition of the smooth clam catches by mesh size and depth is shown in Fig. 7. Kolmogorov–Smirnov comparisons confirmed that the size–frequency composition of the catches collected with both dredge mesh sizes was not significantly different ($D = 0.06$; $p = 0.99$) regardless of the depth. In addition, the Kruskal–Wallis test showed significant differences in the median size of individuals fished by each clam dredge (24 × 24 and 29 × 29 mm) ($H = 168.64$; d.f. = 1; $p < 0.001$). As expected, 95% of the total catch using the larger mesh size (29 × 29 mm) was composed of the bigger smooth clams, ranging between 33 and 47 mm length, whereas 95% of the total catch obtained with the medium mesh size (24 × 24 mm) ranged between 21 and 41 mm length (Fig. 7).

3.5. Clam growth

Two sets of parameters for the VBGM were obtained with the two methods used to study growth.

3.5.1. Modal class progression analysis

A time series of length frequencies in which the progression of the mode can be observed is presented in Fig. 8. At the beginning of the study (February 2005), the method of Bhattacharya identified

three cohorts, each one corresponding to the annual recruitment of the years 2004 (C-04), 2003 (C-03) and 2002 (C-02), with modal sizes of 28.30 mm (SD = 3.62), 42.64 mm (SD = 4.37) and 55.33 mm (SD = 5.57), respectively (Fig. 9). From May 2005, one or two cohorts were detected in the population, corresponding to the recruitments of 2003, 2004 and 2005. During the period of study, a new recruitment (C-05) was observed in August 2005, with juveniles of a medium length of 20.42 mm (SD = 1.05). The modal size of the C-05 recruits increased until 27.88 mm (SD = 3.60) in February 2006. Accordingly, the modal size of the C-04 cohort reached 28.30 mm in February 2005. Growth results of the C-04 cohort showed that growth was faster between April and July 2005, slowed down between August and October and increased again from November 2005 to February 2006.

The parameters estimated from the modal class progression analysis were $L_\infty = 96.97$ mm, $K = 0.205$ year^{-1} and $t_0 = 0.21$ ($N = 1055$, $r^2 = 0.80$).

3.5.2. Mark-recapture data

In the mark-recapture experiment, 47 smooth clams were recovered one year after their release. The lengths of the recovered bivalves ranged from 20 to 69 mm. The percentage of survival differed between experimental cages, being between 70% and 90% in five cages, 50% and 69% in two cages, and 49% in one cage. Two cages showed a mortality of 100% as a consequence of common octopus (*Octopus vulgaris*) sneaking inside seeking refuge and preying on the clams.

Growth rates varied in function of initial shell size, i.e. the bigger the shell length was, the slower was the growth (Fig. 10).
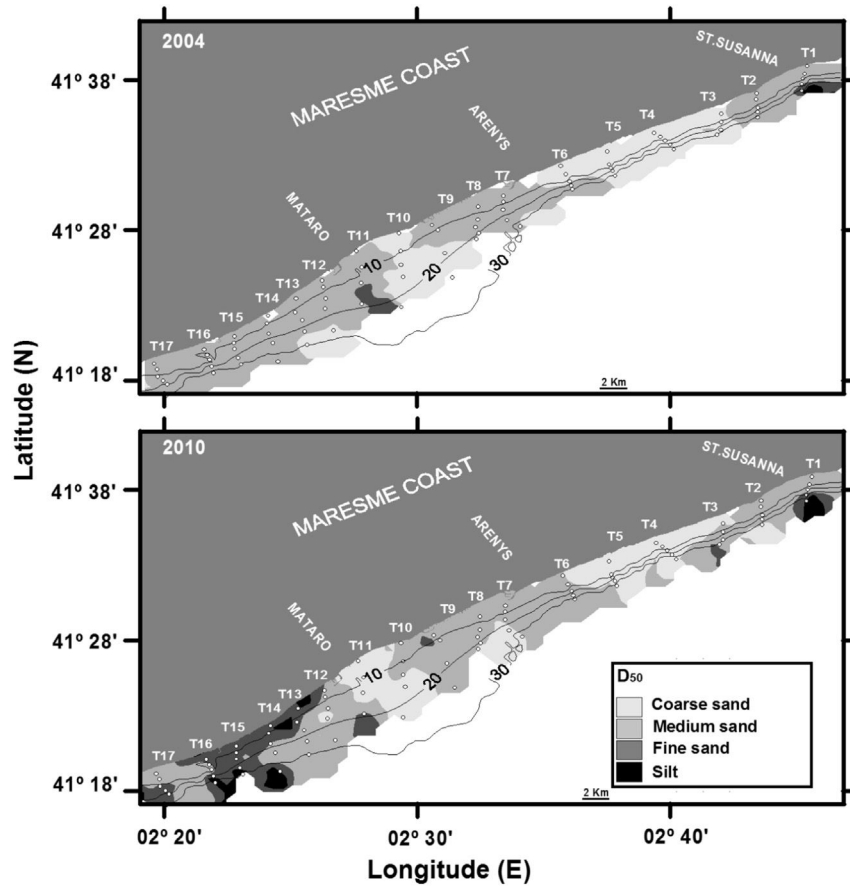
Fig. 5. Median grain size (D50) spatial distribution in the two different sampling periods (2004 and 2010) in the study area. Coarse sand (2.0–0.63 mm); medium sand (0.63–0.2 mm); fine sand (0.2–0.063 mm); silt (0.063–0.0063 mm).

Individuals from the smallest group (20–29 mm) grew at a rate of 8.60 mm year^{-1} (SD = 1.67); the 30–39 mm length group at a rate of 4.19 mm year^{-1} (SD = 1.32); the 40–49 mm length group at a rate of 2.73 mm year^{-1} (SD = 1.15); the 50–59 mm length group at a rate of 2.19 mm year^{-1} (SD = 0.92); and the biggest group, ranging from 60 to 69 mm, at a rate of 0.28 mm year^{-1} (SD = 0.06).

The estimated parameter values for the growth function from the mark-recapture experiment were L_∞ = 107.63 mm and K = 0.147 year^{-1} (N = 47, r^2 = 0.49).

4. Discussion

The present study shows the decrease in density and biomass of the *C. chione* bed by comparing several population parameters in three different periods over 26 years and confirms its impoverishment. Commercial landings peaked in 1997 and then declined steadily, culminating in the collapse of the bivalve fishery at the end of 2005 because of the very low presence of older clams above the minimum legal size. In 2010, 90% of the population was composed of individuals smaller than 45 mm long which, according to our growth estimations, corresponds to ages below 4 years. The presence of only 2% of individuals over the legal commercial size (60 mm length, 5–6 years old), explains the collapse of the fishery. The clams in the study population are very young compared with other populations in the Mediterranean Sea, for which ages between 5 and 15 years have been reported (Ezgeta-Balić et al., 2011; Leontarakis and Richardson, 2005; Metaxatos, 2004).

The shell growth rate of *C. chione* is not continuous through life; growth occurs rapidly in the first 5–6 years of life and then gradually slows down until it is practically inappreciable (Ezgeta-Balić et al., 2011; Keller et al., 2002; Moura et al., 2009). Information on growth and longevity of this species differs among geographical areas and locations, giving different estimations of parameters of the von Bertalanffy growth function. In the eastern Mediterranean Sea and Portugal, its lifespan has been estimated at between 12 and 20 years (Ezgeta-Balić et al., 2011; Hall et al., 1974; Keller et al., 2002; Leontarakis and Richardson, 2005; Metaxatos, 2004; Moura et al., 2009; Strada and Zocco, 1985). Accordingly, our estimated VBGF values are in the range of previously published data, although the methodologies used are different. The previous studies use surface growth ring and/or internal shell micro-growth line readings; in contrast, both our methods for estimating growth are based on field observations (monthly samples and mark-recapture experiments). The two methodologies here used to estimate growth gave us very similar growth curves, especially at sizes under 12 years, which is larger than the sizes found in the study population. Therefore, although the estimation with the mark-recapture experiment was based on one sample year, and on only 47 clams, we are confident of the results. Our results suggest that *C. chione* on the Maresme coast grows rapidly in the initial 4–5 years, and during the first year of life; moreover, the clams have higher growth rates in winter and early summer months. Similar growth seasonality was found in this species by Hall et al. (1974) and Moura et al. (2009) in the Atlantic Ocean. In the western Mediterranean, Ramón and Richardson (1992) reported for the
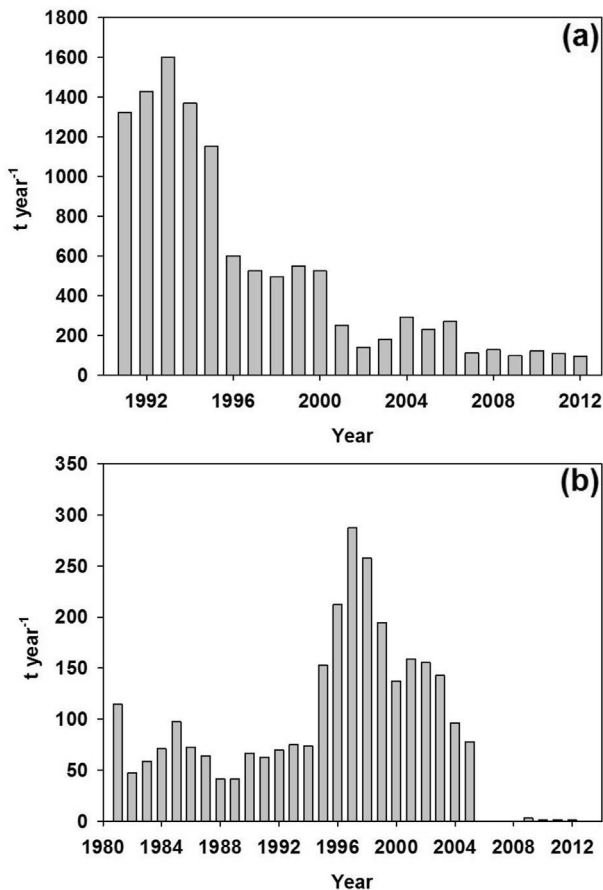
Fig. 6. Evolution of landings: (a) Total bivalve annual landings in Catalonia; (b) *Callista chione* annual landings on the Maresme coast.

bivalve *C. gallina* a high growth rate in winter and late spring and slow growth between August and October, following the maximum summer sea water temperature, similarly to the findings of our study for *C. chione*.

Determining the factors that led to the decline of the *C. chione* bed is a complex task owing to the multiple factors influencing species inhabiting nearshore areas. The shallow soft-bottom sediments of the Maresme coast are continuously affected by man-

Table 4
Number of individuals (*N*), mean density (ind. m^{-2}) and mean biomass (g m^{-2}) of the *Callista chione* population distributed at 10 m depth in three time periods (1984, 2004 and 2010) for transects (T), obtained using the clam dredge provided with a 24 × 24 mm mesh size.

T	N			Ind. m^{-2}			g m^{-2}		
	1984	2004	2010	1984	2004	2010	1984	2004	2010
T1	73	28	2	0.26	0.21	0.01		6.06	1.71
T2	142	74	12	0.59	0.52	0.06	25.25	12.57	1.71
T3	132	51	19	0.73	0.37	0.09	24.82	8.31	2.72
T4	180	91	21	0.75	0.65	0.11	27.15	14.74	4.69
T5	71	96	22	0.59	0.67	0.11	10.70	17.10	4.12
T6	49	49	4	0.41	0.35	0.02	10.39	9.86	0.31
T8	115	44	4	0.48	0.31	0.02	17.33	13.03	1.39
T9	38	55	39	0.16	0.39	0.20	5.76	12.31	2.22
T10	106	58	24	0.44	0.41	0.12	15.95	14.86	1.36
T11	58	29	8	0.24	0.20	0.04	8.75	6.82	0.23
T12	119	59	2	0.50	0.42	0.01	17.90	12.29	0.38
T14	100	60	21	0.42	0.29	0.10	15.08	9.79	0.82
T16	64	36	32	0.27	0.26	0.16	9.20	8.93	1.38

made disturbances: breakwaters, recreational port construction, dredging activities for beach nourishment (a process by which sediment lost is replaced from sources outside the eroding beach), and commercial fisheries (Sardá et al., 2000, 1999). Systematically, the authorities use the sand deposits from the Maresme coast to combat coastal erosion along the nearby beaches. About 10 200 000 m^3 of sand was dredged from the area between 1987 and 2007 (García Rodriguez, 2008). Half of that volume was dredged from the southern area of the *C. chione* bed, between the Tiana intermittent stream and Mataró Port; 36% of the sand was dredged from the central part of the bed (between Mataró and Arenys de Mar harbour), and the rest was obtained from undetermined sources. No sand extraction took place at the northern study sites, between Arenys de Mar harbour and the Tordera River. Our results show a change in the sediment particles size between 2004 and 2010, when fine sand and mud portions clearly increased in the southwestern area of the bed. The increase in fine sand and mud may make this area inhabitable for *C. chione* because, as observed in our study, it prefers medium and coarse sand.

Several studies have analysed the effect of dredging on benthic communities (Bolam et al., 2006; Newell et al., 1998). It is known that the degree and duration of change in sediment composition caused by sand extraction has great implications for the recovery of the benthic fauna (van Dalfsen et al., 2000). In Sitges, a few kilometres south of the study area (Costa Daurada, western Mediterranean), the addition of a thick layer of muddy sediment on top of the native sand had a great impact on the benthic community and populations of commercially exploited mollusk species (*C. chione*, *Murex* sp., *Cerastoderma edule* and *Ensis siliqua*) were almost completely eliminated (van Dalfsen et al., 2000). When areas are depopulated through sand extraction, re-colonization of the disturbed area largely depends on the settlement of larvae and immigration of mobile species. Newell et al. (1998) suggested that long-life and slow-growing species may take several years before larval recruitment and subsequent growth of the juveniles allow the original community composition and biomass to be restored. In fact, Sardá et al. (2000) observed, on the Maresme coast, that the number of species in a dredged area quickly recovered and most populations reached large sizes two years later, with the exception of *C. chione*, whose population was still clearly reduced. Continuous dredging operations in the southwestern part of the bed gradually reduced the distribution area of the smooth clam to the northeast. Therefore, in agreement with Sardá et al. (2000), we consider the impact of continuous sand extraction to be a very likely cause of the decline of the *C. chione* bed.

Resource overexploitation is another possible reason for the decline of the Maresme *C. chione* bed. Unexploited long-life soft bottom bivalve populations are worldwide composed of large-sized, old individuals with slow growth at high densities. Wolff (2005) compared the same bed of the bloody cockle *Anadara senilis* in Banc d'Aguin (Mauritania), first unexploited (1986–1987) and then years after being exploited (2001–2002). The author observed that the initial population was dominated by 10–20-year-old individuals, whereas after exploitation it was composed of 0- to 5-year old individuals. The population structure of the smooth clam on the Maresme coast was dominated by small-sized (30 mm), young individuals (2 years old) at relatively low densities. Furthermore, we have indications that smooth clams of 39–40 mm (2–2.5 years) had been fished and commercialized, especially during the last period when low quantities of legal commercial sizes remained in the bed. Though no data on fishing effort are available, it is most likely that the reduction of the distribution area of the smooth clam to the northeast part of the Maresme coast forced fishermen to progressively concentrate their activity in a smaller area, with the consequent increase in fishing effort in the
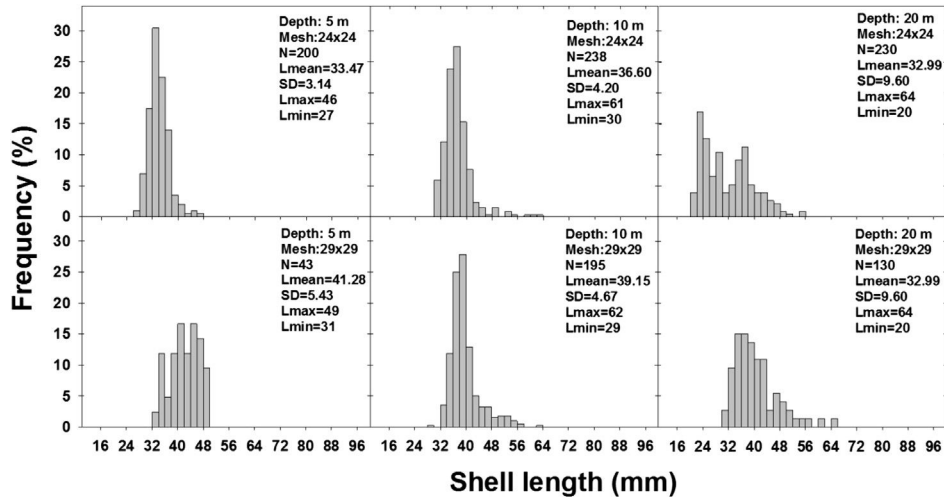
Fig. 7. Length–frequency distribution of *Callista chione* catches (by depth) performed with commercial dredges provided with two different mesh sizes (24 × 24 on top and 29 × 29 on bottom).

northern sites. Therefore, reduced adult density due to overfishing is another highly probable cause of the decline of the *C. chione* bed.

Predation is another factor influencing bivalve populations. Though predation can be very high, it is mainly focused on recruits (Cattaneo-Vietti et al., 1997; Malinowski, 1993; Wolff, 2005). In the study area, there is a strong predation on smooth clam juveniles by the sea star *Astropecten aranciacus* (Baeta and Ramón, 2013). Individuals over 30 mm long have few predators: occasionally *O. vulgaris*, and the gastropods *Natica haebrea* and *Natica dillwynii*. The number of empty shells found in the smooth clam bed was very low, so it is very unlikely that predation could be a determining cause of the decline of the *C. chione* bed.

Pathologies or diseases can cause mass mortality episodes in bivalves. Rickettsia-like formations were found in a histopathological study of the *C. chione* population on the Maresme coast performed in April, July, and October 2007 (unpublished results from the Pathological Diagnostic Service in Fish from the Veterinary Faculty of the Universitat Autònoma de Barcelona). These parasitic formations have been reported to cause high mortalities in bivalve beds (Villalba et al., 1999; Zhu et al., 2012). Nevertheless, as the number of empty shells found in the study area was low, and the parasitic prevalences found were around 5–30%, we think that Rickettsia-like formations are unlikely to be the cause of the decline of the *C. chione* bed.

Other non-studied parameters such as primary production, recruitment fluctuations and pollution can also influence the survivorship of *C. chione* in the Maresme bed. Romanelli et al. (2009)

reviewed the literature related to the clam *C. gallina* fishery in the Adriatic Sea and suggested that fishing pressure and the reduction in primary production both played an important role in the reduction of the clam population. Two time series in coastal ecosystems from the Adriatic Sea showed a consistent decrease in phytoplankton abundance and biomass over the last 20 years (Mozetič et al., 2010; Ninčević Gladan et al., 2010). To our knowledge, time series of phytoplankton dynamics are not available on the western Mediterranean coast to ascertain whether this phenomenon also occurs there. Booms and busts in the abundance of bivalve populations are also often attributed to fluctuations in larval recruitment (Beukers-Stewart et al., 2003; Sissenwine, 1984; Vause et al., 2007).

The present study is one of the few existing works in the literature reporting the impoverishment of a bivalve bed on the basis of field work and putting together the main causes that led to this situation. Although establishing a cause and effect is difficult, we can assert that the absence of an integrated management of this coastal area has led the *C. chione* population to a critical situation and its fishery to collapse. Information on the smooth clam bed on
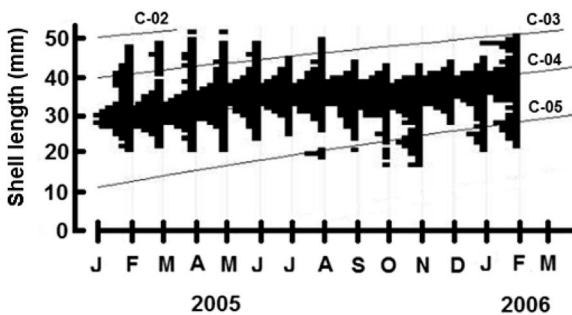
Fig. 8. Length–frequency histograms and the corresponding von Bertalanffy growth curves for *Callista chione* during the period 2005–2006.
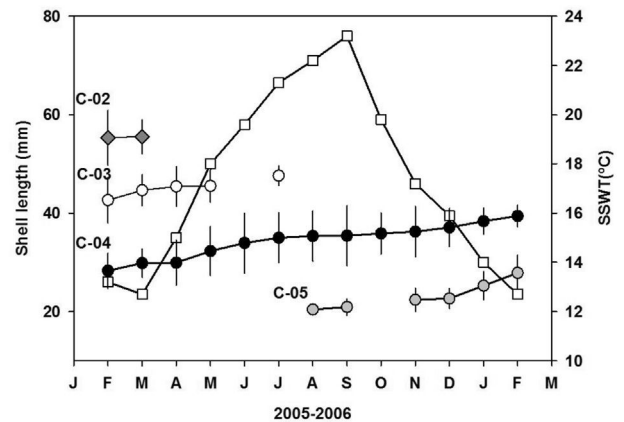
Fig. 9. *Callista chione* shell length from four cohorts between February 2005 and February 2006, determined from monthly progression of mean size of each cohort in length–frequency distributions. White squares correspond to surface sea water temperature (SSWT). Other symbols correspond to a different smooth clam cohort (±SD): grey diamonds (C-02), white circles (C-03), black circles (C-04), and grey circles (C-05).

$$y = 32.52^{(-0.056x)}$$
$$R^2 = 0.80$$

Fig. 10. *Callista chione* growth rates as a function of initial shell length measured in cage experiments from February 2005 to February 2006.

the Maresme coast has been collected from several sources (commercial landing data, biomass and density data from 1984, and information on locations and volume of dredged sand, 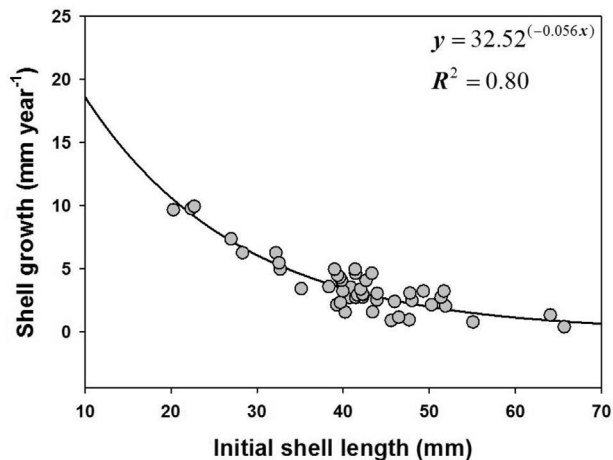and the prevalence of pathologies) and analysed in this present study together with our own data. After integrating all the information available, we are fairly certain that the decline of the bed is mainly caused by the interaction of two coastal uses: (i) sand dredging, which has been occurring periodically; and (ii) overfishing, which has eliminated the larger, more fertile clams, aggravating the situation of an impoverished population.

5. Conclusions

The present study demonstrates the decline of the *C. chione* population on the Maresme coast over 26 years. Two main causes seem to be responsible for the current status of the bed: continuous dredging operations in the southwestern and central part of the bed for beach nourishment, and overfishing. Appropriate management plans are needed to sufficiently recover the population to sustain harvesting. We suggest the following management guidelines: (1) banning artisanal clam dredging until the population has recovered; and (2) implementing other alternatives to beach nourishment to mitigate coastal erosion. If no alternatives to beach nourishment are found, sand dredging should be restricted to the southern area and preferably to depths at which there are no vulnerable species.

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7.2. Feeding ecology of three species of Astropecten (Asteroidea) coexisting on shallow sandy bottoms of the northwestern Mediterranean Sea

Abstract

Predation is one of the most important biotic interactions influencing populations and communities in marine soft sediments. Sea stars are ubiquitous predators with diverse diets that play functionally important roles in the benthos. Here we examined the diet and the ecological roles of three sympatric species of the genus *Astropecten* (*A. aranciacus, A. irregularis pentacanthus* and *A. platyacanthus*. The study was performed between March 2010 and February 2011 on the Maresme coast. Their main diet consists of gastropods and bivalves, with some dominant prey species. The analysis of the infaunal community composition and stomach contents indicated that food selection was not associated with prey availability. Diet varied between species and seasons, but no between size classes. Ontogenic patterns of prey size use were recognized in the three species. *A. irregularis pentacanthus* does not compete with the other two species for the available resources. A large overlap was detected between *A. aranciacus* and *A. platyacanthus* in winter, which indicates competitive interactions. These results demonstrate that *A. aranciacus* and *A. platyacanthus* predation is an important factor controlling the populations of the commercial bivalve *Callista chione*.

Figures 10 and **11:** *A. aranciacus* stomach contents.

Resumen

La predación es una de las principales interacciones biólógicas que influencia a las poblaciones y comunidades biológicas de los sedimentos blandos marinos. Las estrellas de mar son depredadores omnipresentes, con dietas muy diversas, que juegan un papel muy importante en las comunidades bentónicas. Se ha examinado la dieta y el papel ecológico de tres especies de estrellas simpátricas pertenecientes al género *Astropecten* (*A. aranciacus, A. irregularis pentacanthus* and *A. platyacanthus*). Este estudio se llevó a cabo entre marzo de 2010 y febrero de 2011 en la costa del Maresme (Noreste del Mar Mediterráneo). Los resultados muestran que su dieta está formada esencialmente por gasterópodos y bivalvos, dominando determinadas especies. El análisis de la comunidad infaunal y de los contenidos estomacales indicó que la selección de las especies ingeridas no tenía relación su disponibilidad en el medio. Las dietas variaron entre especies y estaciones, pero no entre grupos de tallas. También se observaron patrones ontogénicos en la selección del tamaño de las presas, en las tres especies. Se observó que *A. irregularis pentacanthus* no competía por los recursos disponibles con ninguna de las otras dos especies de estrellas. No obstante, se detectó un fuerte solapamiento alimentario entre *A. aranciacus* y *A. platyacanthus* en los meses de invierno. Además, los resultados mostraron que la depredación de *A. aranciacus* and *A. platyacanthus* sobre el bivalvo comercial *Callista chione* ejerce un papel importante en el control de sus poblaciones.

Participación de los distintos autores

Todos los coautores participaron en la elaboración y corrección del manuscrito

Trabajo del doctorando

El doctorando ha participado en el diseño experimental de los muestreos, la recogida y posterior análisis de las muestras en el laboratorio, así como el análisis de los datos y la posterior redacción y corrección del manuscrito.

ORIGINAL PAPER

Feeding ecology of three species of *Astropecten* (Asteroidea) coexisting on shallow sandy bottoms of the northwestern Mediterranean Sea

Marc Baeta · Montserrat Ramón

Abstract Predation and competition are important biotic interactions influencing populations and communities in marine soft sediments. Sea stars are ubiquitous predators with diverse diets that play functionally important roles in the benthos. In this study, we examined the diet and the ecological roles of three sympatric species of the genus *Astropecten* (*A. aranciacus*, *A. irregularis pentacanthus* and *A. platyacanthus*). The study was performed between March 2010 and February 2011 on the Maresme coast (northwestern Mediterranean Sea). Results showed that their main diet consisted on gastropods and bivalves, such as *Glycymeris glycymeris*, *Callista chione*, *Gibbula guttadauri* and *Cyclope neritea*. Food competition between species was avoided by partition of prey resources. Intra-specific differences in the dietary compositions between seasons were found, but not between size classes. Ontogenetic patterns of prey size consumption were recognized in the three species. A large diet overlap was detected between *A. aranciacus* and *A. platyacanthus* in winter, due to changes in prey availability. Nevertheless, the analysis of the infaunal community composition and stomach contents indicated that food selection was not associated with prey availability.

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Introduction

Marine soft sediments are the most common habitat on earth and are increasingly being subjected to broad-scale anthropogenic disturbances due to, for example, eutrophication, hypoxia, fishing, sedimentation and pollution (Norkko et al. 2006; Zajac et al. 1998; Ellis et al. 2000). Predation and competition are considered to be the most important biotic interactions influencing populations and communities in these habitats (Evans 1983). Asteroids of the genus *Astropecten* are efficient predators common throughout the world in intertidal and subtidal sandy and muddy environments (Tortonese 1965; Wells and Lalli 2003). Paxillosid sea stars have an intra-oral feeding mechanism: They swallow their prey intact, which then remains in the stomach for a variable period of time (Christensen 1970; Beddingfield and McClintock 1993). Therefore, analysing the stomach contents of these invertebrates can provide reliable information on their diet, which is composed of a wide variety of prey, but is usually dominated by bivalves (Christensen 1970; Schwartz and Porter 1977) and gastropods (Massé 1963; Edwards 1969). Like other predators, sea stars exert a strong influence on the structure and function of the community they prey on, promoting heterogeneity and diversity in the community (Gaymer et al. 2004).

Three paxillosid sea star species of the genus *Astropecten* inhabit the coastal grounds of the northwestern Mediterranean: *A. aranciacus* (Linnaeus 1758), *A. irregularis pentacanthus* (Delle Chiaje 1827) and *A. platyacanthus* (Philippi 1837). *Astropecten aranciacus* occurs in the Mediterranean Sea and the eastern Atlantic from Portugal to Angola, including the Canary, Madeira and Cape Verde Islands. It lives on sandy, muddy and detrital aggregate bottoms, as well as in seagrass beds. The geographical

distribution of *A. irregularis pentacanthus* encompasses the eastern Atlantic from northern Norway to Angola, including the Canary and Cape Verde Islands. It inhabits sandy and muddy bottoms from the sublittoral to depths of about 900 m (Koehler 1921; Tortonese 1965; Sierra et al. 1978; Southward and Campbell 2006) and dominates the epibenthic community in the northwestern Mediterranean fishing grounds (De Juan et al. 2007). The geographical distribution of *A. platyacanthus* is restricted to the Mediterranean Sea, and it lives on sandy and muddy bottoms from 2 to 100 m depth.

Predation is often the most important cause of mortality in bivalve populations (Salas et al. 2001). In some areas, sea stars are thought to be the most effective predators of bivalves (Dame 1996). For instance, *Asterias rubens* controls the abundance and distribution of mussels in both intertidal and subtidal areas (Sloan 1980; Saier 2001). Sea scallop recruitment in the Mid-Atlantic Bight is significantly related to depth and to the abundances of *Astropecten americanus* and *Asterias spp.* (Hart 2006). *Spisula subtruncata* was almost eliminated in Danish waters as a result of *A. irregularis* predation (Muus 1966; Freeman et al. 2001). Moreover, the negative effect of some sea stars has also been documented in aquaculture. For instance, in Japan, an outbreak of *Asterias amurensis* can produce serious damage to natural and cultured bivalve beds (Nojima et al. 1986). The three *Astropecten* species here studied are regularly caught as bycatch in an important artisanal bivalve fishery to the northeast of Barcelona (northwestern Mediterranean Sea) that targets the smooth clam *Callista chione* (Linnaeus, 1758). A previous study on the faunistic assemblages associated with the *C. chione* beds in the same area found that *Astropecten spp.* appeared in 48 % of the samples analysed (Pubill et al. 2011). Nevertheless, there are so far no data in the literature on the potential of *Astropecten spp.* as predators of commercially important shellfish beds in the Mediterranean.

The dietary composition of a predator has important implications not only for the predator species itself but also for its impact on sympatric species (Schoener 1974). Understanding the factors that affect species coexistence is an important focus area in ecology. Interspecific competition has been recognized as an important factor for structuring communities (Carrete et al. 2010). The coexistence of different species of the genus *Astropecten* has been previously documented in Venezuela (Bitter 2000) and Queensland (Australia) (Lemmen et al. 1995) as well as in the Mediterranean Sea, that is, in Sardinia (Ribi et al. 1977) and Almeria (Sierra et al. 1978), but the ecological relationships among these species are still poorly understood. Competition theory dictates that complete competitors cannot coexist (Gause 1934), and therefore, under the stress of competition, specializations or niche differences will evolve.

Seasonal variability of prey in the stomachs of *A. americanus* has been related to shifts in the abundance of the bivalve *Arctica islandica* (Franz and Worley 1982). Macroinfaunal abundance and biomass in the Northwestern Mediterranean soft bottoms was found to vary seasonally with a peak during spring, decreasing sharply in summer, and reaching low values in winter (Pinedo et al. 1997). There is no information on the existence of seasonality on the diet of the *Astropecten* species inhabiting in these bottoms.

Ontogenetic changes in diet composition have been reported for other asteroids (Himmelman and Dutil 1991; Manzur et al. 2010). Differences in prey size selected by small and large *Pisaster ochraceus* can be critical for juvenile survival (Menge and Menge 1974).

The main objective of this study was to investigate the trophic relationships of three sympatric *Astropecten* species (*A. aranciacus*, *A. platyacanthus*, and *A. irregularis pentacanthus*) that inhabit the shallow bottoms of the northwestern Mediterranean. This paper examines its feeding strategy, diet overlap, ontogenetic changes in the preys consumed (species and sizes) and prey selection. Temporal patterns related to diet composition are also analysed.

Materials and methods

Study site

The study site was located on the Maresme coast (northeast Barcelona, Spain), between port Balís and the village of Sant Pol (Fig. 1), at depths between 7 and 12 m. The beaches are of the reflective type with coarse sediments originating from the erosion of degraded granite from the nearby mountains and transported by short rivers, such as the Tordera, and seasonal intermittent streams. The mean surface water temperature is approximately 12 °C in winter and 23 °C in summer (http://www.meteoestartit.cat).

Sampling and stomach content analysis

Samples were collected in four seasons (spring, summer, autumn and winter), with three samplings within each season (once a month) to have a better approach of the seasonal variability. Sampling was carried out between March 2010 and February 2011 in daylight onboard the artisanal fishing boat "Esparta" (10 m in length; 100 HP) from the bivalve *C. chione* fishery fleet. A clam dredge, locally known as a "gàbia de lluenta", was used to take samples. This gear is comprised of a metallic frame (mouth length: 70 cm; mouth height: 53 cm), a toothed lower bar and a rectangular metallic grid box (mesh size:

Fig. 1 Map of the study area
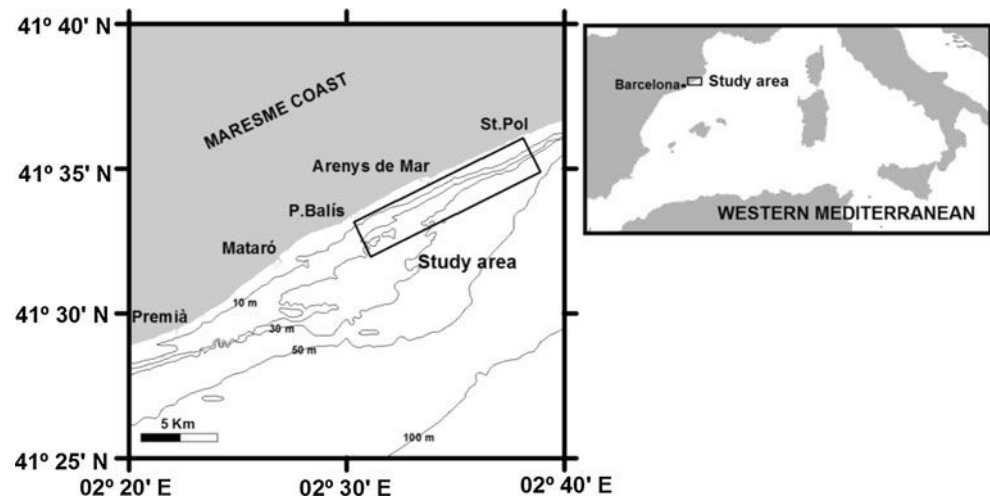
29 × 29 mm). A mean of 12 tows were carried out per sampling journey. Each tow lasted approximately 30 min at a speed of 1–1.2 knots, and the mean towed area was around 800 m². All the sea stars of the genus *Astropecten* caught were transported to the laboratory in a cool box (4 °C).

The sea stars were identified and weighed in the laboratory; the length or major radius (R = distance from the centre of the oral disc to the tip of the longest arm) was measured to the nearest 0.1 mm using callipers. The oral surface was opened by separating the plates along the ambulacral grooves to expose the stomach. The stomach contents, often including the thin stomach wall so as to collect any small prey hidden in its folds, were carefully removed, washed through a 200 μm sieve and weighed. Stomach contents were preserved in 70 % ethanol and then examined under a binocular compound microscope. All prey items were identified to the lowest possible taxonomic category, counted and weighed. Molluscs were also measured (total length) to the nearest 0.01 mm using callipers. These data were used to analyse diet composition (by species, season and size class), ontogenetic changes in the prey consumed, diet overlap and feeding strategy.

Additionally, we chose three stations in the study area located in front of Port Balís, Arenys and St Pol (Fig. 1) for a specific analysis of prey selection. Three sediment samples were collected with a Van Veen grab (0.1 m²) at each station, and afterwards, a short tow (5 min at a speed of 1–1.2 knots) was performed at the same location to collect sea stars. This sampling was conducted once in March, August and November 2010 and in February 2011. Sediment samples were sieved through a 0.5 mm mesh screen and preserved in formalin. Stomach contents were processed as indicated above. All prey items were identified to the lowest possible taxonomic category.

Diet composition analysis

Data on diet were analysed by multidimensional scaling (MDS) techniques. We reduced the high number of dietary samples (127 stomachs) of *A. aranciacus* to a level that was manageable but which still allowed any trends in the MDS ordination plots to be readily identified. Therefore, samples for each size class of *A. aranciacus* in each season were first randomly sorted into groups of three to five, depending on the total number of sea stars in the samples (Platell and Potter 2001; Lek et al. 2011). The composition of the different dietary categories in each group comprising the various size classes and seasons was then averaged. Dietary data of *A. platyacanthus* and *A. irregularis pentacanthus* did not need any grouping as the number of stomachs analysed was much lower (31 and 22, respectively). The resultant abundances were log-transformed to avoid any tendency for the main dietary components to be excessively dominant. Similarities between samples were calculated using the Bray–Curtis similarity coefficient. An MDS was applied to the combined dietary results of the sea star species to analyse possible resource partitioning between them. ANOSIM was used to test whether the dietary samples of each species were significantly different from other species. Similarity percentages (SIMPER) were used to define the dietary categories that typified each particular group and contributed to the dissimilarities between the different groups (Clarke and Gorley 2006).

Seasonal and size class variations in the diet of each sea star species were also analysed by MDS. Sea stars were divided into several size categories to assess size-related changes in food habits. *A. aranciacus* was classified into six different size classes: SC1 between 20 and 39 mm ($n = 15$), SC2 between 40 and 59 mm ($n = 44$), SC3 between 60 and 79 mm ($n = 27$), SC4 between 80 and 99 mm ($n = 29$), SC5 between 100 and 119 mm ($n = 15$)

and SC6 greater than 120 mm ($n = 6$). *A. irregularis pentacanthus* was classified into three different size classes: SC1 between 20 and 39 mm ($n = 10$), SC2 between 40 and 59 mm ($n = 9$), SC3 between 60 and 79 mm ($n = 3$). *A. platyacanthus* was classified into four different size classes: SC1 between 20 and 39 mm ($n = 13$), SC2 between 40 and 59 mm ($n = 8$), SC3 between 60 and 79 mm ($n = 8$) and SC5-6 greater than 100 mm ($n = 2$). The feeding components of the three asteroids were also grouped by season: spring (March–May 2010), summer (June–August 2010), autumn (September–November 2010) and winter (December 2010–February 2011). ANOSIM tests were applied to identify significant differences among size class and season. SIMPER was applied to identify those prey items that contributed most to the characterization of each main group. All the analyses were performed using PRIMER v6 software (Clarke and Gorley 2006).

Variation in the ontogenetic patterns of prey size use

Regression analysis was used to analyse interspecific variability and changes in prey size use in relation to ontogeny. Scatter diagrams (prey size vs predator size) were plotted, and least-square regressions were generated for each sea star species versus the two major groups of prey (gastropods and bivalves) in order to estimate their relationships (StataCorp. 1999). To determine changes in minimum and maximum prey size with increasing predator size, the upper and lower limits of each scatter diagram were analysed with quantile regression procedures (Scharf et al. 1998; Cade et al. 1999). The range between the 90th and 99th quantiles was used to determine the upper and lower bounds. Correlation analyses were carried out between maximum, minimum and mean prey size slope estimates to analyse whether increases in the mean prey size were a result of changes in the minimum or maximum prey size (Scharf et al. 2000). Analysis of covariance (ANCOVA) was used to test differences between slopes of the regression equations in order to analyse interspecific prey size use. Previously, $\text{Log}_{(x+1)}$ transformation of data was performed to achieve normality and homoscedasticity.

Diet overlap

The degree of overlap in the diets of the three sea stars species in relation to seasons was evaluated using Morisita's index (Morisita 1959; Horn 1966), which is defined as:

$$C_{\lambda} = \frac{2 \sum_{i=1}^{S} P_{A,i} x P_{B,i}}{\sum_{i=1}^{S} P_{A,i}^{2} + \sum_{i=1}^{S} P_{B,i}^{2}}$$

where C_{λ} is the Morisita-Horn index of overlap between predator species A and B; S the total number of identified

prey items in the feeding regime of both predators; $P_{A,i}$ is the proportion prey i makes up of the total prey consumed by predator A; and $P_{B,i}$ is the proportion prey i makes up of the total prey consumed by predator B. The possible values of C_{λ} range from 0, when no prey is shared, to 1, when the diets are identical.

Feeding strategy

Feeding strategy, prey importance and inter- and intra-individual components of niche breadth were also analysed using a modification of the traditional Costello graphical method proposed by Amundsen et al. (1996). A two-dimensional representation is obtained by plotting the prey-specific abundance of prey i (P_i), defined as the percentage a prey taxon makes up of all the prey items in only those predators in which that particular prey item has been found, against the frequency of occurrence. The prey-specific abundance (P_i) is mathematically expressed as:

$$P_i = (\Sigma S_i)/(\Sigma S_{ti}) * 100$$

where S_i is the stomach content (number) composed of prey i and S_{ti} the total stomach content in only those predators with prey i in their stomachs (Amundsen et al. 1996).

The diagram can be interpreted by examining the distribution of points along the diagonals and axes of the graph. The importance of the prey is represented on the diagonal from the lower left (rare prey) to the upper right (dominant prey). The vertical axis represents the feeding strategy of the predator in terms of specialization or generalization. The prey positioned in the upper part of the graph is prey on which the predator has specialized, whereas prey positioned in the lower part is only eaten occasionally (generalization). Prey points located in the upper left part of the diagram are indicative of specialization by individual predators, and those in the upper right part represent specialization of the entire predator population. Finally, in terms of niche breadth, it is possible to envision a population with a high between-phenotype component, as different individuals specialize on different resource types, as well as a high within-population component, as most of the individuals use many resource types simultaneously. Both phenotype components can be observed in the diagram. Prey with a high specific abundance and low occurrence (upper left) were consumed by a few individuals displaying specialization, whereas prey with a low abundance and high occurrence (lower right) were eaten occasionally by most individuals.

Prey selection

The Ivlev's electivity index (Ivlev 1961), commonly used in the literature, was chosen to assess prey selection:

$$E_i = \%A - P_i/\%A + P_i$$

where %A is the relative proportion of preys eaten and P_i is the relative proportion of preys available in the environment. $E_i = -1$ corresponds to total avoidance, $E_i = 0$ represents nonselective feeding and $E_i = 1$ shows exclusive feeding on a given prey item.

Results

The number of sea stars analysed per species and basic information about the percentage of stomachs containing prey items, predator length (range and mean) and prey number (range and mean/predator) are given in Table 1. Although all the specimens captured were analysed, far fewer individuals of *A. irregularis pentacanthus* and *A. platyacanthus* were examined than *A. aranciacus* due to their lower density in the studied site. *A. platyacanthus* is more voracious, as it had a mean number of 70 prey items in each stomach compared to 25 in *A. aranciacus* and 13 in *A. irregularis pentacanthus*.

The studied sea stars show a mollusc-dominated diet (specifically, bivalves and gastropods) and a wide feeding spectrum inside this group. The presence of other zoological groups (sea urchins, crustaceans, polychaetes, fish and sea squirts) are extremely low (Table 2) and when they are present, appear in low abundance. A total of 61 molluscan species were found in *A. aranciacus* stomachs (31 gastropods, 29 bivalves and 1 scaphopod), 38 species were found in *A. irregularis pentacanthus* (20 gastropods and 18 bivalves) and 46 species were found in *A. platyacanthus* (23 gastropods and 23 bivalves).

Diet composition analysis

An overall MDS showed three well-defined groups, separated by species (Fig. 2a). The dietary samples of *A. aranciacus* formed a well-defined group on the upper side of the plot, and the *A. platyacanthus* samples formed a second group on the bottom left. The dietary samples of *A. irregularis pentacanthus* formed a third group on the right site of the plot. ANOSIM demonstrated that the diet of the three *Astropecten* species differed significantly between them ($p < 0.01$; global $R = 0.633$). The R statistic values for the pairwise comparisons between species were high for *A. aranciacus* versus *A. irregularis pentacanthus* ($R = 0.725$; $p < 0.01$), and also for *A. aranciacus* versus *A. platyacanthus* ($R = 0.625$; $p < 0.01$), but they were slightly lower for *A. platyacanthus* versus *A. irregularis pentacanthus* ($R = 0.561$; $p < 0.01$). A SIMPER analysis showed the importance in the diet of *A. aranciacus* of the bivalves' *Glycymeris glycymeris* and *C. chione* and the gastropods *C. neritea* and *G. guttadauri* that together account for 75.25 % of the prey abundance. The bivalves *Goodallia triangularis* and *C. chione* and the gastropods and *C. neritea* account for % of the preys abundance in the diet of *A. platyacanthus*, while in the diet of *A. irregularis pentacanthus* the gastropods *C. neritea* and *Nassarius pygmaeus* account for 65.81 % of the prey abundance.

An MDS performed separately for each sea star species (Fig. 2b–d) indicated a grouping of samples by season. The two-way ANOSIM showed significant differences between seasons in the dietary compositions ($p < 0.001$; global $R = 0.66$ in A. *aranciacus*, global $R = 0.97$ in A. *platyacanthus* and global $R = 0.92$ in A. *irregularis pentacanthus*). No significant differences were found between size classes ($p < 0.05$). In the case of *A. aranciacus*, significant differences ($p < 0.05$) were found between all seasons except among spring versus winter ($p < 0.1$). SIMPER showed that both bivalves *G. glycymeris* and *C. chione* dominated *A. aranciacus* stomachs in spring and winter (49 and 48 % diet contribution, respectively); the gastropods *G. guttadauri* and *N. pygmaeus* dominated in autumn (58 % contribution), and the bivalves *G. glycymeris* and *Corbula gibba* in summer (46 % contribution). In *A. platyacanthus* differences were found between all seasons ($p < 0.05$) except summer versus spring and summer versus autumn ($p < 0.1$). SIMPER showed that *G. triangularis* represented a diet contribution of 40 % in summer and

Table 1 Information on the sea stars and stomachs analysed

	A. aranciacus	A. irregularis p.	A.platyacanthus
Individuals analysed	132	26	31
Individuals with prey in the stomach	127 (96.21 %)	22 (84.62 %)	31 (100 %)
Length range (R, mm)	24.95–154	23.44–63.64	22.01–171
Mean length (R, mm)	70.04	41.148	52.369
Std. error	2.497	2.237	5.335
Prey item range (N)	0–112	0–74	15–173
Mean number of prey items × ind.	25.038	12.955	69.968
Std. Error	1.832	3.459	6.856

Table 2 Diet composition to the lowest possible taxon of three sea star species from the Maresme coast (northwestern Mediterranean)

	A. aranciacus	*A. irregularis p.*	*A. platyacanthus*
Phylum Mollusca			
Class Gastropoda			
Family Trochidae			
Gibbula guttadauri	X	X	X
Gibbula magus	X	0	0
Gibbula philberti	X	X	X
Phorcus richardi	X	0	0
Gibbula umbilicalis	X	X	0
Gibbula varia	X	0	X
Family Cerithiidae			
Bittium submamillatum	0	0	X
Cerithium vulgatum	X	0	X
Bittium latreillii	X	X	X
Bittium reticulatum	X	X	X
Cerithium vulgatum	X	0	X
Family Turritellidae			
Turritella communis	X	0	X
Family Rissoidae			
Pusillina inconspicua	X	X	X
Obtusella intersecta	X	X	X
Family Caecidae			
Caecum auriculatum	X	0	0
Caecum trachea	X	0	X
Caecum subannulatum	X	X	0
Family Tornidae			
Circulus striatus	0	0	X
Family Calyptraeidae			
Calyptraea chinensis	X	X	X
Family Naticidae			
Natica dillwynii	X	0	X
Natica hebraea	X	X	X
Euspira pulchella	X	X	X
Family Nassariidae			
Nassarius incrassatus	X	0	0
Nassarius pygmaeus	X	X	X
Nassarius reticulatus	X	0	0
Cyclope neritea	X	X	X
Family Mangeliidae			
Bela nebula	X	X	0
Mangelia costulata	X	X	0
Mangelia tenuicostata	X	0	0
Family Ocenebrinae			
Ocinebrina edwardsii	X	0	0
Family Turridae			
Haedropleura septangularis	X	X	0
Family Architectonicidae			
Heliacus fallaciosus	X	0	0
Family Murchisonellidae			
Ebala pointeli	0	X	X
Family Pyramidellidae			
Odostomia angusta	X	X	X
Odostomia turriculata	X	0	X

Table 2 continued

	A. aranciacus	A. irregularis p.	A. platyacanthus
Family Retusidae			
Retusa mammillata	X	X	X
Family Philinidae			
Philine aperta	X	0	0
Class Bivalvia			
Family Corbulidae			
Corbula gibba	X	X	X
Family Mytilidae			
Crenella arenaria	0	0	X
Modiolula phaseolina	X	0	0
Modiolus adriaticus	X	X	X
Mytilus galloprovincialis	0	X	0
Family Limidae			
Limatula subauriculata	X	X	0
Family Montacutidae			
Kurtiella bidentata	X	0	X
Family Cardiidae			
Acanthocardia paucicostata	X	0	0
Acanthocardia tuberculata	X	0	0
Laevicarvium crassum	X	0	X
Parvicardium scabrum	X	X	X
Parvicardium scriptum	X	X	X
Plagiocardium papillosum	X	X	X
Family Mactridae			
Mactra glauca	X	0	X
Spisula subtruncata	X	0	X
Family Tellinidae			
Arcopagia crassa	0	0	X
Tellina pygmaea	X	X	0
Tellina sp I.	X	X	0
Tellina sp II.	X	X	0
Family Donacidae			
Donax variegatus	X	X	X
Family Psammobiidae			
Gari costulata	X	0	X
Family Veneridae			
Callista chione	X	0	X
Clausinella fasciata	X	X	X
Chamelea gallina	0	0	X
Dosinia exoleta	X	X	X
Dosinia lupinus	X	X	X
Gouldia minima	X	X	X
Paphia aurea	X	X	X
Pitar rudis	X	X	X
Timoclea ovata	X	0	0
Family Lasaeidae			
Hemilepton nitidum	X	0	0
Family Mesodesmatidae			
Donacilla cornea	0	0	X
Family Astartidae			
Goodallia triangularis	X	X	X

Table 2 continued

	A. aranciacus	A. irregularis p.		A. platyacanthus
Class Scaphopoda				
Family Dentaliidae				
Antalis vulgaris	X	0		0
Phyllum Echinodermata				
Class Echinoidea				
Family Echinocyamidae				
Echinocyamus pusillus	X	0		X
Family Loveniidae				
Echinocardium sp.	X	0		X
Family Parechinidae				
Psammechinus microtuberculatus	X	0		0
Phyllum Arthropoda				
Class Malacostraca				
Family Leucosiidae				
Ilia nucleus	X	0		0
Family Parthenopidae				
Parthenope sp.	X	0		0
Family Diogenidae				
Diogenes pugilator	X	0		0
Family Gammaridae				
Gammaridae I	X	0		0
Phylum Annelida				
Class Polychaeta				
Family Eunicidae				
Eunicidae I	X	X		X
Family Polynoidae				
Eunoe sp.	X	0		0
Family Lumbrineridae				
Lumbrineris sp.	X	0		0
Family Oweniidae				
Oweniidae I	X	0		X
Family Onuphidae				
Hyalinoecia tubicola	X	0		0
Phyllum Chordata				
Class Osteichthyes				
Fish I	X	0		0
Fish II	0	0	X	X
Fish III	0	X	0	0
Fish IV	0	X	0	0
Class Ascidiacea				
Family Ascidiidae				
Ascidia sp.	X	0	0	0

87 % in autumn, while *C. chione* and *G. glycymeris* dominated the diet in winter (67 %) and *Retusa mammillata* (20 %) in spring. In the case of *A. irregularis pentacanthus*, significant differences were only found among autumn and the rest of the seasons. The gastropod *N. pygmaeus* constituted the 96.37 % of its diet in autumn, while in the rest of the seasons, the diet is more diverse, that is, *C. neritea* dominated in winter (30 %) and spring (76 %), and *Caecum trachea* dominated in summer (33 %).

Variation in ontogenetic patterns of prey size use

The size of the prey eaten increased significantly with increasing predator length (R) for *A. aranciacus*, *A. platyacanthus* and *A. irregularis pentacanthus* (Fig. 3a–f). In addition, as the size of the predators increased, the increase in minimum prey sizes was only significant for bivalves and gastropods in *A. aranciacus* and only for bivalves in *A. platyacanthus*. Asymmetric predator size–
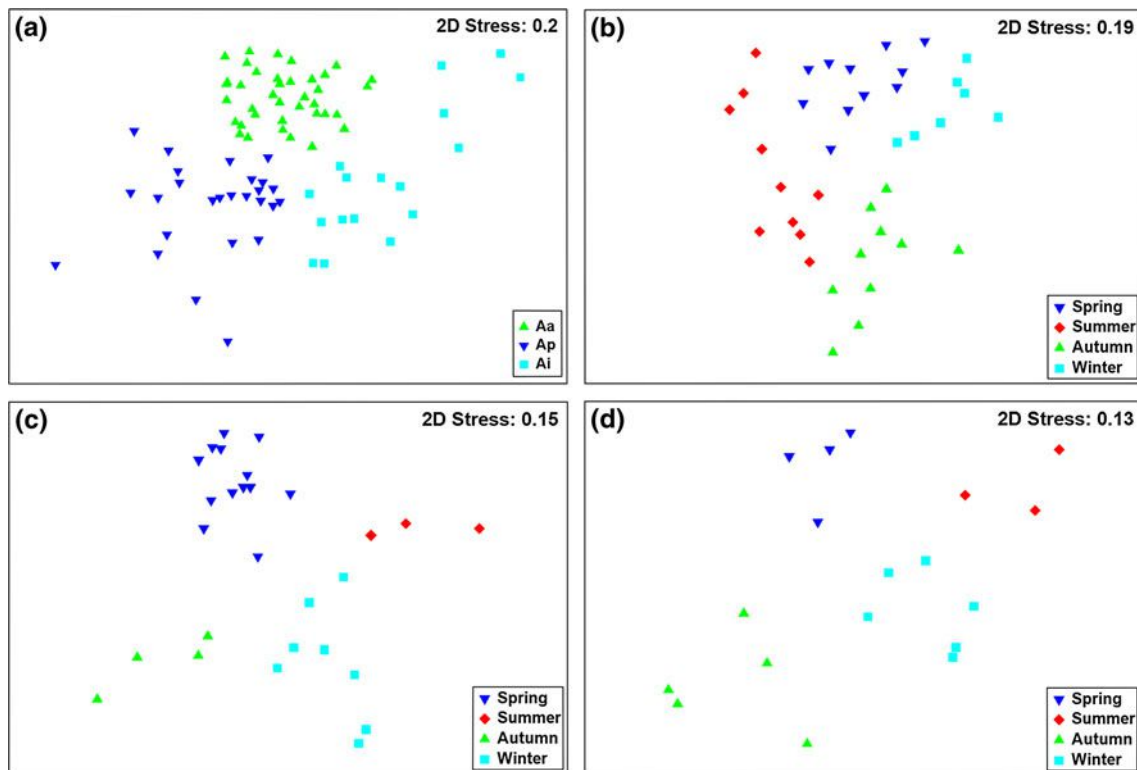
Fig. 2 Non-metric multidimensional scaling ordination of dietary samples performed on **a** the three sea star species; **b** *A. aranciacus*, **c** *A. platyacanthus* and **d** *A. irregularis pentacanthus*. Symbols indicate **a** *Aa* for *A. aranciacus*, *Ap* for *A. platyacanthus* and *Ai* for *A.* *irregularis pentacanthus* and **b**, **c**, **d** *spring* (March–May 2010), *summer* (June–August 2010), *autumn* (September–November 2010) and *winter* (December 2010–February 2011)

prey size distributions were frequently observed because small preys were part of the diet of the entire range of predator body sizes. Upper-bound slopes of predators ranged from 0.007 to 0.1121, while lower-bound slopes showed higher interspecific variation, ranging from 0.001 to 0.0258.

There was a positive correlation between the slopes of the upper bound and the slopes of the mean for all three sea star species analysed ($p < 0.001$), and also between the significant lower bound and the mean ($p < 0.001$) that means that in *A. aranciacus* and *A. platyacanthus* ontogenetic changes in mean prey sizes eaten were driven by changes in maximum and minimum prey sizes consumed, whereas in *A. irregularis* were driven primarily by changes in maximum prey sizes consumed.

Significant differences in the slope of the regression equations were detected between the three star species. In the case of gastropods, the "*b*" value was higher for *A. irregularis*, followed by *A. aranciacus* and *A. platyacanthus* (ANCOVA, $F_{(2,20)} = 50.49$, $p < 0.0001$). In the case of bivalves, the "*b*" value was higher for *A. aranciacus*, followed by *A. irregularis* and *A. platyacanthus* (ANCOVA, $F_{(2,20)} = 191.5$, $p < 0.0001$).

Diet overlap

Considering the data from the entire year, the diet overlap was low between all species, with Morisita's index values ranging from 0.13 to 0.34 (Table 3). Focusing on seasonal data, a high diet overlap was observed in winter among *A. aranciacus* and *A. platyacanthus* ($C_\lambda = 0.85$), and a medium diet overlap among *A. aranciacus* and *A. irregularis* ($C_\lambda = 0.53$).

Feeding strategy

The feeding strategy plots (Fig. 4a) of the main components of the diets of all sea star species between March 2010 and February 2011 showed that most of the prey points are located in the lower part of the graph, attaining a low prey-specific abundance. Consequently, the three species can be considered generalist feeders, with some differences between them. The sea star *A. aranciacus* showed varying degrees of specialization and generalization on different prey types (Fig. 4b). The gastropod *G. guttadauri* and the bivalves *G. glycymeris* and *C. chione* were its dominant prey, making a high contribution to the stomach contents (>22 %) and also occurring frequently.

(a) Aa vs. Gas
$Y_{95th} = 0.0940PD + 2.178$
$Y_{MEAN} = 0.0479PD + 0.991$
$Y_{05th} = 0.0192PD + 0.324$
N = 1742

(b) Aa vs. Biv
$Y_{95th} = 0.0070PD + 7.885$
$Y_{MEAN} = 0.0040PD + 3.372$
$Y_{05th} = 0.0227PD + 0.748$
N = 1506

(c) Ap vs. Gas
$Y_{99th} = 0.0563PD + 9.720$
$Y_{MEAN} = 0.0516PD + 0.633$
$Y_{01th} = 0.0227PD + 0.748^*$
N = 974

(d) Ap vs. Biv
$Y_{90th} = 0.0824PD + 1.870$
$Y_{MEAN} = 0.0040PD + 1.129$
$Y_{10th} = 0.0163PD + 0.816$
N = 1133

(e) Ai vs. Gas
$Y_{90th} = 0.0916PD + 2.343$
$Y_{MEAN} = 0.0760PD + 0.832$
$Y_{10th} = 0.0258PD + 0.662^*$
N = 215

(f) Ai vs. Biv
$Y_{90th} = 0.1121PD + 2.084$
$Y_{MEAN} = 0.0040PD + 1.904$
$Y_{10th} = 0.0057PD + 1.225^*$
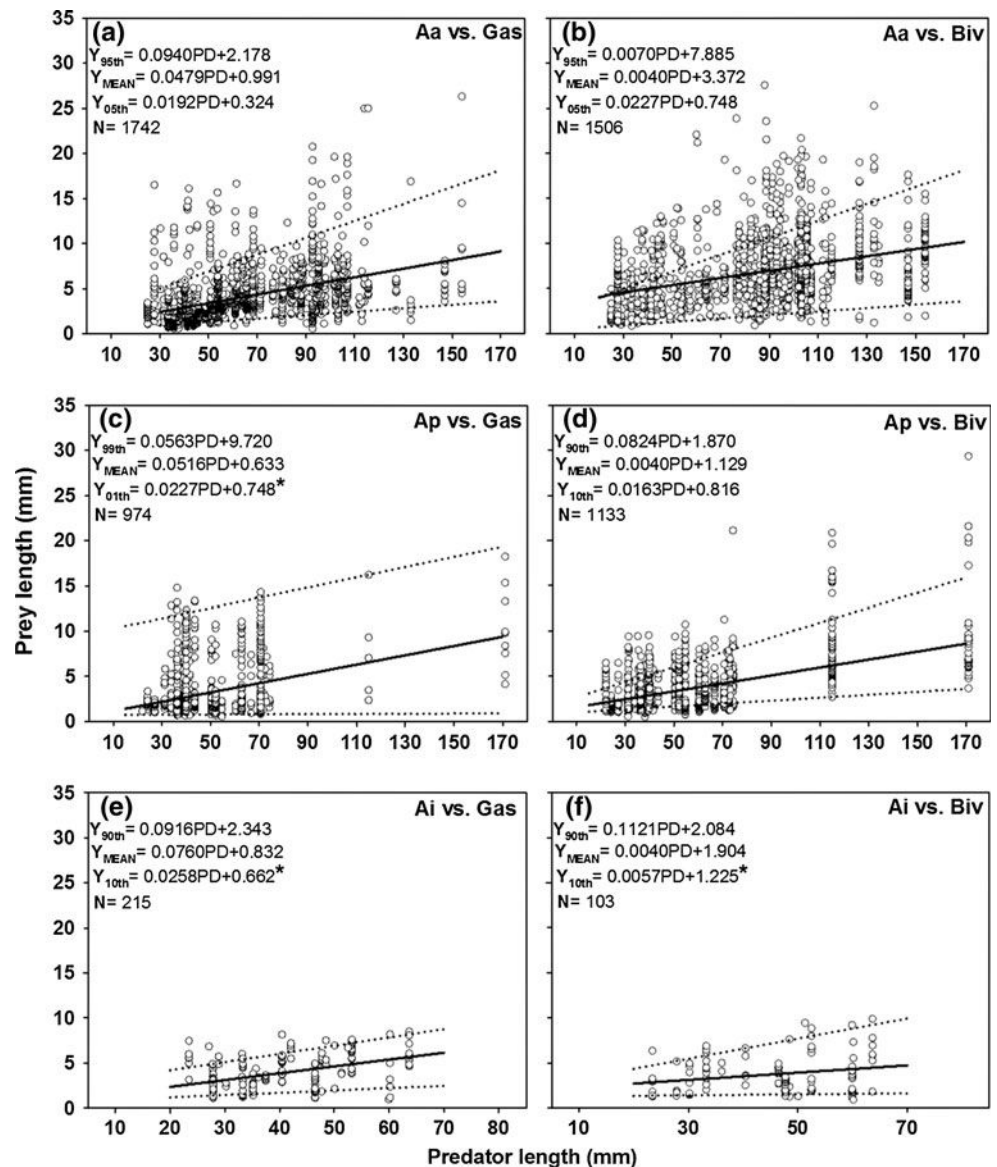N = 103

Prey length (mm) — Predator length (mm)

Table 3 Morisita-Horn index of overlap (C_λ) between seasons for *A. aranciacus*, *A. irregularis* and *A. platyacanthus*

Pairs compared	N_1	N_2	All year data	Spring	Summer	Autumn	Winter
Aa–Ai	127	22	0.13	0.18	0.35	0.05	0.57
Aa–Ap	127	31	0.34	0.33	0.15	0.01	0.85
Ai–Ap	22	31	0.15	0.25	0.20	0.01	0.10

Seasons: spring (March–May 10), summer (June–August 10), autumn (September–November 10) and winter (December 10–February 11)

N_1 and N_2 = Number of sea stars of each species analysed

A lot of other species appear in small proportions, indicating that they are rare or less frequent prey (low frequency and abundance) and thus only consumed occasionally. The diet of *A. irregularis pentacanthus* showed some specialization on *C. neritea*, as it is the only prey point positioned in the upper right part of the graph and to a lesser extent on *N. pygmaeus*. Most individuals of this sea star fed on these dominant prey taxon, but other prey types were also frequent and abundant (Fig. 4c). Isolated individuals of *A. irregularis pentacanthus* specialized on other gastropods, such as *C. trachea*. *A. platyacanthus* is the species that showed more generalist diet; the most important prey taxa, like *G. triangularis* and *R. mamillata*, had been eaten by more than half of the sea stars but their contribution to the stomach content was low (<20 %), that is, most individuals used many prey types simultaneously (Fig. 4d).

In terms of the niche width contribution, the location of most of the prey indicates that the within-phenotype component in the utilization of food resources is larger than the between-phenotype component.
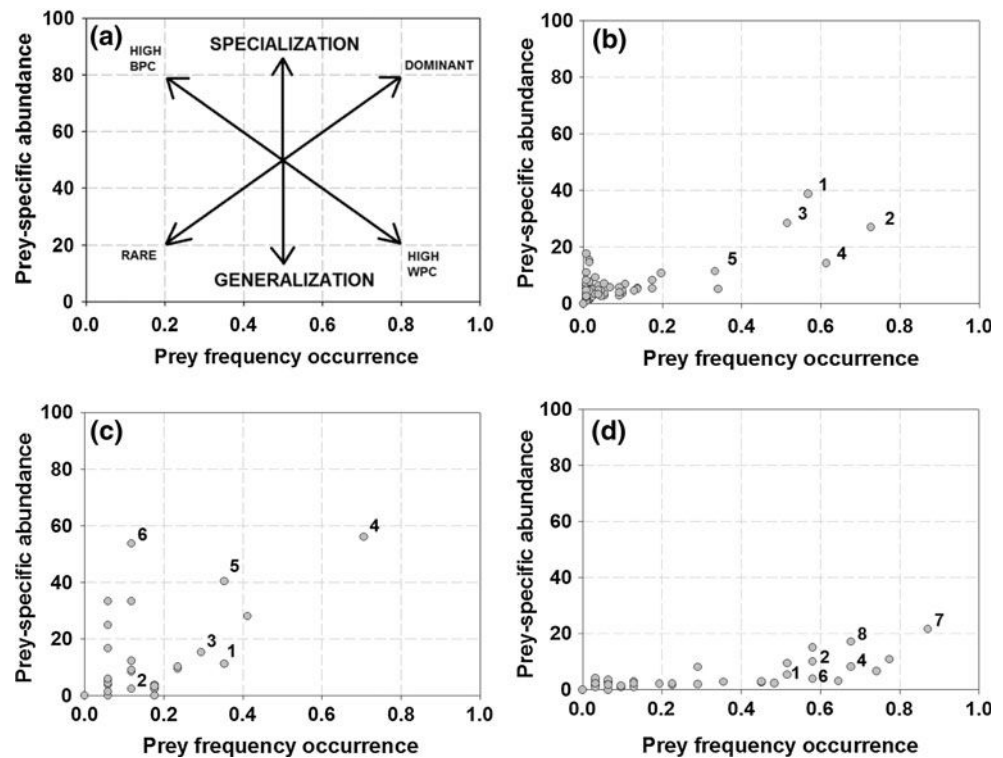
Prey selection

The infaunal community co-occurring with the sea stars was numerically composed by polychaetes (87.46 %), isopods (5.68 %), amphipods (0.59 %), decapods (0.10 %), ophiuroids (0.40 %), echinoids (2.02 %), ascidians (0.94 %) and molluscs (0.15 %). However, sea stars ignored most of these faunistic groups and concentrated its predation on gastropods and bivalves (Table 4). The most abundant molluscs species in the sediment were the bivalve *G. triangularis* and the gastropod *C. trachea* in the 4 months studied. With the exception of *A. platyacanthus*, the other two sea star species studied did not show any preference for *G. triangularis* (E_i values near zero) and most individuals avoided *C. trachea* as prey. The smooth clam *C. chione* and the nasariid *C. neritea* were positively selected by the three sea star species. Nevertheless, *G. glycymeris* was positively selected by *A. aranciacus* and *A. platyacanthus*, but totally avoided by *A. irregularis pentacanthus*. The gastropods *R. mamillata* and *Bittium reticulatum* were relatively abundant in the sediment, but they were not selected or even avoided by the three sea star species.

Astropecten aranciacus exhibited highest prey preference (by decreasing electivity value) for *G. glycymeris*, *C. neritea*, *C. chione* and *Natica haebrea*; *A. irregularis pentacanthus* for *C. neritea*, *Pitar rudis*, *N. pygmaeus*, *C. gibba* and *C. chione*; and *A. platyacanthus* showed a preference for *C. neritea*, *C. chione*, *G. triangularis*, *G.*

glycymeris and *Dosinia exoleta*. It is to point out that most of these species that the three sea stars studied preferred to ingest were not abundant or were even rare in the sediment (Table 4).

Discussion

The diet of the three sea star species that inhabits on shallow bottoms of the northwestern Mediterranean Sea was mainly based on bivalves and gastropods, although they were not the dominant infaunal taxa. The bivalves *G. glycymeris* and *C. chione,* together with the gastropod *C. neritea,* predominated in the stomachs of *A. aranciacus.* The bivalves *G. triangularis* and *C. chione* were abundant in *A. platyacanthus* stomachs, while the gastropods *C. neritea* and *N. pygmaeus* were common in the diet of *A. irregularis pentacanthus*. All these preys were not the most abundant molluscs in the environment. The selectivity index indicated little or no selection for the most abundant prey species, whereas some rare preys were strongly selected. The diet of *Astropecten* species has attracted attention since the end of the nineteenth century, specially related to *A. irregularis pentacanthus* (Power 1857; Eichelbaum 1910; Hunt 1925; Kisch 1958). In the Mediterranean Sea, Giribet and Peñas (1997) reported a total of 118 mollusc species in the stomach contents of *A. irregularis* and *A. aranciacus* collected in south Barcelona. The dominant gastropod was *Alvania*

Table 4 Preys available in the environment (mean no. m^{-2}), prey numerical abundance in the stomachs (%A) and Ivlev's electivity index (E_i) by month for *A. aranciacus*, *A. irregularis pentacanthus* and *A. platyacanthus*

Prey	Density (no. m^{-2})					p_i	%A			Ivlev's electivity (E_i)		
	Mar	Jun	Oct	Dec	Mean		Aa	Ai	Ap	Aa	Ai	Ap
Callista chione	6	2	2	2	3	0.30	22.61	3.85	3.21	0.97	0.86	0.83
Glycymeris glycymeris	2	2	2	1	2	0.19	37.42	0.00	1.33	0.99	−1.00	0.75
Goodallia triangularis	141	159	53	23	94	9.15	6.05	7.69	78.86	−0.20	−0.09	0.79
Corbula gibba	3	6	1	1	3	0.27	2.55	19.23	1.41	0.81	0.97	0.68
Donax variegatus	9	9	7	2	7	0.64	1.75	3.85	0.23	0.46	0.71	−0.46
Parvicardium scriptum	0	8	0	1	2	0.21	0.00	0.00	0.08	−1.00	−1.00	−0.46
Dosinia exoleta	4	0	0	1	1	0.13	1.67	0.00	0.78	0.85	−1.00	0.71
Pitar rudis	0	1	0	0	0	0.03	0.00	3.85	0.00	−1.00	0.99	−1.00
Modiolus adriaticus	2	17	2	1	6	0.54	0.96	0.00	0.63	0.28	−1.00	0.08
Minority bivalve species	53	150	116	85	101	9.82	7.96	11.54	3.21	−0.10	0.08	−0.51
Total bivalvia	271	753	183	117	219	21.28	80.97	50.00	89.74	0.58	0.40	0.62
Gibbula guttadauri	0	0	1	4	1	0.12	1.04	0.00	0.55	0.79	−1.00	0.63
Cyclope neritea	1	0	0	1	1	0.05	5.33	26.92	1.41	0.98	1.00	0.93
Nassarius pygmaeus	1	1	0	1	1	0.08	1.59	7.69	0.16	0.91	0.98	0.33
Natica haebrea	0	0	1	2	1	0.08	2.63	0.00	0.31	0.94	−1.00	0.61
Cerithium vulgatum	1	3	0	0	1	0.11	0.48	0.00	0.31	0.63	−1.00	0.49
Retusa mammillata	37	31	2	3	18	1.78	0.32	0.00	4.15	−0.70	−1.00	0.40
Bittium reticulatum	42	1	14	2	15	1.45	0.32	7.69	0.47	−0.64	0.68	−0.51
Caecum trachea	423	298	253	42	254	24.72	0.88	0.00	1.02	−0.93	−1.00	−0.92
Minority gastropod sp.	16	13	11	5	11	1.09	2.31	7.69	0.63	0.36	0.75	−0.27
Total gastropoda	521	468	283	60	303	29.48	18.39	50.00	10.57	−0.23	0.26	−0.47
Other taxa	413	482	799	332	507	49.28	2.39	0	0.47	−0.91	−1.00	−0.98
Total	1206	1703	1265	509	1028	100	100	100	100			

testae, and the dominant bivalve was *Timoclea ovata*. Regarding *A. aranciacus*, Ribi et al. (1977) studied its diet on the coast of Sardinia, on sandy sediment bottoms at 8 m depth (very similar conditions to our study area), and found a preference for the sea urchin *Echinocardium mediterraneum*, which represented 56.3 % of the stomach content, compared to molluscs, which represented 50.1 %. There were ten species of prey molluscs, and the most abundant was the bivalve *Chamelea gallina* (27.1 %). Sierra et al. (1978) studied the diet of three *Astropecten* species collected in Almeria between 6 and 400 m depth and found a preference for gastropods in *A. aranciacus* and *A. platyacanthus*, whereas the preferences of *A. irregularis pentacanthus* varied depending on the sediment type. De Juan et al. (2007) concluded that more than 90 % of the diet of *A. irregularis* inhabiting muddy sediments of the Ebro Delta (NW Mediterranean) between 30 and 80 m depth consisted of three gastropods (*Turritella communis*, *Odostomia sp*, *Hyala vitrea*) and three bivalves (*Corbula gibba*, *Parvicardium minimum* and *T. ovata*), even though these prey species were not abundant in the environment. The existing information indicates that astropectinids are able to exploit the different food resources available in the marine benthic ecosystems where they live.

According to the niche theory, when sympatric species overlap in the use of a shared resource along one dimension, they must differ along another resource to coexist (Hutchinson 1959; MacArthur 1958). Several factors can reduce competitive interactions. Periodical migrations by sea stars have been related to food seeking (Kashenko 2003; Gallagher et al. 2008). Pabst and Vicentini (1978) observed seasonal migrations of *Astropecten jonstoni*, which moved to deeper waters in winter to avoid the impacts of seasonal marine storms and strong waves, returning to shallow waters in spring to escape from *A. aranciacus*. It has also been suggested that segregation on a small spatial scale is important to avoid competition (Menge and Menge 1974; Gaymer et al. 2001a). Ribi et al. (1977) concluded that *A. aranciacus* and *A. bispinosus* in Costa Colostrai (Sardinia, Italy) could coexist because *A. bispinous* was not present on coarse sand, as opposed to *A. aranciacus*. In our study, all samples were caught in a narrow depth stratum (7–12 m), on coarse or medium sand; therefore, the coexistence of the three sea stars cannot be attributed to the granulometry. Another factor that is

considered to favour the coexistence of asteroids is to have different daily activity patterns. Ribi and Jost (1978) showed that *Astropecten aranciacus, A. bispinosus* and *A. jonstoni* have different peaks of daily activity, but this kind of information does not exist for *A. platyacanthus* and *A. irregularis pentacanthus*. In accordance with the concept of niche complementarity, coexisting species often display different food needs or feeding habits (Schoener 1974; Garneau et al. 2007). Partition of prey by species or size has often been suggested to be a mechanism for reducing competition between coexisting species (Menge and Menge 1974; Schoener 1982; Arrontes and Underwood 1991). In the shallow bottoms here studied, the diet composition of coexisting asteroids was significantly different between species, with little food overlap. These results suggest that the contrasting feeding strategy of the sea stars results in the use of sufficiently different resources to avoid competition. The clear preference of *A. irregularis pentacanthus* for gastropods over bivalves indicates that *A. irregularis pentacanthus* does not compete with the other two sea star species for the available resources. The only exceptional value reflecting high diet overlap for *A. aranciacus* and *A. platyacanthus* in winter could be related to the lowest densities of preferred preys observed in the benthos during December. According to SIMPER results, both sea star species fed heavily on *C. chione* and *G. glycymeris* during winter. However, during the other seasons, *A. platyacanthus* preyed on *G. triangularis* and *R. mamillata*, which were not selected by *A. aranciacus*.

An intraspecific analysis of the prey species that constitutes the diet of the sea stars here studied has shown changes throughout the year, but no differences between size classes. Seasonal changes could be related to annual feeding cycles, which have been reported previously in other asteroid species (Brun 1972; Christensen 1970), and attributed to variations in exogenous (temperature, prey availability and prey energy value) and endogenous factors (reproductive state, physiological status and handling cost) (Jangoux 1982; McClintock and Lawrence 1985; Beddingfield and McClintock 1993; Micheli 1995; Gaymer et al. 2001a, b). Our results showed that these seasonal changes in the diet can affect food overlap, as it was the case for *A. aranciacus* and *A. platyacanthus* in winter.

We reported for the first time interspecific variation in the ontogenetic patterns of prey size consumption for the three astropectinids. The mean and maximum size of the prey items (gastropods and bivalves) increased as the predator grew, although small preys were eaten by all the sea star sizes. Therefore, the range of its potential prey items becomes wider as the sea star increases in size. This behaviour may be related to factors linked to optimizing the energetic intake, such as the time needed for capturing and consuming each prey and the energetic value of the

prey (Gaymer et al. 2001b). It is possible that larger sea stars would try to maximize the energy intake by increasing the consumption of larger preys. In addition, *A. aranciacus* (preying on gastropods and bivalves) and *A. platyacanthus* (preying on bivalves) showed a significant increase in the minimum prey size consumed. *A. platyacanthus* did not increase the lower limit of the gastropod prey items. This behaviour did not occur with bivalve prey items perhaps as a consequence of the morphological differences between the two groups or their different energetic values, which could lead to small gastropods being included in the sea star diets and bivalves of the same size being excluded. Finally, *A. irregularis pentacanthus* did not increase the lower limit of either of the prey items categories.

Astropecten aranciacus showed a high dietary diversity in the studied area, with a total of 73 different prey species in the stomachs, compared to *A. irregularis pentacanthus,* which preyed on 32 species, and to previous information found for other areas (Ribi et al. 1977; Ribi and Jost 1978, Giribet and Peñas 1997). *A. platyacanthus* was the most voracious species judging by the elevated number of preys in its stomach. Two main feeding strategies (mixed and generalist) have been detected in this study. *A. aranciacus* and *A. platyacanthus* populations had a relatively high within-phenotype contribution to niche width. The most important prey taxa had been eaten by more than half of the sea stars, but their average contribution to the stomach contents of these sea stars was low, indicating a generalized feeding strategy, especially in *A. platyacanthus*. In contrast, *A. irregularis pentacanthus* showed a mixed feeding strategy, with varying degrees of specialization and generalization on different prey types. Most individuals had been feeding on the dominant prey taxon (*C. neritea*) but also other important prey (*N. pygmaeus, C. trachea*) was included occasionally in the diet of some individuals.

Asteroids may play a major role in structuring bivalve populations in soft-sediment habitats (e.g. Christensen 1970; Anger et al. 1977). In benthic communities where *Astropecten* species are common, seasonal changes in the abundance of these predators can have a profound influence on the population structure and density of many of the infaunal invertebrates on which they prey (Christensen 1970; Massé 1975; Morin et al. 1985; Freeman et al. 2001). In the study area, the smooth shell clam *C. chione* is targeted by an artisanal fishery. The importance of this commercially exploited bivalve as a prey varied for the different paxillosid sea stars studied. It was common in the diets of both *A. aranciacus* and *A. platyacanthus,* but it was not relevant in the diet of *A. irregularis pentacanthus*. The composition of the stomach contents does not necessarily reflect the relative amounts of prey eaten because the time needed for digestion differs between prey species (Christensen 1970). For instance, bivalves such us *C. gallina* are

retained in *A. aranciacus* for an average of 12 days (Massé 1975), whereas other species, like *S. subtruncata*, are retained for less than 2 days (Christensen 1970). There are no data in the literature on the retention time for the smooth clam *C. chione* neither on the number of spat that can pick up and digest within 24 h. Therefore, our preliminary estimations of the impact on the bivalve beds can only be based on our knowledge of the average number of *C. chione* in stomachs and the sea star density. An average of five *C. chione* per stomach was found in *A. aranciacus* and *A. platyacanthus*. Assuming that this number is their daily consumption rate, it can be estimated that each sea star can eat more than 1500 *C. chione* juveniles during a year. Experimental research needs to be carried out to determine the daily consumption of smooth shell clams as well as the size preferences in order to accurately evaluate the impact of sea stars on the bivalve beds on the Maresme coast.

The coexistence of three species of astropectinids on shallow bottoms of the northwestern Mediterranean Sea can be explained by partition of resources, each sea star preys on different species of bivalves and/or gastropods. This mechanism for reducing interspecific competition is maintained all year round, with the exception of winter, when the availability of preys decreases. Astropectinids can be considered generalist predators as a general rule; their populations are able to specialize and occupy different ecological niches in order to avoid competition and according to local prey spectrum availability.

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7.3. Spatio-temporal changes in Astropecten populations inhabiting soft bottoms of the Maresme coast (northwestern Mediterranean Sea).

Abstract

Sea stars are voracious predators at or near the top of the coastal food chain and variations in their populations can therefore have cascading influences on the ecosystems. *Astropecten* species inhabit soft bottom habitats worldwide, from intertidal areas to the deep sea. Sympatric *Astropecten* species (*A. aranciacus*, *A. irregularis pentacanthus*, *A. platyacanthus A. jonstoni* and *A. spinulosus*) co-occur in the shallow coastal area of the Maresme coast (northwestern Mediterranean Sea). This study analyzes medium-term (between 2004-2006 and 2010-2011) asteroidean population dynamics in an area that has suffered habitat (sediment grain size) and prey abundance shifts as a result of human pressures (sand extractions for beach nourishment and overfishing). Our results revealed changes in *Astropecten* species composition, abundance, spatial distribution and population structure. Moreover, we found that each sea star has specific habitat requirements that allow microhabitat partitioning to avoid competition. Our findings strongly suggest that *Astropecten* species have been affected by human impacts and that *A. aranciacus* is the most vulnerable.

Figures 12 y **13:** Smooth clam catches in the Maresme coast

Resumen

Las estrellas de mar son depredadores voraces que se encuentran en la cúspide de la red trófica o cerca de ella y las variaciones de sus poblaciones pueden tener incidencia sobre el conjunto del ecosistema. Las estrellas de mar del género *Astropecten* habitan los fondos marinos blandos alrededor del mundo, desde la zona intermareal hasta el mar profundo. Distintas especies de este género cohabitan en las aguas costeras y poco profundas de la costa del Maresme (noroeste del Mar Mediterráneo). Este estudio analiza la dinámica de sus poblaciones a medio plazo (entre 2004-2006 y 2010-2011) en una zona que ha sufrido importantes cambios en su hábitat (granulometría del sedimento) y en la abundancia de presas como resultado de presiones humanas (extracción de arenas para la regeneración de playas y sobrepesca). Los resultados muestran cambios en la composición, abundancia, distribución espacial y estructura de las poblaciones de *Astropecten* spp. Por otra parte, las estrellas de mar muestran requerimientos de hábitat específicos que permiten el reparto de microhabitats para evitar la competencia. Los resultados sugieren que las especies de *Astropecten* spp. se han visto afectadas por el impacto humano y que *A. aranciacus* es la especie más vulnerable a dichas presiones.

Participación de los distintos autores

Todos los coautores participaron en la elaboración y corrección del manuscrito.

Trabajo del doctorando

El doctorando ha participado en el diseño experimental de los muestreos, la recogida y posterior análisis de las muestras en el laboratorio, así como el análisis de los datos y la posterior redacción y corrección del manuscrito.

Spatio-temporal changes in sea star populations of the genus *Astropecten* inhabiting soft-bottoms in the northwestern Mediterranean Sea

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Abstract.

Sea stars are voracious predators at or near the top of the coastal food chain and variations in their populations can therefore have cascading influences on the ecosystems. *Astropecten* species inhabit soft bottom habitats worldwide, from intertidal areas to the deep sea. Sympatric *Astropecten* species (*A. aranciacus*, *A. irregularis pentacanthus*, *A. platyacanthus A. jonstoni* and *A. spinulosus*) co-occur in the shallow coastal area of the Maresme coast (northwestern Mediterranean Sea). This study analyzes medium-term (between 2004-2006 and 2010-2011)asteroidean population dynamics in an area that has suffered habitat (sediment grain size) and prey abundance shifts as a result of human pressures (sand extractions for beach nourishment and overfishing). Our results revealed changes in *Astropecten* species composition, abundance, spatial distribution and population structure. Moreover, we found that each sea star has specific habitat requirements that allow microhabitat partitioning to avoid competition. Our findings strongly suggest that*Astropecten* species have been affected by human impacts and that*A. aranciacus* is the most vulnerable.

Additional keywords: spatial distribution**,** starfish, benthos, ecological requirements, anthropogenic impacts.

Running head: Spatio-temporal changes in *Astropecten* spp. populations.

Introduction

Sea stars are studied widely in the fields of paleontology, evolutionary biology, reproduction, development, conservation, genetics, biochemistry and biogeography. They play significant ecological roles and are model organisms for understanding climate change (Lawrence 2013). *Astropecten* is one of the genera with most species among sea stars and its members are distributed worldwide, inhabiting soft-bottom ecosystems from polar to tropical seas and from intertidal areas to the deep sea (Zulliger and Lessios 2010). This genus includes six species in the Mediterranean Sea: *A. aranciacus* (Linnaeus 1758), *A. bispinosus* (Otto 1823), *A. irregularis pentacanthus* (Pennant 1777), *A. platyacanthus* (Philippi 1837), *A. jonstoni* (Delle Chiaje 1827) and *A. spinulosus* (Philippi 1837); the last three are endemic to the Mediterranean. *Astropecten* spp. are voracious predators feeding mainly on mollusks (gastropods and bivalves). They swallow whole preys and have intra-oral digestion (Christensen 1970). Though they were first described as non-selective feeders (Wells *et al.* 1961), some feeding selection and specialization has been observed (Gaymer *et al.* 2001). They have chemoreceptive abilities to distinguish prey quality, choosing preferentially those that have a higher nutrient composition and provide more energy (Beddingfield and McClintock 1993).

Coastal areas are among the most productive and threatened systems in the world, providing important services related to human well-being (Agardy *et al.* 2005). Marine species composition, distribution and abundance have been strongly altered in coastal areas over the last few decades and species occupying high trophic levels have been particularly affected (Menge *et al.* 1994; Jackson *et al.* 2001; Hutchings and Baum 2005). Marine top predators play an essential role in ecosystem health and their decline can initiate trophic cascades, strongly altering marine communities (Heithaus *et al.* 2008). For example, Paine (1969) explained how the zonation of the mussel *Mytilus californianus* rapidly changed after the top predator sea star *Pisaster ochraceus* was removed from the site, thus introducing the keystone species concept. Therefore, as top predators, sea stars can be particularly affected by coastal ecosystem degradation and changes in their population can cause modifications in the ecosystem.

Over the last few decades, a significant decline in coastal bivalve beds has been reported on the Mediterranean coast of Spain (Ramón *et al.* 2005; Baeta *et al.* 2014). The Maresme coast (Catalonia, northwestern Mediterranean Sea) is one of the main shellfish areas in which an artisanal clam fishery was maintained until recently, with the

smooth clam (*Callista chione*) as the target species. The megabenthic community in the area was described by Pubill *et al.* (2011), who reported that, among all bivalves, the commonest and dominant species (in density) was *C. chione*, which was present in about 86% of the samples. The importance of *C. chione* in the diet of its main top predators, three sympatric sea stars species of the genus *Astropecten*, was analyzed by Baeta and Ramón (2013), who found that *C. chione* was positively selected by *A. aranciacus, A. irregularis pentacanthus and A. platyacanthus*. Baeta *et al.* (2014) reported the collapse of the smooth clam fishery in 2006, suggesting that fishing activities and sand dredge extraction were the causes of this collapse. Nevertheless, the consequences of the *C. chione* bed decline on the sea star populations inhabiting the area remain unknown.

The goal of the present study was to provide new insights into medium-term asteroidean population dynamics by examining spatio-temporal changes in five sea star species of the genus *Astropecten* inhabiting the Maresme coast. To accomplish this goal, we analyzed *Astropecten* spp. population composition, abundance, spatial distribution and size structure in two sampling periods, 2004-2006 and 2010-2011. In addition, we investigated the factors affecting the distribution of the *Astropecten* spp.

Materials and methods

Study site

The study site was located on the Maresme coast (Catalonia, northwestern Mediterranean Sea), a narrow and shallow (5-30 m depth) strip approximately 51 km long parallel to the coast line between the Tordera River (northeast) and the seasonal Tiana River (southwest) (Fig. 1). The site is characterized by a large infralittoral plain (0-30 m depth) of soft-bottoms dominated by coarse granitic sand and reflective beaches.

Sampling procedure

Several daily surveys were performed during two periods, from 23 November to 16 December 2004, and from 1 May to 15 May 2010, to study medium-term spatial changes in sea star species composition, spatial distribution and abundance. Sampling stations were located along 17 parallel transects 3 km from each other and perpendicular to the coastline, covering the entire study area. They were numbered consecutively from northeastern to southwestern (T1-T17). Five stations corresponding to depths of 5, 10,

15, 20, and 25 m were sampled in each transect whenever possible (avoiding the existence of sea grass, rocky outcrops and submarine outfalls) (Fig. 1). Samples were collected at sea on board the F/V *Nautes* (10 m in length; 100 HP), which is involved in the smooth clam fishery of the area. The sampling gear used for this study was a commercial cage stile clam dredge (mouth width, 70 cm; mouth height, 53 cm; depth, 120 cm) provided with an experimental metal wire mesh of 12×12 mm. Each tow, whose geographical position was recorded using GPS, lasted 30 minutes at a towing speed of 1-1.2 knots. All the sea stars collected were transported in a cooler with ice (4ºC) to the laboratory, where they were identified and counted for each transect and depth. Densities were standardized to N.ha^{-1}.

Factors influencing *Astropecten* spp. distribution were analyzed during the second survey period (from 1 May to 15 May 2010). For this purpose, abundance of the sea stars and the bivalve *C. chione* and sediment characteristics (granulometry and organic matter content) were quantified. Specimens were collected at each station (for each transect and depth) using the above method and were identified and counted in the laboratory. In addition, surface sediment samples were taken with a Van Veen grab (0.1 m^2) to analyze the granulometric composition and the percentage of organic matter content. Sediment was treated according to the standard protocol: oven-drying at 70ºC for 72h, treating with 0.2 NaOH solution, and stirring to release silt and clay particles. The sediment was finally sieved through decreasing mesh-sized sieves and classified as follows: 2 mm (gravel), 2.0-1.0 mm (very coarse sand), 1.0-0.5 mm (coarse sand), 0.5-0.25 mm (medium sand), 0.25-0.125 mm (fine sand), 0.125-0.063 mm (very fine sand); smaller particles were classified as silt-clay. The median size of the particles (D50) was also calculated. The organic matter content was estimated as the loss in weight of dried sediment (l00°C, 24h) after combustion (500°C, 3h) (Heithaus *et al.* 2008).

Medium-term changes in sea star density and population structure were analyzed in transects T3 and T5. From the initial 17 transects, only two were randomly chosen because of the timing and logistics of the project. Monthly samplings were performed from January 2005 to January 2006 and from January 2010 to January 2011.

Medium-term diet changes of the most common sea star species found, *A. aranciacus,* were studied by examining stomach contents in two annual periods (January 2005–January 2006 and January 2010–January 2011). The oral surface was opened by separating the plates along the ambulacral grooves to expose the stomach. The stomach content, including the thin stomach wall to collect any small prey hidden

in the folds, was carefully removed and washed through a 200-µm sieve. Stomach contents were preserved in 70% ethanol and examined under a stereo microscope. All prey items were identified to the lowest possible taxonomic category and counted.

Data analyses

Several standard measures of absolute and relative abundance were used to assess the importance of each sea star species in the area: (i) sea star density per sampling station, calculated as number of individuals per area (N. ha^{-1}); (ii) relative density of the different sea stars, which represents the density of one species as a percentage of total density (all sea star species together); and (iii) frequency of occurrence (F), which expresses the percentage of stations where a sea star species was collected. Differences in density of each sea star species by sampling station and year (2004 and 2010) were tested with a two-way ANOVA (significance level was set at p<0.05) after testing the data for normality and homoscedasticity.

The geographic distribution of the astropectinids in both annual surveys (2004 and 2010) was examined by species using the Kriging interpolation algorithm (SURFER 8® Golden Software, Colorado). Kriging is a geostatistical gridding method based on the assumption that the value of a non-sampled location can be interpolated from a random field based on the measured values of the random field at nearby locations. Data from stations were used to create gridded data and a 2000 × 2000 m grid was generated for both years. To measure spatial autocorrelation, we used Moran's I statistic (Cliff and Ord 1973; Upton and Fingleton 1985), which indicates whether similar sea star densities are in close proximity in a plot of mapped data (two-dimensional method). This methodology was previously used in echinoderms by Fisher and Owens (2004):

$$I = \frac{N}{\sum_i \sum_j w_{ij}} \frac{\left(\sum_i \sum_j w_{ij}(X_i - \overline{X})(X_j - \overline{X})\right)}{\sum_i (X_i - \overline{X})^2}$$

where N is the number of spatial observations indexed by i and j in the whole study area in each sampling period (2004 and 2010), $\overline{x}$ is the mean of x, and w$_{ij}$ is the spatial weight (w) between samples (quadrants) of i and j. The weight matrix represents the relationship between an element and its surrounding elements. Values range from −1 (indicating perfect dispersion) to +1 (indicating perfect clustering); zero value means a random spatial pattern. Moran's I index and two measures of the test significance (z-

value and p-value) were calculated using GeoDA software (Anselin *et al* 2006). The z-value indicates whether the apparent similarity (a spatial clustering of either high or low values) or dissimilarity (a spatial outlier) is more pronounced than one would expect in a random distribution. A high positive z-value indicates that the surrounding features have similar values and a low negative z-value indicates a spatial outlier.

During the second survey (1 May to 15 May 2010), we assessed the relationships between the density of *A. aranciacus, A. irregularis pentacanthus* and *A. platyacanthus* and the independent variables depth, transect (spatial location), sediment size classification (D50), sediment organic matter content *C. chione* density and the co-occurring sea star species density, using a generalized linear model (GLM) analysis (STATA v 1.2 statistical Software (Stata Corporation, College Station, TX, USA). For the GLM analysis, the dependent variable (sea star density) was normalized ($\log_{x+1}$ transformed) to incorporate independent variables: density of sympatric sea stars *A. aranciacus*; *A. irregularis pentacanthus*; *A. platyacanthus*), density of *C. chione*, percentage of organic content in the sediment (%MO), sediment granulometry (D50) and depth (5, 10, 15, 20 and 25 m). A Gaussian error distribution was used in the analysis. The coefficient obtained is the value for predicting the influence of the independent variables on the dependent variable. A positive coefficient indicates an increase in the independent variable with the increase in the dependent variable, whereas a negative coefficient indicates a decrease in the independent variable with the increase in the dependent variable.

The length frequency distributions of *A. aranciacus*, *A. irregularis pentacanthus* and *A. platyacanthus* were compared between the two sampling periods with the non-parametric Kolmogorov-Smirnov test. The relative abundance (A%) of each prey item of *A. aranciacus* was calculated as the relationship between the number of each prey and the total number of prey. Annual data on stomach contents were based on monthly sampling. A chi-square test was used to compare the diet composition between the two annual sampling periods (2005-2006 and 2010-2011) ($p<0.05$). Sea star length-frequency distributions were decomposed into their components to identify cohorts using Bhattacharya's method (Bhattacharya, 1967), included in the FiSAT II software (Gayanilo *et al.* 2005).

Results

Medium-term spatial changes in sea star species composition, distribution and abundance

Five of the six Mediterranean species belonging to the genus *Astropecten* were found inhabiting the Maresme coast: *A. aranciacus*, *A. irregularis pentacanthus*, *A. jonstoni*, *A. spinulosus* and *A. platyacanthus* (Table 1). The most abundant sea star in 2004 was *A. aranciacus,* which was dominant at all depths and present at 64.8% of the stations. The population was distributed at the two ends of the sampled area (Fig. 2a). In 2010, *A. aranciacus* still showed the highest frequency of occurrence, appearing at 39.7% of the stations (Table 1) but a significant relative density reduction took place between the two sampling years ($F_{(1,100)}$= 4.25; p=0.04) and it disappeared from the south western transects (Fig. 2b). *A. irregularis pentacanthus* was the second most abundant species (Table 1), located in two main areas in 2004 (Fig. 2c). Despite a density reduction in 2010 at 5, 10, and 20 m depth, high densities were found at 15 m depth, which could not be sampled in 2004 (Table 1). The frequency of occurrence of *A. irregularis pentacanthus* decreased in 2010, but the relative density increased slightly from 25.4% to 45.1%, although it was not significantly different ($F_{(1,100)}$= 0.07; p=0.79) to the previous findings. In 2004, the distribution was more concentrated, especially in the north area (Fig. 2d). *A. jonstoni* and *A. spinulosus* were observed in very low densities in 2004 at depths above 10 m but no specimen appeared in 2010 (Table 1). *A. platyacanthus* was not found in the 2004 sampling but became quite abundant in 2010 (Table 1), increasing its density with depth. The distribution was concentrated mainly in the southwestern area (Fig. 2g). The four sea star species that coexisted on the Maresme coast in 2004 overlapped their spatial distribution in some transects, whereas in 2010 the three remaining sea star species occupied different transects with no overlap.

Moran's I statistic of autocorrelation resulted in values between 0.22 and 0.69 (Table 2), indicating that sea stars had a patchy spatial distribution on the Maresme coast. The two most abundant species (*A. aranciacus* and *A. irregularis pentacanthus*) became more concentrated with time, as seen by an increase in Moran's I statistic between the two sampling years: Moran's I value for *A. aranciacus* rose from 0.44 to 0.65, while the value for *A. irregularis pentacanthus* rose from 0.45 to 0.58.

Factors influencing Astropecten spp. distribution

GLM results on the influence of several parameters upon the sea stars density are shown in Table 3. *A. aranciacus* predominated in areas with presence of the bivalve *C. chione* ($p=0.001$), coarse grain ($p=0.0001$), and higher depths ($p=0.013$), as seen for the significant positive β value. By contrast, significant negative β values indicated that the species was scarce in sediments with high concentrations of organic matter ($p=0.033$). *A. irregularis pentacanthus* was abundant in areas with fine sediments ($p=0.043$) and high percentages of organic matter ($p=0.004$). *A. platyacanthus* predominated in areas with low concentrations of organic matter ($p=0.0001$), greater depth ($p=0.0001$), and the southern transects of the study area ($p=0.0001$). The presence of other *Astropecten* species had no influence on *A. aranciacus* or *A. irregularis pentacanthus* but *A. platyacanthus* was absent when *A. aranciacus* was present ($p=0.023$).

Changes in sea star density and population structure

    A. aranciacus was the most abundant species in 2005-2006 but its density dropped in 2010-2011 (Fig. 3), when it became only slightly higher than that of *A. irregularis pentacanthus* and *A. platyacanthus*. *A. aranciacus* showed a seasonal pattern in both transects (T3 and T5) in 2005-2006, with higher density values (>140 N.ha^{-1}) in winter (from December to March), a decrease in spring (to 50 N.ha^{-1} from March to May-June), a slight increase in summer (June-July and August), a new decrease in September to near-disappearance, and again an increase in October and November. A similar pattern was observed in 2010-2011 in transect T3 but not in T5, in which densities had values of around 30 N.ha^{-1} all year round, except for January and August. *A. irregularis pentacanthus* was scarce in both transects and periods and showed no clear seasonal patterns. The highest densities for transect T3 were found in March and April 2005 (16 N.ha^{-1} and 10 N.ha^{-1}, respectively), and in winter 2010 (between 39-28 N.ha^{-1}). In transect T5 the highest abundances were found in spring, with values of 27 N.ha^{-1} and 7 N.ha^{-1} (in March 2005 and May 2010, respectively) and in summer during both study periods, mainly in August, with values of 18 N.ha^{-1} and 30 N.ha^{-1} (in 2005 and 2010, respectively). *A. platyacanthus* was only present during the whole period of 2010-2011, with the highest densities in transect T3 being observed in February (63 N.ha^{-1}) and August 2010 (>70 N.ha^{-1}) and in January 2011 (95 N.ha^{-1}), whereas the highest densities in transect T5 were observed in August 2010 (70 N.ha^{-1}) and January 2011 (39 N.ha^{-1}).

The Kolmogorov-Smirnov test showed significant differences in the size-frequency distribution in both sampling periods for *A. aranciacus* (D=0.23; *p*<0.0001) and *A. irregularis pentacanthus* (D=0.47; *p*<0.0001) (Fig.4). *A. aranciacus* exhibited a multiple cohort population in 2005-2006, with four cohorts (X_1=19.74±5.32; X_2=51.30±10.19; X_3=88.63±8.63; and X_4=126.76±10.31) with a high proportion of recruits (<20 mm major radius length), while in the second sampling period (2010-2011) these smaller sizes had mostly disappeared (X_1=50.79±8.23; X_2=83.84±17.01; X_3=133.89±9.47). The *A. aranciacus* population increased the mean size from 55.68 mm in 2005-2006 to 67.88 mm in 2010-2011. The *A. irregularis pentacanthus* population showed two cohorts in both sampling periods, 2005-2006 (X_1=16.64±3.77; and X_2=43.92±4.60) and 2010-2011 (X_1=22.77±4.76; and X_2=49.62±3.82). Though its population increased its mean size by about 10 mm from 2005-2006 to 2010-2011, from 23.78 mm to 33.08 mm. *A. platyacanthus*, which was not detected in the first sampling period, showed a plurimodal structure in 2010-2011, with four cohorts (X_1=19.49±4.42; X_2=32.17±4.71; X_3=65.68±3.86; and X_4=77.34±4.86).

Diet changes in A. aranciacus

The diet of *A. aranciacus* was composed of several species of bivalves and gastropods. There were significant differences between the two sampling periods in the diet of *A. aranciacus* (X^2=50.83 dF=20; *p*<0.0001). The abundance of bivalves in the stomach content decreased from 79.72% to 51.61%, and the abundance of gastropods increased from 19.32% to 47.29% (Table 4). The diet was mainly based on the bivalve species *C. chione* (56.56%) and *Glycymeris glycymeris* (16.37%) in the first period of study, whereas it was dominated by three different preys in the second period: the bivalves *G. glycymeris* (24.52%) and *C. chione* (17.95%) and the gastropod *Gibbula guttadauri* (21.17%).

Discussion

Five of the six Mediterranean species belonging to the genus *Astropecten* have been found inhabiting the narrow 51-km strip parallel to the coastline of the Maresme, between 5 and 30 m depth. However, only three or four species coexisted in time depending on the period. The co-occurrence of different species of the genus *Astropecten* has been observed worldwide (Bitter and Penchaszadeh 1983; Lemmen *et al.* 1995; Ventura and Da Costa Fernandes 1995) and they frequently exhibit a patchy

distribution, like most of the echinoderms (Gutt and Starmans 2003; Freeman *et al.* 2001). The patchy distribution of sea stars detected in the study site could be a consequence of several biotic and abiotic factors, such as predation, competition, depth, sediment grain size and organic matter content, as reported in several studies (Ferlin-Lubini and Ribi 1978; Freeman *et al.* 2001; Tuya and Duarte 2012).

Prey competition and potential predation risk could explain the results of the GLM model regarding the fact that *A. platyacanthus* avoided the presence *of A. aranciacus.* Though *A. platyacanthus* showed no relationship with the presence of *C. chione* (GLM results in this study), the two species had a dietary overlap (Baeta and Ramón, 2013). If two species show considerable dietary overlap and are limited in abundance by the food supply available, competition between them is likely to occur (Ribi and Jost 1978). Moreover, *A. aranciacus* has been described as an important predator for other astropectinids (e.g. *A. jonstoni* and *A. bispinousus*) in the northwestern Mediterranean (Pabst and Vicentini 1978; Ferlin-Lubini and Ribi 1978; Schmid and Schaerer 1981) and it may also prey on *A. platyacanthus*, although no mention of this has been found in the literature.

Sediment is also a factor that might have an important effect on species distribution in benthic organisms. Pubill *et al.* (2011) observed three different megabenthic faunistic assemblages in the Maresme area: Medium Sand in Shallow waters (MSS), Coarse Sand in Shallow waters (CSS) and Coarse Sand in Deeper waters (CSD). The smooth clam was dominant in both types of coarse sand, that is, CSS and CSD. According to our results, *A. aranciacus* was also related to coarse sand, *A. irregularis pentacanthus* was found in finer sediments and *A. platyacanthus* was not related to any particular sediment grain size. Baeta *et al.* (2014) reported sediment granulometry changes on the Maresme coast between the same two periods studied herein. The distribution of the median grain size (D50) revealed that the sediments became finer everywhere in 2010, with the appearance of a larger area of fine sand, even with silt in the south of the study area, between transects T12 and T17. The disappearance of *A. aranciacus* from the southern area (T13 to T17) and some parts of the northern side (T3 and T5-T6) can be related to that increase in finer sediments, in agreement with the results of the present study, which show that this species predominates in coarse sand. In contrast, the decrease in the D50 of the sediment favored *A. irregularis pentacanthus* whose abundance increased in the southwest because this species predominates in fine sediments. However, the increase in

abundance of *A. irregularis pentacanthus* in the northeast area, where the sediment grain remained thicker, cannot be explained by sediment characteristics, so it must be related to a factor not analyzed in the present study.

Prey availability has been established as one of the most important factors determining sea star composition, distribution and abundance (Gaymer *et al.* 2001). Baeta *et al.* (2014) reported that the distribution of *C. chione* was hugely reduced on the Maresme coast between 2004 and 2010, showing a sharp decline in density and biomass and a decrease in the mean population size. The present study has shown that *A. aranciacus* re-adapted the feeding habits towards other prey in 2010, probably as a consequence of changes in prey availability. Therefore, even if this species is related to the presence of *C. chione*, it is able to change its diet, suggesting that the type of sediment most likely had a higher influence on sea star distribution than the abundance of smooth clam. The bivalve *G. triangularis*, the preferred prey of *A. platyacanthus* (Baeta and Ramón, 2013), inhabits coarse and medium sands like *C. chione* (Moreira *et al.* 2005; Troncoso *et al.* 2005) and was the most abundant bivalve throughout 2010-2011 in the Maresme coast, when only 3 ind. m^2 of *C. chione* were found (Baeta and Ramón 2013). We infer that the critical situation of the smooth clam bed benefited the expansion of other species such as the micro-bivalve *G. triangularis,* and consequently of its predator, *A. platyacanthus* (Baeta and Ramón 2013). A decline in *A. aranciacus* populations has been observed in other areas within the Mediterranean Sea over the past 20 years (Zulliger *et al.* 2009) but the possible causes of the decline were not reported. In our study, despite the change in feeding habits of *A. aranciacus* in 2010, we hypothesize that *A. platyacanthus* might be progressively occupying the ecological niche of *A. aranciacus* as a result of the sediment changes in the area and the disappearance of *C. chione* (Baeta et al., 2014).

Our results also showed monthly variations in the abundance of the sea star populations, and particularly that of *A. aranciacus*, as has been reported for several *Astropecten* species. For example, Ventura and Da Costa Fernandes (1995) observed changes in the abundance of *A. cingulatus* and *A. brasiliensis* during upwelling periods. Freeman *et al.* (2001) suggested that variations in the density of *A. irregularis* were related to prey dynamics, so when the prey recruitment occurred, sea star density increased. In the area, *C. chione* begins to ripen the gonads in December and is sexually mature until April-May, when spawning occurs (non-published data). Bivalves are reported to be richer in lipids, which have a high energy content when they are ripe

(Pipe 1985; Galap *et al.* 1997; Honkoop *et al.* 1999), so the smooth clam is likely to be more nutritious in the cold months. This period coincides with the increase in *A. aranciacus* density, suggesting a relationship between the two parameters.

High mortality rates and migration of shellfish predators after the collapse of bivalve beds have been reported (Beukema and Cadée 1996; Atkinson *et al.* 2003). We found no diseased, moribund or dead sea stars during our samplings and fishermen never alerted us about morphological signs of disease in the sea star species that could indicate mortality events. However, a combination of absence of recruitment, as observed in our study, and migration to other areas could also have influenced the population decline of *A. aranciacus*. *Astropecten* spp. have the ability to travel long distances (Ferlin-Lubini and Ribi 1978): for example, *A. aranciacus* can move about 10 m d^{-1} (Burla *et al.* 1972). Seasonal migration is a common event in sea star species, particularly in temperate areas (Hinz *et al.* 2004), and can be caused by weather conditions, reproduction, food availability and optimized feeding (Feder and Christensen 1966; Sloan 1980; Menge 1972; Gallagher *et al.* 2008). Absence of recruitment or low recruitment rates are not abnormal in sea stars and other echinoderms because they are highly variable events regulated by the interaction of several biotic and abiotic factors (Loosanoff 1964; Christensen 1970; Balch and Scheibling 2000; Hereu *et al.* 2004; Kinch *et al.* 2008). Future studies are recommended to determine whether the decrease in *A. aranciacus* density and the absence of recruitment in the area is a short-term or a long-term process.

Human pressures has led many marine predators that occupy high trophic levels to a severe decline worldwide in the last few decades at a worrying rate (Heithaus *et al.* 2008). Understanding how species are vulnerable to human pressure is an essential prerequisite for designing effective conservation strategies (Pinsky *et al.* 2011). The present study shows how Mediterranean sea star populations of the genus *Astropecten* responded to previously reported changes in habitat (sediment grain size decrease) and prey abundance (*C. chione* decline) over time. The data presented in this study provide a useful basis for monitoring and detecting medium-term changes in benthic soft-bottom ecosystems.

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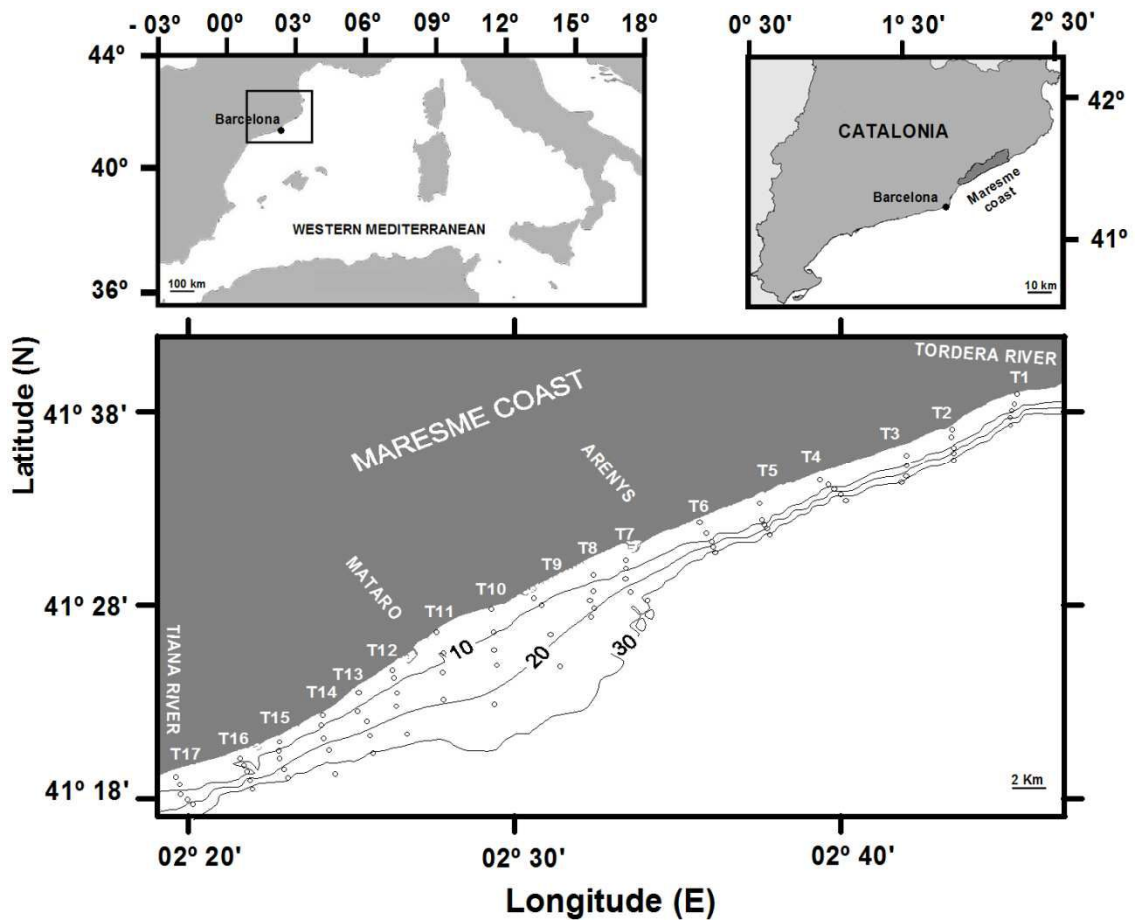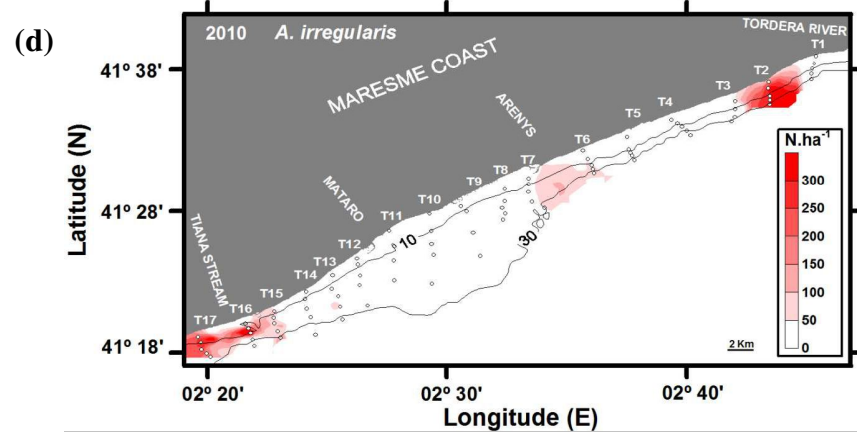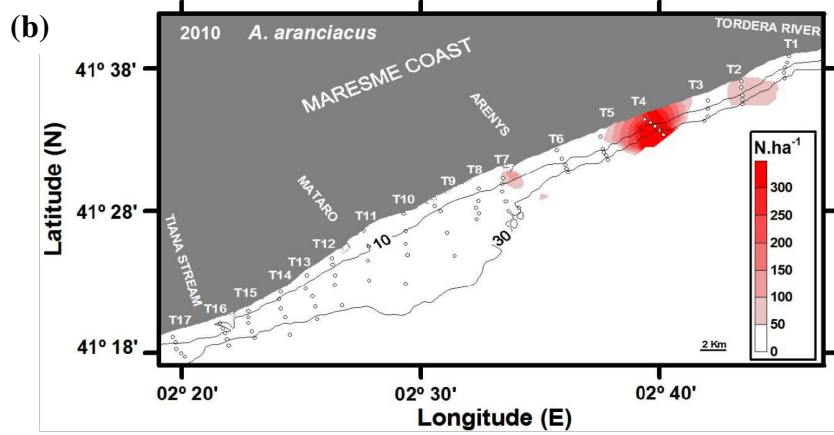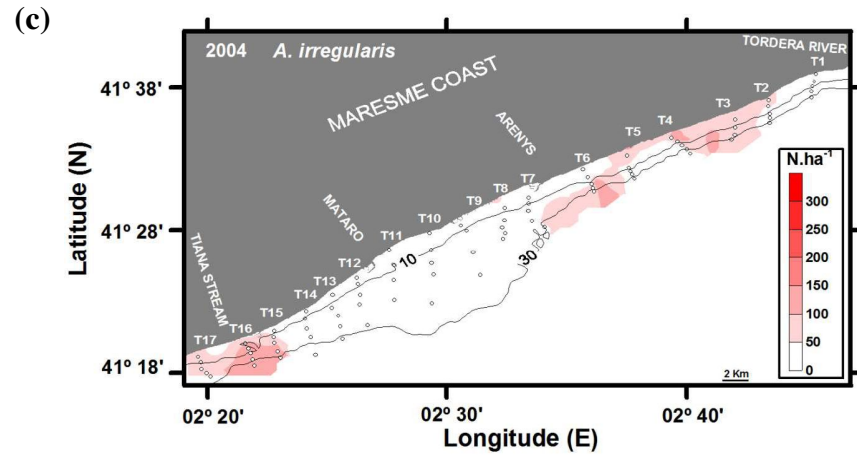
Fig. 1. Study area in the northwestern Mediterranean Sea, showing the distribution of sampling stations (points), transects (T), and isobaths (10, 20 and 30 m).

Fig. 2. Sea star spatial distribution and density (N.ha^{-1}) in the study area for the two periods of study (November-December 2004 and March 2010). *A. aranciacus* (a-b); *A. irregularis pentacanthus* (c-d); *A. jonston*(e); *A. spinulosus* (f); and *A. platyacanthus* (g).

Fig. 3. Monthly sea star density (N.ha^{-1}) in transects T3 and T5 for the two periods of study: January 2005 to January 2006 (grey circle) and January 2010 to January 2011 (white circle). Standard deviation is shown in graph.
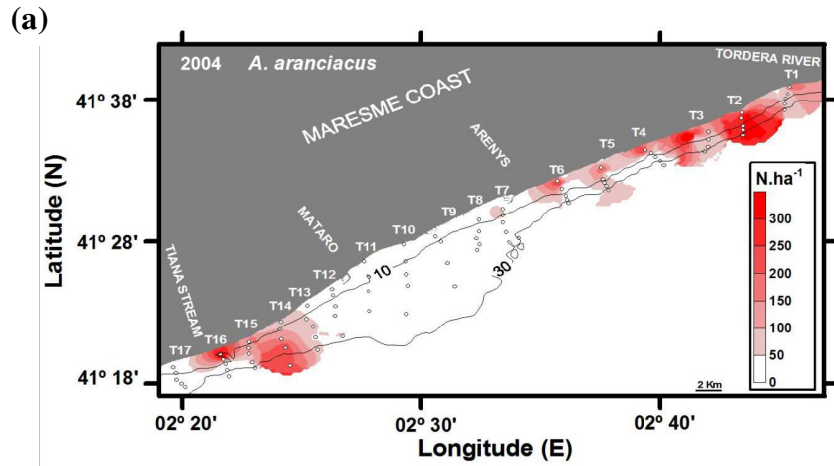
Fig. 1. Study area in the northwestern Mediterranean Sea, showing the distribution of sampling stations (points), transects (T), and isobaths (10, 20 and 30 m).
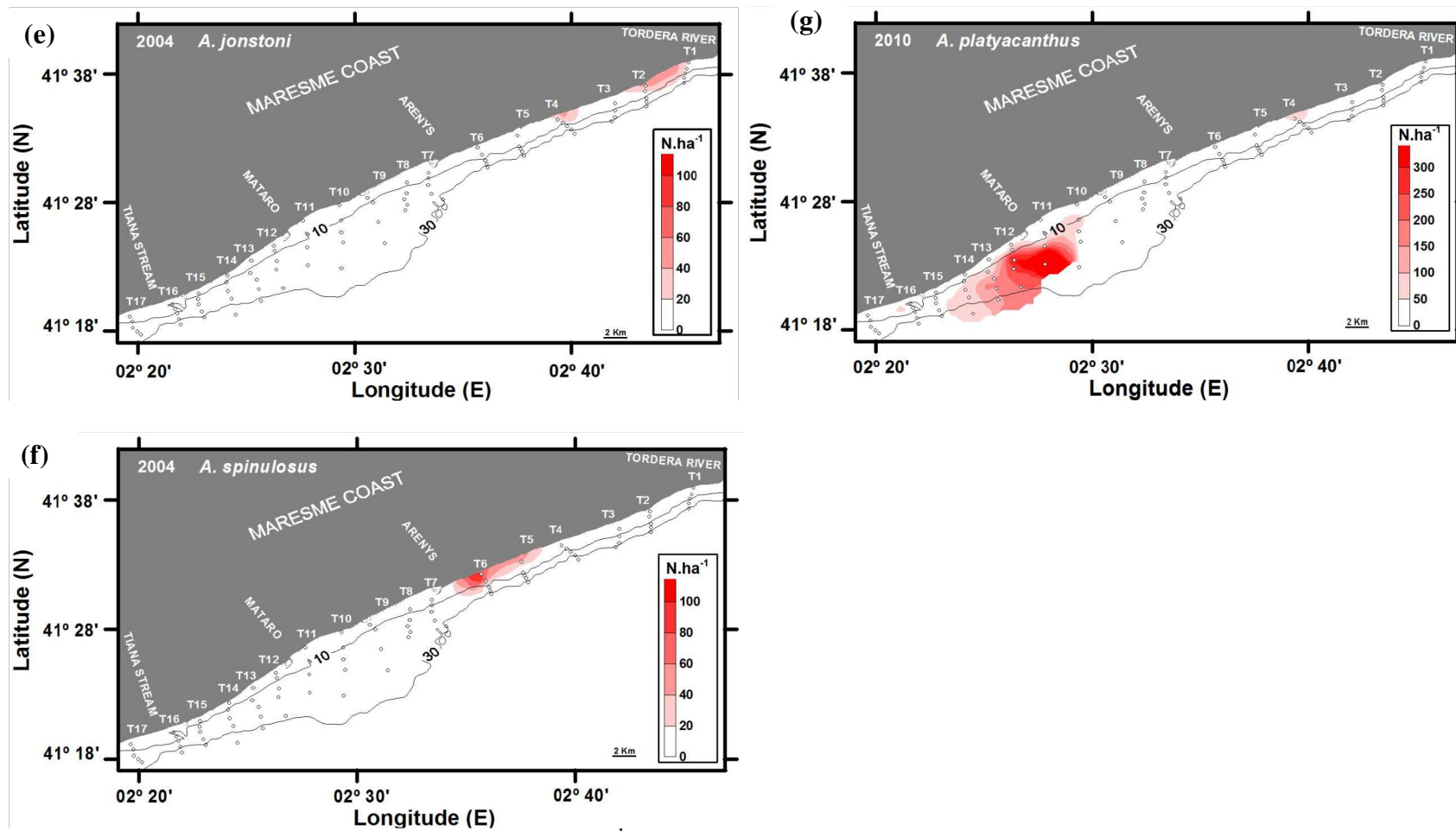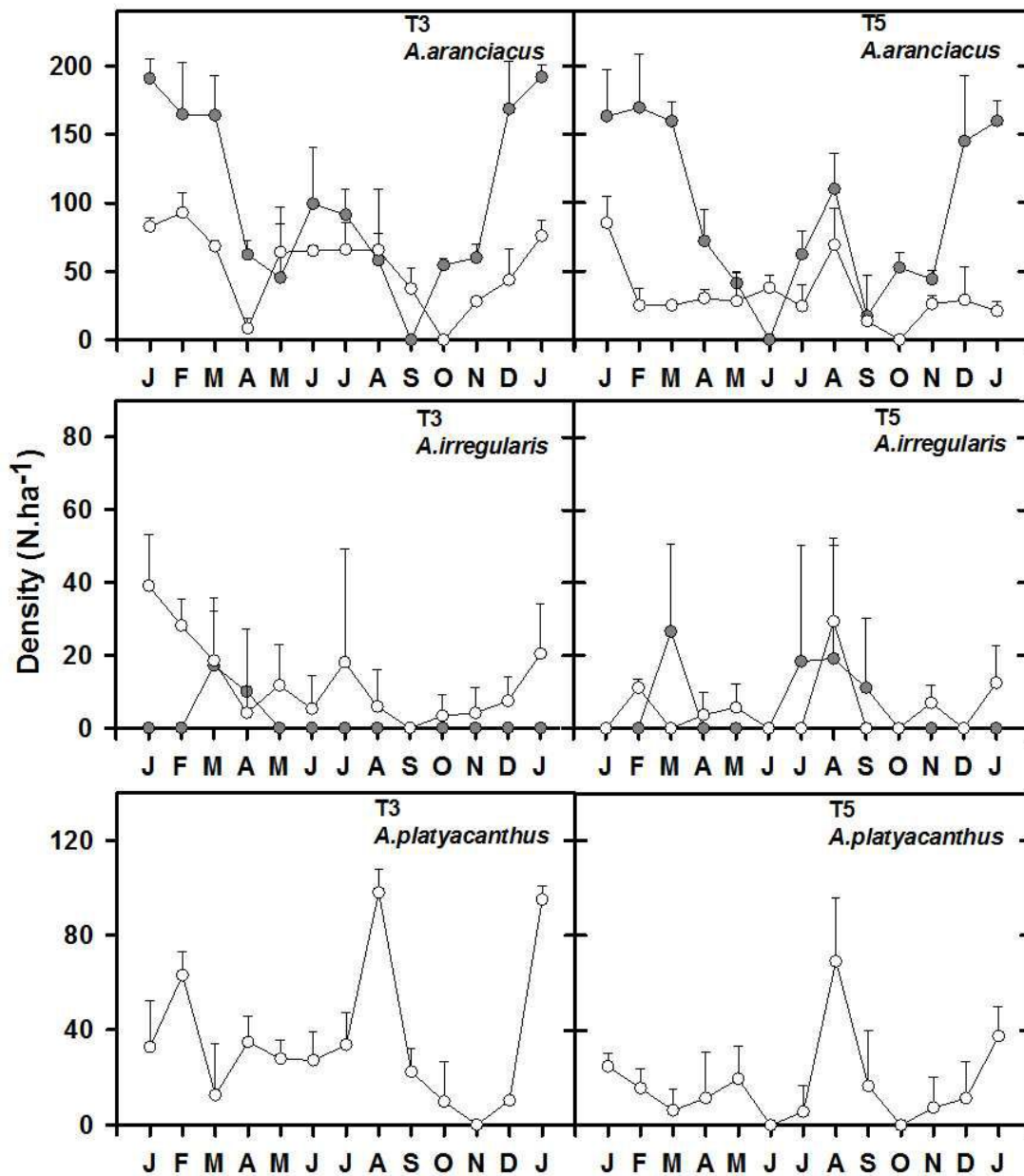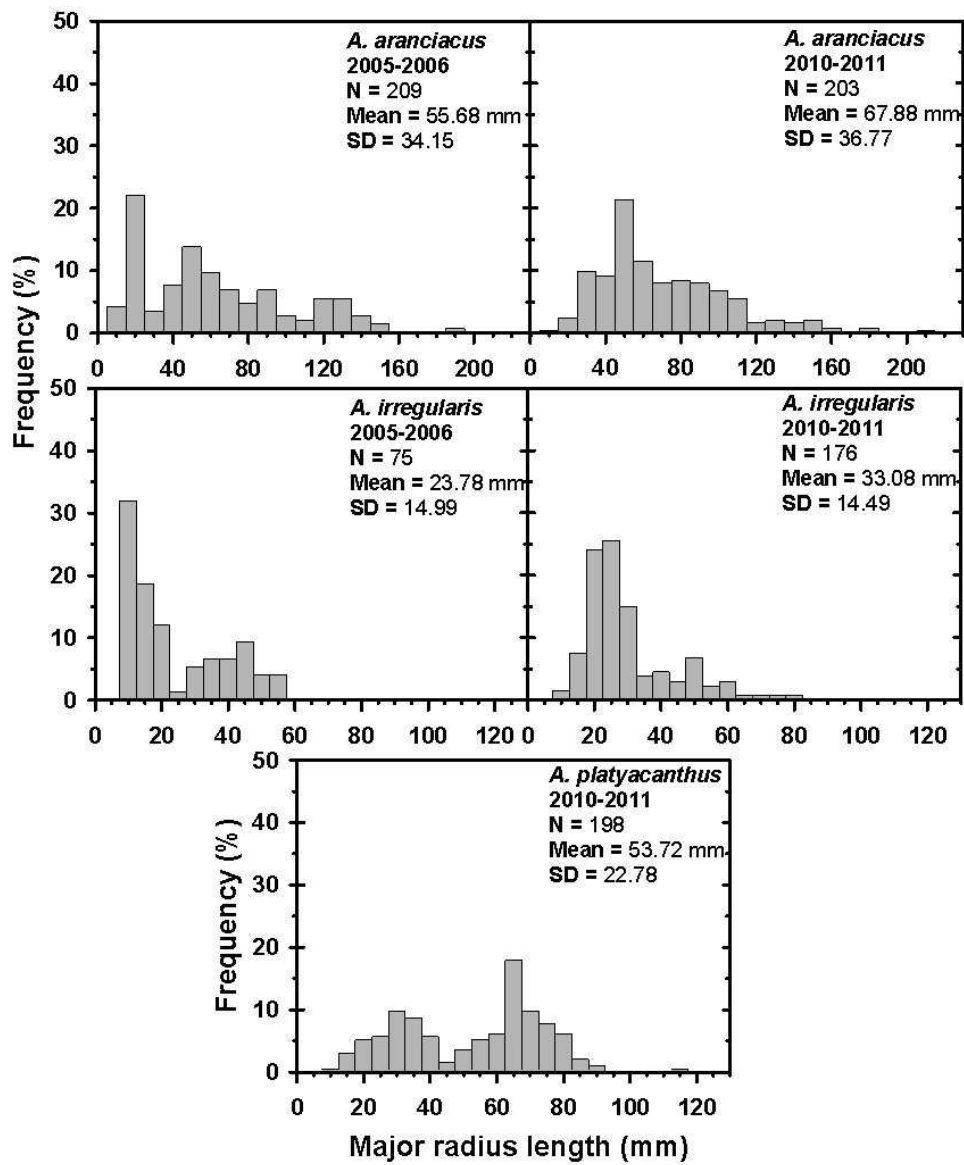
2004

Depth	S(ha)	N.ha⁻¹				
		Aa	**Ai**	**Aj**	**As**	**Ap**
5	0.31	208	138	9	3	0
10	0.34	442	183	0	6	0
15	-	-	-	-	-	-
20	0.27	701	95	0	0	0
25	0.12	122	90	0	0	0
All depth	**1.04**	**369**	**127**	**2**	**2**	**0**
RD (%)		**73.8**	**25.4**	**0.4**	**0.4**	**0**
F (%)		**64.8**	**46.3**	**7.4**	**5.7**	**0**

2010

Depth	S(ha)	N.ha⁻¹				
		Aa	**Ai**	**Aj**	**As**	**Ap**
5	0.28	18	0	0	0	0
10	0.28	32	14	0	0	25
15	0.31	61	214	0	0	29
20	0.31	55	68	0	0	39
25	0.15	134	94	0	0	81
All depth	**1.33**	**60**	**78**	**0**	**0**	**35**
RD (%)		**34.7**	**45.1**	**0**	**0**	**20.2**
F (%)		**39.7**	**28.2**	**0**	**0**	**24.4**

Table 1. Density (N.ha^{-1}) of the sea star species (Aa, *A. aranciacus*; Ai, *A. irregularis pentacanthus*; Aj, *A. jonstoni*; As, *A. spinulosus*; Ap, *A. platyacanthus*) by depth (5, 10, 15, 20, 25 m and whole depth) in 2004 (from 23 November to 16 December) and 2010 (from 1 to 15 May). S (ha), sampled area in hectares; RD, relative density; F, frequency of occurrence. Line means no data.

Species	Year	I	SD	z	*p*
A. aranciacus	2004	0.44	0.06	7.839	<0.001
	2010	0.65	0.08	8.452	<0.001
A. irregularis	2004	0.45	0.06	8.060	<0.001
	2010	0.58	0.07	9.004	<0.001
A. jonstoni	2004	0.32	0.05	6.069	<0.005
	2010	-	-	-	-
A. spinulosus	2004	0.22	0.22	4.516	<0.005
	2010	-	-	-	-
A. platyacanthus	2004	-	-	-	-
	2010	0.69	0.08	8.970	<0.001

Table 2. Pattern of distribution (Moran's I statistic of autocorrelation values) for each *Astropecten* species in both sampling periods (23 November to 16 December 2004; 1 to 15 May 2010). SD is standard deviation; z-value and p-value are measures of statistical significance. Line means no data.

A. aranciacus					
Model term	**β**	**SE**	***p***	**95% CI**	
Ai density	0.0033	0.0009	0.100	0.0016	0.0050
Ap density	-0.0013	0.0015	0.409	-0.0042	0.0017
Cc density	2.9649	0.8921	0.001	1.2161	4.7134
% OM	-1.3340	0.6262	0.033	-2.5614	-0.1066
D50	3.1110	0.7651	0.000	1.6113	4.6107
Depth	0.0539	0.0216	0.013	0.0114	0.0963
Transect	-0.0048	0.0310	0.887	-0.0561	0.6571
A. irregularis pentacanthus					
Model term	**β**	**SE**	***p***	**95% CI**	
Aa density	0.0072	0.0039	0.068	-0.0005	0.0149
Ap density	0.0082	0.0048	0.092	-0.0013	0.0177
Cc density	-1.2137	0.9543	0.203	-3.0843	0.0657
% OM	4.2897	1.4736	0.004	1.4015	7.1778
D50	-4.0994	2.2024	0.043	-8.0674	-0.1313
Depth	-0.0687	0.0429	0.110	-0.1529	0.0156
Transect	-0.2342	0.1321	0.076	-0.0245	-0.4931
A. platyacanthus					
Mode lterm	**β**	**SE**	***p***	**95% CI**	
Aa density	-0.0072	0.0032	0.023	-0.0133	-0.0010
Ai density	-0.0044	0.0034	0.198	-0.0110	0.0023
Cc density	1.0689	0.3968	0.077	0.2915	1.8468
% OM	-2.8159	0.6775	0.000	-4.1447	1.4880
D50	0.2264	1.0882	0.835	-1.9065	2.3593
Depth	0.1341	0.0358	0.000	0.0640	0.2043
Transect	0.2569	0.0703	0.000	0.1190	0.3948

Table 3. Summary results of the generalized linear model (GLM) to detect the influence of environmental parameters (independent variables) on the density of each sea star species (dependent variables). Model term is the list of independent variables for each analysis: Aa, *A. aranciacus*; Ai, *A. irregularis pentacanthus*; Ap, *A. platyacanthus*; Cc, *C. chione*; %OM, organic content of the sediment; D50, median size of the sediment particles; Depth (5, 10, 15, 20 and 25 m); and fishing effort (0-10; 0 means no fishing effort and 10 very high fishing effort) and sand extraction (0-5; 0 means no sand extracted and 5 large amounts of sand extracted). Coefficient (β) is the value for predicting the dependent variable from the independent variable; SE, standard error; *p*, test significance; 95% CI, 95% confidence interval for the coefficient.

Season	Jan05 - Jan06		Jan10 - Jan11	
Sea star (N)	142		107	
Prey items	N	A	N	A
BIVALVIA				
Callista chione	750	56.56	675	17.95
Glycymeris glycymeris	217	16.37	922	24.52
Goodallia triangularis	25	1.89	111	2.95
Corbula gibba	0	0.00	23	0.61
Donax variegatus	4	0.30	36	0.96
Parvicardium scriptum	11	0.83	34	0.90
Dosinia exoleta	12	0.90	25	0.66
Pitar rudis	14	1.06	19	0.51
Modiolus adriaticus	6	0.45	5	0.13
Other bivalves	18	1.36	91	2.42
All bivalves	**1057**	**79.72**	**1941**	**51.61**
GASTROPODA				
Gibbula guttadauri	20	1.51	796	21.17
Cyclope neritea	70	5.28	361	9.60
Nassarius pygmaeus	38	2.87	166	4.41
Natica haebrea	36	2.71	119	3.16
Cerithium vulgatum	2	0.15	88	2.34
Euspira pulchella	81	6.11	49	1.30
Retusa mammillata	2	0.15	34	0.90
Bittium reticulatum	1	0.08	34	0.90
Caecum trachea	1	0.08	13	0.35
Other gastropods	5	0.38	119	3.16
All gastropods	**256**	**19.32**	**1779**	**47.29**
OTHER TAXA	**13**	**0.96**	**40**	**1.10**
TOTAL	**1326**	**100**	**3760**	**100**

Table 4. Stomach content composition of *A. aranciacus* for each sampling period (January 2005–January 2006; January 2010–January 2011) in number (N) and abundance A (%).

7.4. Growth and reproductive biology of the sea star *Astropecten aranciacus* (Echinodermata Asteroidea) on the continental shelf of the Catalan Sea (northwestern Mediterranean).

Abstract

The growth and reproductive biology of the sea star *Astropecten aranciacus* was investigated on the continental shelf of the northwestern Mediterranean Sea. Sea stars were captured monthly at two bathymetric ranges (5-30 and 50-150m), between November 2009 and October 2012. Three cohorts have been identified at each bathymetric range and growth rates estimated. Recruitment was recorded twice nearshore from the whole study period but no recruitment was detected offshore. *A. aranciacus* growth showed seasonality, being higher from June to October in the nearshore cohorts. The growth period was wider offshore (February-October) although the growth rate was lower (about half) in comparison with nearshore values. Histology and organ indexes revealed an annual well-defined reproductive cycle, with a maturation peak occurring between February and April, coinciding with the spring phytoplankton bloom, the increase of sea water temperatures and a short day photoperiod. *A. aranciacus* did not show an inverse relationship between gonad index and pyloric caeca index. Ratio between males and females was proximately 1:1 throughout the year and at both bathymetrical ranges. The size at first maturity (R50%) was estimated to be R=112 mm. This investigation showed the bathymetric segregation by size in *A. aranciacus*; small individuals inhabit shallow areas (5-30 m), while large individuals inhabit deeper areas of the continental shelf (50-150 m).

Figures 14 and **15:** Mature gonads of *A. aranciacus* male (left) and female (right).

Resumen

El crecimiento y la biología reproductiva de la estrella de mar *Astropecten aranciacus* fueron por primera vez investigados. Los ejemplares estudiados fueron capturados mensualmente en dos rangos batimétricos distintos (5-30 y 50-150m) en la costa del Maresme (noroeste del Mar Mediterráneo) entre noviembre de 2009 y octubre de 2012. El crecimiento fue estimado por separado en ambos rangos batimétricos y tres cohortes fueron identificadas en cada uno de ellos. El reclutamiento fue documentado dos veces en la zona costera, aunque no se detectó en la zona más profunda. El período de crecimiento fue estacional en ambos casos siendo más largo en la zona más profunda (entre febrero y marzo) aunque de menor intensidad (aproximdamente la mitad) que en la zona costera. La histología y los índices gonadal y pilórico mostraron un ciclo reproductivo muy bien definido, con un pico de maduración entre los meses de febrero y abril, coincidiendo con el bloom de fitoplancton primaveral, el incremento de las temperaturas marinas y un fotoperíodo corto. *A. aranciacus* no mostró una relación inversa entre el índice gonadal y el pilórico. La ratio machos hebras fue aproximadamente 1:1 durante todo el año. El tamaño de primera madurez (R50%) fue estimado en R=112 mm. Esta investigación muestra que existe una segregación batimétrica por tamaño en *A. aranciacus*, habitando los ejemplares pequeños las zonas poco profundas (5-30 m) y los de mayor tamaño las zonas profundas de la plataforma continental (50-150 m).

Participación de los distintos autores

All authors participated in the elaboration of manuscript, and subsequent correction.

Trabajo del doctorando

El doctorado ha participado desde el diseño experimental de los muestreos, la recogida y posterior análisis de las muertas en el laboratorio, así como el análisis de los datos y la posterior redacción del manuscrito.

Growth and reproductive biology of the sea star *Astropecten aranciacus* (Echinodermata Asteroidea) on the continental shelf of the Catalan Sea (northwestern Mediterranean)

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Abstract

The growth and reproductive biology of the sea star *Astropecten aranciacus* was investigated on the continental shelf of the northwestern Mediterranean Sea. Sea stars were captured monthly at two bathymetric ranges (5-30 and 50-150m), between November 2009 and October 2012. Three cohorts have been identified at each bathymetric range and growth rates estimated. Recruitment was recorded twice nearshore from the whole study period but no recruitment was detected offshore. *A. aranciacus* growth showed seasonality, being higher from June to October in the nearshore cohorts. The growth period was wider offshore (February-October) although the growth rate was lower (about half) in comparison with nearshore values. Histology and organ indexes revealed an annual well-defined reproductive cycle, with a maturation peak occurring between February and April, coinciding with the spring phytoplankton bloom, the increase of sea water temperatures and a short day photoperiod. *A. aranciacus* did not show an inverse relationship between gonad index and pyloric caeca index. Ratio between males and females was proximately 1:1 throughout the year and at both bathymetrical ranges. The size at first maturity (R50%) was estimated to be R=112 mm. This investigation showed the bathymetric segregation by size in *A. aranciacus*; small individuals inhabit shallow areas (5-30 m), while large individuals inhabit deeper areas of the continental shelf (50-150 m).

Keywords: Distribution, reproduction, reproductive cycle, growth, *Astropecten*, sea star and echinoderm.

1

Introduction

Sea stars play an essential ecological role, as high level predators, on the structure and function of intertidal and subtidal benthic communities, where they promote heterogeneity and diversity (Jangoux & Lawrence, 1982). Changes in the abundance of these predators can have far-reaching consequences on the population characteristics of many of the invertebrates on which they prey (Christensen, 1970). Despite their ecological importance, research has been limited to certain species and areas where starfish predation has an economic impact, as they feed on important shellfish and on reef-building corals (Lawrence, 2013).

Astropecten (Fam. Astropectinidae) is one of the most species-rich genus among sea stars and their members are worldwide distributed, from polar to tropical seas and from intertidal areas to the deep sea (Zulliger & Lessios, 2010). They are voracious predators feeding mainly on gastropods and bivalves. These carnivores have an intra-oral feeding mechanism swallowing intact prey (Christensen, 1970). In general they exhibit a patchy spatial distribution as a consequence of a combination of biotic (*e.g.* prey and congeners abundance) and abiotic (*e.g.* depth and sediment properties) factors (Ribi *et al.*, 1976). There is a vast literature on the genus *Astropecten* worldwide, mainly focused on their feeding behaviour, diet characteristics (Christensen, 1970; Baeta & Ramón, 2013) and early stages of development (Hörstadius, 1938; Komatsu & Nojima, 1985). However, aspects of their biology such as growth and reproductive biology have been less analysed in contrast with current knowledge on other sea star genus (Ventura, 2013). Growth in field populations have been studied in both tropical (Ventura, 1999) and temperate waters (Nojima, 1982; Freeman *et al.*, 2001). Freeman *et al.* (2001) observed that *A. irregularis* growth in Red Wharf Bay was highly seasonal with maximum growth occurring between mid-summer and mid to late autumn. *Astropecten* spp. reproduction has analysed in tropical waters (Ventura *et al.*, 1997; Ventura *et al.*, 1998; Marion *et al.*, 1998) and in temperate waters (Christensen, 1970; Grant & Tyler, 1986; Freeman *et al.*, 2001). It is commonly seasonal and spawning occurs coinciding with highest sea water temperatures in temperate waters but there is not a clear trend in tropical waters (Ventura, 2013)

Astropecten aranciacus (Linnaeus 1758) is one of the largest sea stars in the Mediterranean Sea, with a body size up to 60 cm in diameter. *A. aranciacus* lives on sandy, muddy and detrital bottoms, as well as in seagrass beds, including *Zostera*, *Cymodocea* and *Posidonia* beds, between 1 and 200 meters depth (Tortonese, 1965). It

2

inhabits in the Mediterranean Sea and the eastern Atlantic from Portugal to Angola, including the Canary, Madeira and Cape Verde Islands. Recently an important decrease in its population has been detected in the Mediterranean Sea (Zulliger *et al.*, 2009). *A. aranciacus* is the dominant species in the continental shelf of Maresme coast (northwestern Mediterranean Sea), where co-occurs with other species of the same genus (*A. platyacanthus, A. irregularis pentacanthus, A. bispinosus, A. spinulosus* and *A. jonstoni*) (own observations). This species have a defined behavioural pattern: it remains buried in the sand during the daytime, emerges just before sunset looking for prey all night, and buries again just a few hours, after dawn (Ribi *et al.*, 1977). To our knowledge, there are no previous reports on growth and reproduction of the sea star *A. aranciacus*.

Most sea stars have a pair of gonads and a pair of pyloric caeca (digestive organs) located in each arm. Gonad and pyloric caecum indices are widely used as indicators of reproductive effort and nutritional condition. Pyloric caeca stored resources seem to play an important role in the seasonal production of gonads in some asteroid species (Lawrence & Lane, 1982). For example, in *Asterias rubens* an inverse relationship has been found in the annual cycle of the pyloric caeca and gonad indices, interpreted as transfer of material stored in the caeca to the developing gonads, but this relationship is not observed in *Asterias forbesi* (Franz, 1986). There is no information on the role that plays the pyloric caeca on the reproduction of *A. aranciacus*

This paper examines for the first time *A. aranciacus* growth and its reproductive cycle. For the purpose, we used monthly modal size classes, histological techniques and seasonal variations of the pyloric caeca and gonadal indexes. In addition, the influence of exogenous factors such as photoperiod, sea water temperature and chlorophyll (chl-a) concentration on the biology of the species was also analysed.

Materials and Methods

Study site

The study was carried out on the continental shelf of the Catalan Sea (northwestern Mediterranean), between the Tordera River delta (northeast) and the mouth of the Tiana seasonal stream (southwest) (Fig.1). This area is named "Maresme coast" and it is a reflective, sandy and straight, wave dominated plain which displays a NE-SW trend. The continental shelf has a mean width of 21 km, a gradient among 0.01-10º, with the shelf break occurring at 130 m ± 20m (Ercilla *et al.*, 2010). Its seabed

3

consists of coarse to medium-sand bottoms nearshore and mud or/and sandy bottoms offshore (Díaz & Maldonado, 1990).

Sampling

Monthly samples were obtained in the Maresme coast between November 2009 and October 2012. Sampling was performed by fishermen on board two vessels from the Arenys de Mar harbour fishing fleet, that use commercial fishing gears according to their fishing modality (shellfish and trawlers) and fishing grounds. The impossibility to sample the whole study area with the same gear due to local fishing regulations constraint us to subdivide the study site in two nearby areas (Fig.1), i.e. nearshore, where the shellfish fleet operate between 5 to 30 meters depth, and offshore, between 50 to 150 m, where trawlers are allow to operate. The strip between 30 and 50 m depth is not covered by these fishing boats on their daily activities. The nearshore area was sampled during daylight onboard the artisanal fishing boat "Esparta" (10 m in length; 100 HP), which belonged to the smooth clam fishery fleet and used clam dredges. The clam dredge consisted in a metallic frame (mouth length: 70 cm; mouth height: 53 cm), a toothed lower bar and a rectangular metallic grid box (mesh size: 29×29 mm). Each tow lasted approximately 30 min at a speed of 1-1.2 kn, and mean towed area was around 800 m^2. The offshore area was sampled during daylight onboard the small trawl fishing boat "San Benito" (10.75 m in length; 105 CV), which targeted black bellied angler (*Lophius budegassa*) and royal sea cucumber (*Parastichopus regalis*). The trawl net was cone-shaped, with a mouth of 4 m width x 0.5 m high and a quadrangular mesh size of 40 × 40 mm. Each tow lasted approximately 2 hours at a speed of 1.8-2 kn. All the *A. aranciacus* caught, regardless of the gear used, were transported to the laboratory in a cool box (4º C). Sea stars were weighed and measured. The length of the sea stars was defined as R, major radius length or distance from the centre of the oral disc to the tip of the longest arm, and was measured using calipers to the nearest 0.1 mm.

Growth

Length-weight relationship was estimated joining biometrical data from individuals collected in both bathymetrical ranges. The relationship between the length and weight of one organism is usually expressed by the equation, $W = aL^b$, where W is body weight (g), L is length (cm), a is the intercept and b is the allometric coefficient.

4

Values of b significantly different from 3 indicated that growth in weight is relatively faster than that in length (positive allometry (b>3) or lower (negative allometry b<3).

Nearshore and offshore samples were analysed separately to study growth due to the different gear selectivity. Sea star length (R) was categorized into 20-mm classes and grouped every two months to obtain bi-monthly length-frequency distributions. Growth was estimated from the modal class progression analysis in the length-frequency distributions, using the Bhattacharya method (Bhattacharya, 1967), previously used to examine growth in other asteroids (Manzur *et al.*, 2010; Bos *et al.*, 2011) and included in the FISAT II software (Gayanilo *et al.*, 2005). The parameters of the von Bertalanffy growth function ($L_t = L_\infty(1-e^{-k\ (t-\ t_0)})$) were estimated by nonlinear regression using the FiSAT II software package, where, from left to right L_t is the predicted length at time t (mm), L_∞ is the asymptotic length (mm), k is the growth constant (year^{-1}), t the age (year) of the *A. aranciacus*, and t_0 is the age at which L_t=0 (Gulland, 1983).

Reproduction

All nearshore and offshore individuals collected monthly, from May 2011 to September 2012, were used for reproduction analyses. Each sea star was damp-dried and weighed to the nearest 0.001 g. The oral surface was opened by separating the plates along the ambulacral grooves to expose the viscera. The number of immature individuals was annotated and all gonads from adults were examined (between 18 and 34 gonads per month). Gonads and pyloric caeca of the five arms were removed, damp-dried and weighed to 0.001 g accuracy. Gonads were fixed in 10% formalin 24 hours, cleaned with deionised water and preserved with 70% ethanol. The gonad tissue were dehydrated in graded ethanol, and afterward infiltrated and embedded with glycol-methacrylate resin. Gonads were cut into 4µm sections and were stained in Lee's methylene blue-basic fuchsin. Microscopic examination of the sections allowed sex determination and assignation of each individual to a gonad maturation state. Development was divided in five stages based on an adaptation of scales used for other asteroid species, where each stage is determined according to the frequency and characteristics of gametes, presence of phagocytes and cell remains, as well as thickness and shape of the gonadal wall (McClary & Mladenov, 1989; Byrne *et al.*, 1997; Carvalho & Ventura, 2002; Rubilar *et al.*, 2005; Benítez-Villalobos & Martínez-García, 2012).

5

The gonadal index (GI) and the pyloric caeca index (PCI) were calculated as: (wet organ weight/total body wet weight)*100 (Giese, 1966). Size at first maturation (size at which gonads of 50% of the individuals are mature, R50%) was calculated by plotting the percentage of individuals with mature gonads against size (Conand, 1981). To analyse the influence of some exogenous factors on the reproductive biology of this species, surface water temperature was obtained from the Barcelona buoy of "Puertos del Estado" (41.32ºN / 02.20ºE), photoperiod data from "Observatorio Astronómico Nacional, Instituto Geográfico Nacional, Ministerio de Fomento" and chl-a concentration was obtained from MODIS satellite imagery between 2002-2014, using a resolution of 4 km with 0.1 x 0.1 degrees areas.

Statistical analysis

Sex-ratio was tested using a Chi-square (X^2) test. Differences in the mean GSI values between sexes were assessed for each month using Mann–Whitney U test. A Kruskal-Wallis non parametric ANOVA was used to check for differences in pooled GSI and PCI data among months. The relationship between indexes and environmental factors was tested using the Spearman's rank correlation analysis. The correlation coefficient ranges from -1 to +1. Positive values indicated variables tended to increase together. Negative values indicated that one variable tends to decrease while the other increases.

Results

Sea stars collected from both nearshore and offshore areas had different size composition (Fig. 2). *A. aranciacus* major radius length (R) ranged between 11-214 mm in nearshore samples, with a mean size of 81.40 mm (SD = 39.44), whereas R ranged between 47 - 280 mm in offshore individuals, with a mean size of 161.33 mm (SD = 44.47). The arm length-weight relationship can be expressed as: $W = 0.0025L^{3.22}$ (R^2 = 0.95; F (1.487) = 10179, N = 489). Concerning growth types, the length–weight relationship revealed that weight increases isometrically with length for *A. aranciacus*, showing that weigh increase is negative allometric (p < 0.001, t = 35,54), i.e., the sea star become relatively more slender as it grows longer.

Growth

6

The method of Bhattacharya allowed us to identify several cohorts in the *A. aranciacus* length frequency distributions, at both bathymetrical ranges, and to follow the progression of the cohorts along the three years of study (Fig.3). Recruitment nearshore was recorded only twice from the whole period of study, in February 2010 and in April 2012, with mean R sizes of 34.40 mm and 47.56 mm respectively. A cohort (C-1 at Fig.3A) was observed from April 2012 (R = 47.56 mm) to August 2012 (R = 69.15 mm). Another cohort C-2 (Fig.3A) was observed from February 2010 (R = 34.40 mm) to October 2012 (R = 123.62 mm), which is a size increase of 89.22 mm. A third cohort (C3) was also detected (Fig.3A) from December 2009 (R = 113.02 mm) to June 2010 (R = 115.51 mm). In the offshore samples (Fig. 3B) we also observed three cohorts composed by adults but no recruitment or individuals smaller than 100 mm were found. The C-4 cohort (Fig. 3B) was observed from December 2010 (R = 103.04 mm) to October 2012 (R = 144.65 mm); another cohort (C-5, Fig.3B) was found from December 2009 (R = 125.58 mm) to October 2012 (R=171.08 mm), and the last one (C-6, Fig.3B) was occasionally detected from February 2012 (R=206.5 mm) to August 2012 (R = 217.64 mm). Growth rates can be obtained following the mean length of cohorts C-2, C-4 and C-5 along time. The nearshore C-2 cohort showed higher growth rates during summer and autumn (18 - 24 mm from June to October) in the three years studied. The offshore cohort C-4 showed higher growth between February-August 2011 (22.8 mm) and February-October 2012 (10.65 mm). The offshore cohort C-5 showed higher growth between April-August 2010 (14.44 mm). The estimated Von Bertalanffy growth parameters for nearshore individuals were $L\infty$ = 136.75 mm, k = 0. 44 year^{-1}, t_0 = 0.0017 (N = 741; R^2 = 0.73); whereas for offshore individuals were: $L\infty$ = 205 mm, k = 0. 32 year^{-1}, t_0 = 0.0011 (N = 624; R^2 = 0.82).

Gonads morphology and development

The reproductive system of *A. aranciacus* comprises 2 separated gonads in each arm (10 gonads in total). Each gonad was arranged as a series of tufts, located in and attached to the proximal part of each arm, near the disc on the inner face of the lateral wall, below the pyloric caeca, suspended in the coelom along the entire length of the arm. Mature gonads were pale cream in males and deep yellow in females. The gonadal wall consisted of two sac-structures (the inner and the outer sacs) separated by the genital coelom, typical for asteroids.

7

The five stages that characterize the gonadal development of *A. aranciacus* are the following:

Ovogenesis: (Fig.4): *I-Recovery Stage*: ovaries' lumen was partially filled with amorphous material, cell debris and phagocytes. The gonadal wall was thick and the two-sac structures were evident; at advanced recovery stage surface of germinal epithelium was lined with oogonia and sometimes with early vitellogenic oogonia (Fig.4A). *II-Growing Stage*: Early in the growth stage (Fig. 4B), the ovarian surface epithelium was thick and mainly covered by previtellogenic oocytes, although some early vitellogenic oocytes could also be found. Late in the growth stage (Fig. 4C), the ovarian surface epithelium appeared thinner, oocytes accumulated in the lumen and vitellogenic oocytes were dominant. Oocytes showed an eccentric nucleus (Fig.4C). The cytoplasm of the oocytes appeared blue together with oogonia; whereas the nuclei stained in pink. *III-Mature Stage:* Ovaries were densely packed and stacked with fully grown oocytes in the lumen, and the surface epithelium appeared thin. Oogonia and previtellogenic oocytes were uncommon and restricted to the germinal layer. The gonadal wall was the thinnest observed in all the reproductive cycle (Fig.4D). *IV-Partly spawned Stage*: Ovaries were poorly packed with fully grown oocytes in the lumen with important empty spaces; previtellogenic oocytes were scarce and not exclusively restricted to the germinal layer. Relict oocyte debris and phagocytes were present in the lumen. The ovaries wall remained thin (Fig.4E). Sometimes atresia can be observed. *V-Spent stage*: Ovaries were filled with amorphous material with relict oocytes, the gonadal wall becomes thicker and the two-sac structure was more evident. Relict oocyte debris and phagocytes were present in the lumen (Fig.4F).

Spermatogenesis (Fig.5): *I-Recovery Stage*: testes were small and remain contracted; the lumen was almost empty and partially filled with nutritive phagocytes; the gonadal wall was thick and the two gonadal sacs were visible. Spermatogenic columns (consisting in spermatogonia) started to develop and grow (Fig.5A). *II-Growing Stage*: the testes had an intense spermatogenesis activity; they started to widen and become larger. Early in the growth stage, spermatogenic columns were projected into the central lumen and fill almost the totality of the volume; the gonadal wall begins to shrink. As the growth stage progressed, testes enlarged and increased the number of spermatozoa from the border of the columns to the central lumen; at the same time the spermatogenic columns became smaller as the gonadal wall shrinked (Fig.5B-C). *III-*

8

Mature Stage: testes were densely packed and compressed with spermatozoa in the lumen; surrounded by very thin spermatogenic epithelium of spermatogenic columns. The wall of testes was the thinnest observed in all the reproductive cycle (Fig.5D). *IV-Partly spawned Stage:* testes looked similar than those in the mature stage but spermatozoa were poorly packed; there were spaces between patchy concentrations of spermatozoa in the lumen. Sometimes a gap between the peripheral spermatogenic layer and the central mass of spermatozoa is visible. The gonadal wall became thicker, and inner and outer sacs were visible again (Fig.5E). *V-Spent stage:* testes shrunk and became smaller and contracted; the lumen was almost empty with some nutritive phagocytes and isolated spermatozoa. The wall was thick and the two gonadal sacs became evident (Fig.5H).

Reproductive cycle

Results showed that females in Stage I (recovery) were present throughout the whole study. Ovaries in stage II (growing stage) were also found all year round except in spring (May 2011 and from March to May 2012) (Fig.6A). The proportion of females with ovaries in stage II began to increase in June for both studied years, and the maximum frequency of occurrence (90%) was recorded in September 2011. Accordingly, females with mature gonads (stage III) were observed from October 2011 to May 2012, being the period between February and April when more mature females were recorded (>40%). Partially spawned gonads (stage IV) were observed from December to June, with the highest frequency found in May 2012. The majority of the spent ovaries (stage V) were found between March and July for both 2011 and 2012.

Similarly to females, males in Stage I were present throughout the whole study except for March 2012. Spermatogenesis (stage II) started between August and September and lasted in January, but was dominant between October and December (Fig.6B). In accordance, mature testes (stage III) appeared afterwards and were observed in some individuals from December to May. Partially spawned (stage IV) individuals were found between January and July, with a higher frequency in April 2012. Despite that a few spent testes (stage V) were observed in February 2012, most of the individuals in this reproductive stage were observed from March to August.

Sex ratio and size at first maturity

9

Sea stars did not show sexual dimorphism. A total of 313 individuals were collected from nearshore (87 females, 89 males and 136 immature) and 244 individuals from offshore (135 females, 116 males and 2 immature). The Chi-square (X^2) test did not show significant differences between sexes; the ratio between males and females was almost 1:1 throughout the year at both bathymetrical ranges: nearshore (X^2=10.186 dF=15; p > 0.05) and offshore (X^2 = 19.856; dF = 16, p > 0.05). The size of the smallest sea star with gonads was R = 56 mm for females and R = 55 mm for males. The size at first maturity (R50%) was estimated to be R = 112 mm.

Organ indexes

No significant differences among sexes were found when comparing the monthly gonadal and pyloric caeca indexes (Mann-Whitney, p>0.05), and then, values for both sexes were pooled for further analyses. Gonadal index (GI) values for *A. aranciacus* (Fig.7) showed significant differences among months (H = 110.07; dF = 16, p < 0.001). Monthly values revealed a slow and more or less constant increase from September 2011 to March 2012, when GI reached its maximum (3.62 %). After that peak it decreased until July 2012 (0.14%). Significant differences were also observed among months for Pyloric caeca index (PCI) (H = 58.76; dF = 16, p < 0.001). Highest values were recorded between March and May 2012 (> 4.5 %), whereas minimum values were observed in the summer months (June, July, August 2011, and July, August, September 2012). The surface sea water temperature at the study site had maximum values in summer months (July to September) and the minimum values in winter months (January to March) (Fig. 8). The photoperiod dynamics showed maximum day length values in summer and minimum values in winter, with a gradual increase in spring and decrease in autumn (Fig. 8). Figure 8 shows two different chlorophyll-a values. On one side, chl-a monthly values recorded during our study period had lower values between July and September, and two peaks were recorded, one in December 2011 (0.46 mg.m^{-3}) and another in March 2012 (0.93 mg.m^3). On another side, chl-a monthly mean values from years 2002 to 2014 showed the same seasonality as observed in our study from May 2011 to September 2012. The Spearman's rank correlation analysis detected a strong positive correlation between GI and PCI (P<0.01; Table 1). A negative correlation between both indexes and SSWT but positive correlation with chl-a monthly values recorded during our study period. Nevertheless, GI had a negative

10

correlation with photoperiod but no correlation between PCI and photoperiod was observed.

Discussion

  A. aranciacus individuals smaller of 80 mm were abundant in shallow waters (5-30 m depth) whereas large individuals (> 130 mm) were observed mostly offshore (50-150 m depth). The use of different gears to sample both bathymetric ranges in this study may have caused bias collecting small sizes offshore, but no bias for bigger sizes in shallow waters could happen. Therefore, in case of bigger individuals of *A. aranciacus* inhabiting from 5 to 30 m, they would have been collected in our sampling. Burla *et al.* (1972) studied the activity pattern of *A. aranciacus* by scuba diving in Sardinia (Italy) and found only small specimens. These authors suggested that adults and juveniles may dwell in different parts of the ecological zone occupied by the species, the fully-grown specimens invading the deeper waters. Our study is the first that had sampled most of the bathymetrical distribution range of this species, allowing us to confirm a bathymetrical segregation by size in *A. aranciacus*. Size depth trends were also reported for the asteroid *Protoreaster nodosus*, whose large specimens inhabits between 0 and 33 m depth whereas small specimens were exclusively found in shallower habitats (< 5m) (Bos et al., 2008). Young sea stars might prefer shallow areas, where food and shelters to avoid predation are usually more abundant (Manzur et al., 2010).

  The major radius length-weight relationship showed a negative allometry in *A. aranciacus*, as previously observed in other asteroids (Bos *et al.*, 2008; Bos *et al.*, 2011). Absolute growth has been extensively analysed in in sea stars (see references in Lawrence & Lane, 1982) but few studies have established growth rates in natural populations of the genus *Astropecten* (Nojima, 1982; Ventura, 1999; Freeman *et al.*, 2001). The *A. aranciacus* population studied exhibited a seasonal pattern of growth, being higher from June to October in the nearshore cohorts. Growth period was wider offshore (February-October) although the growth rate was lower (about half) in comparison with nearshore values. Seasonal variation in growth has been described in other *Astropecten* species, that usually showed a decrease in growth rate associated with gonad maturation (Nojima, 1982; Ventura, 1999; Freeman et al., 2001), but it was not observed in *A. aranciacus*. Growth rate seems to be related to sea water temperature in *A. aranciacus*. Higher growth was recorded nearshore when sea water temperature was

11

above 21ºC (between June to October). Moreover, sea water temperature increased slightly from February to December offshore, in coincidence with the period of higher growth rate. Ventura (2013) reported that the decrease in *A. brasiliensis* and *A. cingulatus* growth rate coincided with the seasonal upwelling period in Brazil, suggesting that it could be related to sea water temperature decline. Other factors like the amount and quality of available food can also affect growth, as observed by Guillou & Guillaumin (1984) in *Asterias rubens*.

The *A. aranciacus* population here studied seems to have variable reproductive and recruitment success. Recruits were detected on February 2010 and April 2012 nearshore, but they were not detected on 2011. The absence or low rate of recruitment throughout a period of time is not rare in echinoderms, and it has been attributed to hydrological processes and predation upon embryos and larvae (Thorson, 1946; Freeman *et al.*, 2001). Therefore, even if the reproductive cycle is annual, recruitment may not be successful every year.

The histological study of the gonads showed that the structure of the *A. aranciacus* gonads is the typical for asteroids. Both sexes had a synchronous gametogenesis. Notwithstanding, females reached the maturity stage slightly earlier than males (females: October; and males: December). Byrne *et al.* (1997) observed a similar behavior in *Asterias amurensis*. The studied *A. aranciacus* population did not differ significantly in the male-female proportions, in coincidence with previous results in other asteroids (Kim, 1968; Benítez-Villalobos & Martínez-García, 2012). Even though the spawning peak occurs between April and May, the development of the gonads reflected that mature and partially-spawned individuals remained for an extended period of time. The gonadal index value was higher in March, indicating that during that period the gonads of *A. aranciacus* were in maximum development. Spawning likely occurred during April and May, in accordance with the decreased of GI and the presence of post spawning individuals in the histological samples.

In general the reproductive cycles of sea stars are correlated with a combination of endogenous (*i.e.* hormones) and exogenous factors (*i.e.* temperature, photoperiod, food availability, lunar cycle, tidal flux and light intensity) (Mercier & Hamel, 2009). However, the direct influence of each factor remain poorly understood (Mercier & Hamel, 2009). In *Astropecten* species, breeding season commonly coincides with the increase of water temperatures on temperate areas (Grant & Tyler, 1986; Marion *et al.*, 1998; Freeman *et al.*, 2001). For instance, Freeman *et al.* (2001) reported that the

12

spawning periods for *A. irregularis* coincided with the rise from 8ºC to 15ºC in seawater temperatures (North Wales). Our results showed the same pattern, because *A. aranciacus* spawning season was in spring, when the sea water temperatures begun to increase in the Mediterranean. Our findings also showed that spawning occurred during the minimum day length period of the year. This inverse relationship found between GI and photoperiod has not been described previously in the genus *Astropecten*, and it is rare in sea stars although it is common in other echinoderms (Mercier & Hamel, 2009). We also observed that *A. aranciacus* GI was related to the highest chlorophyll-a concentration in the water, which was originated by the spring phytoplankton bloom typical from the Mediterranean Sea. The correlation between phytoplankton concentration and GI has been previously described in other echinoderms, but it is rare in sea stars (Mercier & Hamel, 2009). The majority of the species of the genus *Astropecten* have planktonic larvae (bipinnaria). Bipinnaria larva nourish essentially on detritus, bacteria, phytoplankton (mainly small diatoms and small flagellates) and small zooplankton (Ayukai, 1993). The synchronism between the gonadal development of *A. aranciacus* and the phytoplankton bloom could be a strategy to guaranty higher survival of early developmental stages.

An inverse correlation between GI and PCI has been usually described in most sea stars, suggesting the transference of nutrients from the pyloric caeca to the gonads during gametogenesis (Lawrence & Lane, 1982). Nevertheless, this interaction has not been observed in those species inhabiting areas with stable environmental conditions (Benítez-Villalobos & Martínez-García, 2012). This relationship was not observed in the studied *A. aranciacus* population despite inhabiting in a seasonally changing environment, in accordance with the results obtained by Ventura *et al.* (1998) in *A. cingulatus*. Individuals of *A. aranciacus* collected in the offshore zone of the study area had large amount of preys in the stomach throughout the year. Most of these prey items were the venerid *Timoclea ovata* (>55%, abundance in 224 sea stars analyzed) and each sea star stomach contains a mean of 49 *T. ovata* items of a mean size of 5.77 mm (SD = 5.52, N=9682) (*unpublished data*). Then, food does not seems to be a limiting factor in the Maresme coast, suggesting that sea stars do not need to storage large amount of nutrients in pyloric caecum, because nutrients can be easily obtained from the environment throughout all year. This may be the reason why an inverse correlation between GI and PCI was not observed in *A. aranciacus*.

13

Our findings not only provide a better understanding of the biology of *A. aranciacus* on the NW Mediterranean Sea, but are also relevant for the future conservation of this sea star, since its populations seems to decrease in some places of the Mediterranean Sea.

14

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15

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17

Fig. 1. Study area showing the location of the sampling areas in the Maresme coast (circles) and the 30, 50 and 100 m isobaths.
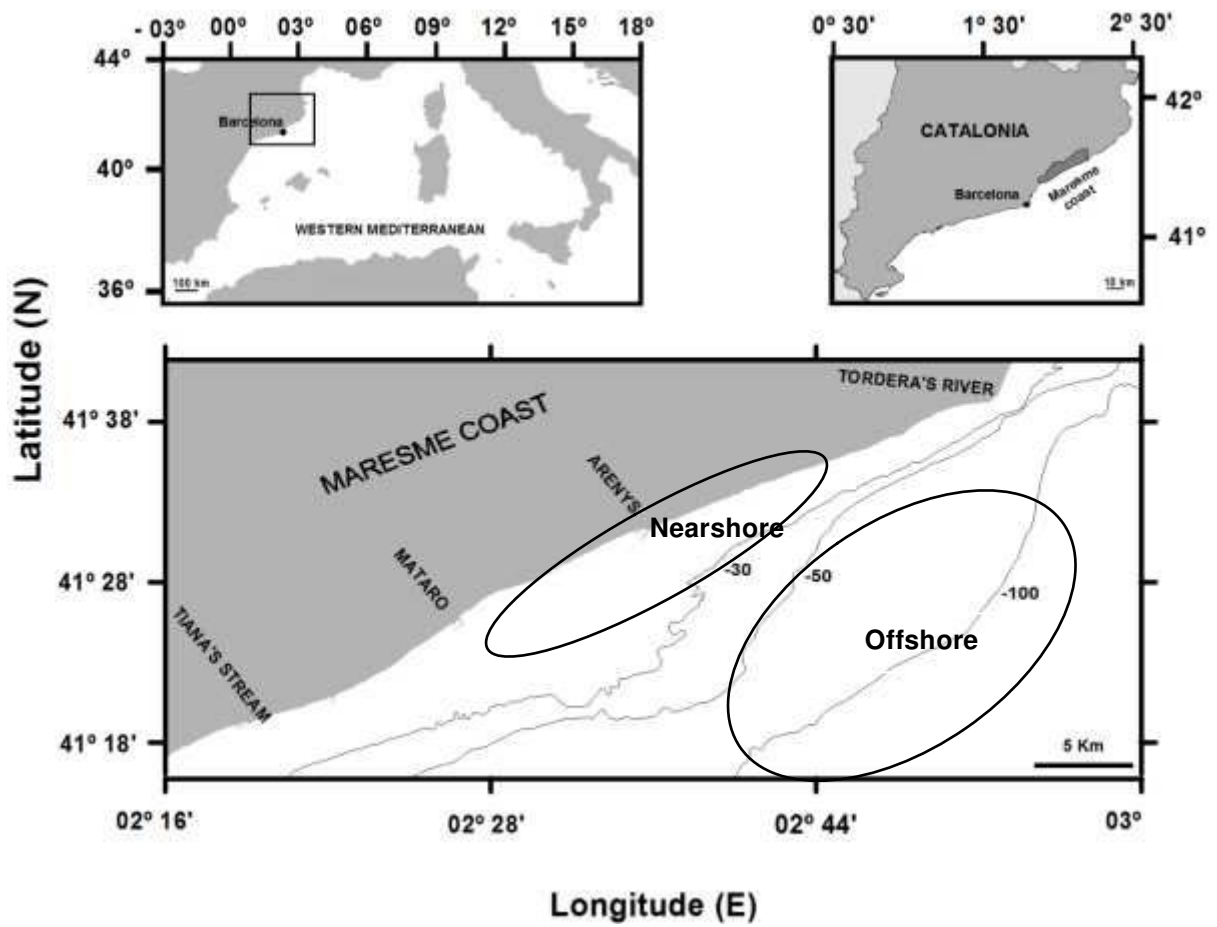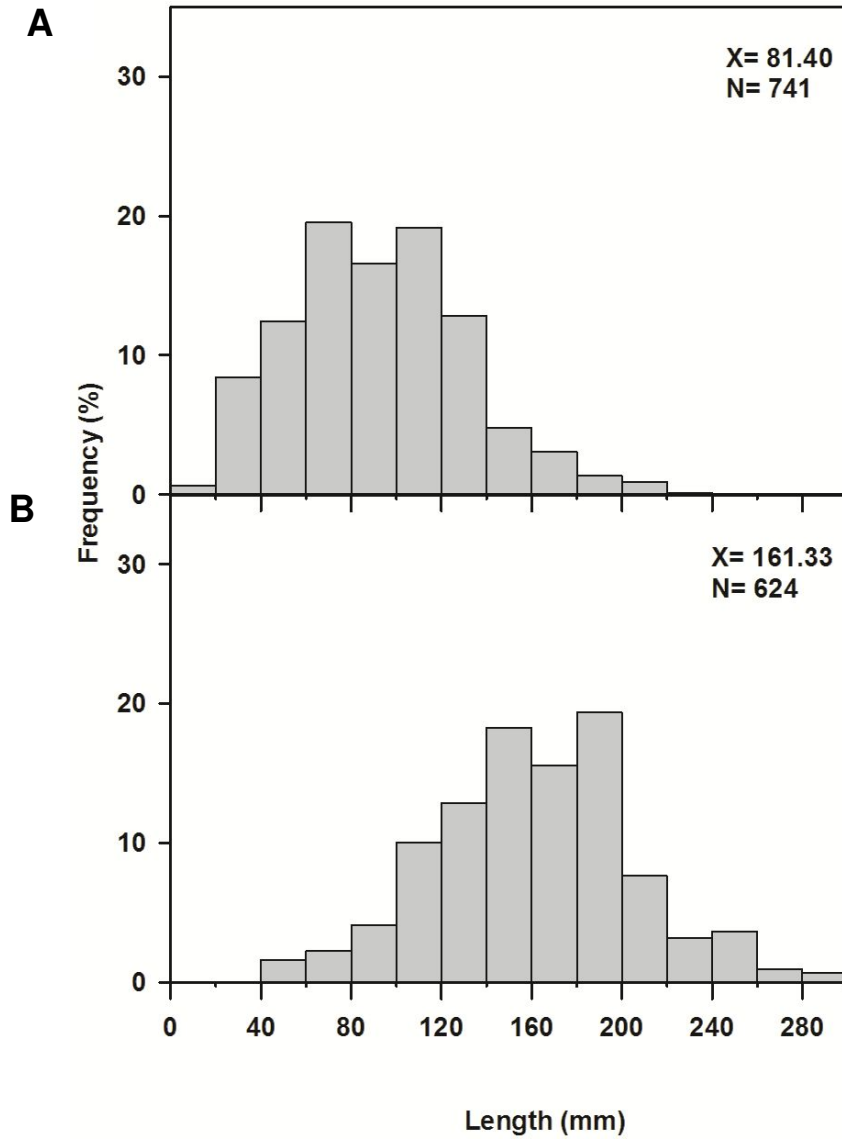
19

Fig. 3. *A. aranciacus* growth between December 2009 and October 2012 estimated from bimonthly progression of mean length of each cohort (±SD) in length frequency distributions, at both bathymetrical ranges (A) 5-30 m and (B) 50-150 m. Each symbol corresponds to different sea star cohorts. In (A) white circles indicate cohort C-1; gray circles C-2 and black circles C-3; in (B) black circles indicate cohort C-4, light grey circles C-5 and dark grey circles C-6. The black line indicates sea water temperature at -20 m (A) and at -80 m (B).
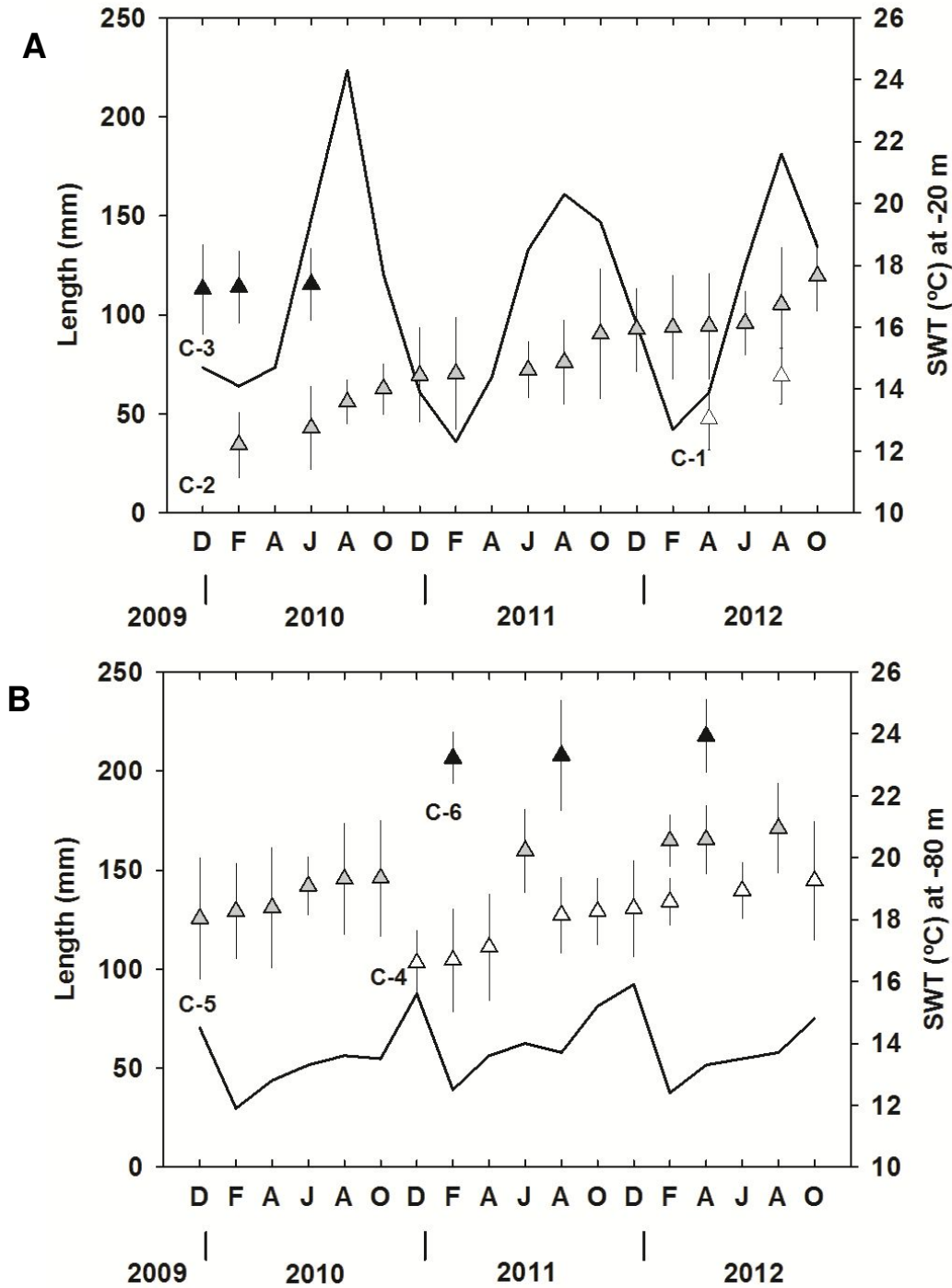

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130

Fig. 4. Photomicrographs of *A. aranciacus* ovaries: (A) Stage I: Recovery Stage; (B-C) Stage II: Growing Stage*;* (D) Stage *III: Mature* Stage*;* (E) *Stage IV: Partly spawned Stage;* (F) Stage V: Spent stage. *hf*: haemal invaginations; *hs*: haemal sinus; *lu*: lumen, *o*:oogonia; *po*: previtelogenic oocyte, *vo*: vitelogenic oocyte; *ro*: relict oocyte and *np*: nutritional phagocytes. Scale bars = 500µm.
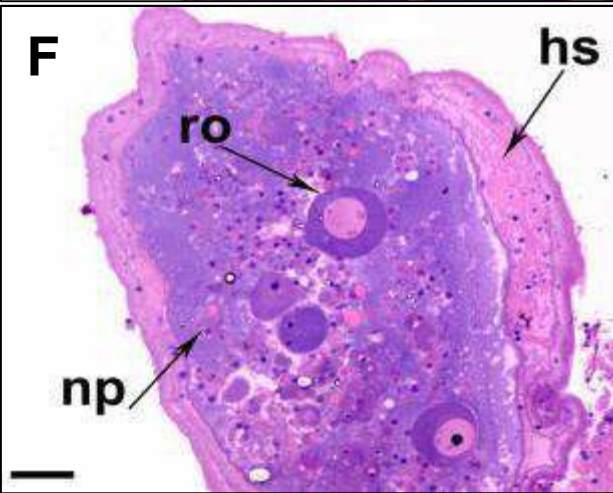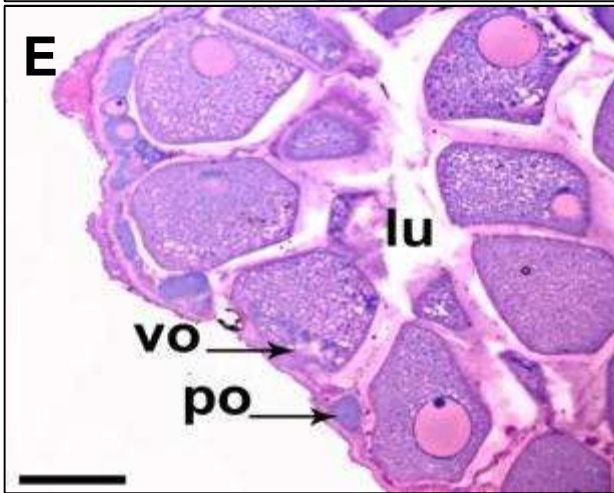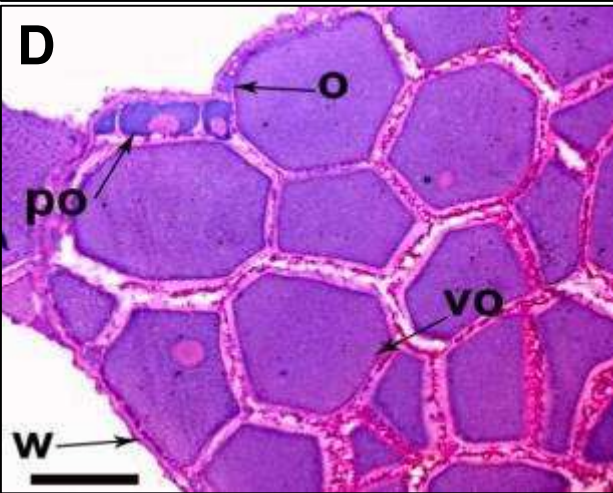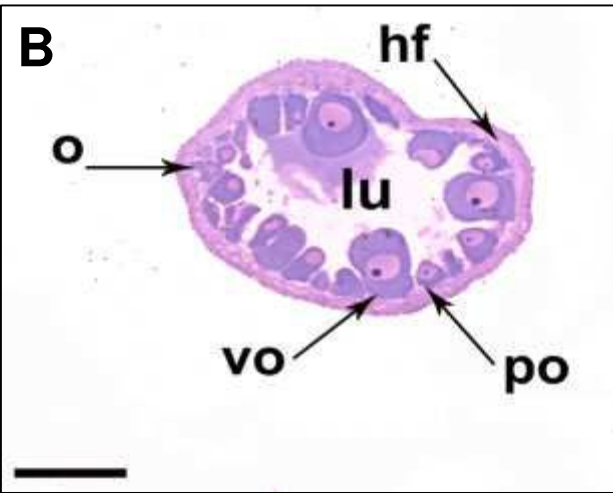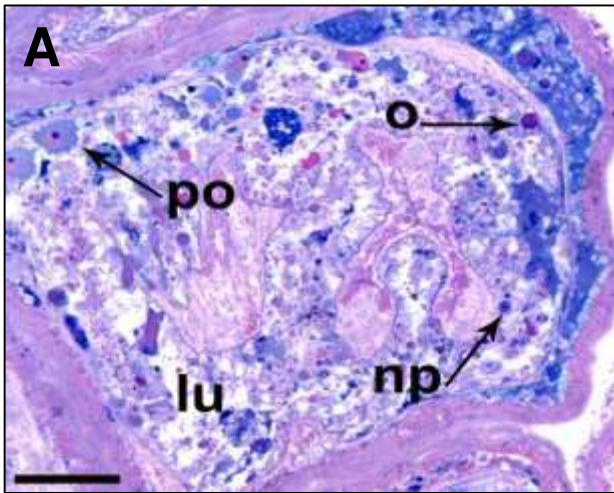
Fig. 5. Photomicrographs of *A.aranciacus* testes: (A) Stage *I: Recovery Stage*, (B-C) Stage *II: Growing Stage;* (D) Stage *III: Mature Stage;* (E) Stage *IV: Partly spawned Stage*, (F) Stage V: *Spent stage. Hf*: haemal invaginations; *hs*: haemal sinus; *lu*: lumen, *sc*: spermatogenic columns; *sp*: spermatogonia; *sm*: spermatids; *s*: spermatozoa; *rs*: residual spermatozoa; and *np*: nutritional phagocytes. Scale bars= 500µm.

23

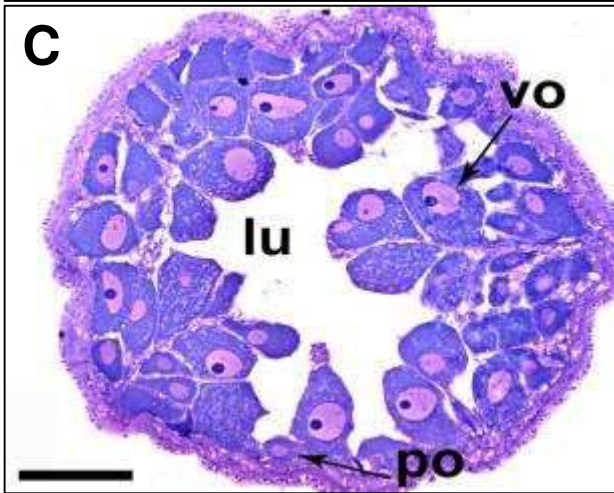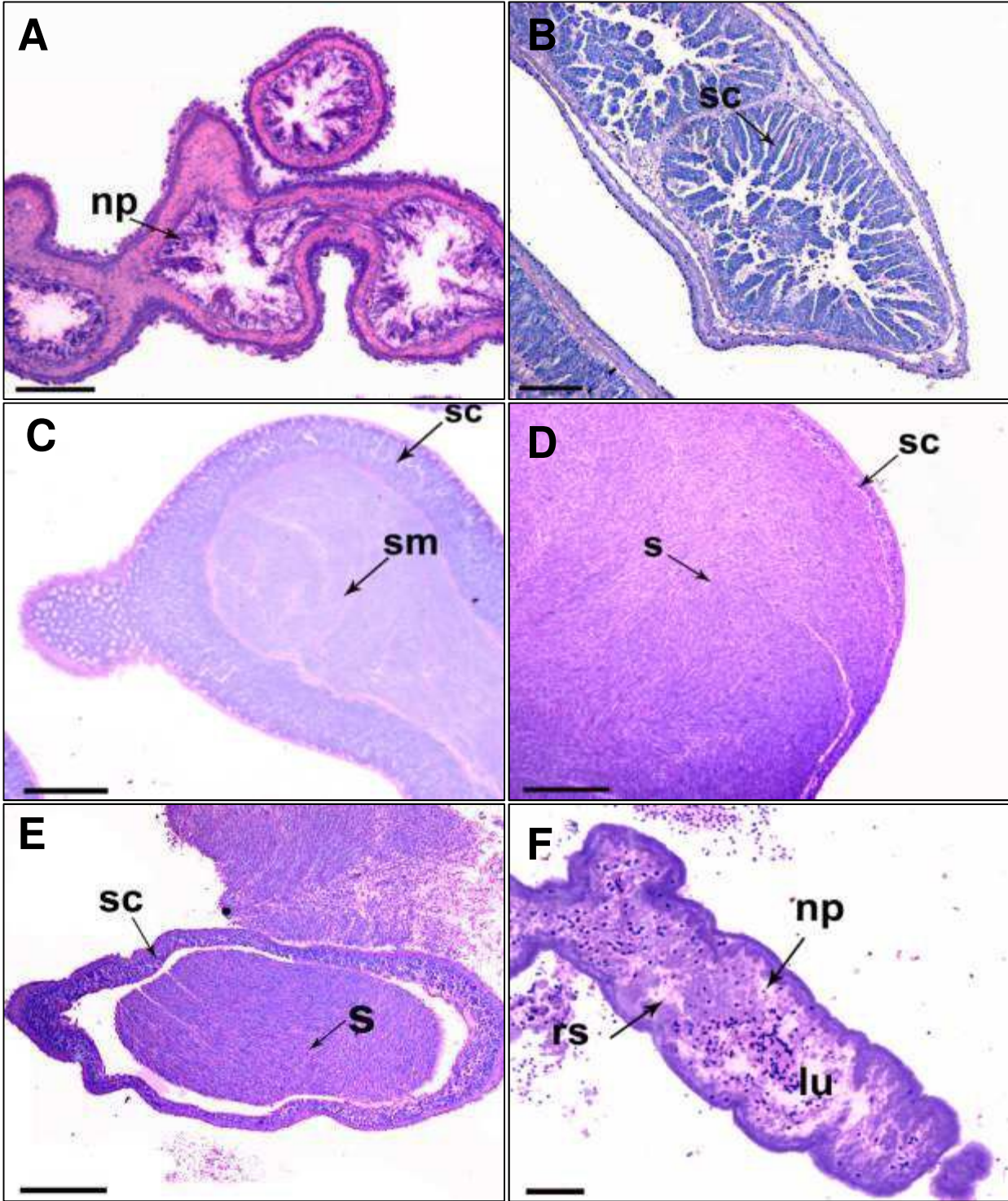**Fig. 6.** Annual gametogenesis cycle of *A. aranciacus* between May 2011 and September 2012. (A) Females; (B) Males. Numbers on the top of each column indicate the number of individuals analyzed monthly per sex.
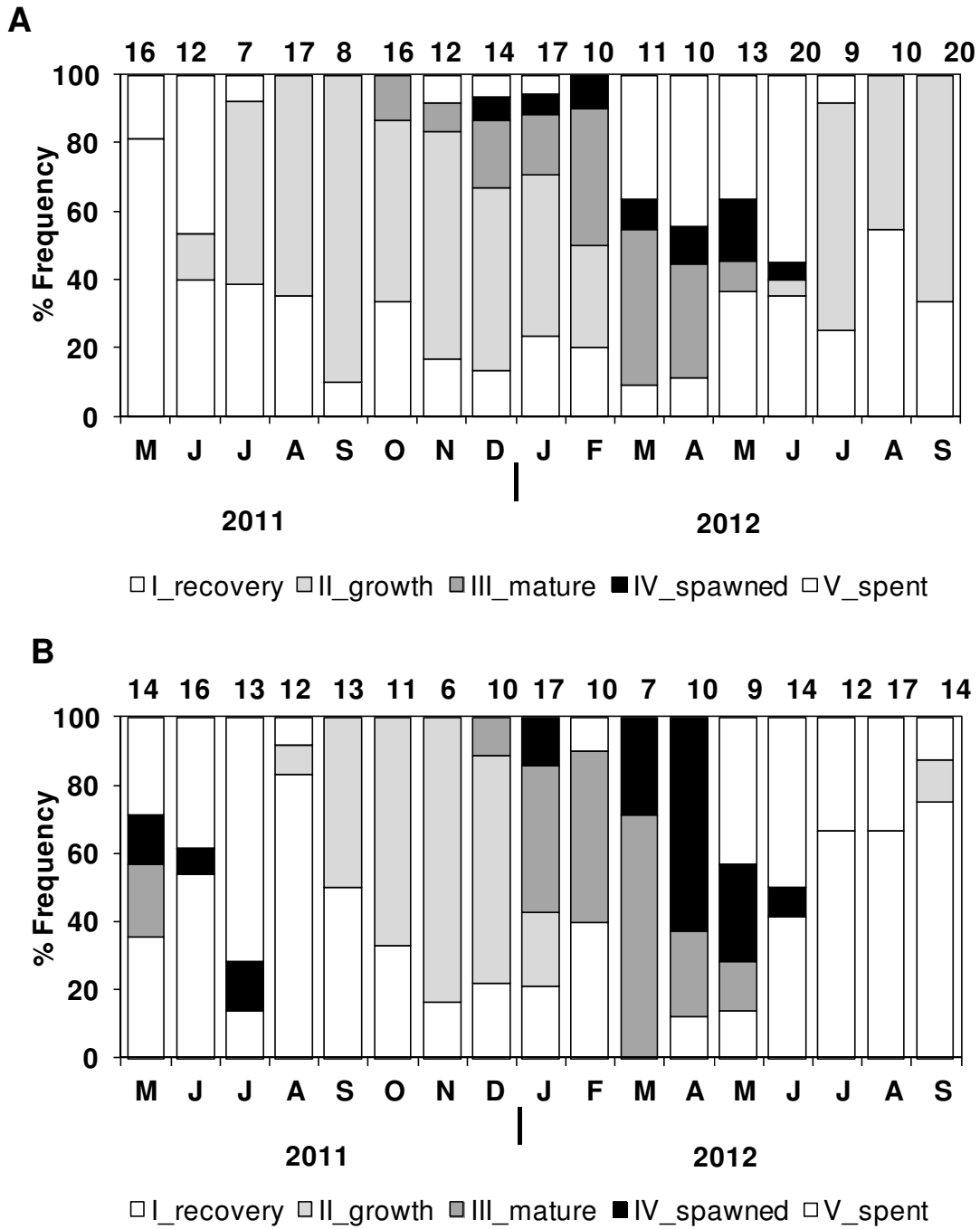
Fig. 7. Seasonal changes in gonadal index (GI, mean,–SE) and pyloric caeca index (PCI, mean, -SE).
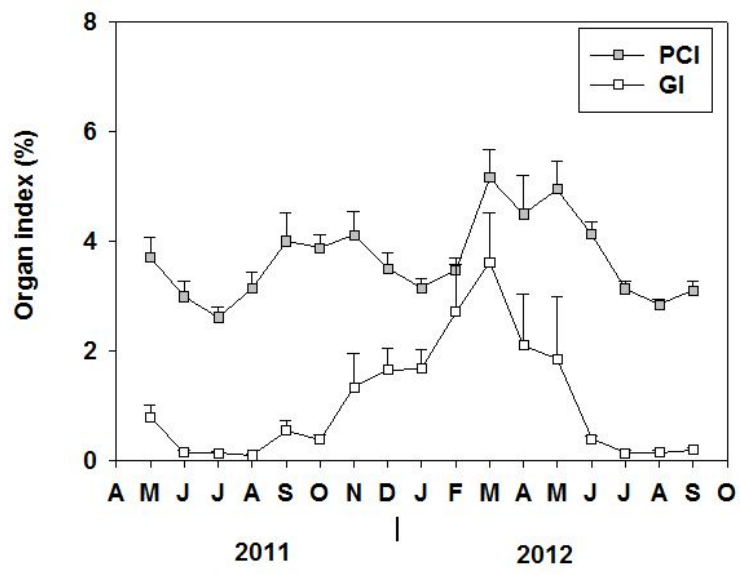
Fig. 8. Monthly mean of surface sea water temperature (SSWT; grey long dash); photoperiod (Photo; grey line), expressed in number of daylight hours every 24 h; mean values of chlorophyll-a (chl-a) concentration from May 2011 to September 2012 (dotted line). Black line indicates the monthly mean of chlorophyll-a (chl-a) concentration throughout the period 2002-2014

27
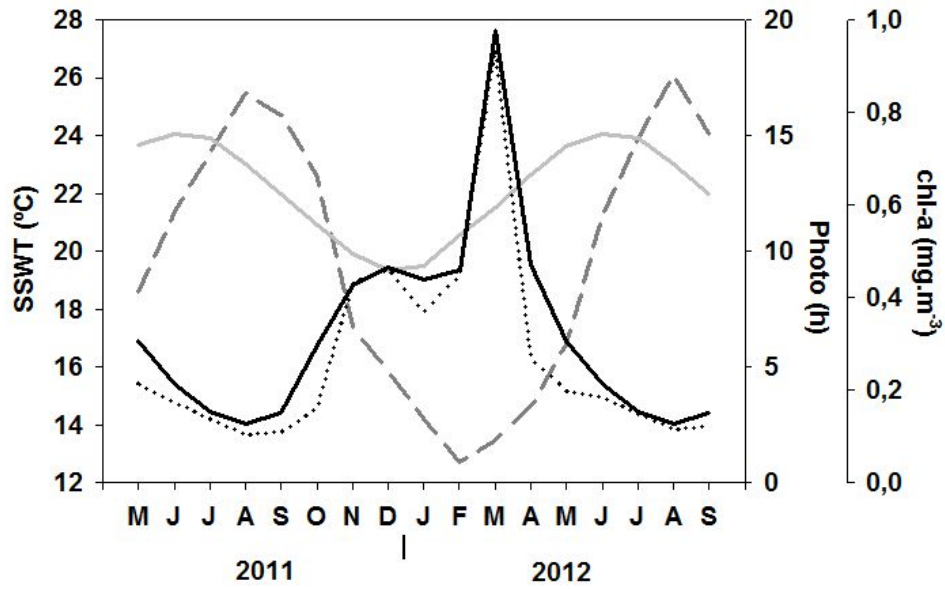
7.5. Other collaborations

In parallel to my work, I have been involved in the following papers as a co-author, both related with some aspects of this Doctoral Thesis.

1. Eva Pubill, Pere Abelló, Montserrat Ramón and Marc Baeta. 2011. Faunistic assemblages of a sublittoral coarse sand habitat of the northwestern Mediterranean. *Scientia Marina* 75 (1): 189-196.

2. Eve Galimany, Marc Baeta, Mercè Durfort, Jordi Lleonart, Montserrat Ramón. 2015. Reproduction and size at first maturity in a Mediterranean exploited *Callista chione* (L. 1758) bivalve bed. *Scientia Marina* (in press).

8. RESUMEN

8.1. Introducción

El concepto de especies clave ha sido amplia e históricamente utilizado en biología y ecología (Simberloff 1998) desde que fue creado por Paine (1966). Las especies clave son aquellas consideradas excepcionales por fomentar y mantener la estructura y la diversidad del conjunto de la comunidad a la que pertenecen (Paine 1969; Mills *et al.* 1993). Entre las especies con estas características se han descrito distintos moluscos bivalvos (ostras, mejillones, almejas, berberechos etc.) que viven formando grandes agregaciones de individuos, así como depredadores que ocupan altos niveles tróficos como las estrellas de mar (Paine 1969; Dame 1996). Desafortunadamente, a pesar de que estas especies tienen un papel crucial en los ecosistemas, su ecología ha sido a menudo poco estudiado, y a veces como en el caso muchas especies de estrellas de mar sigue siendo una gran desconocida.

La biodiversidad mundial está disminuyendo a un ritmo alarmante debido a las actividades humanas (Jenkins *et al.* 2003). Estudios recientes sugieren que nos encontramos frente a la sexta extinción en masa que ha experimentado el planeta Tierra desde que se inició la vida (Barnosky *et al.* 2011). A lo largo de las últimas décadas expertos conservacionistas han fijado su atención en la identificación de las áreas más importantes para preservar la diversidad genética, las especies y los ecosistemas; y fruto de su estudio se han identificado 25 zonas clave para la preservación de la biodiversidad, siendo la cuenca del Mar Mediterráneo una de ellas (Myers *et al.* 2000; Shi *et al.* 2005). Se especula que habitan este mar aproximadamente unas 17000 especies, aunque el estado de conservación de la mayoría de ellas es una verdadera incógnita (Coll *et al.* 2010).

Esta Tesis Doctoral ha contribuido a mejorar el conocimiento de la biología y la ecología de algunas de estas especies clave; la concha fina *C. chione* y las estrellas de mar del género *Astropecten*. La concha fina es actualmente una de las pocas especies de bivalvos con una cierta importancia comercial en el Mar Mediterráneo, que históricamente ha constituido un importante recurso en la costa del Maresme (Cataluña), dónde ha sustentado una importante pesquería artesanal asociada. En la misma zona la presencia de distintas especies de estrellas de mar del género *Astropecten* aparecen regularmente como "by-catch" de la pesquería de dicho bivalvo. Estas estrellas de mar se caracterizan por ser voraces depredadores en la cúspide de la red trófica, o cerca de ella; y desempeñan un papel esencial en los ecosistemas de fondos blandos, donde pueden llegar a influir las poblaciones de bivalvos comerciales. A pesar de ello, su ecología y el rol que desempeñan en la población de concha fina del Maresme eran desconocidos.

El término Mediterráneo deriva del latín "*Mediterraneus*" que significa "entre tierras", ya que se encuentra localizado entre tres continentes Europa, Asia y África. El Mar Mediterráneo cubre una extensión aproximada de 2.5 millones de Km^2, con una profundidad media de 1500 metros, un volumen de 3.7 millones de Km^3 y tiene un periodo de renovación de 80 años (Ambroggi 1977; Vanney and Gennesseaux 1985). Es además el mayor mar semi-cerrado de la tierra (Tyler 2003) y se caracteriza por ser oligotrófico con una baja producción primaria en comparación con otros océanos y mares. La concentración de nutrientes decrece de oeste a este (Danovaro *et al.* 2010), presenta una temperatura constante (12.5-14.5ºC), por debajo de los 200 metros de

profundidad a lo largo de todo el año, una elevada salinidad (38.0-39.5‰) y elevadas concentraciones de oxígeno (4.5-5 ml/l), alcanzando niveles de saturación en la superficie (Hopkins 1985).

Como ya se ha comentado previamente, el Mar Mediterráneo es también una de las zonas que concentra unos mayores niveles de biodiversidad del planeta Tierra (Myers *et al.* 2000; Shi *et al.* 2005). Sin embargo, a su vez se encuentra sujeto a una importante presión antrópica y a un sinfín de impactos producidos por las actividades humanas (infraestructuras costeras, superpoblación, contaminación, turismo, erosión, especies invasoras etc.). Entre todas ellas, Costello *et al.* (2010) identificó la sobrepesca, la pérdida de hábitats y la contaminación como las principales amenazas para la conservación de su biodiversidad. Aunque dichas amenazas existen para todo el Mar Mediterráneo son más intensas en las zonas costeras (Coll *et al.* 2010).

Existe una cierta controversia en el mundo académico sobre la definición de zonas costeras, aunque la más aceptada es la que incluye "el área geográfica marina situada entre el la zona intermareal y el borde de la plataforma continental" (Creel 2003). Las zonas costeras se caracterizan por presentar una elevada productividad primaria y secundaria, así como por concentrar una elevada diversidad de fauna y flora (Beck *et al.* 2001). Además, juegan un papel vital para muchas especies de peces e invertebrados que la utilizan durante parte o la totalidad de su ciclo vital (Elliott and Dewailly 1995). Estas zonas también han sido ampliamente reconocidas como refugio para juveniles de muchas especies (Rozas and Odum 1988). No obstante, son lugares con sistemas altamente variables, ya que están fuertemente influenciadas por variaciones en los parámetros ambientales (temperatura, salinidad, irradiación solar etc.) y por las zonas terrestres anexas (ríos, vertidos de aguas residuales urbanas e industriales, etc.). Dichas variaciones se ven reflejadas en la dinámica poblacional de las especies que las habitan (Calbet *et al.* 2001).

El conjunto de estudios que se han desarrollado en la presente Tesis Doctoral se ha desarrollado exclusivamente en la zona costera del Maresme (Barcelona, Cataluña, España) situada en noroeste del Mar Mediterráneo. El Maresme se halla localizado al noroeste de la ciudad de Barcelona, en el interior de su área metropolitana y es una de las zonas más altamente pobladas de la costa de España. Su costa tiene una longitud de 51 Km entre la desembocadura del Río Tordera (noroeste) y de la Riera de Tiana (suroeste) (Ercilla *et al.* 2010) (Fig. 1). Esta zona ha concentrado en los últimos 70 años un fuerte incremento poblacional y por lo tanto una fuerte presión antrópica sobre el medio ambiente marino, el cual se ha visto fuertemente alterado (Ercilla *et al.* 2010). La zona costera del Maresme se caracteriza por estar dominada por fondos blandos de arenas gruesas (0.63-2.0 mm). Esta tipología de fondos marinos es relativamente escasa en el Mediterráneo Occidental y además de la zona de estudio (Maresme-Costa Brava) únicamente se detecta en el Mar de Alboran (costa Mediterránea de Andalucía) en la costa española del Mar Mediterráneo (Pubill *et al.* 2011).

Los fondos blandos marinos se caracterizan por ser los mayores y más antiguos hábitats del planeta Tierra (Gray 2002). Alojan una gran variedad de organismos y desempeñan un papel fundamental en el funcionamiento de los ecosistemas marinos (Lohrer and Hancock 2004). La actividad de dichos organismos tiene una fuerte influencia sobre en el ciclo global del carbono, del nitrógeno y del azufre; el transporte, precipitación y procesos metabólicos de muchos contaminantes; la producción secundaria (incluyendo

las especies comerciales); y el transporte sedimentos (Snelgrove 1998; Díaz-Castañeda and Harris 2004).

La existencia de una correlación entre ciertos grupos de organismos y sedimentos con unas características morfológicas concretas a una profundidad específica fue descrita por primera vez por Petersen (1914). Años después también se definió dicha correlación para el Mar Mediterráneo (Pérès and Picard 1964; Picard 1965; Pérès 1982). Los fondos blandos que se encuentran en la plataforma continental están sujetos a fuertes presiones antrópicas, aunque es la pesca (esencialmente de arrastre y con dragas) la actividad que más severamente impacta y deteriora estas zonas y sus comunidades biológicas (Dayton *et al.* 1995; Jennings and Kaiser 1998; Thrush and Dayton 2002). En las últimas décadas se ha incrementado de forma alarmante la extracción de arenas para distintos usos (construcción, industrial, y para combatir la erosión) (van Dalfsen *et al.* 2000). Esta actividad se ha observado que es también muy impactante sobre las comunidades biológicas que habitan en dichos fondos, siendo especialmente severa en especies de crecimiento lento y larga esperanza de vida (Newell *et al.* 1998; Sardá *et al.* 2000; Bolam *et al.* 2006).

Las comunidades biológicas son agrupaciones de organismos cuya composición y aspecto vienen determinados por las propiedades del medio ambiente y por las interacciones de los organismos que las conforman entre sí (Krebs 2009). Estas interacciones pueden ocurrir de forma directa (vía interferencia competitiva, depredación, parasitismo, comensalismo y mutualismo) o de forma indirecta (vía alteraciones bióticas de la condiciones, competencia por los recursos y competición aparente) (Siepielski and McPeek 2010). Los trabajos desarrollados en la presente Tesis Doctoral han pretendido desarrollar el estudio las dos interacciones siguientes: competencia por los recursos (entre las distintas especies de estrellas de mar) y la depredación (de las estrellas sobre los moluscos esencialmente bivalvos y en menor medida gasterópodos).

Algunas especies juegan un papel clave en las comunidades biológicas, y su desaparición puede producir una reducción de la diversidad de especies así como provocar cambios en la estructura y la dinámica de sus especies, estas especies han sido denominadas "*Keystone species*" o especies clave (Jones et al., 1994). Desafortunadamente muchas de estas especies son absolutamente desconocidas hasta que ya es demasiado tarde y fruto de alguna actividad humana desaparecen, provocando cambios irreversibles en las comunidades biológicas a las que pertenecen y por extensión en los ecosistemas marinos. La detección de estas especies singulares es muy difícil, no obstante debe ser una prioridad para la conservación de la biodiversidad global. Según mi opinión los gestores y los gobiernos no están prestando suficiente atención a estas especies y las consecuencias de su desaparición pueden ser impredecibles.

Existen distintas tipologías de especies clave en función del papel funcional que desarrollan en las comunidades biológicas en las que se encuentran. Esta Tesis Doctoral ha centrado su atención en dos tipologías distintas: depredadores y modificadores de hábitat y/o ingenieros. (1) Depredadores: cuando un único depredador determina la estructura, diversidad, composición de tallas y distribución de varias especies de presas en una comunidad. Corresponde a la primera definición que dio Paine (1966) a las especies clave. Muchas especies de estrellas de mar se han considerado pertenecientes a

este grupo, de hecho Paine (1966) se inspiró en una estrella de mar intermareal para formular ésta definición. (2) Ingenieros y/o modificadores de hábitat: especies que modifican las características del hábitat en el que viven y que a su vez tienen efectos tróficos directos sobre otras especies, modificando por ejemplo su supervivencia (Mills *et al.* 1993). Se ha considerado pertenecientes a éste grupo por ejemplo las grandes agrupaciones de moluscos bivalvos. (Dame 1996).

Las grandes agrupaciones de bivalvos se encuentran a menudo en zonas costeras y/o estuáricas, dónde juegan un papel clave en la biogeoquímica de los sedimentos, así como el control de la dinámica planctónica de la columna de agua y su turbidez (Dame 1996). Estas grandes concentraciones de moluscos han sido explotadas desde tiempos remotos (Paleolítico) por los homínidos (*Homo sapiens* y *Homo neanderthalensis*) (Colonese *et al.* 2011). Su explotación fue más o menos sostenible hasta mediados del siglo XVIII y principios del siglo XIX, cuando con la Revolución Industrial se mejoraron las técnicas de recolección y explotación y se detectaron los primeros síntomas de sobreexplotación en los bancos de bivalvos de Europa y Norte América. Desde entonces se ha producido el colapso de muchas de sus pesquerías, que no ha dejado de producirse hasta nuestros días (MacKenzie *et al.* 1997b; MacKenzie *et al.* 1997a; MacKenzie *et al.* 1997c).

En el Mar Mediterráneo, la industrialización de esta pesquería se produjo ya bien entrado el siglo XX. Aunque no fue hasta principios de los años 80 y los 90 en que las capturas de la mayoría de especies explotadas empezaron a disminuir de forma notable. Esta reducción se produjo en especies como la coquina y la chirla y se detectó en los principales países que las explotaban comercialmente: Grecia, Italia y España (Ramón *et al.* 2005; Koutsoubas *et al.* 2007; Romanelli *et al.* 2009; Baeta *et al.* 2014). En la costa mediterránea de España por ejemplo actualmente la mayoría de pesquerías de bivalvos han desaparecido y únicamente quedan algunos ejemplos muy localizados geográficamente de lo que fue antaño esta pesquería. El declive de las poblaciones moluscos bivalvos ha tenido un efecto muy importante sobre la economía de las zonas costeras. No obstante el efecto que ha tenido sobre los ecosistemas costeros y estuáricos no ha sido estudiado.

La dicotomía de fuerzas "*top-down*" (de arriba abajo) y "*bottom-up*" (de abajo a arriba) que actúan sobre especies que conforman las comunidades ha motivado el estudio y la investigación en ecología desde sus inicios. Dichas fuerzas son las que controlan y rigen las comunidades biológicas. Cuando dichas fuerzas son alteradas se puede producir un efecto cascada en ambos sentidos. Las cascadas "*top-down*" suceden cuando la red trófica se ve alterada por la eliminación de un superdepredador o un depredador que ocupa altos niveles tróficos. Por otro lado, las cascadas "*bottom-up*" se producen cuando los productores primarios o algún consumidor que ocupan bajos niveles tróficos se ven alterados (Krebs 2009). Habitualmente en los fondos blandos marinos las comunidades biológicas a escala local (<1 km) están controladas por los depredadores como las estrellas de mar que determinan el reclutamiento, la abundancia y la distribución de sus presas ("*top-down*") (Hart 2006). No obstante a mayor escala (>1 km), son las fuerzas "*bottom-up*" las que controlan el sistema (Seitz 2011). Es decir es la disponibilidad de presas es la que controla a los depredadores (su comportamiento, desarrollo y abundancia)(Barahona and Navarrete 2010).

8.2. Marco de la Tesis Doctoral

En las últimas décadas se ha detectado un declive significativo en los stocks de moluscos bivalvos en toda la costa mediterránea de España (Ramón *et al.* 2005; Baeta *et al.* 2014). La costa del Maresme (Cataluña, Noroeste del Mar Mediterráneo) ha sido históricamente una de las principales zonas de explotación de moluscos bivalvos, donde una importante actividad pesquera se ha desarrollado hasta hace relativamente poco tiempo. La principal especie objetivo de la flota pesquera ha sido la concha fina (*C. chione*). Sus capturas empezaron a caer en 1997 y en consecuencia las autoridades locales (La Generalitat de Catalunya) encargaron un estudio para evaluar su estado. Los resultados de dicho estudio recomendaron el cierre inmediato del banco a la explotación pesquera y su pesca se prohibió entre marzo de 2008 y abril de 2009. También se decretó el cierre estacional entre marzo y abril para los siguientes años. La pesquería fue reabierta en abril de 2009, no obstante la mayoría de pescadores tuvieron que abandonar la actividad pesquera fruto de la escasez de producto y el mal estado en que se encontraba en stock. El primer objetivo de esta Tesis Doctoral fue el estudio de las causas que habían provocado dicho declive para dar una respuesta a la administración y al propio sector. Así como proponer medidas la futura recuperación del banco. Por ello se amplió el estudio de la biología y ecología de la concha fina de la zona del Maresme.

La concha fina *C. chione* es un molusco bivalvo suspensívoro (Charles *et al.* 1999) que vive en arenas limpias poco profundas en la zona costera, siendo más abundante entre los 5 y los 30 metros de profundidad. Es una especie de vida larga que puede vivir más allá de 40 años (Forster 1981). Se distribuye en el Mar Mediterráneo y en la costa Este del Océano Atlántico entre las Islas Británicas y Marruecos, incluyendo las Islas Canarias y las Azores (Tebble 1966). Es una especie objetivo de la pesquería de bivalvos y tiene importancia económica en la costa mediterránea de España (especialmente en Málaga y el Maresme-Costa Brava) Portugal, Italia, Francia, Croacia, Grecia, Turquía y Marruecos. Se pesca con distintas modalidades de dragas para la captura de bivalvos y en algunos lugares del Mediterráneo Oriental es también recolectada manualmente por buzos (Gaspar *et al.* 2001; Metaxatos 2004; Pubill *et al.* 2011).

Distintas especies de estrellas de mar del género *Astropecten* son capturadas frecuentemente y con abundancia notoria como by-catch de la pesquería de *C. chione* en el Maresme. Esta Tesis Doctoral ha puesto también su atención en estos equinodermos para determinar qué papel ecológico juegan en banco de marisqueo. Además ha investigado en profundidad sus relaciones tróficas, así como su ecología; especialmente la especie más abundante *A. aranciacus*.

Astropecten (Asteroidea, Astropectinidae) es el género de estrellas de mar que más especies contiene, sus miembros están ampliamente distribuidos por todo el mundo desde zonas polares a zonas tropicales y desde zonas intramareales a zonas profundas, aunque siempre habitando fondos blandos (Zulliger and Lessios 2010). Este género incluye seis especies que habitan en el Mar Mediterráneo *A. aranciacus* (Linnaeus 1758); *A. bispinosus* (Otto 1823); *A. irregularis pentacanthus* (Pennant 1777); *A. platyacanthus* (Philippi 1837); *A. jonstoni* (Delle Chiaje 1827); and *A. spinulosus* (Philippi 1837); siendo las últimas tres endémicas del Mar Mediterráneo. Estas estrellas de mar son voraces depredadores que se alimentan esencialmente de moluscos (gasterópodos y bivalvos) y presentan una digestión intra-oral (Christensen 1970). A pesar de que inicialmente fueron descritos como especies que no seleccionaban las

presas, es decir generalistas (Wells *et al.* 1961), en esta Tesis Doctoral se ha podido comprobar que contrariamente a lo que se creía presentan una cierta especialización en la selección de las presas consumidas (Baeta and Ramón 2013). Como depredadores que ocupan altos niveles tróficos de la red trófica, las estrellas de mar se pueden ver especialmente afectadas por la degradación de los ecosistemas costeros y a su vez por su papel como especies clave pueden producir efectos impredecibles en las comunidades biológicas donde habitan. Por lo tanto su estudio es de vital importancia para la conservación y la gestión adecuada de los recursos marinos y especialmente para la concha fina del Maresme.

8.3. *Objetivos*

El objetivo principal de la presente Tesis Doctoral es mejorar el conocimiento en la ecología de la concha fina (*C. chione*), así como de sus potenciales depredadores las distintas especies del género *Astropecten* que se distribuyen en la misma zona geográfica situada en la costa del Maresme, Cataluña, noroeste de España. Al mismo tiempo incidir en el estudio de las relaciones tróficas existentes entre estas especies y comprender cuál es su nivel de vulnerabilidad ante las presiones antrópicas.

Los objetivos específicos que se plantearon fueron:

I. Caracterizar la población de concha fina *C. chione* existente en la zona del Maresme, describiendo el crecimiento, la estructura de la población, la pesquería y los patrones de variación espacial y temporal.

II. Analizar las causas potenciales que produjeron el descenso en las capturas de *C. chione,* así como su posterior colapso pesquero.

III. Identificar que especies de estrellas de mar (del género *Astropecten*) se distribuyen en el banco de la concha fina *C. chione* del Maresme. Analizar las relaciones tróficas que existen entre las distintas especies, a partir de su estrategia alimentaria, el solapamiento de sus dietas y las variaciones ontogénicas en la selección de sus presas; con especial énfasis en su depredación sobre la concha fina *C. chione.*

IV. Aportar nuevos conocimentos sobre las distintas especies de estrellas de mar que cohabitan en la costa del Maresme*,* a través del estudio de sus dinámicas poblacionales a medio plazo. En concreto sobre las estrellas de mar del género *Astropecten*, estudiando su composición, población, distribución espacial y temporal y su estructura.

V. Analizar distintos factores bióticos y abióticos que pueden afectar la distribución de *Astropecten* spp. en la zona de estudio.

VI. Mejorar el conocimiento de la ecología de la estrella de mar *A. aranciacus,* describiendo por primera vez su crecimiento, ciclo reproductivo y distribución.

8.4. Resultados y Discusión

Los resultados obtenidos en esta Tesis Doctoral demuestran que se ha producido un progresivo descenso en la biomasa y la densidad de concha fina *C. chione* a lo largo de las últimas décadas en la costa del Maresme. Los registros de las lonjas de la zona muestran como los desembarcos de este molusco fueron de 110 t año^{-1} entre 1980 y 1994, posteriormente registraron un máximo de alrededor de 290 t año^{-1} en 1997, para finalmente ir progresivamente descendiendo hasta únicamente alcanzar las 80 toneladas en 2005. Esta tendencia culminó con el colapso de la pesquería a finales de 2005. Después del cierre decretado por la administración local (la Generalitat de Catalunya) entre marzo de 2008 y abril de 2009, se observó que el 90% de los ejemplares capturados eran inferiores a la talla de 45 mm, que de acuerdo con nuestras estimaciones corresponde a ejemplares de no más de 4 años de vida. Además únicamente un 2% de ejemplares se encontraba por encima de la talla mínima legal (60 mm). La población encontrada estaba forma por ejemplares muy jóvenes en comparación con otras poblaciones explotadas comercialmente dentro de su rango de distribución geográfica, y en que la edad media de los ejmeplares capturados se sitúa entre los 5 y los 15 años (Leontarakis and Richardson 2005; Ezgeta-Balić *et al.* 2011).

Los resultados de esta Tesis Doctoral corroboran que la concha fina *C. chione* es una especie de molusco bivalvo con un crecimiento lento, alcanzando los 60 mm de longitud (la talla mínima legal) entre los 5 y los 6 años de vida. Los parámetros de crecimiento de *C. chione* descritos en la zona de estudio difieren ligeramente con los previamente hallados en otras zonas geográficas. La esperanza de vida descrita para esta especie descrita en ésta Tesis Doctoral también coincide con la previamente descrita por otros autores en otras zonas, situándose entre los 12 y los 20 años. (Hall *et al.* 1974; Strada and Zocco 1985; Keller *et al.* 2002; Metaxatos 2004; Leontarakis and Richardson 2005; Moura *et al.* 2009; Ezgeta-Balić *et al.* 2011).

Los resultados obtenidos muestran un cambio significativo en la granulometría del sedimento de la zona de estudio entre 2004 y 2010. Entre ambos períodos se incrementó la proporción de arenas finas y fangos especialmente en la zona suroeste del banco haciéndola inhabitable para *C. chione*, que según se ha podido constar en este estudio prefiere zonas con arenas más gruesas. Los persistentes dragados realizados en la zona de estudio desde 1987 han ido reduciendo paulatinamente la zona de distribución de *C. chione* hacia el noroeste de su distribución original en la costa del Maresme. Consecuentemente la actividad pesquera se ha ido concentrando cada vez más en una menor extensión geográfica en el noroeste, incrementando en ella el esfuerzo pesquero. Por lo tanto los resultados demuestran claramente como el declive de *C. chione* en la zona de la costa del Maresme se produjo fruto de la interacción de dos usos antrópicos de la costa: la extracción de arenas para la regeneración de playas y la pesca artesanal de la concha fina.

Para la recuperación de *C. chione* de la costa del Maresme esta Tesis Doctoral propone las siguientes medidas de gestión: (1) Prohibición de la actividad pesquera con rastros (pesca de la concha fina) en la zona hasta que la población se haya recuperado totalmente. (2) La aplicación de otras alternativas a la regeneración de playas para mitigar la erosión costera. En el caso de no encontrar otras alternativas, se propone restringir a la zona suroeste del banco dichas actividades. (3) Se debe elaborar un plan para la recuperación del stock pesquero de *C. chione,* liderado por científicos, financiado por las administraciones públicas (Gobierno Autonómico y Central) y debe

incluir todos los actores locales (Ayuntamientos, Consejos Comarcales, Cofradías de pescadores, pescadores de concha fina, puertos recreativos etc.). Este plan deberá incluir medidas que se han demostrado exitosas en otras zonas del mundo que se han encontrado ante la misma situación, como por ejemplo: (a) la creación de un santuario de individuos de gran tamaño, (b) repoblar el banco con ejemplares juveniles producidos mediante técnicas de acuicultura, (c) estudiar y evaluar el efecto de la desaparición del banco de *C. chione* para el conjunto del ecosistema, y (d) hacer campañas de concienciación.

La coexistencia de distintas especies de estrellas del género *Astropecten* ha sido documentada alrededor del mundo y no es un hecho inusual, por ejemplo ha sido descrita en Venezuela (Bitter 2000), Brasil (Ventura 1999), Japón (Nojima 1984), Australia (Lemmens *et al.* 1995) y en el Mar Mediterráneo (Ribi and Jost 1978). A pesar de ello, los mecanismos que explican cómo dicha coexistencia es posible han sido muy poco estudiados. Para explicar la coexistencia de otras especies de estrellas de mar, a menudo ha sido propuesta la partición de las especies de presas y de las tallas de estas presas como el mecanismo empleado para reducir potenciales interacciones competitivas (Menge and Menge 1974; Schoener and Schoener 1982). Esta Tesis Doctoral ha explorado esta posibilidad en las especies del género *Astropecten* y se ha podido comprobar cómo efectivamente este mecanismo es también utilizado por ellas. De este modo, y cada especie depreda mayoritariamente sobre unas especies de bivalvos y/o gasterópodos en concreto. Durante los trabajos desarrollados únicamente se detectó una potencial interacción competitiva entre las especies *A. aranciacus* y *A. platyacanthus* durante los meses de invierno. Otro mecanismo que ha sido descrito para evitar una situación de competencia entre distintas especies es la partición de hábitats (MacArthur and Wilson 1967). En esta Tesis Doctoral también se ha explorado esta posibilidad y los resultados han demostrado que cada especie ocupa un microhábitat con distintas características bióticas y abióticas concretas. Es decir, aunque cohabitan en el banco de *C. chione* del Maresme, no coexisten. Por lo tanto, los resultados muestran claramente que aunque distintas especies del género *Astropecten* coexisten en la zona de estudio no existe competencia entre ellas. En la literatura también se han descrito otros mecanismos para evitar la competencia entre especies de estrellas de mar, por ejemplo presentar distintos patrones de actividad durante el día (Ribi and Jost 1978), aunque éstos no han sido explorados en esta esta Tesis Doctoral.

Las presiones antrópicas sobre los ecosistemas marinos han llevado a muchas especies que ocupan altos niveles tróficos a severos declives en sus poblaciones a un ritmo alarmante en las últimas décadas (Heithaus *et al.* 2008). Comprender como estas especies son vulnerables a dichas presiones antrópicas es un prerrequisito indispensable para diseñar y definir estrategias para su gestión (Pinsky *et al.* 2011). Esta Tesis Doctoral ha demostrado como las distintas especies de estrellas de mar del género *Astropecten* que habitan la costa del Maresme se han visto afectadas a medio plazo (entre 2004-2006 y 2010-2011) por cambios en el hábitat (la granulometría) y la abundancia de presas (esencialmente *C. chione*) como resultado de las presiones antrópicas (extracciones de playas para la regeneración de playas y la sobrepesca). En concreto se ha documentado por primera vez cambios en su composición, abundancia, distribución espacial, estructura de las poblaciones y también en la dieta de *A. aranciacus*. Además se ha constatado que la estrella de mar *A. aranciacus* es la especie más vulnerable a dichas presiones antrópicas.

Por otro lado, los resultados obtenidos también muestran que los ejemplares de *A. aranciacus* inferiores a 80 mm son más abundantes en las zonas costeras y poco profundas (5-30 m), mientras que los ejemplares de mayor tamaño (>130 mm) lo son principalmente en las zonas más profundas (50-150 m). El uso de diferentes artes de pesca para los muestreos utilizados en ambos rangos batimétricos podría sugerir un sesgo en la recogida de ejemplares de tamaños pequeños en la zona más profunda (50-150 m). No obstante, dicho sesgo no pudo existir en la ausencia de ejemplares de mayor tamaño en la zona costera, ya que en caso de habitar la zona entre 5 y 30 metros habrían sido capturados. Burla *et al.* (1972) estudiaron el patrón de actividad de *A. aranciacus* mediante muestreos submarinos en Cerdeña, Italia. Estos autores sugirieron que los adultos y los jóvenes vivían en diferentes partes de la zona ecológica ocupada por la especie, habitando los especímenes de mayor medida las aguas más profundas. Nuestro estudio es el primero que ha muestreado la mayor parte del rango batimétrico de distribución de *A. aranciacus***,** permitiéndonos confirmar la existencia de una segregación batimétrica por tamaño. Similares resultados fueron documentados para la estrella de mar *Protoreaster nodosus*, en que sus ejemplares de mayor talla habitan entre los 0 y los 30 metros de profundidad, mientras que los especímenes de menor talla se encuentran exclusivamente en las zonas poco profundas por debajo de los 5 metros (Bos *et al.* 2008). Los ejemplares jóvenes de estrellas de mar suelen preferir zonas poco profundas, con mayor cantidad de alimentos y refugios para reducir la depredación (Manzur *et al.* 2010).

La población estudiada de *A. aranciacus* mostró un patrón de crecimiento estacional, siendo mayor entre junio y octubre en las cohortes presentes en la zona situada a menor profundidad. Dicho período de mayor crecimiento fue más amplio (entre febrero y octubre) en las cohortes presentes en la zona situada a más profundidad, aunque el ratio de crecimiento fue menor que el detectado en la zona costera (aproximadamente la mitad). Un patrón estacional de crecimiento ha sido también descrito en otras especies de estrellas del género *Astropecten*. Habitualmente se ha observado la disminución de del crecimiento coincidiendo con la maduración gonadal (Nojima 1982; Ventura 1999; Freeman *et al.* 2001), aunque esta correlación no ha sido observada en *A. aranciacus*. En *A. aranciacus* el crecimiento parece también estar relacionado con la temperatura de agua. En la zona costera se ha observado la coincidencia de un mayor crecimiento con el período de temperaturas más elevadas del agua, en concreto cuando la temperatura es superior a los 21ºC (entre los meses de junio y octubre). En la zona más profunda se observó un mayor crecimiento los meses en que la temperatura del agua de mar se incrementa a -80 m. Ventura (2013) observó que el descenso en el crecimiento de *A. brasiliensis* and *A. cingulatus* coincidía con el período estacional de upwelling en la costa de Brasil, sugiriendo que dicha disminución podía estar relacionada con una disminución de la temperatura del agua.

Los resultados mostraron dos períodos de reclutamiento en la zona costera (febrero 2010 y abril 2012), aunque no se observó en la zona más profunda. Tampoco se detectó reclutamiento durante el año 2011. La ausencia o los bajos ratios de reclutamiento durante periodos de tiempo es un suceso habitual en las estrellas de mar, así como en otros equinodermos y ha sido atribuido a procesos hidrológicos en la dispersión de los gametos y las larvas, así como a su depredación (Thorson 1946; Freeman *et al.* 2001). Por lo tanto, aunque *A. aranciacus* tiene un ciclo de reproducción anual, aunque su reclutamiento no tiene éxito cada año.

En general los ciclos reproductivos de las estrellas de mar están correlacionados con una combinación de factores endógenos (hormonas) y exógenos (temperatura, fotoperiodo, disponibilidad de alimento, ciclo lunar y mareas) (Mercier and Hamel 2009). No obstante, la influencia directa de cada factor sigue siendo poco comprendido (Mercier and Hamel 2009). En las especies de estrellas del género *Astropecten*, el período reproductivo habitualmente coincide con el incremento de la temperatura del agua de mar en las zonas temperadas (Grant and Tyler 1986; Marion *et al.* 1998; Freeman *et al.* 2001). Nuestros resultados también muestran el mismo patrón, ya que el período de reproducción de *A. aranciacus* (primavera) ocurre cuando las temperaturas del agua de mar empiezan a incrementarse en el Mediterráneo. Estos también muestran que el período de puesta coincide con la época del año con un bajo fotoperiodo. Esta relación inversa entre GI y fotoperiodo no ha sido descrita en otras especies de estrellas del género *Astropecten*, y es rara en otras estrellas de mar, aunque es común en otros equinodermos (Mercier and Hamel 2009). También nuestros resultados evidencian que el período de puesta está relacionado con la época del año en que mayor concentración de clorofila a se encuentra en el agua de mar, y que es causada por el bloom de fitoplancton de primaveral, típico del noroeste del Mar Mediterráneo. La mayoría de estrellas del género *Astropecten* tienen una larva planctónica (bipinaria), dichas larvas se alimentan fundamentalmente de detritus, baterías, fitoplancton (esencialmente de pequeñas diatomeas y dinoflagelados) y zooplancton pequeño (Ayukai 1993). Por lo tanto esta estrategia alimentaria podría explicar el sincronismo entre el desarrollo gonadal de *A. aranciacus* y el bloom de fitoplancton primaveral, liberando los gametos, cuando mayor concentración de chl-a se encuentra en el agua.

Una correlación inversa entre GI and PCI ha sido descrita habitualmente en la mayoría de estrellas de mar, sugiriendo que existe una transferencia de nutrientes desde el ciego pilórico hacia las gónadas durante la gametogénesis (Lawrence and Lane 1982). Aunque esta interacción no ha sido observada en aquellas especies que habitan áreas con condiciones ambientales estables (Benítez-Villalobos and Martínez-García 2012). Nosotros tampoco hemos observado dicha correlación en *A. aranciacus* a pesar de que habita una zona con variaciones estacionales. Otra excepción también ha sido descrita por Ventura *et al.* (1998) en *A. cingulatus*, aunque su causa es desconocida. Los individuos de *A. aranciacus* capturados en la zona más profunda de estudio presentaban gran cantidad de presas en el estómago a lo largo de todo el año. La mayoría de las presas correspondían al venérido *Timoclea ovata* (>55% de abundancia en 224 estrellas de mar analizadas) y cada estómago de cada estrella contenía una media de 49 *T. ovata* ejemplares con una talla media de 5.77 mm (SD=5.52, N=9682) (*unpublished data*). Por lo tanto, el alimento no parece ser un factor limitante en *A. aranciacus*, esto sugiere que las estrellas de mar no necesitan almacenar grandes cantidades de nutrientes en el ciego pilórico para ser posteriormente transferidos a las gónadas durante la maduración gonadal, ya que éstos pueden ser obtenidos rápida y fácilmente del medio a lo largo de todo el año. Esta podría ser la razón por la cual no se ha observado una correlación inversa de GI y PCI en *A. aranciacus*.

Las especies clave ejercen una fuerte influencia sobre otras especies y su declive puede afectar de una forma significativa la conservación de la biodiversidad. Por lo tanto, los esfuerzos destinados a su adecuada gestión y/o protección pueden ayudar a estabilizar el conjunto de las comunidades biológicas preservando en consecuencia dicha biodiversidad. No obstante para su adecuada gestión y/o protección es esencial el conocimiento de su biología y ecología, así como el estado de sus poblaciones. Esta

Tesis Doctoral realizó un esfuerzo para mejorar el conocimiento de algunas de estas especies: la concha fina y las estrellas de mar del género *Astropecten*, proporcionando nueva información científica que pretende ayudar a la mejor gestión de la concha fina y a la mejora en la conservación las estrellas de mar estudiadas.

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