

THE INVASIVE SPECIES *ASPARAGOPSIS TAXIFORMIS* (BONNEMAISONIALES, RHODOPHYTA) ON ANDALUSIAN COASTS (SOUTHERN SPAIN): REPRODUCTIVE STAGES, NEW RECORDS AND INVADED COMMUNITIES

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ABSTRACT. *The invasive species Asparagopsis taxiformis (Bonnemaisoniales, Rhodophyta) on Andalusian coasts (Southern Spain): reproductive stages, new records and invaded communities.* The present study provides new records from Andalusian coasts of the exotic invasive seaweed *Asparagopsis taxiformis* (Delile) Trevisan. These records demonstrate that *A. taxiformis* has rapidly and widely expanded its distribution range in this region, from Almería to Cádiz (Strait of Gibraltar). The latter locality may represent the western geographical limit of the species in the Mediterranean Sea. Spermatangial heads and cystocarps were observed in the collected gametophytes. Additionally, we report the first record of the tetrasporophytic stage, *Falkenbergia hillebrandii* (Bornet) Falkenberg from the Andalusian coast, although tetraspores were not encountered in these samples. Consequently, information on the affected communities and arguments for considering *A. taxiformis* as an invasive species in the Andalusian coast are provided.

Key words. *Asparagopsis taxiformis*, Bonnemaisoniales, distribution, *Falkenbergia hillebrandii*, invasive species, Mediterranean Sea, new record, reproductive stage, Rhodophyta

RESUMEN. *La especie invasora Asparagopsis taxiformis (Bonnemaisoniales, Rhodophyta) en las costas andaluzas (Sur de España): fases reproductivas, nuevas citas y comunidades invadidas.* El

presente trabajo aporta nuevas citas para las costas andaluzas de la especie exótica invasora de macroalga *Asparagopsis taxiformis* (Delile) Trevisan. Estas citas muestran que la especie ha aumentado ampliamente su área de distribución de manera rápida en esta región, desde Almería hasta Cádiz (Estrecho de Gibraltar). Esta última localidad representaría el límite occidental de la especie en el mar Mediterráneo. En las muestras recogidas de gametofitos se pudieron observar ramas espermatangiales y cistocarpos. Se aporta la primera cita del estadio tetrasporofítico, *Falkenbergia hillebrandii* (Bornet) Falkenberg en las costas andaluzas, aunque no se observaron tetrásporas en estas muestras. Se informa sobre las comunidades afectadas y se dan argumentos para considerar a *A. taxiformis* invasora en las costas andaluzas.

Palabras clave. *Asparagopsis taxiformis*, Bonnemaisoniales, distribución, especie invasora, estadio reproductivo, *Falkenbergia hillebrandii*, mar Mediterráneo, nueva cita, Rhodophyta

INTRODUCTION

Biological invasions are one of the major threats to biodiversity, ecosystem functions and services, both in terrestrial and marine environments (Norse 1993; Grosholz 2002). In coastal habitats, macroalgae constitute an important component of introduced biota, ranging from 8 to 38% of the total number of the recorded non-indigenous species (Schaffelke *et al.* 2006). According to Boudouresque & Verlaque (2002) there are 85 introduced seaweeds in the Mediterranean Sea, compared to only 49 species detected along the European Atlantic coasts (Ribera 2003). However, these numbers are probably higher due to the existence of cryptic and/or cryptogenic species (Carlton 1996). In fact, the Mediterranean Sea is considered a hot spot of exotic marine macroalgae due to the diversity of environmental habitats, the intense maritime traffic, the connectivity with the Atlantic and the Indo-Pacific Oceans via the Strait of Gibraltar and the Suez Canal respectively, aquaculture activities and the low number of large perennial algae and herbivores (Ribera 2003).

In the list of introduced marine macroalgae in the Mediterranean Sea, both species of the genus *Asparagopsis*, *A. armata* Harvey and *A. taxiformis* (Delile) Trevisan,

are included (Boudouresque & Verlaque 2002), with different introduction times. *Asparagopsis armata*, a temperate distributed species, is considered a Lessepsian immigrant, first reported from the Algerian coasts in 1923 (Feldmann & Feldmann 1942). *Asparagopsis taxiformis*, a tropical to warm temperate species, is considered a pre-Lessepsian immigrant or native in the eastern Mediterranean (Andreakis *et al.* 2004), since the first record in the Mediterranean Sea was given in Egypt in 1813 (Delile 1813). Both taxa exhibit a strong invasive behaviour, and are included in the list of the “Worst invasive alien species threatening biodiversity in Europe” (EEA 2007) and also in the list of the 100 “Worst Invasives in the Mediterranean Sea” (Streftaris & Zenetos 2006).

The first record of *Asparagopsis armata* on Andalusian coasts was in 1965 (Seoane 1965), on the Atlantic coast of Cádiz. Nowadays, the species can be found from Cádiz to Almería (Conde *et al.* 1996), forming natural vegetation belts on exposed coasts between 0 and -15m depth (Ballesteros & Pinedo 2004), representing the first reported macroalgal invasion in Andalusian coasts.

The introduction of *A. taxiformis* is much more recent, as it was cited for the first time in Alboran Sea (Chafarinas Islands) in

1999 (Altamirano 1999). Later the species was found in Andalusian coast, in Punta de la Mona (Granada) (Báez *et al.* 2001), Cala Rijana (Granada) and Punta de la Polacra, P.N. Cabo de Gata (Almería) (Ballesteros & Pinedo 2004), but in none of these cases the species was considered invasive. Whether the species can complete its diplohaplontic heteromorphic life-cycle or not in Andalusian coasts, is still unclear, as only non-reproductive gametophytes have been found, and the tetrasporophytic stage, *Falkenbergia hillebrandi* (Bornet) Falkenberg, has never been reported before.

The present work provides new records of gametophytes of *A. taxiformis* in Andalusian coasts, and the first record of the tetrasporophyte, “*Falkenbergia*-stage”, in this region. Habitat and reproductive information is also provided, and arguments for considering this species as invasive on Andalusian coasts are exposed.

MATERIAL AND METHODS

Samples of gametophytes and tetrasporophytes of *Asparagopsis taxiformis* were collected between 2005 and 2007 at the infralittoral zone of different locations in Cádiz, Málaga, Granada and Almería provinces (Andalusia, Southern Spain), by snorkeling and SCUBA diving. Several locations in Huelva province were also visited. Samples were preserved in 4% of formaline in seawater. Recognition of the “*Falkenbergia*-stage” was achieved according to Ní Chualáin *et al.* (2004), considering the length and width of one of the three pericentral cells at cells 30, 40 and 50 from the apex of one branch of twenty specimens. Microscopic samples were studied using a microscope Nikon Eclipse E800; photographs were obtained with a digital camera Nikon DXM 1200. Identified

samples were pressed and prepared for herbarium sheets to be included in the Herbarium of the University of Málaga (MGC). Herbarium acronyms follow Holmgren *et al.* (1990).

RESULTS

Gametophytes of *A. taxiformis* (fig. 1) were found between 0 and -17m depth on rocky substratum in eleven new locations in Andalusia from March to December (fig. 2, tab. 1). Four new locations are given for Almería, three for Granada, three for Málaga and one for Cádiz yet, no populations were encountered in Huelva. Spermatangial branches were observed in one specimen from Málaga (fig. 3) in July, and cystocarps were observed in specimens from Almería (fig. 4) in September. In several locations, such as Paraje Natural de los Acantilados de Maro-Cerro Gordo (Málaga-Granada), gametophytes of *A. taxiformis* formed conspicuous monospecific stands. In these sites, the species appeared to act as a keystone species. In other sampling sites, such as Marina del Este (Granada), the species was observed inhabiting on the community of *Cystoseira tamariscifolia* (Hudson) Papenfuss. In Parque Natural Cabo de Gata (Almería) gametophytes were observed growing on rhizomes of the seagrass *Posidonia oceanica* L. Often *A. taxiformis* occurred in sympatry with *A. armata*. In these cases the former was found deeper in the infralittoral zone, although both species overlap for a few meters at approximately -6m depth.

In October 2007, when gametophytes of *A. taxiformis* were observed, but no *A. armata*, *Falkenbergia* filaments were collected in Marina del Este (Granada) (fig. 5). Cell length of pericentral cells at cells 30, 40 and 50 from the apex ($58,3 \pm 9,5$ mm,

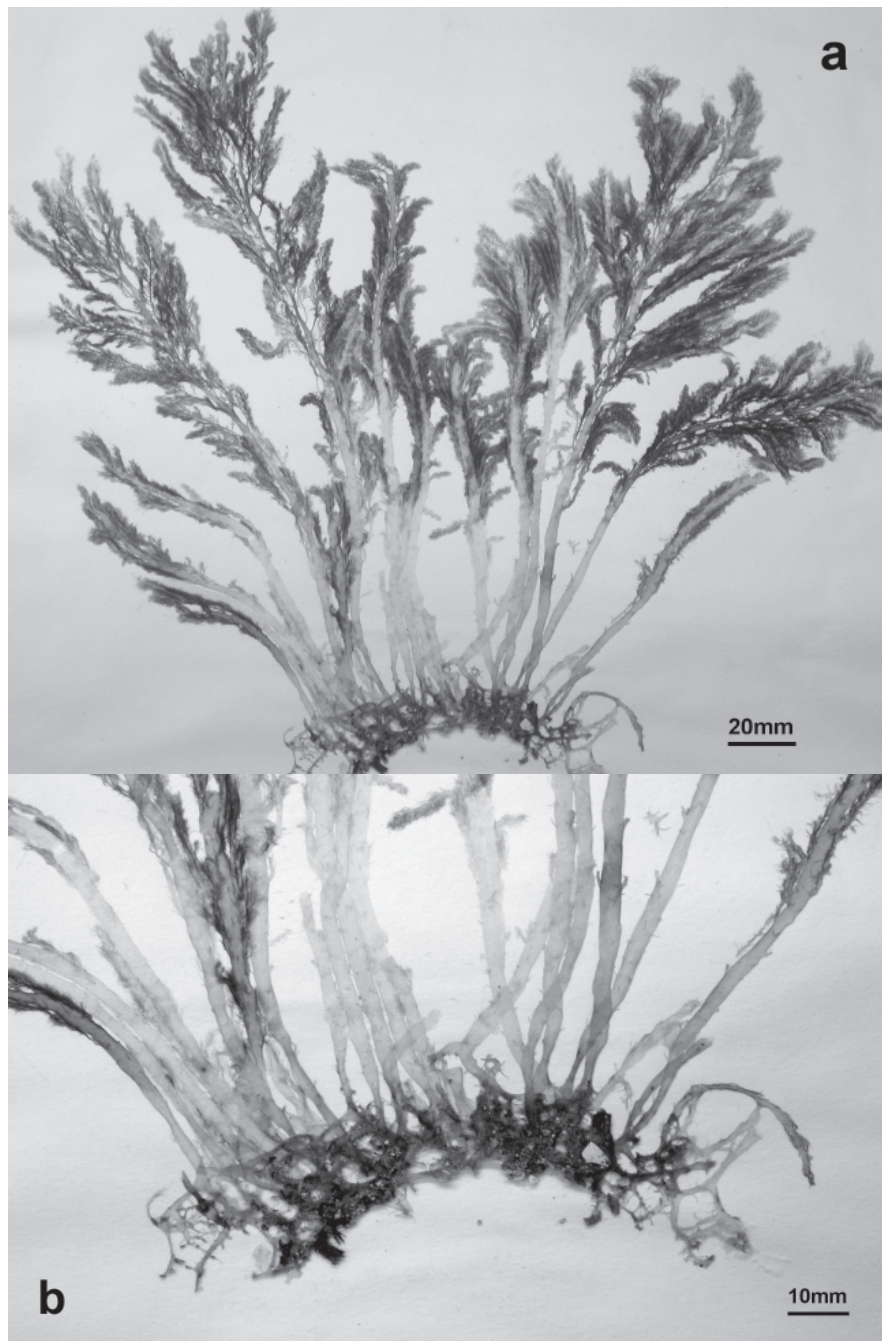


Figure 1. Gametophytes of *Asparagopsis taxiformis*. a) Habitat and b) basal stolons and rhizoids (MGC-Phyc 3844). Gametofitos de *Asparagopsis taxiformis*. a) Hábito y b) estolones basales y rizoides (MGC-Phyc 3844).

Sample site	Acronym	Collection date	Phase	MGC	Reproductive	Coordinates	Observations
Almería							
Cala del Bergantín, P.N. Cabo de Gata	CB	01-03-2006	G	3844	No	589055X4079400Y	In <i>Posidonia oceanica</i> meadows, -14m
Acantillado de la Vela Blanca, P.N. Cabo de Gata	VB	29-08-2006	G	3852	No	575921X4065571Y	-1m
Cala Rajá, P. N. Cabo de Gata	CR	27-08-2006	G	3851	No	583817X4072892Y	-2/-3m
Guardias Viejas	GV	21-09-2006	G	3855	Cystocarps	512704X4061737Y	-4m
Granada							
Acantillado de Calahonda	AC	30-04-2006	G	3843	No	463645X4062064Y	-8m
Marina del Este	ME	28-05-2006	G	3841	No	435502X4065352Y	-0,5m
Marina del Este	ME	07-10-2007	T	3915	No	435502X4065352Y	-0,5m
Marina del Este	ME	07-10-2007	G	3914	No	435502X4065352Y	-1m
Peñón del Fraile, Paraje Natural de Maro-Cerro Gordo	PF	12-12-2007	G	3930	No	430254X4066456Y	On <i>Cystoseira tamariscifolia</i> , -11m
Málaga							
Playa del Cañuelo, Paraje Natural de Maro Cerro-Gordo	CÑ	09-07-2006	G	3835	Spermatangial heads	429754X4066838Y	-1m
Cantarriján	PC	09-07-2006	G	3834	No	430941X4066030Y	On <i>Cystoseira tamariscifolia</i> , below <i>A. armata</i> , -5/-9m
Cala de Maro, Paraje Natural de Maro-Cerro Gordo	CG	08-04-2006	G	3840	No	425108X4068002Y	
Cádiz							
Punta del Parque Eólico, P.N. del Estrecho	PE	28-11-2005	G	3832	No	273382X3991249Y	Below <i>A. armata</i> , -6/-16m

MGC: Málaga University Herbarium record; G: gametophyte; T: tetrasporophyte

Table 1. New records of *A. taxiformis* in Andalusian coasts. *Citas nuevas de A. taxiformis en las costas andaluzas.*

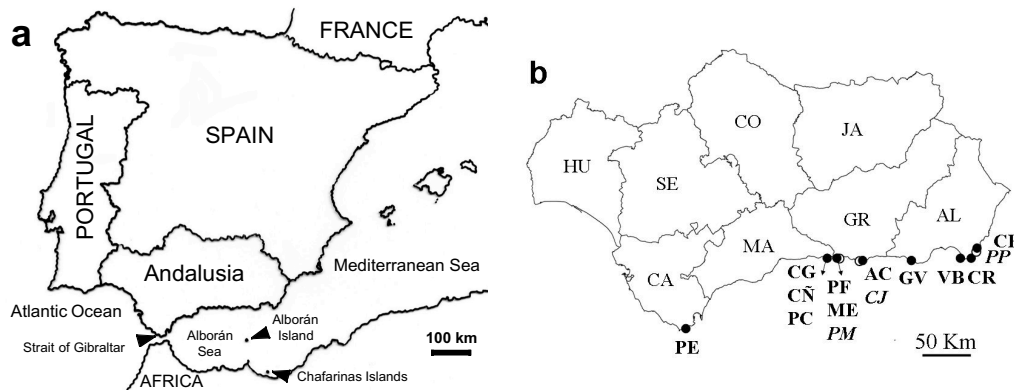


Figure 2. a) Location of the study area, Andalusia, in the Iberian Peninsula. b) Distribution of *Asparagopsis taxiformis* in Andalusia. Black dots show new records with acronym meanings given in Table 1; previous records are shown with white dots with acronyms in italics (PM: Punta de la Mona, Granada, CJ: Cala Rijana, Granada, PP: Punta de la Polacra, Almería). HU: Huelva, SE: Sevilla, CO: Córdoba, JA: Jaén, AL: Almería, GR: Granada, MA: Málaga, CA: Cádiz. a) *Localización del área de estudio, Andalucía, en la Península Ibérica.* b) *Distribución de *Asparagopsis taxiformis* en Andalucía.* Los puntos negros muestran las citas nuevas con los acrónimos de las localidades, cuyos significados se dan en la Tabla 1; las citas anteriores se muestran con puntos blancos y los acrónimos de sus localidades en cursiva (PM: Punta de la Mona, Granada, CJ: Cala Rijana, Granada, PP: Punta de la Polacra, Almería). HU: Huelva, SE: Sevilla, CO: Córdoba, JA: Jaén, AL: Almería, GR: Granada, MA: Málaga, CA: Cádiz.

66,9±8,5mm, 70,3±9,5mm, respectively) (fig. 6) was in the range given by Ní Chualáin *et al.* (2004) for the *A. taxiformis* Caribbean clade, but longer than values provided by these authors for *A. armata*. Cell width of these cells (20,0±2,7mm, 23,3±3,8mm, 23,0±1,9mm, respectively) (fig. 6) was intermediate in size between *A. armata* and *A. taxiformis* clades reported by Ní Chualáin *et al.* (2004). Given these results, we assign tetrasporophytes found in Granada to *Falkenbergia hillebrandii* on the basis of cell biometry differences obtained by Ní Chualáin *et al.* (2004) for cultured isolates. No tetrasporangia were observed in these samples. Tetrasporophytes grew between 0 and -1,5m depth in sheltered waters, epiphyte on *Halopteris filicina* (Grateloup) Kützinger, *Corallina officinalis* L. and *Jania rubens* (L.) Lamouroux.

Sea hares, *Aplysia fasciata* Poiret

(Aplysiidae, Mollusca) were observed feeding on gametophytes of *A. taxiformis* in Paraje Natural de los Acantilados de Maro-Cerro Gordo.

DISCUSSION

The present work provides the first records of the exotic invasive seaweed *Asparagopsis taxiformis* from the provinces of Málaga and Cádiz, the latter representing the up to date western geographical limit of the species in the Mediterranean Sea. We also report the first record of the tetrasporophyte of this species for Andalusian coasts, as cell size of the filaments were in the ranges of those given by Ní Chualáin *et al.* (2004) for *A. taxiformis* tetrasporophytes in culture, although, it should be necessary to clarify if differences between both *Asparagopsis*

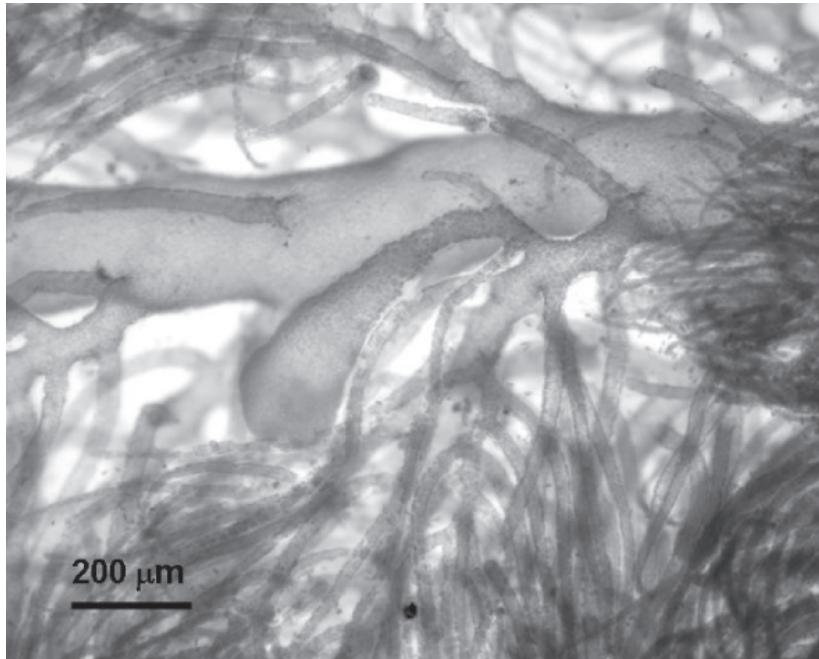


Figure 3. Spermatangial branches of *Asparagopsis taxiformis* (MGC-Phyc 3835). *Ramas espermatangiales de Asparagopsis taxiformis* (MGC-Phyc 3835).

species tetrasporophytes obtained in culture remains in wild specimens. The absence of *Asparagopsis* from the Huelva province might be related to the sandy conditions of the coastline, where suitable rocky substrata for the establishment of *Asparagopsis* populations are very scarce.

Recently, *A. taxiformis* has rapidly expanded its distribution range along the Andalusian coast. Granada has been reported as the geographical limit of the species in the western Mediterranean until 2004 (Ballesteros & Pinedo 2004). One year later *Asparagopsis* was found at the Strait of Gibraltar, approximately 210km to the west. Prolific vegetative reproduction may explain the fast dispersal rates of the species, which also exhibits an attaching system consisting in basal stolons and rhizoids (Figure 1) (Womersley 1996), able to facilitate the establishment of the propagules. However,

sexual reproduction also occurs, as proved by the presence of gametangia in some of the recorded samples. Yet, we cannot state the fulfilling of the complete life-cycle because, although tetrasporophytes were found, no tetrasporangia could be observed.

The origin of the Andalusian populations of *A. taxiformis* is unknown. A recent study on the phylogeography of the species has revealed that two genetically divergent lineages coexist in the Mediterranean Sea, which are considered biologically distinct but morphologically cryptic species (lineages 2 and 3, Andreakis *et al.* 2007). Following these authors, lineage 2 is distributed in the south of Portugal, central Mediterranean coasts and Indo-Pacific waters; lineage 3 is found in the Atlantic Ocean and the eastern Mediterranean coast of Lebanon. Several hypotheses have been proposed to explain

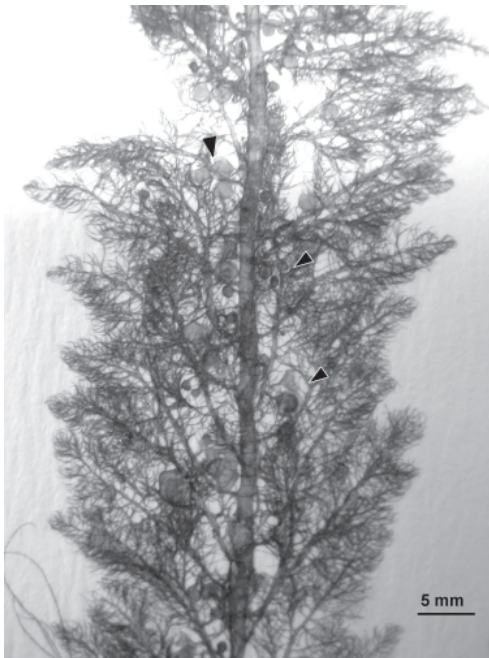


Figure 4. Female gametophyte of *Asparagopsis taxiformis* presenting globular cystocarps (MGC-Phyc 3855) (arrow shows cystocarps). *Gametofito femenino de Asparagopsis taxiformis con cistocarpos globulares (MGC-Phyc 3855) (la flecha muestra los cistocarpos).*

the existence of these two *A. taxiformis* lineages in the Mediterranean Sea, related to immigration and invasions at different time scales. A recent invasion through the Suez Canal has been suggested for both of them, although a more ancient immigration is argued for lineage 3, linked to the reopening of the Strait of Gibraltar 5 million years ago (Andreakis *et al.* 2007). The new populations of *A. taxiformis* revealed by this work were not included in the aforementioned studies. Therefore, the affiliation of our specimens to any of the two lineages occurring in the Mediterranean Sea or the possibility of an hybrid origin for the Andalusian *A. taxiformis* remain unclear. However, the presence of the Indo-Pacific Mediterranean

lineage 2 in Faro (Southern Portugal) (Andreakis *et al.* 2007) suggests that Andalusian populations of *A. taxiformis* may represent an invasion of the latter lineage into the Atlantic Ocean, probably due to anthropogenic mediated vectors such as ballast water (Flagella *et al.* 2007), hull's fouling or entangled propagules in fishing nets or ropes (Sant *et al.* 1996; Schaffelke & Deane 2005). Furthermore, global warming may have favoured the dispersal of the species in transforming new western habitats physiologically suitable for its survival. However, owing to the special characteristics of Alboran Sea water bodies due to the proximity of the Strait of Gibraltar and the importance of this relatively narrow channel in the introduction of non-indigenous species in the Mediterranean, the hypothesis of an invasion of the Atlantic lineage 3 to our study area cannot be rejected.

A recent study on “*Falkenbergia*-phase” specimens of both species of *Asparagopsis* demonstrated that thermal ranges for tetrasporangial formation differ among isolates collected from different regions of the world (Ní Chualáin *et al.* 2004). Our tetrasporophytes were not reproductive at 20 °C (water temperature at the collecting time), which may fit our samples to the thermal limits of Caribbean, Japanese or Italian *Falkenbergia* isolates (Ní Chualáin *et al.* 2004). This observation increases the debate on the affiliation and origins of Andalusian populations of *A. taxiformis*.

Independently of its origin, it remains the fact that *A. taxiformis* was not an Andalusian marine macroalgal resident until recently, yet it has widened its distribution range westerly for more than two hundred kilometres within few years. In our study area, the species colonizes protected habitats such as *Posidonia oceanica* meadows (European Union 1992), and forms conspicuously established and self-sustained

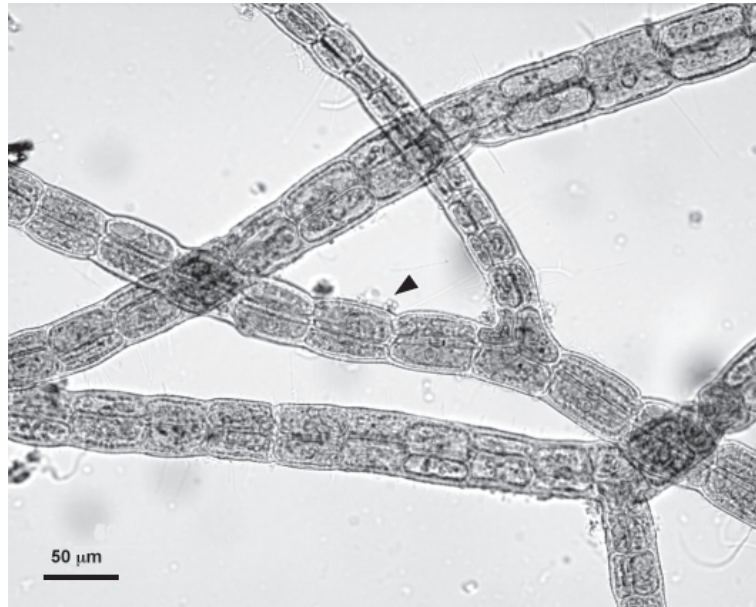


Figure 5. Tetrasporophyte of *Asparagopsis taxiformis*, *Falkenbergia hillebrandii* (MGC-Phyc 3915). Arrow shows pericentral cell at cell number 30 from the apex. *Tetrasporofito de Asparagopsis taxiformis*, *Falkenbergia hillebrandii* (MGC-Phyc 3915). La flecha muestra la célula pericentral número 30 desde el ápice.

stands in protected zones threatening the integrity of native Mediterranean marine communities. Herein, in accordance to the IUCN Guidelines (The World Conservation Union 2000), we state that *A. taxiformis* exhibits an invasive behaviour in Andalusian coasts. Consequently, *in situ* studies to confirm the ecological role and assess the impact of the species on the native communities are essential as this kind of records on this invasive species remain unknown in the Mediterranean Sea.

In Andalusian coasts *Asparagopsis taxiformis* is invading localities previously invaded by *A. armata*. The former colonizes the same substratum for a few meters, for which both species seem to compete. In these cases *A. armata* seems to be more competent at shallower waters than *A. taxiformis*, as the latter remains under *A. armata* belts at deeper

spots. Nevertheless, *A. taxiformis* can be found at very shallow waters (-0,5m) in other localities where *A. armata* is absent. The dynamics of this competition process remains unknown. The only presence of *A. taxiformis* in places where *A. armata* was present before (de la Rosa & Altamirano, pers. obs.) indicates that there might be several distinct stages in the invasive dynamics of *A. taxiformis*, when competing with *A. armata*, in which physiological adaptations, coupling of seasonal growth and reproductive cycles of both species may play an important role. In these cases, in which *A. taxiformis* clearly competes with another species, the study of the factors determining the susceptibility of the local communities to the invasion attempt, may provide valuable information on the general knowledge of the evolution of the invasion processes in temporal and spatial scales.

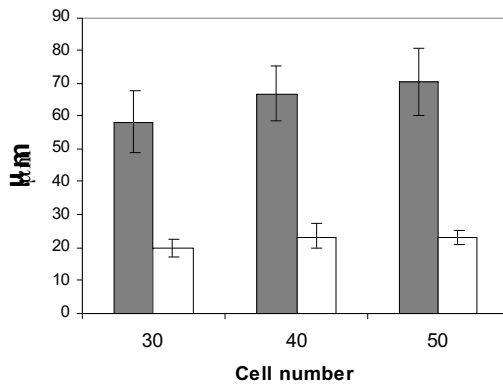


Figure 6. Cell length (shaded bars) and width (white bars) of tetrasporophytes of *Asparagopsis taxiformis* (*Falkenbergia hillebrandii*) collected in Granada, at cell numbers 30, 40 and 50 from the apex. Data are shown as mean value \pm 1SD. *Longitud* (barras sombreadas) y *anchura* (barras blancas) de las células número 30, 40 y 50 desde el ápice de tetrasporofitos de *Asparagopsis taxiformis* (*Falkenbergia hillebrandii*) recogidos en Granada. Los datos se muestran como media \pm 1SD.

Although we have no data on the effects that this invasion is causing on marine communities of Southern Spain, we have observed that the species has a predator, the sea hare *Aplysia fasciata*, which has been actively recorded feeding on individuals of *A. taxiformis*. Whether this herbivorous is able to naturally control the invasion is not entirely clear. Effective biocontrol of macroalgal invasions by herbivores has been reported before. For example, a local population of the invasive green algae *Codium fragile* ssp. *tomentosoides* (Van Goor) Silva, was diminished in Scotland by natural populations of the herbivorous sea slug *Placida dentritica* Alder and Hancock, which are themselves controlled by water motion (Trowbridge 2002; Harris & Jones 2005). However, effective biocontrol may be possible only at the first stages of the invasion process.

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