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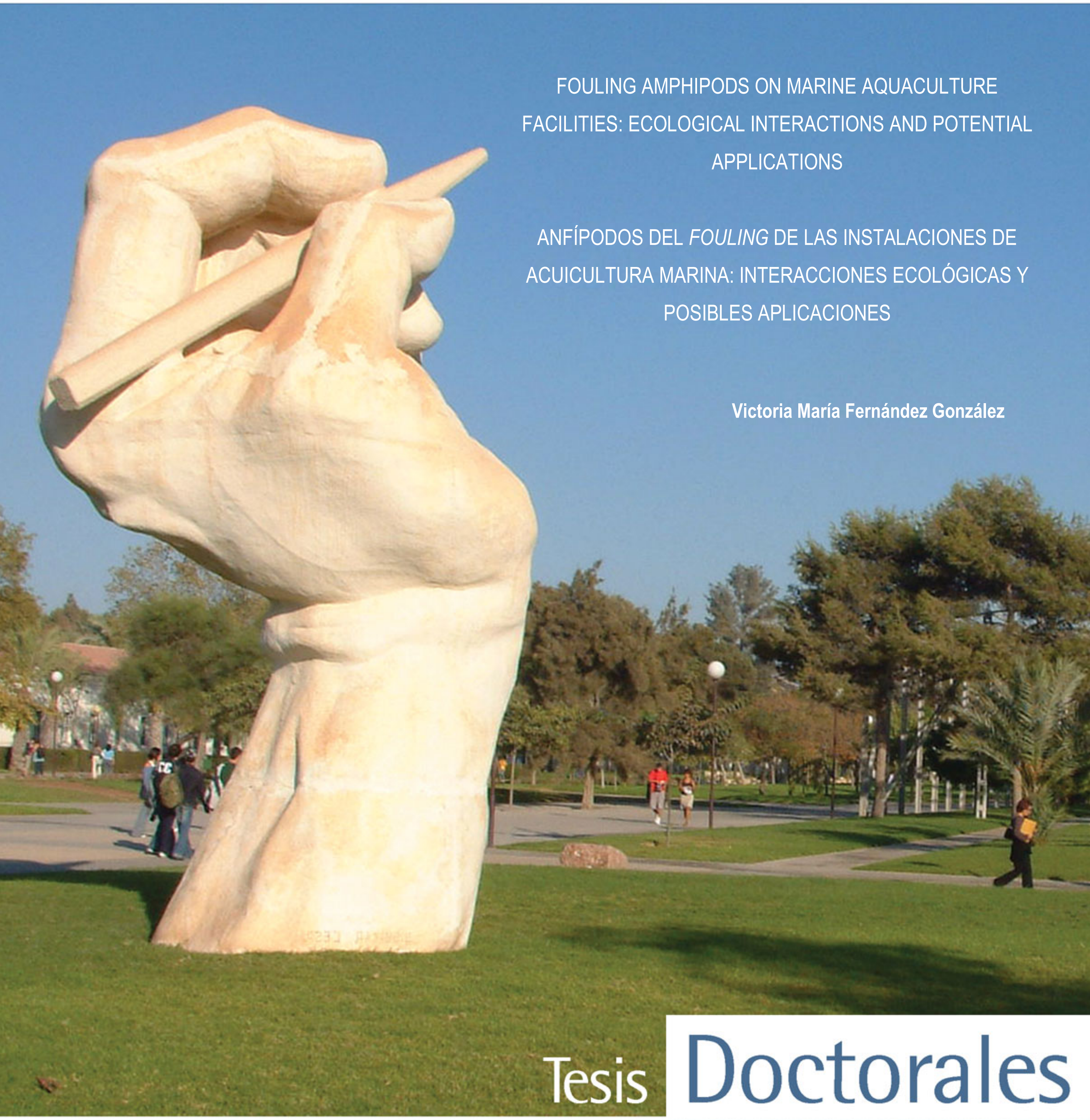

# FOULING AMPHIPODS ON MARINE AQUACULTURE FACILITIES: ECOLOGICAL INTERACTIONS AND POTENTIAL APPLICATIONS

# ANFÍPODOS DEL *FOULING* DE LAS INSTALACIONES DE ACUICULTURA MARINA: INTERACCIONES ECOLÓGICAS Y POSIBLES APLICACIONES

**Victoria María Fernández González**

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# Fouling Amphipods on Marine Aquaculture Facilities: Ecological Interactions and Potential Applications

Victoria Fernández González

PhD Thesis

2017

Universitat d'Alacant
Universidad de Alicante

**Design and Layout**
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Victoria M. Fernández González

**Photos**
Pablo Arechavala López

**Illustrations**
Victoria M. Fernández González
Rafael Fernández Pedregosa (Page 221)

**Printing and Binding**
University of Alicante printing services

Universitat d'Alacant
Universidad de Alicante

DEPARTAMENTO DE CIENCIAS DEL MAR Y BIOLOGÍA APLICADA
FACULTAD DE CIENCIAS

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# ANFÍPODOS DEL *FOULING* DE LAS INSTALACIONES DE ACUICULTURA MARINA: INTERACCIONES ECOLÓGICAS Y POSIBLES APLICACIONES



VICTORIA MARÍA FERNÁNDEZ GONZÁLEZ

Tesis presentada para aspirar al grado de
DOCTORA POR LA UNIVERSIDAD DE ALICANTE

MENCIÓN DE DOCTORA INTERNACIONAL
DOCTORADO DE CIENCIAS DEL MAR Y BIOLOGÍA APLICADA

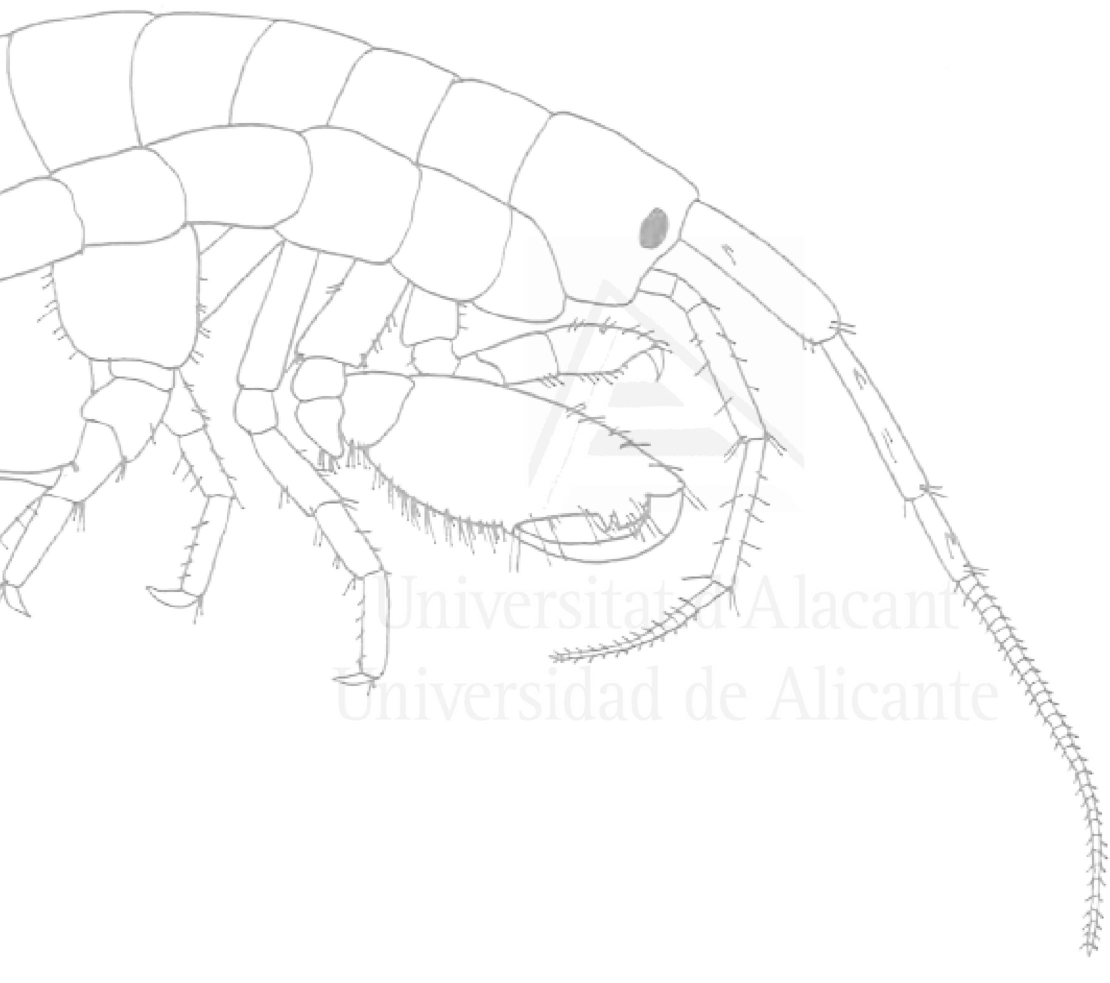
Dirigida por:
Dr. PABLO J. SÁNCHEZ JEREZ

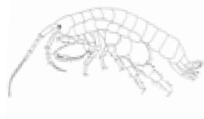
A Kilian,
Quien no ha soltado mi mano
en todo este tiempo

**CONTENTS**



# General Introduction





## Definition of *fouling*

According to Wahl (1989) the term *fouling* refers to "the colonisation process of a solid surface, be it living or dead". Like him, some authors have described fouling communities as assemblages of organisms on any natural substrate. However, a vast part of the literature uses this term to almost exclusively describe the colonisation of man-made structures rather than natural objects. In fact, Dürr and Thomason (2009) in their book *Biofouling* define the general term fouling as "the process of accumulation of unwanted material at an interface", referring to problems of this type arising in industries such as shipping, offshore oil or aquaculture from a human point of view, comparable to the term weeds in agriculture and gardening. The same authors point out that the word *fouling* is applied in the book as a noun and verb (since it is actually the gerund of the verb foul), although strictly speaking it is used incorrectly as a noun, given the widespread use of this term in the literature. These are just examples of the many definitions of *fouling*, depending on its context and particularly what surface is fouled.

In this PhD thesis, the terms *fouling* or *biofouling* are used indistinctly as both noun, adjective and occasionally as the verb to foul and is considered as "the process of accumulation of material, mainly marine organisms, resulting of the colonisation of an artificial surface", thereby avoiding its use to define the colonisation process of both living organisms or natural substrates such as rocky reefs and also the negative connotations generated by a human perception. This definition is, in turn, in agreement with that reported by other authors (e.g. Guillermes et al. 1994, Kocak et al. 1999, Madin et al. 2009)

## Development of fouling communities on artificial surfaces

Any clean surfaces exposed to sea water go through a succession of changes that promote their colonisation by marine organisms. Thus, colonisation of a new surface is composed of four phases constituting an overlapping time sequence: biochemical conditioning, bacterial colonisation, micro- and finally macrofouling settlement and development (Wahl 1989). Just after immersion, dissolved organic compounds adhere to the surface within seconds or a few hours and form a thin conditioning film referred to as molecular fouling (Callow & Callow 2002). Bacteria are among the first colonisers to establish contact with the conditioning film (Qian et al. 2007), followed by the arrival of protozoa and more predominantly, diatoms (Scheer 1945, Wahl 1989; Fig. I.1). The attachment of these communities involves the secretion of an extracellular polymeric substance matrix, mainly formed of polysaccharides, proteins, nucleic acids and lipids, which may cover wide substratum areas (Flemming & Wingender 2010). The term *biofilm* is commonly used to define this microbial community as a whole (Dürr & Thomason 2009). This phase usually take several days and covers different successional stages (Wahl 1989). Only after that, the last phase of macrofouling colonisation begins with the settlement of planktonic larvae, marine invertebrates and algal spores (Corner et al. 2007). Chemical factors produced by the microbial film have been recognised to elicit settlement of cnidarians, polychaetes, molluscs and echinoderms among other groups (Pawlik 1992). Colonisation by macrofouling species involves the presence of sessile organisms and also free-living species (Hincapié-Cárdenas 2007). Growth and development of sessile species may determine the formation of macrohabitats, in such a way that sessile organisms act as ecosystem engineers through the provision of food and/or shelter for associated epifauna, conditioning their presence (Jones et al. 1994).

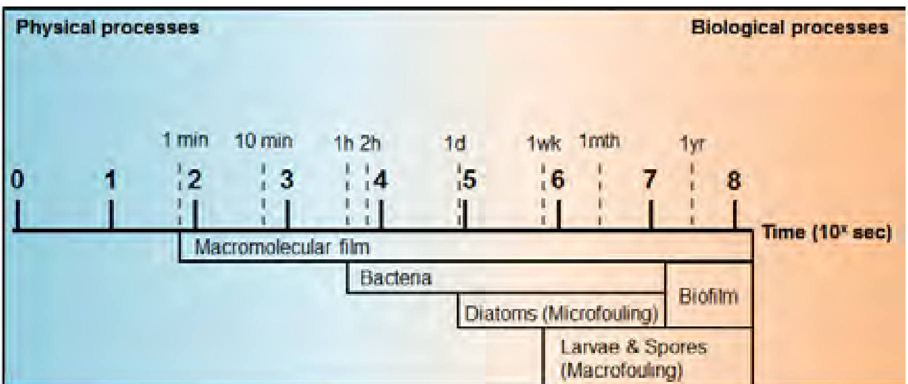



**Figure I.1.** Colonising sequence leading to the establishment of a fouling community (adapted from Wahl 1989).

Successional changes and different mechanisms like facilitation, inhibition or tolerance as well as disturbing factors such as predation or environmental impacts will determine a 'climax' community or stable final stage of long-lived individuals (Connell & Slatyer 1977, Keough & Downes 1982). Thus, multiple stable points may be reached depending on the different species composition and the external drivers during the colonisation process (Connell & Slatyer 1977).

## Aquaculture facilities as artificial structures in coastal areas

The practice of intensive marine aquaculture has steadily increased in many countries during the last five decades (FAO 2014). Aquaculture facilities involve mooring a large amount of artificial structures at a particular position in the sea, which then remain there for long periods. A set of guidelines has been established to distinguish between coastal, off-coast and offshore farming based on parameters such as distance from the coast, water depth or exposure to currents (Holmer 2010). Thus, coastal farming is carried out in shallow waters (< 10 m) near the shore (< 0.5 km), off-coast farming between 10 to 50 m depth, 0.5 to 3 km from the shore and offshore farming further out, in areas more exposed to swells, currents and winds, at water depths up to 50 m and several km from the coast (Holmer 2010).



Mirroring the global trend, aquaculture production is expanding in the Mediterranean Sea (APROMAR 2016) with more than 800 shellfish and finfish farms along the entire Mediterranean coast (estimated from Cardia & Lovatelli 2008, Trujillo et al. 2012). Aquaculture production is mainly focused on the culture of gilthead sea bream *Sparus aurata* and European sea bass *Dicentrarchus labrax*, characteristically developed in off-coast areas and to a lesser extent, in the fattening of young Atlantic bluefin tuna *Thunnus thynnus* captured in the wild, and shellfish such as *Mytilus* spp. and *Ostrea edulis* (APROMAR 2016).

Nearly all Mediterranean production is carried out in circular floating cages with a surface collar structure mostly made of high-density polyethylene (HDPE, Cardia & Lovatelli 2008). The surface collar normally consists of two flotation rings, which hold a net hanging into the water column. Cage shape and volume are maintained by attaching the net to a weights system or by the deployment of a bottom ring sinker system in the lower portion of the net (Klebert et al. 2013). The mooring system consists of a complex framework of ropes, chains and buoys, which are fixed to the sea bottom at several anchorage points (Fig. I.2).

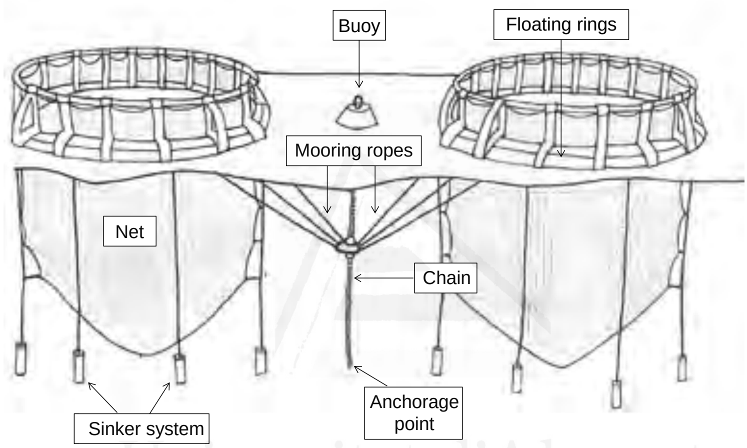



**Figure I.2.** Schematic view of a fish farm, consisting of several circular floating cages (gravity-type; Loverich & Gace 1997).



All the nets, ropes and buoys provide suitable surfaces for a wide group of marine species able to colonise and settle on off-coast structures and form diverse fouling communities (Sarà et al. 2007, Fitridge et al. 2012; Fig. I.3).

### Aquaculture features affecting fouling development

Several characteristics related to farming activity may condition the fouling of fish farms in comparison with other fouling communities. Given the location of aquaculture facilities and certain operational practices, potential differential factors may be the following:

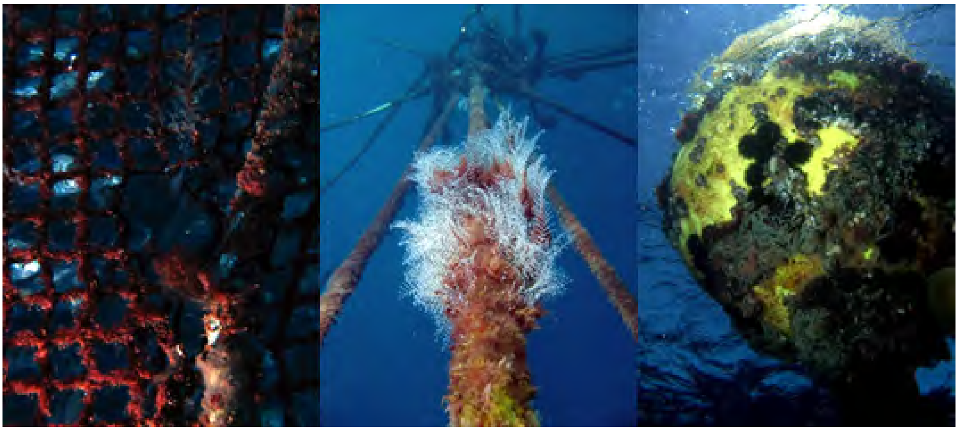


**Figure I.3.** Different fouling communities on nets, ropes and buoys at a fish farm during the study period (Photos: Pablo Arechavala).

- *Position mostly isolated from the sea bottom*: as mentioned above, the newly available surfaces provided by aquaculture facilities are located several kilometres from the shore and tens of metres to the sea bottom (except for the anchorage points). Different development of fouling communities has been observed on substrates attached to the sea bottom and to suspended fish cages (Greene & Grizzle 2007). Hydroids seem to dominate fouling communities of substrates connected to the seafloor, while they are replaced by mussel communities in fish-farm fouling at the early stages of colonisation (Greene & Grizzle 2007). These authors hypothesised that the observed differences were potentially due to distance from seafloor, absence of predators, light availability, position in the waterway and the floating nature of fish farms.

- *Floating features of the facilities:* Floating installations are usually fouled in greater abundance by filter feeders, when compared to fixed installations (Perkol-Finkel et al. 2008). Moving or rotating substrata can attract greater abundances of barnacles, sponges and ascidians, which can double the biomass reached in fixed structures (Glasby 2001). Similarly, a higher presence of bryozoans, bivalves and barnacles is observed on floating installations due to greater exposure to the hydrodynamic conditions (Perkol-Finkel et al. 2008).

- *Influence of aquaculture facilities on hydrodynamics:* The complex structural framework of aquaculture facilities alters the local oceanographic conditions by blocking current flow in front of the first cages, increasing the flow speed on both sides and reducing current speed in their wake (Plew et al. 2005, Klebert et al. 2013). Dispersing stages of marine species transported by sea currents can be consistently held inside the aquaculture framework and rapidly colonise these structures.

- *Food availability:* One of the most studied effects of aquaculture are the organic-enriched wastes generated by uneaten fish feed and faecal material, which are accumulated on marine sediment and can cause negative effects on benthic fauna (Gowen & Bradbury 1987, Wu 1995, Kalantzi & Karakassis 2006). Dissolved and particulate organic matter released into the water column may influence the development of fouling communities in aquaculture facilities. Indeed, higher biomass of biofilm can be found with high organic matter loads in fish farms (Sanz-Lázaro et al. 2011). Hence, biomass of colonising organisms and the presence of heterotrophic filter-feeders also increases in artificial structures near fish farms, with respect to reference sites. This suggests that aquaculture wastes provide an enhanced food supply to fouling communities (Cook et al. 2006). This is supported by Gonzalez-Silvera et al. (2015), who concluded using fatty-acid profiles that macroinvertebrates present in farm fouling are able to assimilate the organic matter deriving from fish farms as a trophic resource.

- *Antifouling strategies*: Biofouling may cause problems in marine aquaculture when either the target cultured species and/or infrastructure can be affected. In fish farms, colonising organisms result in added weight and drag to the structures, affecting cage behaviour and reducing water flow, leading to poorer water quality for farmed fish (Swift et al. 2006, Corner et al. 2007). In shellfish farms they can even damage the target cultured organisms themselves

(Antoniadou et al. 2013). They involve additional economic cost to the aquaculture industry because of the need for cleaning to prevent negative effects on production (Ross et al. 2004, Willemsen 2005). Copper coatings are also often used on nets to prevent the weave of netting being filled by fouling organisms, blocking pores (Corner et al. 2007, Guenther et al. 2010, Fitridge et al. 2012). Additionally, farm staffs normally carry out a routine mechanical cleaning of ropes and other structures in the mooring system, during which most of the organisms are removed (CRAB 2007, Fitridge et al. 2012). This procedure creates opportunities for colonisation by additional species, initiating an ecological succession in the absence of an established climax community structure (Greene & Grizzle 2007).

## Common organisms fouling aquaculture facilities

Since intensive aquaculture started to develop in coastal areas five decades ago, many studies have focused on determining what macrobenthic organisms are able to settle on floating cage structures, owing to the specific problems they cause and their economic cost to the aquaculture industry. Net panels have been deployed at farms in order to describe the development of fouling communities and their species composition in aquaculture facilities (e.g. Hodson et al. 2000, Corner et al. 2007, Greene & Grizzle 2007). These studies have mainly been focused on the sessile species. Despite biogeographical variations, the most important groups found in fish farms are: bivalves especially mussels, hydroids, algae and tunicates (Cook et al. 2006, CRAB 2007, Fitridge et al. 2012). Together with barnacles and sponges, they are the main fouling species in shellfish farms (Khalaman 2001, Fitridge et al. 2012, Antoniadou et al. 2013, Watts et al. 2015). Additionally, free-living and epifaunal inhabitants are crustaceans (e.g. Hincapié-Cárdenas 2007, Madin et al. 2009, Watts et al. 2015), polychaetes (e.g. Hodson et al. 2000, Cook et al. 2006, Fitridge et al. 2012), gastropods (Sarà et al. 2007, Guenther et al. 2010), echinoderms (Greene & Grizzle 2007, Watts et al. 2015, Gonzalez-Silvera et al. 2015), sipunculids (Gonzalez-Silvera et al. 2015) and platyhelminths (Fitridge et al. 2012). Amphipods are however without doubt the most reported group in aquaculture facilities, notably tube-building amphipods (CRAB 2007, Greene & Grizzle 2007, Madin et al. 2009, Gonzalez-Silvera et al. 2015) and caprellids (Hodson et al. 2000, Cook et al. 2006, Swift et al. 2006, Greene & Grizzle 2007, Guenther et al. 2010, Fernandez-Gonzalez & Sanchez-Jerez 2013, Gonzalez-Silvera et al. 2015, Watts et al. 2015). Nevertheless, although they have been reported as early colonisers and also as an abundant component of fouling communities in fish farms (Greene & Grizzle 2007) they have received little research attention in this context.

## Amphipods as a representative group of epifauna

### *Systematics*

The order Amphipoda contains 215 families and more than 9,900 described species (Horton et al. 2016). The classification of the taxon is as below:

| | |
|---|---|
| Phylum: | Arthropoda |
| Subphylum: | Crustacea |
| Superclass: | Multicrustacea |
| Class: | Malacostraca |
| Subclass: | Eumalacostraca |
| Superorder: | Peracarida |
| Order: | Amphipoda |

It traditionally included four suborders: Gammaridea (which contained most of the taxa and the amphipods showing the typical laterally flattened or cylindrical body morphology), Caprellidea (with a characteristically elongated body and a degeneration of the abdomen and pleopods), Hyperiidea (containing all the holoplanktonic amphipods) and Ingolfiellidea (with few species, and a vermiform body with pleopods reduced in size). A few years ago, the Order was rearranged to improve the classification based on the phylogeny. Thus, a new suborder Senticaudata was created, encompassing the previous Caprellidea and part of the old suborder Gammaridea (Lowry & Myers 2013).

### *Biology*

Amphipod species exhibit a degree of sexual dimorphism that permits differentiating males and females. The sex-ratio of populations is often female-biased (Thiel 1998a, Kevrekidis 2004, Prato & Biandolino 2006) and most of them are iteroparous annuals, producing several generations during a year (Sainte-Marie 1991). Median life-span is 14 months (Sainte-Marie 1991), and sexual maturation is reached before 30 days approx. (Takeuchi & Hirano 1991, Cunha et al. 2000, Baeza-Rojano et al. 2011, 2013c). As in the rest of peracarids, amphipods undergo direct development so embryos are carried by females in a ventral brood pouch or marsupium, from which fully-developed juveniles emerge (Thiel 1998b). The brooding period lasts around 10 days (Takeuchi & Hirano 1991, Cunha et al. 2000, Baeza-Rojano et al. 2011, 2013c) and brood size is related to the female size and varies greatly among species between 2-630 (median value = 25) eggs per female (for a review see Sainte-Marie 1991).



### *Ecology*

Most amphipods are marine organisms, but they are also found in brackish and fresh-water environments. Most of them live associated with benthic habitats, except for members of the suborder Hyperiidea, which are holoplanktonic. Amphipods are one of the most abundant groups among benthic fauna (Marti 1989, Thomas 1993, Sanchez-Jerez et al. 1999a, Vázquez-Luis et al. 2009, De-la-Ossa-Carretero et al. 2010, Carvalho et al. 2012) and their sensitivity to pollution is higher than other macrobenthic assemblages. This has allowed them to be applied accordingly as bioindicators for different types of environmental impact (Bellan-Santini 1980, Conradi et al. 1997, Gómez-Gesteira & Dauvin 2000, Guerra-García & García-Gomez 2001, De-la-Ossa-Carretero et al. 2012).

Amphipods are mainly detritivorous, but omnivororous, carnivorous and herbivorous strategies can also be observed (Guerra-García et al. 2014a). They are an important link in the food web, constituting a preferential food for small crustaceans, polychaetes and many fish species (Ruffo 1998, Jiménez-Prada et al. 2015).

Despite lacking pelagic larvae, which is otherwise the main dispersal phase of most marine invertebrates, other routes such as passive drifting (Cummings et al. 1995) or rafting on artificial or natural floating materials (Highsmith 1985, Thiel & Gutow 2005) enable some amphipod species to attain or maintain a broad geographic distribution.

**Justification and general aims**

Taking into account all the factors described above, we find that although sessile fouling communities are well-studied from the point of view of controlling this community on aquaculture facilities, little is known about the epifaunal mobile species inhabiting these artificial structures. The paucity of knowledge is especially the case for amphipod assemblages. Despite being detected in high abundances in several studies, they have not been studied regarding their species composition and relation to the habitats created by the sessile species.

Hence, the overall purposes of this thesis are to:

1) assess the composition of fouling assemblages on aquaculture facilities in the Mediterranean Sea, focusing on the importance of amphipods and comparing these fouling communities with others such as those in harbours, marinas, offshore structures and floating elements.

2) quantify the importance of amphipods in fish-farm fouling and elucidate the role of the main sessile species in supporting such amphipod communities.

3) determine how fish farm structures affect the species composition and

nocturnal distribution of planktonic amphipods with different habitat preferences (pelagic, fouling and soft-bottom).

4) investigate the influence of amphipod species in fouling communities as a potential source of colonisers during the recolonisation of defaunated sediments.

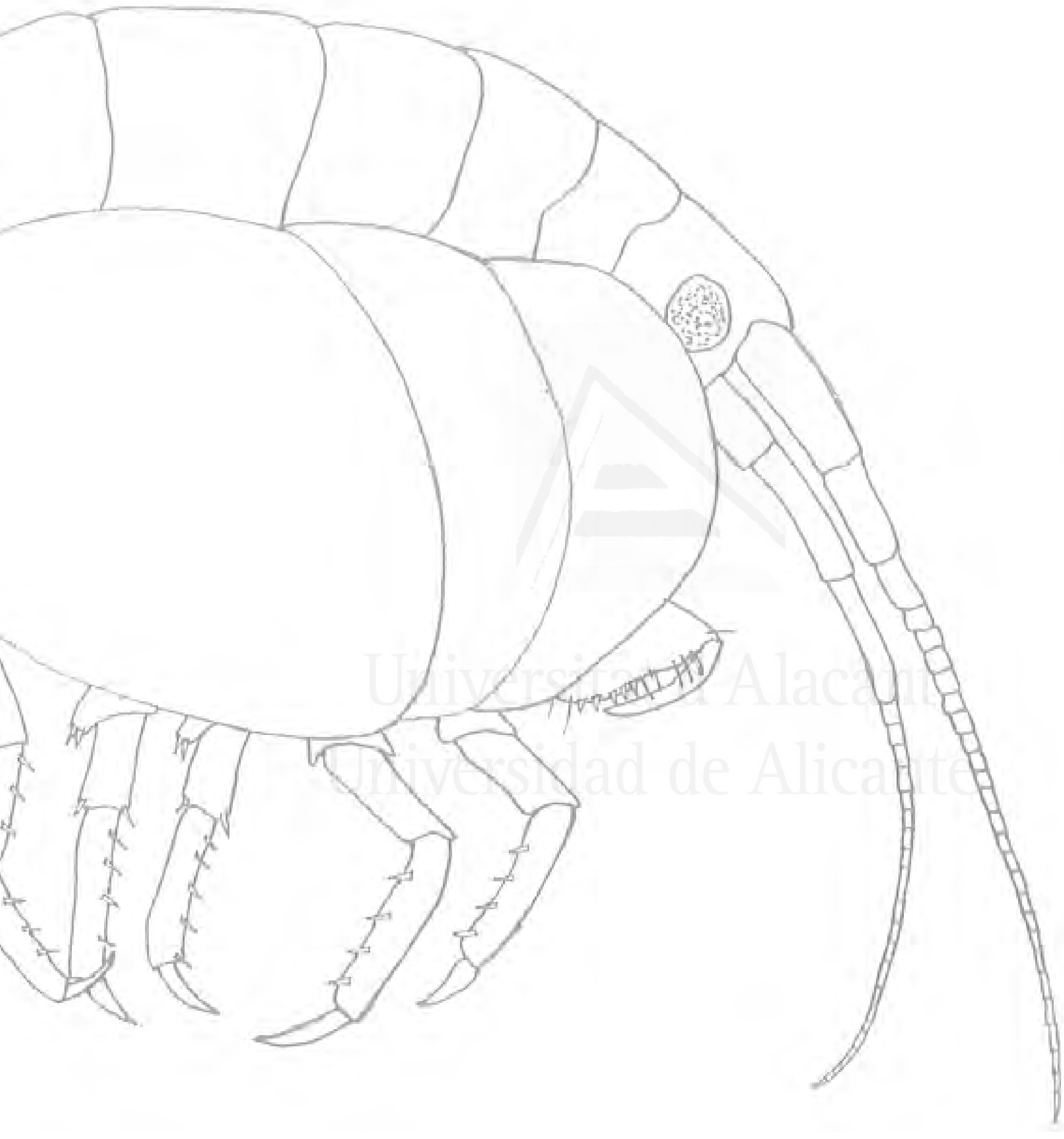
5) analyse the potential role of fish-farm fouling as a source population of amphipods dispersing towards surrounding habitats in the water column.

6) test the applicability of amphipods as an accessory culture in an offshore integrated multi-trophic aquaculture (IMTA) system with finfish as main fed species.



# Chapter 1

## Fouling assemblages associated with off-coast aquaculture facilities: an overall assessment of the Mediterranean Sea



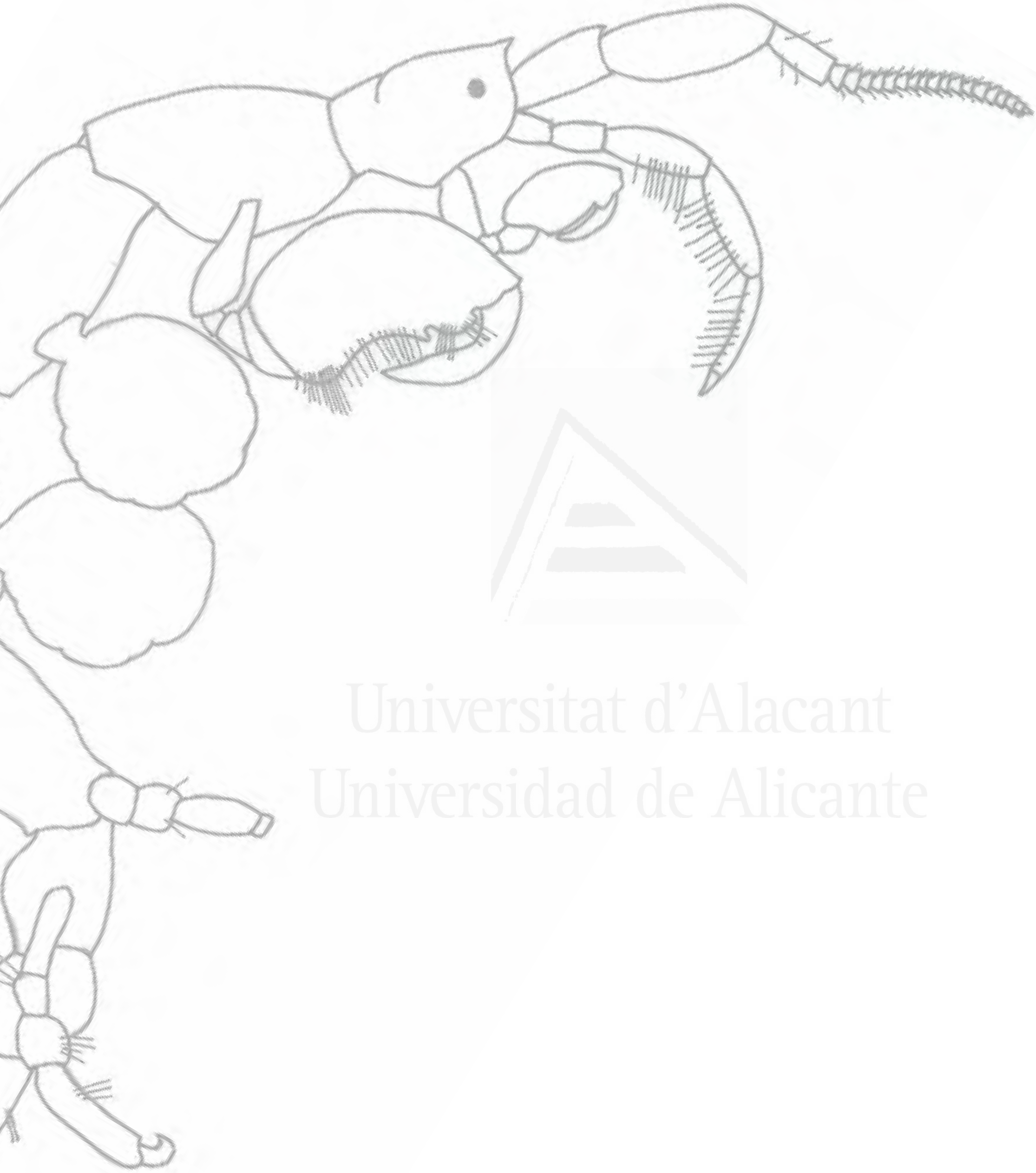
This chapter has been published as:

Fernandez-Gonzalez V, Sanchez-Jerez P (*in press*) Fouling assemblages associated with off-coast aquaculture facilities: an overall assessment on the Mediterranean Sea. Medit Mar Sci. Doi: 10.12681/mms.1806



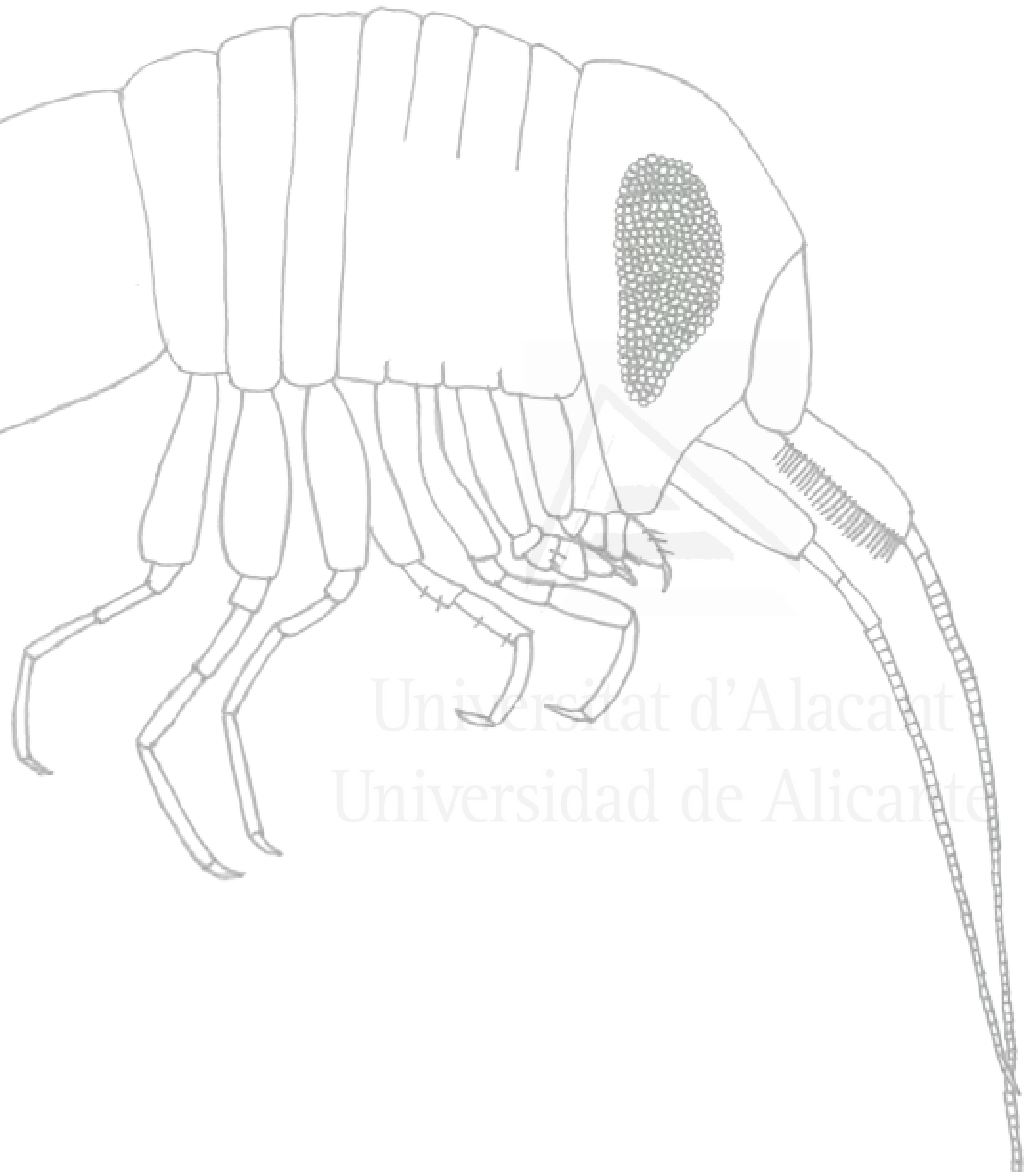
# Chapter 2

## The importance of macro and microhabitats in holding extremely high densities of amphipods at fish farms



# Chapter 3

## Changes in nocturnal planktonic assemblages of amphipods due to the presence of coastal aquaculture cages



This chapter has been published as:

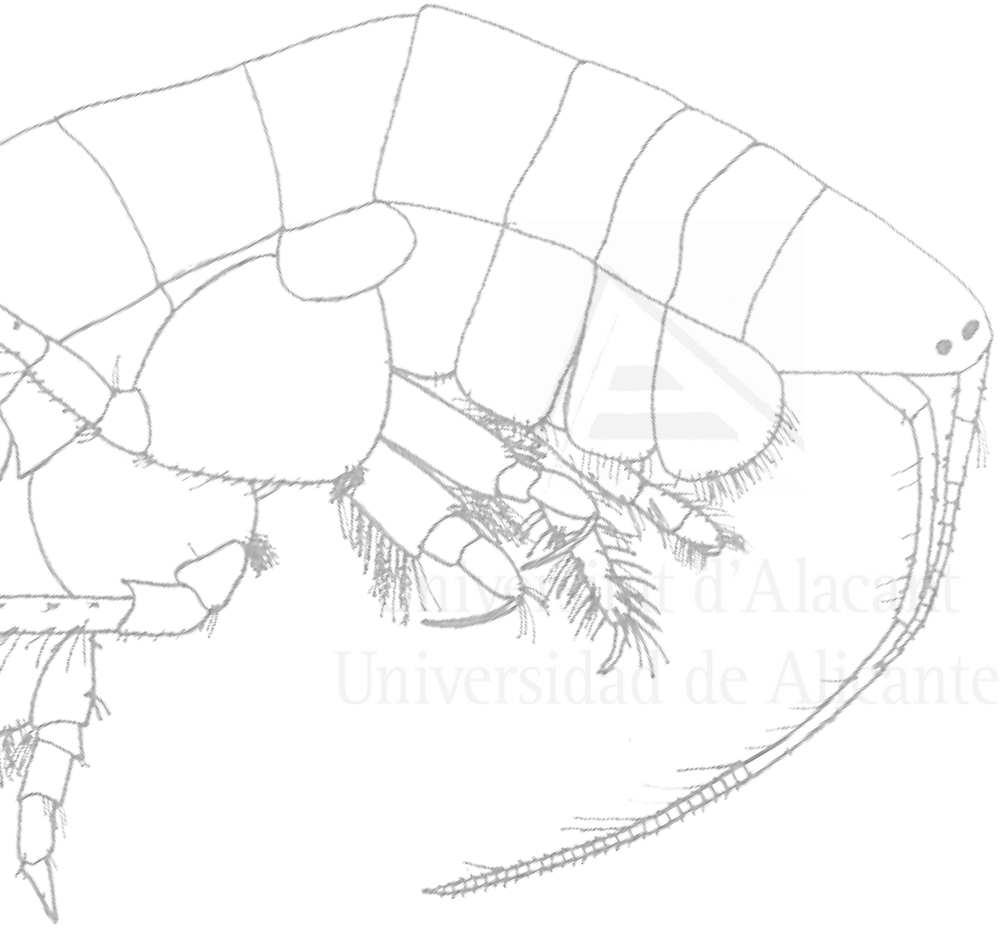
Fernandez-Gonzalez V, Fernandez-Jover D, Toledo-Guedes K, Valero-Rodriguez JM, Sanchez-Jerez P (2014) Nocturnal planktonic assemblages of amphipods vary due to the presence of coastal aquaculture cages. Mar Environ Res 101: 22-28.

http://www.sciencedirect.com/science/article/pii/S0141113614001433



# Chapter 4

## Role of fish-farm fouling in recolonisation of nearby soft-bottom habitats affected by coastal aquaculture



This chapter has been published as:

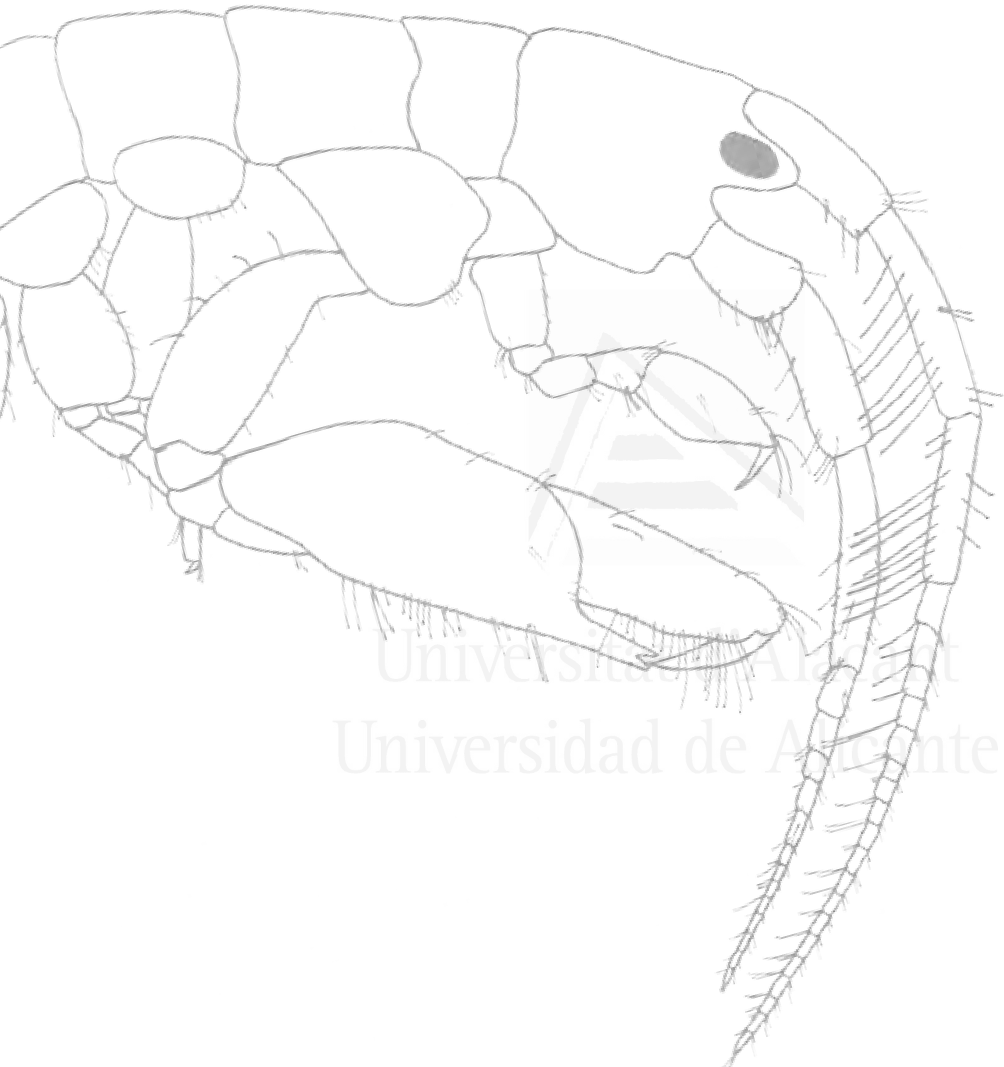
Fernandez-Gonzalez V, Martinez-Garcia E, Sanchez-Jerez P (2016) Role of fish farm fouling in recolonisation of nearby soft-bottom habitats affected by coastal aquaculture. J Exp Mar Biol Ecol 474: 210-215.

http://www.sciencedirect.com/science/article/pii/S0022098115300502



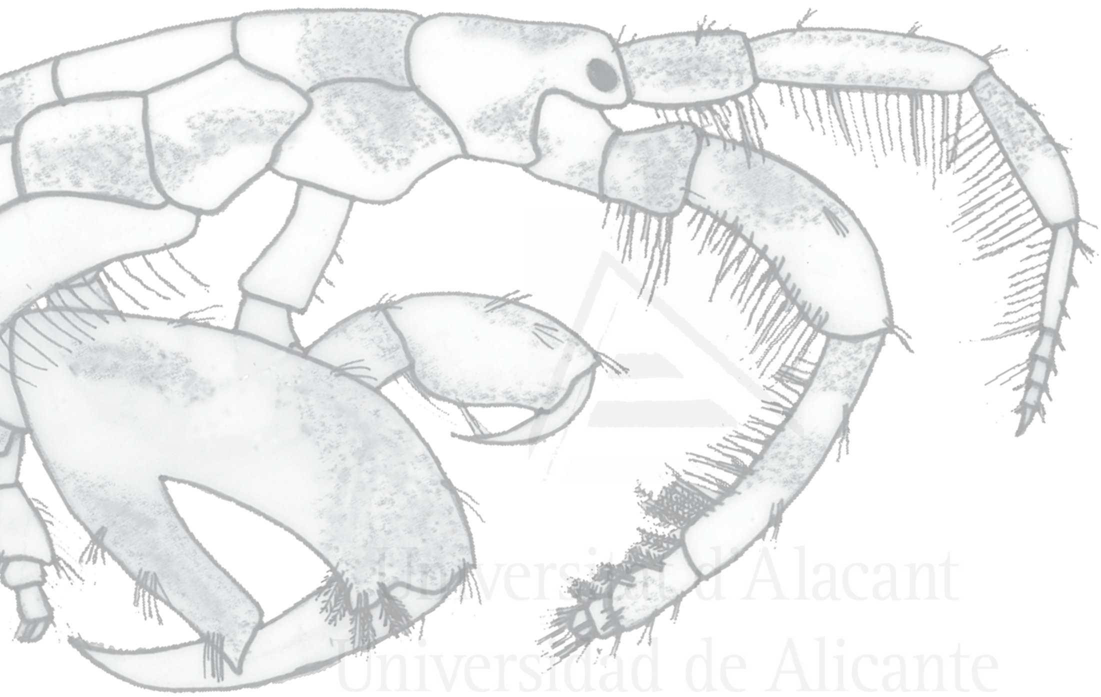
# Chapter 5

## The influence of fish-farm fouling as source population of amphipods in the establishment and maintenance of local metapopulations



# Chapter 6

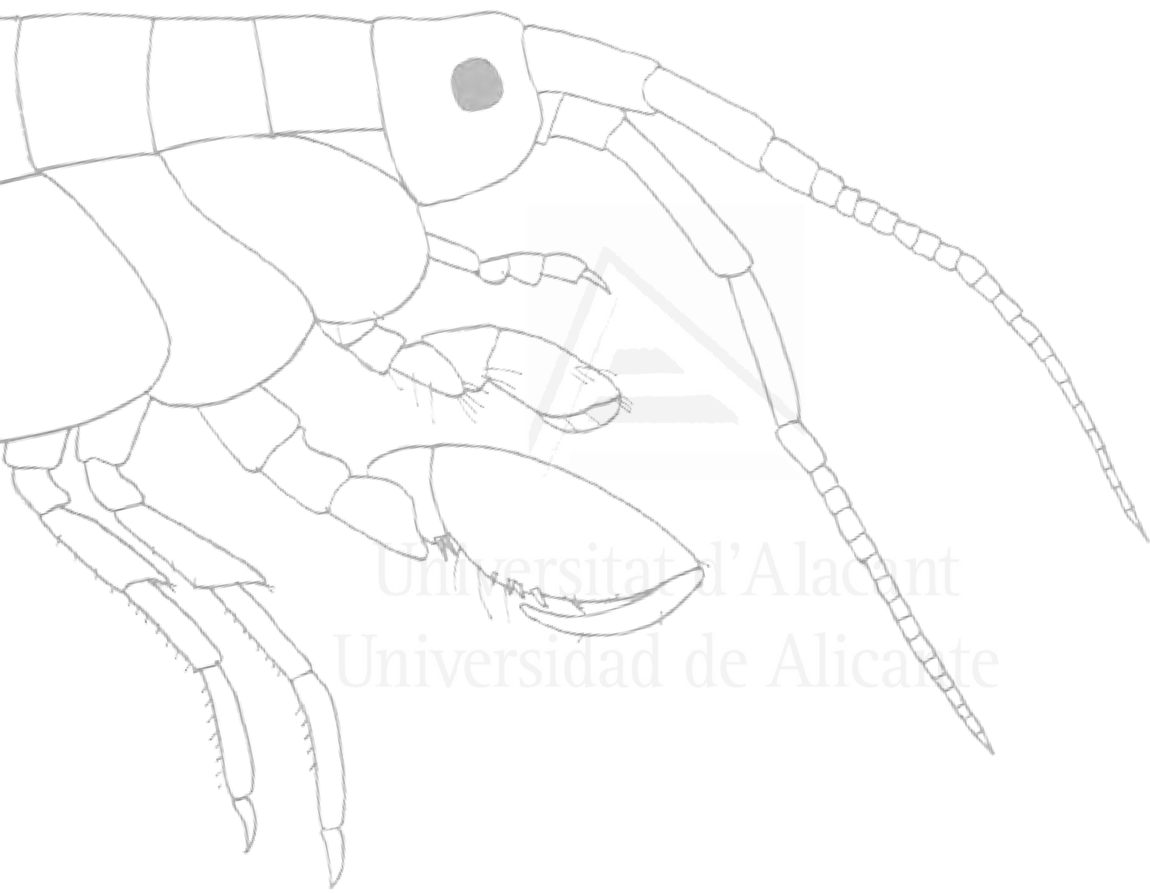
## Harvesting amphipods applying the Integrated Multitrophic Aquaculture (IMTA) concept in off-shore areas.





This experiment was carried out in collaboration with Cultivos del Ponto and Piscifactoría de Aguadulce (CULMAREX GROUP) and Centro Tecnológico de la Acuicultura (CTAQUA) as part of the project "Desarrollo de sistemas acuícolas multitróficos integrados asistidos por tecnología submarina avanzada (SUMERGI+DOS)", financed by FEDER-INNTERCONECTA program (CDTI + Junta de Andalucía).

# General Discussion and Conclusions



## Discussion

Throughout this thesis it has been shown that fish-farming activities affect the amphipod assemblage in several ways. They provide new inhabitable niches with an input of organic-enriched wastes and alter the local hydrodynamics. These changes in turn favour the establishment of high population densities of fouling amphipods at aquaculture sites in the Mediterranean Sea. The complexity and heterogeneity of sessile organisms growing on fish farm structures has an important influence on amphipod assemblage composition and abundance, particularly as they undergo constant or regular successional disturbance due to cleaning operations. Moreover, the presence of fish farms in off-coast areas causes changes in the migration behaviour of amphipods, promoting an intimate connectivity between different subpopulations. As a result, a new potential commercial application arises from the possibility of using them as biofilters of aquaculture wastes, within an off-coast integrated multitrophic aquaculture system (Fig. D.1).

### Homogenisation in fouling communities in the Mediterranean Sea: Can it be extrapolated to the rest of the world?



Aquaculture facilities provide substrates for a wide diversity of marine organisms that are able to settle and colonise these structures. The presence of hard substrata in off-coast areas is extremely limited in comparison to the surfaces available in shallow coastal waters, with natural rocky habitats, breakwaters and jetties (Bulleri & Chapman 2010). Most of the amphipod species living on aquaculture facilities have also been found in many different kinds of fouling communities, including harbours, platforms, buoys or even on sea turtles (Chapter 1). The innate need for an attachment to a substratum in the water column may make amphipods non-selectively attach to any object available in the open sea (Gutow et al. 2015). In addition to new substrata, aquaculture facilities offer great quantities of trophic resources in the form of organic-enriched wastes that enable associated fauna to maintain thriving populations. Epifauna inhabiting Mediterranean aquaculture facilities are strongly marked by the abundance of amphipods, showing a homogeneous assemblage with seven common abundant species (*E. rapax*, *J. marmorata*, *J. slatteryi*, *E. punctatus*, *S. tergestina*, *C. equilibra* and *C. dilatata*) throughout all the Mediterranean coasts sampled. These species are commonly reported as rafters, organisms that cling efficiently to floating items and maintain high numbers on them (Thiel & Gutow 2005). The rafting ability of these species, the scarcity of available habitat and the use of the new trophic resources all favour the homogenisation of amphipod assemblages in the fouling communities on Mediterranean aquaculture facilities.

A similar utilisation pattern of the new surfaces available might also be expected for sessile species on aquaculture facilities, which appear to select their attachment substrata opportunistically. Sessile species in the different kinds of fouling assemblages found throughout the Mediterranean Sea are represented mainly by algae, bivalves, bryozoans and hydroids. These matching well with the most representative fouling species found on shellfish and finfish aquaculture facilities reported in the literature (Table D.1). However, further to this finding of the same characteristic groups in fouling on floating structures, the same genera or even the same species are also found in aquaculture facilities worldwide, most of them frequently reported as facultative rafters on floating items (Thiel & Gutow 2005).

Sessile fouling organisms play an important role in supporting the high densities of amphipods, due to habitat complexity, especially on a small scale. In fact, different amphipod species composition depending on the habitat-forming species, mussels, hydroids or algae, were primarily attributable to the diverse microhabitats created by secondary colonising organisms. The relationship of amphipod species with a specific kind of habitat, e.g. *C. dilatata* with branched upright hydroids or *E. rapax* with Ceramiales algae, can consequently lead to cosmopolitan distributions based on their host preferences, if the latter are fouling species commonly found at aquaculture sites on all the world´s seas.

In contrast, some amphipods have also been reported as naturally early colonisers of newly available hard substrata, even clean surfaces or those

**Table D.1.** Comparison of the main sessile fouling organisms found in this study and their presence at finfish (FF) and shellfish (SF) aquaculture facilities worldwide: Mediterranean Sea (Med), Eastern Atlantic Ocean (EAtl), Western Atlantic Ocean (WAtl), North Sea (NS), White Sea (WS), Red Sea (Red), Indian Ocean (Ind.), Pacific Ocean (Pac.) and worldwide review (WW). References are: (1) Cook et al. 2006, (2) Fitridge et al. 2012, (3) Sliskovic et al. 2011, (4) Watts et al. 2015, (5) Hodson et al. 2000, (6) Gonzalez-Silvera et al. 2015, (7) Madin et al. 2009, (8) Antoniadou et al. 2013, (9) Sarà et al. 2007, (10) CRAB 2007, (11) Khalaman 2001, (12) Greene & Grizzle 2007, (13) Bakır & Katağan 2011, (14) Guenther et al. 2010 and Atalah et al. 2016.

| Taxon | Species in this thesis | Species in other studies | Region | Site | Ref. |
|---|---|---|---|---|---|
| Algae | *Antithamnion cruciatum* | *Antithamnion* sp. | Med., WW | FF | 1, 2 |
| | | *A. cruciatum* | Med. | FF | 3 |
| | *Ceramium* spp. | *Ceramium* sp. | Med., Pac. | FF, SF | 1, 4 |
| | | *C. affine*, *C. tasmanicum*, *C. uncinatum* | Pac. | FF, SF | 5,15 |
| | | *C. ciliatum*, *C. diaphanum* | Med. | FF | 3, 6 |
| | *Cladophora* spp | *Cladophora* sp. | Med., Pac. WW | FF, SF | 1, 2, 3,4, 6 |
| | | *C. dalmatica* | Med. | FF | 3 |
| | *Jania* sp | *Jania* sp | Red | FF | 1 |
| | | *J. rubens* | Med. | FF | 6 |
| | *Polysiphonia* spp. | *Polysiphonia* sp. | Med., Ind. | FF | 1, 3, 7 |
| | | *P. brodiei* | Pac. | FF | 5 |
| | | *P. scopulorum* | Med. | FF | 3 |
| | *Spyridia filamentosa* | *S. filamentosa* | Med. | FF | 3 |
| Anthozoans | *Actinia* spp | *Actinia* sp. | Med. | FF | 6 |
| | | *A. tenebrosa* | Pac. | SF | 15 |
| Bryozoans | *Bugula neritina* | *B. neritina* | Med., Pac. | SF | 4, 8, 15 |
| | *Schizoporella errata* | *Schizoporella* sp. | Med. | FF | 6 |
| Crustaceans | *Chthamalus* sp. | *C. stellatus* | Med. | FF | 9 |
| | - | *Balanus* sp. | Med. | FF | 6 |
| | | *B. balanus* | Med., EAtl. | FF | 1 |
| | | *B. crenatus* | W | SF | 11 |
| | | *B. trigonus* | Med., Pac. | SF | 4, 8, 9, 15 |
| | | *Amphibalanus amphitrite* | EAtl., Ind. WW | FF, SF | 2, 7, 8, 10 |
| | | *Perforatus perforatus* | Med., EAtl. | FF, SF | 8, 9, 10 |
| Hydroids | *Aglaophenia* sp. | *Aglaophenia* sp. | Med. | FF | 6 |
| | *Obelia* sp. | *Obelia* sp. | Med., Pac. | FF, SF | 1, 8, 15 |
| | | *O. bidentata* | WW | SF | 2 |
| | | *O. dichotoma* | Pac., WW | FF | 2, 5 |
| | | *O. longissima* | EAtl., WS | FF, SF | 1, 11 |
| | *Pennaria disticha* | *P. disticha* | Med. | FF | 6 |
| | *Tubularia* sp. | *Tubularia* sp. | Med., NS, EAtl., WAtl, WW | FF, SF | 2, 10, 12 |
| Molluscs | *Hiatella arctica* | *H. arctica* | EAtl., WAtl., Pac. | FF, SF | 1, 12, 15 |
| | *Mytilus galloprovincialis* | *M. galloprovincialis* | Med., Pac. | FF, SF | 4, 6 , 9, 13, 15 |
| | | *M. edulis* | EAtl., NS, WS, WAtl., WW | FF, SF | 1, 2, 10, 11, 12, 14 |
| | | *Mytilus* spp. | EAtl., Med., WW | SF | 2, 10 |
| | *Ostrea edulis* | O. edulis | Med. | FF, SF | 8, 9 |
| | | *Ostrea* sp | Med. | FF | 1 |
| Ascidiaceans | - | *Botryllus schlosseri* | Med., Pac., WW | FF, SF | 1, 2, 4 |
| | - | *Ciona intestinalis* | EAtl., NS, Pac., WW | FF, SF | 1, 2, 4, 10 |
| | - | *Styela clava* | WW review | SF | 2 |
| | | *S. plicata* | Med., WW | FF, SF | 2, 8 |
| | | *S. rustica* | WS | SF | 11 |
| | | *S. truncata* | Red | | 1 |

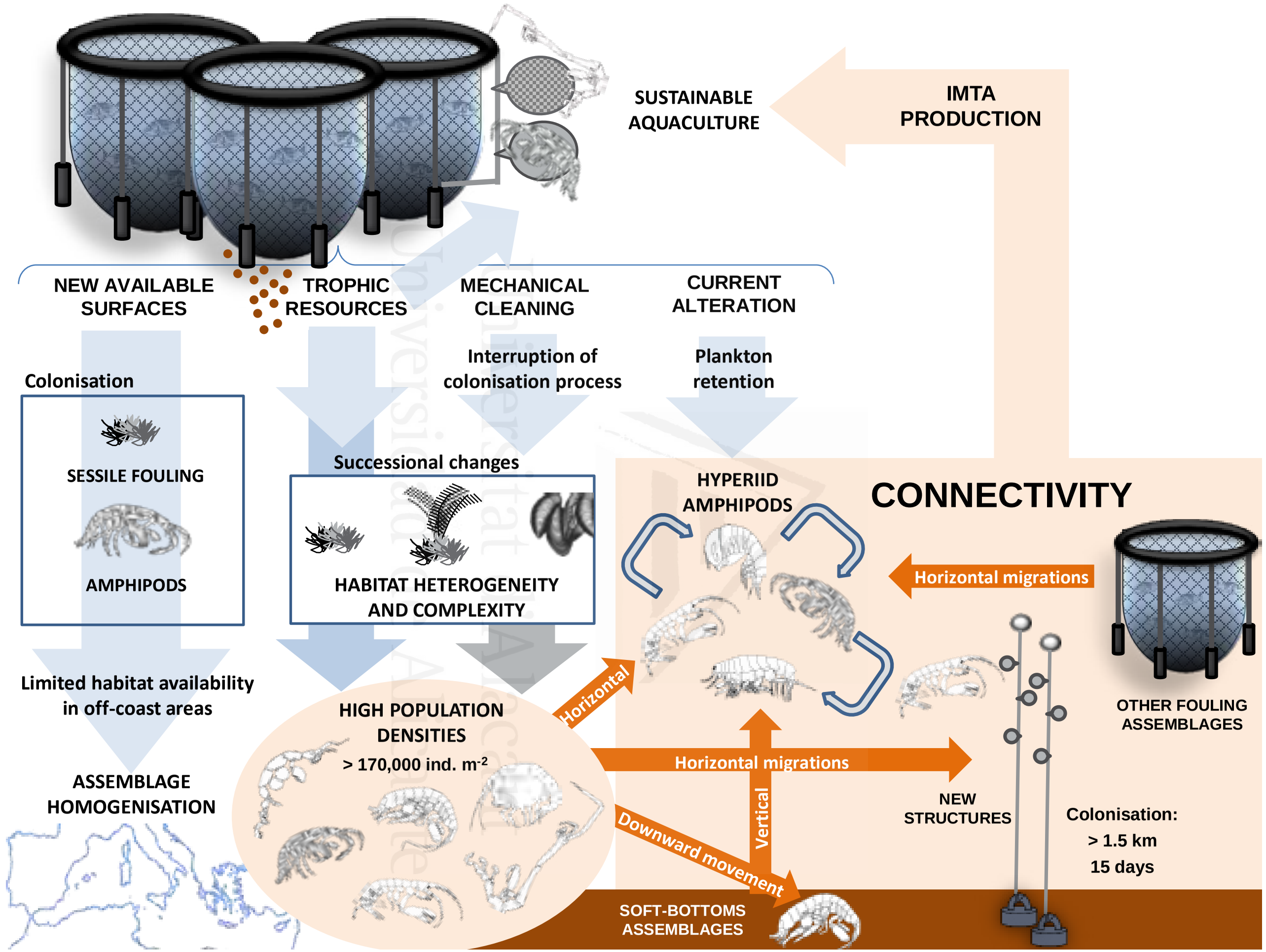



**Figure D.1.** Conceptual model of factors related to aquaculture activity affecting fouling communities, including ecological interactions between amphipod assemblages detected in this thesis and their potential applications.

in an initial stage of colonisation. Examples can be found in tube-building amphipods such as *Jassa* species (Beermann 2014) or caprellids (Iikura 1987 in Takeuchi et al. 2001), both in concordance with the results obtained for *E. punctatus*, *J. slatteryi* and *C. equilibra* in the colonisation experiment in this PhD thesis (see Chapter 5). In fact, species of these genera have been reported as abundant inhabitants of aquaculture facilities worldwide (e.g. *Caprella* spp., Hodson et al. 2000, Swift et al. 2006, Greene & Grizzle 2007, Guenther et al. 2010, Watts et al. 2015, Atalah et al. 2016; *Jassa* spp., Cook et al. 2006, Greene & Grizzle 2007, Atalah et al. 2016).

As we have seen, hard substrata are of limited availability in off-coast areas and they are used opportunistically by early colonisers like sessile and amphipod species. These two factors may be responsible for the high level of homogeneity found in fouling amphipod assemblages in the Mediterranean and that expected for aquaculture facilities worldwide. This is in stark contrast with the high variability observed in other marine habitats such as soft bottoms (Fernandez-Gonzalez et al. 2013) or seagrass meadows (Sturaro et al. 2015), where changes in amphipod assemblages are observable on a scale of metres.



### Connectivity among local amphipod assemblages: Retention *vs* Migration

In the Mediterranean Sea, fish farms are usually located in semi-exposed conditions with the aim of achieving good water renewal in cages, which leads to better culturing conditions and less environmental impact than at farms in semi-enclosed bays (Maldonado et al. 2005).

The structural framework of the farms and the movement of fish swimming inside a circular pattern results in alteration of the local oceanographic conditions through a complex hydrodynamic model that reduces current velocity and consequently favours the retention of particles (Gansel et al. 2014, Klebert et al. 2013). In fact, most plankton groups are concentrated within fish-farm facilities, especially copepods and crustacean larvae. These are up to 20 times more abundant around cages compared to control locations without influence from aquaculture (Fernandez-Jover et al. 2016). This could also explain the rapid colonisation of farm structures by sessile fouling species because of such larval retention.

Amphipods seem to undergo a similar influence from fish farms. Not only hyperiids and other plankton groups are retained in the water column under the structural framework of the farms, but so are the migrant individuals from soft bottoms and fouling communities. Juveniles and adults of many benthic invertebrates often migrate vertically, generally at night, for diverse ecological reasons. It may be to feed in more productive areas, colonise new habitats or to mate (Mills 1967, Laval 1980, Alldredge & King 1985, DeWitt 1987, Conlan 1991, Sanchez-Jerez et al. 1999b). Thus, both the particulate organic matter generated by farming activity and the retention of potential prey such as copepods (Guerra-García et al. 2014a) promote the feeding of amphipods in these productive waters. Furthermore, aquaculture facilities may connect the different amphipod assemblages in off-coast areas, by retaining migrant amphipods that are dispersing passively from both the seabed and other fouling assemblages looking for new habitats (Fig. D.1).

Off-coast connectivity is also promoted by the exchange through horizontal migration of individuals between the amphipod subpopulations within and outside aquaculture sites. The almost saturated populations found in fouling communities promote the dispersal of individuals ready to start breeding immediately, such as ovigerous females and even less fit individuals such as juveniles migrate if the habitat is overly saturated (Hansson 1991). When competition for space and resources is hard, individuals can be spurred to abandon the original habitat, undertaking migrations to the seabed, or to other floating habitats.

Amphipod assemblages greatly differ between fouling communities and soft bottoms influenced by aquaculture (Fernandez-Gonzalez et al. 2013). However, an important flow of fouling amphipods seems to be forced to recolonise benthic habitats. They appear as abundant initial colonisers of defaunated sediments under the cages. Further research is necessary to understand how this downward movement may contribute to reducing the impact of fish farming on the sea bottom. This spillover effect could help reduce the effects on the oxygen and sulphide contents in the distressed sea bottom, where fouling amphipods would increase the bioturbation of the sediment and prepare it for further recolonisation by typical benthic species (Modig & Olafsson 2001). Indeed, it is interesting to know the role of amphipods from fouling communities in the successional process in benthic habitats, since they are thought to be replaced by other species at a latter successional stage (Berge 1990, Lu & Wu 1998).

Complex connectivity processes also operate between aquaculture sites and the surrounding floating habitats, where farm fouling acts as the source point of amphipods, exporting biomass to nearby coastal areas. Given that the experimental collector units used in this thesis were totally submerged, active swimming or floating -even when no rafts are available- seem to be the potential dispersal mechanisms for colonising these new habitats (Highsmith 1985), since peracarids in the water column have a great ability to attach or cling to floating substrata if they make contact with them (Thiel & Gutow 2005). In all cases, the presence or not of hard substrata in off-coast areas is likely be the limiting factor that determines the colonisation of any floating structure by amphipods, which migrate via currents that favour transport to a new settlement site (Kingsford et al. 2002).

Individuals of all life-stages have been detected in both cases: downward movement and horizontal migration. However, dispersal as ovigerous females was frequently observed in this research, which would facilitate the colonisation process and may explain population persistence even at very low densities in the new habitats (Gilpin 2012). Successional studies should be performed to complete our knowledge of the colonisation of off-coast structures by amphipods, as well as the role of a resident population and/or local factors -such as competition or predation- in successful colonisation.

Nonetheless, high connectivity between floating habitats may occur on a regional scale given the extent of dispersal, over 1.5 km from the fish farm in only 2 weeks, and the more than 20,000 offshore floating cages within 10 km of the entire Mediterranean coast (Trujillo et al. 2012). These individual exchanges might widen the genetic diversity of amphipod populations in recipient fouling communities in down-current localities (Gutow et al. 2015). However, further studies are necessary to assess this and other possible consequences of connectivity between floating artificial habitats in off-coast areas and the role of these migrant individuals in the pelagic system, such as their being a trophic resource for plankton-feeding fish.

**Role of farm fouling in the dispersion of alien species**

It is worth noting that the above-mentioned connectivity between off-coast artificial structures may have repercussions on the non-indigenous species (NIS) that reach these off-coast structures. Two NIS have been detected in Mediterranean aquaculture facilities: *Caprella scaura* and *Stenothoe georgiana*, besides others at farms in different countries and seas.

The most striking example of an NIS in farms is the case of *Caprella mutica*. Over the past 40 years this species originating from the Sea of Japan has become successfully established along many of the Pacific, Atlantic and North Sea coastlines (Boos et al. 2011). In regions outside its native range, *C. mutica* is strongly associated with aquaculture activity, being reported principally on fish cage netting and mussel lines (Cook et al. 2007) in Canada, the United States, Scotland, Ireland, Norway, the Netherlands, Spain and New Zealand (Ashton 2006, Boos et al. 2011, Almón et al. 2014). Similarly, another two species, *C. scaura* in the Mediterranean (Fernandez-Gonzalez & Sanchez-Jerez 2013) and *Caprella andreae* in New Zealand (Woods et al. 2014) have also been reported from fish farms outside their native range. Farm fouling can include living substrata where NIS often occur (e.g. *C. scaura* on *Bugula neritina,* Ros et al. 2014; *C. mutica* on *Cladophora* spp., Cook et al. 2007; Table D.1). Therefore, the factors making it a unique habitat where amphipod assemblages show high population densities can lead to fish farms acting as source points of NIS (Boos et al. 2011). Such connectivity observed in off-coast facilities may generate a stepping-stone effect, enhancing opportunities for secondary spread in non-native areas (Cook et al. 2007, Fernandez-Gonzalez & Sanchez-Jerez 2013).

Furthermore, aquaculture facilities are strongly connected with ports and marinas. Fish-farm boats, moving around for regular feeding and maintenance checks, and commercial and recreational vessels fishing around different farms along the same coastal area (Arechavala-Lopez et al. 2011), could also spread NIS between coastal and off-coast locations and also from one farm to another (Fernandez-Gonzalez & Sanchez-Jerez 2013). The ecological impact on coastal systems of NIS dispersal due to fish farming should be tackled in future research.

**Aquaculture of carnivorous species: taking advantage of wastes**

One of the main problems of current aquaculture concerns the nutritional requirements of target cultured species. The number of fed species is increasing each year in such a way that in 2012, 69.2 % of world aquaculture production consisted of these species at the expense of non-fed species e.g. bivalves, macroalgae or cyprinids (FAO 2014). In fact, an important part of European aquaculture is focussed on high-trophic level (i.e. carnivorous) species such as salmon, sea bass, sea bream or meagre, probably because of their higher marketability (APROMAR 2016, FAO 2016). Indeed, 85% of Mediterranean aquaculture is based on sea bass and sea bream (Cardia & Lovatelli 2008).

Culturing carnivorous species has depended on the use of fish meal and fish oil to manufacture formulated pellets. Traditionally, wild fish stocks, mainly small pelagic fish such as Peruvian anchovy, have been used to supply the nutritional requirements of cultured fish. This situation is likely be unsustainable from both environmental and economic points of view, so the search for new alternative sources of marine protein and oil is becoming essential. Efforts to diminish these ingredients have been made and fish oil is being partially replaced by vegetable oils, and fish meal by feedstuff from very different sources: plant-based protein, terrestrial animal or seafood by-products, etc. (NRC 1993). However, new combinations of protein and oil sources are still of particular interest nowadays.

Feeding fish with formulated pellets under aquaculture conditions in floating sea cages makes for an input of particulate organic matter into the marine environment. Depending on factors such as feeding practices, fish behaviour or the local hydrodynamic conditions, a large quantity of supplied but uneaten feed and wastes are lost vertically to the sea bottom or laterally through the sides of the sea cages in all directions (Ballester-Moltó 2016). Approximately 20% of particulate aquaculture wastes flow through the nets horizontally (Ballester-Moltó 2016). Integrated multi-trophic aquaculture (IMTA) arises from the idea of incorporating species at lower trophic levels, which are able to assimilate these wastes from the water column. Amphipods are potentially exploitable in restated IMTA, based on species naturally growing in fish-farm fouling, which ensures they are adapted to local conditions and enhances the sustainability of the farming operation. Thus, amphipods together with mussels (*Mytilus galloprovincialis)*, oysters (*Ostraea edulis*) and sea urchins (*Paracentrotus lividus*) appear to be the most suitable species to fulfil these requirements in the Mediterranean (Fernandez-Gonzalez & Sanchez-Jerez 2015). They present other advantages regarding the best use of the facilities' legal concession and the reduced initial cost of the IMTA system. Moreover, if these organisms are considered as quantities of nitrogen otherwise lost to the environment that are recycled back into marine proteins and lipids, they offer clear opportunities for reincorporation into fish feed and increased productivity versus costs. This should be immediately meaningful and attractive to the farming enterprise (Hughes & Black 2016). IMTA aquaculture is already being actively promoted at a national or European level through various research frameworks (e.g. the JACUMAR IMTA project http://www.mapama.gob.es/app/jacumar/planes_nacionales/Documentos/101_IFP_MULTITROFICOS.pdf; IDREEAM project, http://www.idreem.eu/). Further research about annual variability in terms of potential production and profitability, accompanied by economic analyses, is necessary before IMTA systems become a commercial reality in the Mediterranean Sea.

## CONCLUSIONS

1. Fouling communities at aquaculture facilities in the Mediterranean Sea are made up of mainly bivalves, algae, hydroids and bryozoans. Their epifauna is dominated largely by amphipods, usually representing more than 80 % of motile fauna associated with these organisms.

2. Fouling communities of Mediterranean aquaculture facilities are characterised by a homogeneous amphipod assemblage consisting of seven frequent and dominant species: *Elasmopus rapax*, *Jassa marmorata*, *Jassa slatteryi*, *Ericthonius punctatus*, *Stenothoe tergestina*, *Caprella equilibra* and *Caprella dilatata*.

3. Mean amphipod densities observed in fish-farm fouling amounted to 176,000 ind./m$^2$ and reached maxima up to 1,000,000 ind./m$^2$, exceeding the maximum values reported from the most productive ecosystems worldwide.



4. Macrohabitats formed by the mussel *Mytilus galloprovincialis* on the mooring ropes of aquaculture facilities host the highest abundances of amphipods. However, they were directly related with the microhabitats arising from the epiphytic species of algae and hydroids on the shells. For instance, *E. rapax* was widely present in Ceramiales turf while *E. punctatus* and *C. equilibra* were linked to the microhabitat formed by the hydroid *Aglaophenia* sp.

5. The second most important macrohabitats were characterised by dense colonies of the hydroid *Pennaria disticha.* These were strongly dominated by the caprellid *C. dilatata* and secondarily by the gammarid *J. slatteryi.* The latter seems to compete for space with its congener *J. marmorata*, which colonises the centre of all the studied macrohabitats, limiting the distribution of *J. slatteryi* to more exposed surfaces such as the stems of *P. disticha.*

6. Fish farms induce a retention effect on planktonic amphipods near such facilities, noticeable in the increased abundance of hyperiids. The inputs of amphipods migrating both vertically from soft sediments and horizontally to and from fouling communities were also important.

7. The nocturnal presence of amphipods in the study area is related to the lunar cycle. Hyperiids, particularly *Lestrigonus schizogeneios,* seemed to be mainly influenced by the full moon phase, while benthic amphipods from both seabed and fouling communities were more common in the water column during the quarter moon nights.

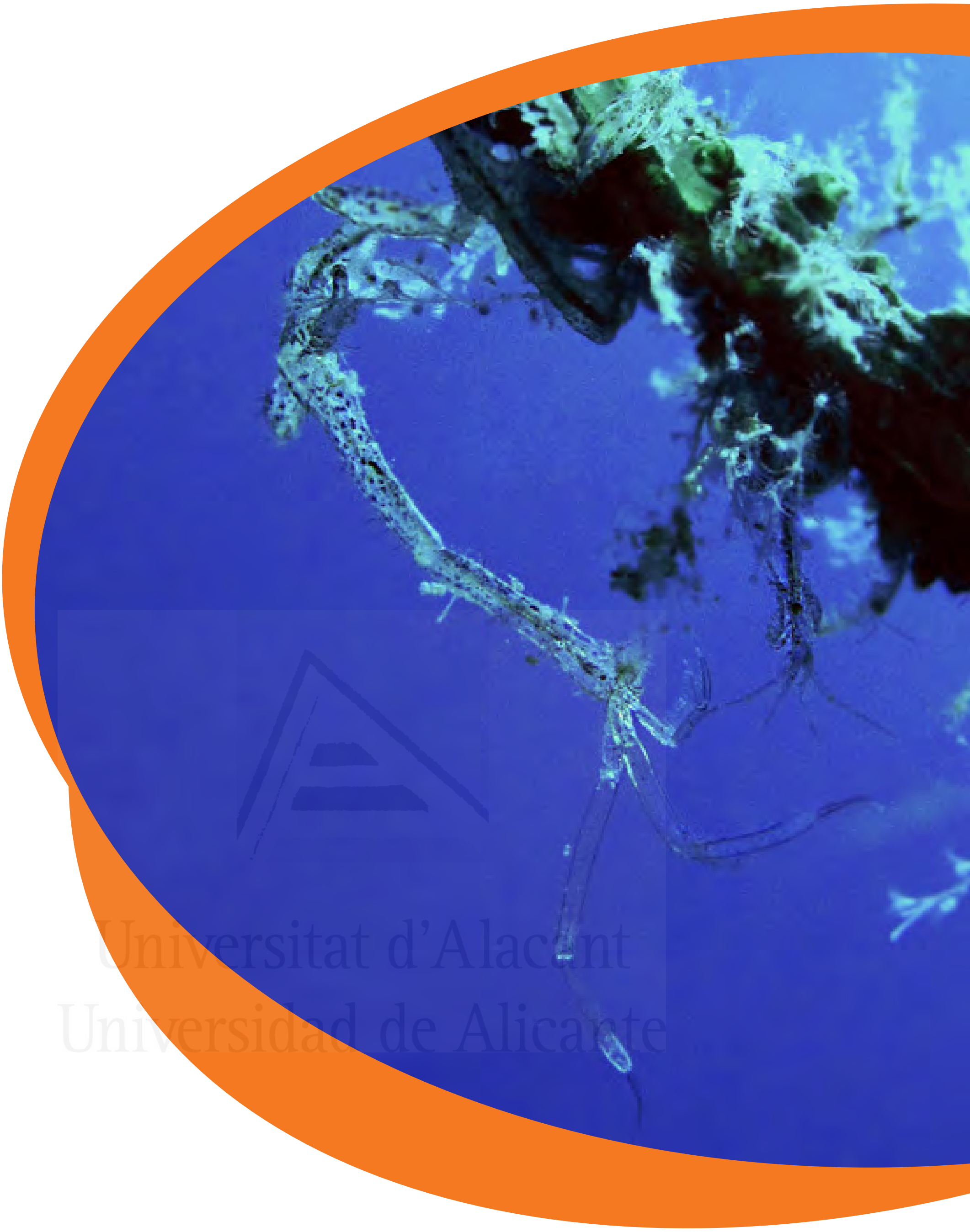
8. The high densities of fouling amphipods in the aquaculture facilities influence surrounding habitats, acting as source population of migrants to soft-bottom and floating communities.

9. Fouling amphipods have great ability as early colonisers, especially the tube-building amphipods *E. punctatus* and *Jassa* spp., which successfully colonise defaunated sediments and other fouling communities, the latter even in an initial stage of colonisation.

10. Aquaculture facilities promote an intimate connectivity between highly spatially structured populations of amphipods, where exchange of individuals is feasible at a scale of hundreds of metres in short periods of time. Distance between the source and receiving habitats and their position further down the main current are determinant factors in this connectivity.

11. Harvesting amphipods from farm fouling is a viable and attractive alternative for developing IMTA systems, in order to diversify cultivable species and develop a more sustainable model of aquaculture.

12. The nutritional value of the amphipod-based product obtained from the offshore IMTA makes it an excellent natural ingredient with promising commercial applications.





# Resumen General

## Introducción general

### *Definición de* fouling

El término *fouling* puede tener diferentes definiciones dependiendo del contexto en el que sea usado. Wahl (1989) lo define como "el proceso de colonización de una superficie sólida, viva o muerta". Sin embargo, Dürr y Thomason (2009) hacen referencia a él como "el proceso de acumulación de material indeseado sobre una superficie", haciendo referencia a los problemas que genera para las industrias en barcos, plataformas petrolíferas o instalaciones de acuicultura.

En castellano, no existe una traducción directa de la palabra *fouling*, por lo que el término es comúnmente usado como un anglicismo en los ámbitos marítimo y científico, haciendo uso de esta palabra como un nombre aunque no esté aceptada por la RAE. Ejemplos de este uso pueden encontrarse en artículos publicados en revistas españolas o latinoamericanas (p. ej. Guillermes et al. 1994, Pérez-Schultheiss 2009, Portillo 2011).

En esta tesis, la palabra *fouling* o *biofouling* se usará haciendo referencia a "el proceso de acumulación de material, principalmente organismos marinos, que se genera de la colonización de una superficie artificial", evitando así su uso para definir el proceso de colonización de organismos o sustratos naturales, como fondos rocosos, y también las connotaciones negativas generadas por la percepción humana. Esta definición además, está en concordancia con la aportada por otros autores en la bibliografía (p.ej. Kocak et al. 1999, Madin et al. 2009).



### *El desarrollo del* fouling *sobre superficies artificiales*

Cuando una superficie limpia se expone al agua de mar sufre una serie de cambios que permiten que sea colonizada por organismos marinos. Esta colonización está compuesta por cuatro fases que pueden solaparse en el tiempo y que incluyen: el acondicionamiento bioquímico, la colonización bacteriana, la fijación y desarrollo del *microfouling* y finalmente, la fijación y desarrollo del *macrofouling* (Wahl 1989). Justo después de que el objeto sea sumergido, la materia orgánica disuelta empieza a adherirse a la superficie y forma una fina capa de acondicionamiento que se denomina *fouling* molecular, en un proceso que puede durar desde segundos a unas pocas horas (Callow y Callow 2002). Esta capa de acondicionamiento es colonizada inicialmente por bacterias (Qian et al. 2007) y posteriormente por protozoos y, sobretodo, diatomeas (Scheer 1945, Wahl 1989; Fig. R.1). La adhesión de estos microorganismos tiene lugar mediante la secreción de una sustancia extracelular polimérica, compuesta principalmente por polisacáridos, proteínas, ácidos nucleicos y lípidos, que puede cubrir áreas muy grandes del sustrato (Flemming y Wingender 2010). Todo el conjunto de bacterias y microorganismos recibe el nombre de *biofilm* (Dürr y Thomason 2009) y conlleva varios estadios de sucesión que suelen durar varios días (Wahl 1989). Sólo después de que esta fase haya transcurrido, la última fase de colonización del *macrofouling* puede llevarse a cabo mediante la fijación de larvas planctónicas de invertebrados marinos o de esporas de algas (Corner et al. 2007). El *biofilm* suele producir compuestos químicos que inducen el asentamiento de cnidarios, poliquetos, moluscos y equinodermos entre otros organismos (Pawlik 1992).



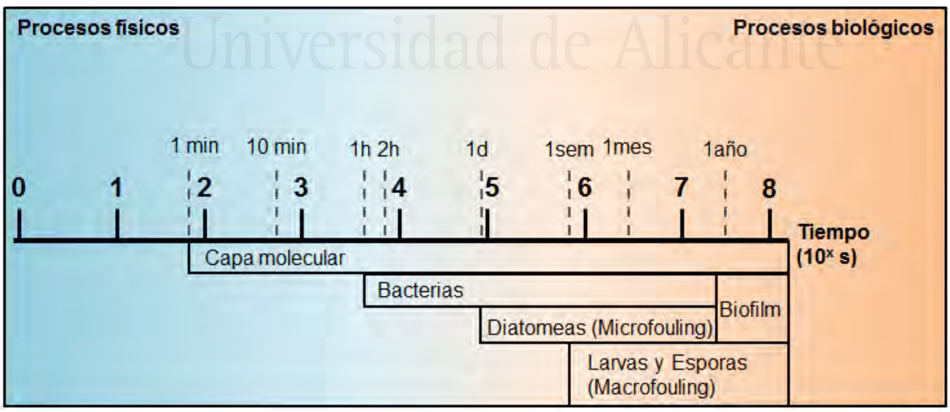



**Figura R.1.** Esquema de las distintas fases de proceso de colonización del *fouling* (adaptado de Wahl 1989).

Dentro del *macrofouling* se incluyen principalmente organismos sésiles, pero también organismos de vida libre (Hincapié-Cárdenas 2007). El crecimiento y desarrollo de los primeros determina la formación de macrohábitats, que actúan como "ingenieros ecosistémicos" y generan refugio y/o proporcionan alimento a la epifauna asociada (Jones et al. 1994).

El *macrofouling* puede sufrir también varios cambios sucesionales, donde la intervención de diferentes mecanismos, como la facilitación, la inhibición o la tolerancia, o de perturbaciones, como la depredación o los impactos ambientales, determinaran la creación de una comunidad final estable compuesta por organismos perennes denominada comunidad clímax (Connell y Slatyer 1977, Keough y Downes 1982). Existen varios estados de comunidad clímax dependiendo tanto de las diferentes composiciones de especies posibles como de los factores externos que puedan influir durante el proceso de colonización (Connell y Slatyer 1977).

### *Las instalaciones de acuicultura como estructuras artificiales en las zonas costeras*

La acuicultura marina intensiva ha ido aumentando constantemente durante las últimas cinco décadas (FAO 2014). La instalación de una granja de acuicultura significa la introducción de una gran cantidad de material artificial en el mar, que se fija en una posición determinada y permanece allí durante un largo periodo de tiempo. Existen distintos tipos de instalaciones: cercanas a costa (*coastal*), lejanas a costa (*off-coast*) y en mar abierto (*offshore*), que se diferencian por una serie de parámetros como la distancia a costa, la profundidad o la exposición al hidrodinamismo (Holmer 2010). De esta forma, las instalaciones cercanas a costa serían las situadas a menos de 500 m de la costa y en aguas poco profundas; las instalaciones lejanas a costa las localizadas entre 500 m y 3 km de la costa y a profundidades de entre 10 y 50 m; y las instalaciones en mar abierto serían las que están en zonas más expuestas al oleaje, a las corrientes y a los vientos, en profundidades superiores a los 50 metros y a varios kilómetros de costa (Holmer 2010).

Siguiendo la tendencia global, la acuicultura sigue aumentando en el Mediterráneo (APROMAR 2016) con alrededor de 800 instalaciones de producción de peces y bivalvos en todo su litoral costero (dato estimado a partir de Cardia y Lovatelli 2008, Trujillo et al. 2012). La producción en el Mediterráneo está centrada principalmente en el cultivo de dorada (*Sparus aurata*) y lubina (*Dicentrarchus labrax*) en instalaciones habitualmente alejadas de la costa (distancia intermedia según Holmer 2010), aunque también existe producción dedicada al engorde de juveniles de atún capturados del medio (*Thunnus thynnus*) y al cultivo de bivalvos como el mejillón *Mytilus* spp. y la ostra *Ostrea edulis* pero en menor proporción (APROMAR 2016).

Casi toda la producción del Mediterráneo se lleva a cabo en jaulas flotantes (Cardia y Lovatelli 2008). Estas jaulas están compuestas por una estructura superficial, formada normalmente por dos anillos de flotación de PVC, que mantienen una red suspendida en la columna de agua. La forma de la jaula y el volumen de la red se mantienen mediante un sistema de pesos o anticorrientes que se fijan a la red (Klebert et al. 2013). El sistema de anclaje consiste en un entramado complejo de boyas, cabos y cadenas que mantienen la instalación fija al fondo en varios puntos (Fig. R.2).

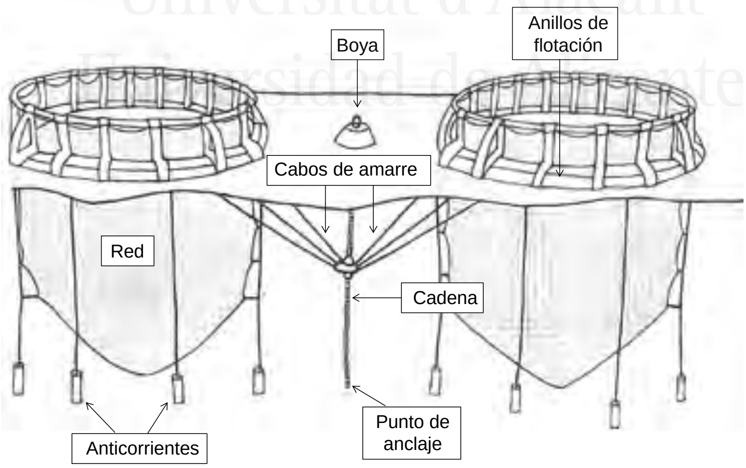



**Figura R.2.** Esquema de una piscifactoría marina con varias jaulas flotantes (Loverich y Gace 1997).

Las redes, los cabos y las boyas ofrecen una superficie disponible a un gran número de especies marinas que son capaces de fijarse y colonizar estas estructuras, formando comunidades de *fouling* muy diversas sobre ellas (Sarà et al. 2007, Fitridge et al. 2012; Fig. R.3).

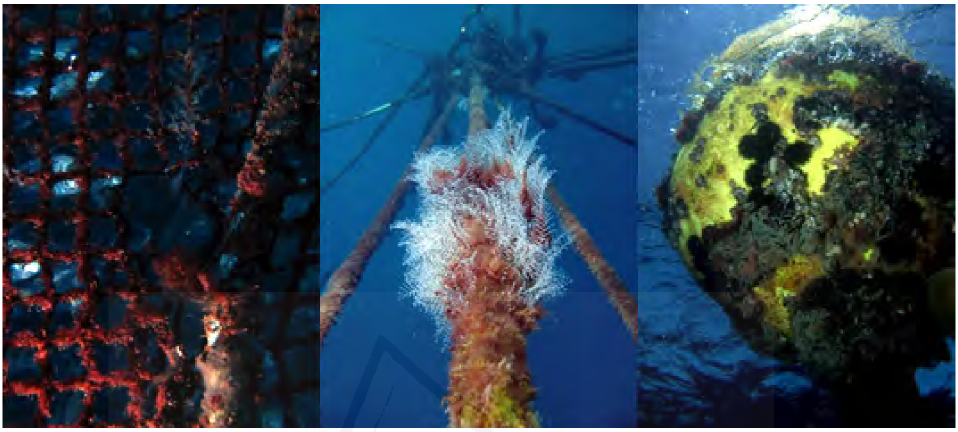


**Figura R.3.** Diferentes comunidades de *fouling* en las redes, cabos y boyas de una instalación de acuicultura durante el periodo de estudio (Fotos: Pablo Arechavala).

*Factores de la acuicultura que afectan al desarrollo del* fouling



La acuicultura presenta varias características que pueden condicionar el desarrollo del *fouling* y que lo diferencian del encontrado en otros lugares. Debido a la localización de las instalaciones y a ciertas prácticas operacionales, las posibles diferencias se basan en:

- <u>Posición prácticamente aislada del fondo:</u> Toda la superficie disponible proporcionada por las instalaciones de acuicultura se localiza a varios kilómetros de la costa y a decenas de metros del fondo marino (excepto por los puntos de anclaje). Esto determina que el desarrollo del *fouling* en jaulas flotantes sea diferente del que aparece en sustratos en contacto con el fondo marino. En profundidad, los hidrozoos suelen dominar las comunidades de *fouling*, mientras que en las jaulas, estos suelen ser remplazados por mejillones desde los primeros estadios de desarrollo (Greene y Grizzle 2007). Según estos autores las diferencias pueden deberse a varios factores como la distancia al fondo, la ausencia de depredadores, la disponibilidad lumínica, la posición respecto a las corrientes o la flotabilidad de las jaulas de cultivo.

- Flotabilidad de las instalaciones: Los objetos flotantes suelen presentar una mayor cantidad de organismos filtradores en comparación con superficies fijas (Perkol-Finkel et al. 2008). El movimiento o la rotación de un sustrato puede determinar la presencia de grandes abundancias de cirrípedos, esponjas o ascidias que pueden llegar a doblar la biomasa alcanzada en estructuras de las mismas características pero fijas (Glasby 2001). En las superficies flotantes, por ejemplo, se observa mayor presencia de briozoos, bivalvos y cirrípedos debido a una mayor exposición al hidrodinamismo (Perkol-Finkel et al. 2008).

- Influencia de las instalaciones de acuicultura en el hidrodinamismo: El complejo entramado estructural de las instalaciones de acuicultura modifica las condiciones oceanográficas locales, ya que la parte frontal de las primeras jaulas bloquea el flujo de las corrientes, lo cual incrementa la velocidad de la corriente a ambos lados y la reduce en la parte posterior de estas, causando un efecto de sombra o estela (Plew et al. 2005, Klebert et al. 2013). Ello hace que los estadios larvarios de las especies marinas, que se dispersan a través de las corrientes, puedan verse retenidos en el interior del entramado de las instalaciones, favoreciendo una colonización más rápida de las estructuras.

- Disponibilidad de alimento: Uno de los efectos más estudiados de la acuicultura es la acumulación de los desechos orgánicos, generados por el exceso de pienso no ingerido y las heces de peces, sobre el sedimento marino y los efectos negativos que esto provoca en la fauna bentónica (Gowen y Bradbury 1987, Wu 1995, Kalantzi y Karakassis 2006). La materia orgánica disuelta y particulada que se libera en la columna de agua pueden influenciar también el desarrollo del *fouling* en las instalaciones de acuicultura. Por ejemplo, la cantidad de *biofilm* en zonas cercanas a las piscifactorías, con grandes aportes de materia orgánica, es mayor comparado con zonas más alejadas (Sanz-Lázaro et al. 2011). La biomasa de *macrofouling*, principalmente filtradores heterótrofos, también es mayor en estructuras artificiales cerca de las jaulas, lo que sugiere que los desechos de acuicultura proporcionan un suplemento alimenticio para estos organismos (Cook et al. 2006). Efectivamente, Gonzalez-Silvera et al. (2015), usando los perfiles de ácidos grasos, concluyó que la macrofauna de invertebrados presente en el *fouling* de las jaulas era capaz de asimilar la materia orgánica de la acuicultura como un nuevo recurso trófico.

- Estrategias *antifouling*: El *fouling* puede ser un problema para la acuicultura cuando la especie objetivo, las infraestructuras o ambas se ven afectadas. En las piscifactorías los organismos colonizadores provocan un peso añadido, que genera una resistencia en las estructuras y afecta al diseño de las jaulas, reduciendo el flujo de agua y dejando agua de peor calidad para los peces cultivados (Swift et al. 2006, Corner et al. 2007). En las instalaciones de bivalvos el *fouling* puede además dañar directamente a los organismos cultivados (Antoniadou et al. 2013). Todo ello provoca un coste adicional a las empresas debido a las limpiezas rutinarias de las instalaciones llevadas a cabo con el fin de evitar los efectos negativos en la producción (Ross et al. 2004, Willemsen 2005). En el caso de las redes, suelen usarse revestimientos *antifouling* con base de cobre que evitan el colapso de la malla por los organismos colonizadores (Corner et al. 2007, Guenther et al. 2010, Fitridge et al. 2012). En el caso de los cabos y otras estructuras del entramado de anclaje, el personal de la instalación suele llevar a cabo limpiezas mecánicas que eliminan la mayor parte de los organismos del *fouling* (CRAB 2007, Fitridge et al. 2012), lo cual crea oportunidades de colonización para otras especies, ya que se reinicia el proceso de sucesión ecológica debido a la ausencia de una comunidad clímax (Greene y Grizzle 2007).

*Especies de* fouling *comunes en las instalaciones de acuicultura*

Desde que la acuicultura intensiva empezó a desarrollarse hace cinco décadas, muchos estudios se han centrado en determinar las especies que son capaces de fijarse a las jaulas flotantes, debido a los problemas anteriormente mencionados y a los costes adicionales que provocan para las empresas de acuicultura. Estos estudios se han centrado principalmente en la descripción de los organismos sésiles, mediante la instalación de paneles de red en las instalaciones (p. ej. Hodson et al. 2000, Corner et al. 2007, Greene y Grizzle 2007). Así, a pesar de algunas diferencias biogeográficas, se ha determinado que los grupos más importantes en las piscifactorías son los bivalvos, principalmente mejillones, los hidrozoos, las algas y los tunicados (Cook et al. 2006, CRAB 2007, Fitridge et al. 2012), mientras que estos mismos grupos junto con los cirrípedos y las esponjas son también los organismos mayoritarios en las instalaciones de bivalvos (Khalaman 2001, Fitridge et al. 2012, Antoniadou et al. 2013, Watts et al. 2015). Es posible encontrar también organismos de vida libre como crustáceos (p. ej. Hincapié-Cárdenas 2007, Madin et al. 2009, Watts et al. 2015), poliquetos (p. ej. Hodson et al. 2000, Cook et al. 2006, Fitridge et al. 2012), gasterópodos (Sarà et al. 2007, Guenther et al. 2010), equinodermos (Greene y Grizzle 2007, Watts et al. 2015, Gonzalez-Silvera et al. 2015), sipuncúlidos (Gonzalez-Silvera et al. 2015) y platelmintos (Fitridge et al. 2012). De todos ellos, los crustáceos anfípodos son el grupo que más veces ha sido citado en la bibliografía, resaltando la presencia de anfípodos tubícolas (CRAB 2007, Greene y Grizzle 2007, Madin et al. 2009, Gonzalez-Silvera et al. 2015) y caprélidos (Hodson et al. 2000, Cook et al. 2006, Swift et al. 2006, Greene y Grizzle 2007, Guenther et al. 2010, Fernandez-Gonzalez y Sanchez-Jerez 2013, Gonzalez-Silvera et al. 2015, Watts et al. 2015). Aunque los anfípodos han mostrado una gran capacidad de colonización de estas estructuras, y se encuentran en grandes abundancias (Greene y Grizzle 2007), su estudio en las instalaciones de acuicultura ha recibido muy poca atención.

*Anfípodos como grupo representativo de la epifauna*

El orden Amphipoda contiene 215 familias y más de 9.900 especies (Horton et al. 2016). La mayor parte de los anfípodos son marinos, pero también hay organismos de agua dulce o salobre. La mayoría suelen vivir asociados a los hábitats bentónicos, excepto los miembros del suborden Hiperiidea que son todos planctónicos. Los anfípodos son uno de los grupos más abundantes de la fauna bentónica (Marti 1989, Thomas 1993, Sanchez-Jerez et al. 1999a, Vázquez-Luis et al. 2009, Carvalho et al. 2012) y su sensibilidad a la contaminación, mayor que la de otro grupos de macroinvertebrados, ha determinado su uso como bioindicadores de diversos tipos de impactos ambientales (Bellan-Santini 1980, Conradi et al. 1997, Gómez-Gesteira y Dauvin 2000, Guerra-García y García-Gómez 2001, De-la-Ossa-Carretero et al. 2012). Son principalmente detritívoros, pero también existen omnívoros, carnívoros y herbívoros (Guerra-García et al. 2014a), y constituyen un eslabón importante de la cadena trófica, siendo presa principal para otros crustáceos, poliquetos y muchas especies de peces (Ruffo 1998, Jiménez-Prada et al. 2015).

Los anfípodos suelen presentar un dimorfismo sexual que permite distinguir los machos de las hembras. La proporción machos-hembras en las poblaciones suele estar a favor de las hembras (Thiel 1998a, Kevrekidis 2004, Prato y Biandolino 2006) y la mayoría de ellos son iteróparos anuales, reproduciéndose varias veces durante todo el año (Sainte-Marie 1991). La vida media es de 14 meses (Sainte-Marie 1991), y alcanzan la madurez sexual aproximadamente después de 30 días (Takeuchi y Hirano 1991, Cunha et al. 2000, Baeza-Rojano et al. 2011, 2013c). Los anfípodos como el resto de los crustáceos peracáridos (tanaidáceos, isópodos, misidáceos y cumáceos) tienen un desarrollo directo, las hembras llevan los huevos en un saco ventral o marsupio, del cual salen pequeños juveniles totalmente desarrollados (Sainte-Marie 1991, Thiel 1998b). El periodo de incubación tiene una duración aproximada de 10 días (Takeuchi y Hirano 1991, Cunha et al. 2000, Baeza-Rojano et al. 2011, 2013c) y el número de huevos está relacionado con el tamaño de la hembra, variando mucho entre especies, desde 2 a 630 (mediana = 25) huevos por hembra (Sainte-Marie 1991). La falta de larva pelágica, principal fase de dispersión para la mayor parte de invertebrados marinos, hace que los anfípodos se hayan adaptado a otros métodos de dispersión pasivos, bien a través de las corrientes (Cummings et al. 1995) o enganchados (*rafting*) a objetos flotantes de origen natural o artificial como boyas, maderas, algas, etc. (Highsmith 1985, Thiel y Gutow 2005), permitiéndoles a muchas especies de anfípodos tener distribuciones geográficas muy amplias.

**Justificación y objetivos generales**

Teniendo en cuenta todos los factores descritos anteriormente, encontramos que aunque las comunidades de *fouling* sésiles han sido bien estudiadas desde el punto de vista de su control en las instalaciones de acuicultura, poco se sabe sobre la epifauna que habita estas estructuras artificiales. La ausencia de estudios es especialmente relevante en las poblaciones de anfípodos, las cuales a pesar de ser detectadas en grandes abundancias en varios estudios, no han sido todavía estudiadas en cuanto a la composición de especies y a su relación con los hábitats creados por los organismos sésiles.

Por lo tanto, los objetivos generales de esta tesis son:

1) Evaluar la composición de las comunidades de *fouling* en el Mediterráneo, centrándose en la importancia de los anfípodos y comparando estas comunidades con las desarrolladas en otras estructuras artificiales tanto en puertos y marinas como en estructuras y en objetos flotantes alejados de la costa.

2) Cuantificar la importancia de los anfípodos en el *fouling* de las instalaciones de acuicultura y explicar el papel de las principales especies sésiles en mantener las poblaciones de anfípodos.

3) Determinar cómo las estructuras de las piscifactorías afectan a la composición de especies y la distribución nocturna de los anfípodos

planctónicos procedentes de diferentes hábitats (pelágicos, *fouling* y fondos blandos).

4) Investigar la influencia de los anfípodos del *fouling* como posible fuente de colonizadores en la recolonización de sedimentos defaunados cercanos.

5) Analizar el potencial del *fouling* de piscifactorías como fuente de exportación de anfípodos hacia otros hábitats flotantes.

6) Testar la aplicabilidad de los anfípodos como cultivo accesorio en un sistema de acuicultura multitrófica alejado de costa con peces como especie principal.

**Capítulo 1: Comunidades de *fouling* asociadas a instalaciones de acuicultura: una evaluación a través del Mediterráneo**

El primer estudio tuvo como objetivo determinar la composición de las comunidades de *fouling* en el Mediterráneo, con especial interés en la epifauna y en los anfípodos como grupo principal. Se muestrearon 17 instalaciones de acuicultura a lo largo de toda la costa mediterránea, realizando raspados de los cabos de amarre de las instalaciones. Además, se realizó una revisión bibliográfica de 30 publicaciones de estudios llevados a cabo en el Mediterráneo con el objetivo de valorar la similaridad del *fouling* de las instalaciones de acuicultura con el desarrollado en otras estructuras. Los resultados obtenidos reflejan que el 80 % de la epifauna asociada a las comunidades de *fouling* de acuicultura son anfípodos. El poblamiento se caracteriza principalmente por la presencia de siete especies de anfípodos, que resultaron frecuentes y dominantes: *Elasmopus rapax*, *Jassa marmorata*, *Jassa slatteryi*, *Ericthonius punctatus*, *Stenothoe tergestina*, *Caprella equilibra* y *Caprella dilatata*, demostrando que están bien adaptadas a colonizar y sobrevivir en estos hábitats alejados de la costa. La mayoría de las especies encontradas en las jaulas también han sido encontradas en zonas costeras como puertos y marinas y en mar abierto como en boyas, plataformas petrolíferas o incluso sobre tortugas marinas, lo que demuestra también una gran tolerancia a áreas contaminadas pero también una gran adaptación a la dispersión mediante la adhesión a objetos flotantes (*rafting*). En este estudio se identificaron dos especies exóticas: *Caprella scaura* y *Stenothoe georgiana*, siendo esta última la primera cita para el Mediterráneo y además se confirmó la presencia de *Jassa slatteryi*, que había sido hasta ahora subestimada en el Mediterráneo.

**Capítulo 2: Importancia de los macro y microhábitats en el mantenimiento de las altas densidades de anfípodos en las piscifactorías**

La complejidad estructural de un hábitat es un factor determinante en la diversidad de las comunidades asociadas. En las instalaciones de acuicultura, las comunidades de *fouling* sésiles forman una matriz tridimensional que da lugar a diferentes macrohábitats. Sin embargo, aún no se sabe la relación que hay entre estos organismos y las comunidades de epifauna asociadas. Este estudio tuvo como objetivo definir la composición de especies y las densidades de población de los anfípodos en cada uno de los principales macrohábitats, analizando la relación entre cada especie de anfípodo y la complejidad de hábitat creada tanto por los organismos sésiles mayoritarios como por los organismos secundarios responsables de formar diferentes microhábitats. Las comunidades de *fouling* se muestrearon mediante raspados de los cabos de amarre de dos piscifactorías del Mediterráneo, seleccionando los macrohábitats formados por el mejillón *Mytilus galloprovincialis*, por el hidrozoo *Pennaria disticha* y por algas cespitosas, principalmente Ceramiales. La densidad media de anfípodos fue de 176.000 ind./m$^2$ con un valor máximo de más de 1.000.000 ind./m$^2$, sobrepasando los valores máximos obtenidos en algunos de los ecosistemas más productivos del mundo. El análisis DistLM indicó relaciones significativas entre las especies de anfípodos y las especies sésiles que generan los microhábitats. Así dentro del macrohábitat formado por *M. galloprovincialis*, las mayores abundancias de anfípodos estuvieron directamente relacionadas con las especies epífitas de algas e hidrozoos que crecen sobre las valvas, de forma que *E. rapax,* se encontró principalmente en las algas Ceramiales, mientras que *E. punctatus* y *C. equilibra* estuvieron relacionados con el hidrozoo *Aglaophenia* sp. El macrohábitat formado por *P. disticha* estuvo fuertemente dominado por el caprélido *Caprella dilatata* y secundariamente por el gammárido *Jassa slatteryi.* Este último parece competir por el espacio con su congénere *J. marmorata*, el cual colonizó la parte central de todos los macrohábitats estudiados, limitando la distribución de *J. slatteryi* a las zonas más expuestas como las ramas de *P. disticha.*

**Capítulo 3: Cambios en las poblaciones nocturnas de anfípodos debido a la presencia de jaulas de acuicultura**

Las migraciones a la columna de agua durante la noche son una actividad diaria común de muchos peracáridos en los ecosistemas marinos. Las instalaciones de acuicultura en las zonas costeras modifican las condiciones oceanográficas locales y, por tanto, pueden afectar la distribución de las comunidades pelágicas. El objetivo de este estudio fue determinar si la abundancia nocturna y la composición de especies del poblamiento de anfípodos planctónicos se ven afectadas por la infraestructura de las jaulas. El estudio se llevó a cabo en dos instalaciones de acuicultura, usando trampas de luz como método de recolección. Un total de 809 anfípodos pertenecientes a 21 especies se capturaron en zonas de acuicultura, comparado con los 42 individuos de 11 especies encontrados en zonas control. Las especies que más contribuyeron a las diferencias entre zonas de acuicultura y zonas control fueron el hipérido *Lestrigonus schizogeneios*, los anfípodos del *fouling E. punctatus*, *J. marmorata*, *Stenothoe sp.* y *Caprella equilibra*, y los del fondo marino *Perioculodes aequimanus* y *Urothoe pulchella*. La gran concentración de anfípodos planctónicos en las instalaciones de acuicultura es el resultado de un aporte directo de individuos desde las comunidades de *fouling*, unido a un efecto de retención de los anfípodos de la columna de agua, incluyendo a los estrictamente planctónicos, los hipéridos, y los que migran desde el sedimento.

### Capítulo 4: Papel del *fouling* en la recolonización de fondos blandos cercanos afectados por la acuicultura

El enriquecimiento orgánico provocado por la acuicultura produce un importante impacto en el sedimento marino, reduciendo la abundancia y la riqueza de especies bentónicas y creando parches de sedimento degradados en el fondo marino. En este estudio se analizaron los cambios en la recolonización del sedimento con los siguientes objetivos: (1) evaluar los efectos de las jaulas de acuicultura en los procesos de colonización de anfípodos de sedimentos defaunados y (2) definir la influencia de los hábitats circundantes naturales o artificiales como fuentes de primeros colonizadores. El diseño experimental incluyó 36 bandejas de plástico rellenas de sedimento defaunado, colocadas en el fondo marino (25-28 m de profundidad) en zonas de piscifactorías y en zonas control y recogidas un mes después. Se encontraron diferencias significativas entre la composición de anfípodos en las zonas control y en las zonas de piscifactorías, de forma que la recolonización en las zonas control dependió de las especies presentes en los sedimentos adyacentes a las bandejas experimentales, mientras que en las zonas de acuicultura la recolonización dependió fuertemente de la aportación de anfípodos desde las comunidades de *fouling*. Es la primera vez que se detecta un efecto de exportación de individuos desde el *fouling* de hábitats flotantes hacia el bentos en las zonas costeras. Si el enriquecimiento orgánico de los sedimentos afectados por la acuicultura es moderado, los servicios ecológicos de los hábitats bentónicos podrían ser compensados, al menos parcialmente, por el aporte de biomasa de las comunidades de *fouling* de las mismas jaulas.

### Capítulo 5: Influencia del *fouling* de las instalaciones de acuicultura como población fuente en el mantenimiento de poblaciones locales

Entender los patrones de dispersión de las especies es vital para conocer aspectos como la persistencia de una población o las dinámicas de la comunidad entre diferentes poblaciones. Los anfípodos, como otros peracáridos, tienen un desarrollo directo y carecen de larva pelágica, de forma que la dispersión se lleva a cabo mediante la migración activa de juveniles o adultos. Las grandes densidades observadas en el *fouling* de las jaulas de acuicultura pueden determinar la competencia entre juveniles adultos y la dispersión a nuevos hábitats. En este estudio, se analizó el papel del *fouling* de acuicultura como población 'fuente' de anfípodos hacia los hábitats circundantes localizados en la columna de agua, con el objetivo de entender los patrones de conectividad en hábitats marinos fragmentados. Se llevó a cabo un experimento de campo en el cual se colocaron 72 colectores artificiales de tres tipos diferentes: 'Hábitat' compuesto por una bolsa de malla rellena de tiras de rafia, con un volumen aproximado de 250 ml; 'Pienso', como los anteriores pero con pienso en su interior, igual al usado en la piscifactoría; y 'control', sólo con la bolsa de malla exterior. Cada tipo de colector se colocó en cabos diferentes para evitar interacciones y se fondearon de tal manera que quedaron a una profundidad de entre 5 y 8 metros. En el mar, cada una de estas estructuras se colocaron cerca (10 m) y lejos (más de 1.5 km) de la instalación, a favor y en contra de la corriente, y en dos sitios diferentes, para testar el efecto de la distancia y la corriente. Transcurridos 15 días los colectores se cubrieron con una bolsa de plástico y se recogieron. Este estudio evidencia la fuerte influencia que un hábitat saturado como las jaulas tiene en el mantenimiento de los hábitats circundantes mediante la exportación de individuos. La distancia fue el primer factor condicionante de la dispersión, de forma que todos los colectores cercanos fueron colonizados, independientemente de la corriente, aunque se hallaron mayores abundancias en los colectores que estaban localizados a favor de la corriente, llegando hasta 1000 anfípodos por colector. Sin embargo, no se encontraron diferencias significativas entre los hábitats que contenían pienso y los que no lo contenían. Este experimento confirma la gran conectividad que existe entre distintos hábitats flotantes generada por las instalaciones de acuicultura, donde los anfípodos fueron capaces de colonizar nuevas superficies a más de 1.5 km en sólo dos semanas.

### Capítulo 6: Recolección de anfípodos aplicando el concepto de acuicultura multitrófica integrada (AMTI) en mar abierto

La tendencia actual de la acuicultura se dirige hacia una acuicultura más sostenible, buscando fuentes de proteínas alternativas para la elaboración de piensos, diversificando las especies cultivables o implantando modelos más respetuosos con el medio ambiente como los sistemas de acuicultura multitrófica integrada (AMTI).

En este estudio se pretendió evaluar la aplicabilidad de los anfípodos como un cultivo accesorio en un sistema AMTI en mar abierto con dorada y lubina como cultivo principal. Para ello se plantearon los siguientes objetivos: 1) determinar la eficiencia y selectividad de un método de extracción de anfípodos; 2) valorar la biomasa y la composición de anfípodos según el tipo y la profundidad del colector; 3) verificar la eficiencia de los anfípodos como biofiltros de los residuos de acuicultura; y 4) analizar el contenido nutricional del producto obtenido. Dos experimentos de AMTI se llevaron a cabo, utilizando dos tipos de colectores diferentes, uno compuesto por rafia y otro por conchas de mejillón secas, ambos con un volumen aproximado de 5 l. Los colectores se colocaron a 5 y 15 metros a fin de comprobar una profundidad óptima de recolección de anfípodos. Al final del experimento, los anfípodos fueron extraídos introduciendo los colectores en agua dulce durante tres minutos, filtrados a 500 µm y congelados. Este es el primer estudio piloto de un cultivo AMTI con anfípodos en mar abierto. El método de extracción recuperó más del 80 % de la fauna asociada a los colectores, obteniendo una producción al mes de 10 g de peso húmedo por colector. El producto obtenido contenía más de un 86% de pureza en anfípodos, y unos valores nutricionales de proteínas, ácidos grasos y aminoácidos adecuados para su uso como ingrediente natural en la composición de piensos de acuicultura o acuariofilia, o incluso como suplemento nutricional para el hombre. El cultivo de anfípodos aprovechó los residuos del cultivo principal garantizando así un desarrollo más sostenible de la acuicultura en el medio marino.

**Discusión general**

A lo largo de esta tesis, se ha demostrado que la acuicultura afecta a las poblaciones de anfípodos en varios aspectos. La creación de nuevos nichos habitables, el aporte de materia de materia orgánica procedente de la producción y la modificación del hidrodinamismo local determinan el

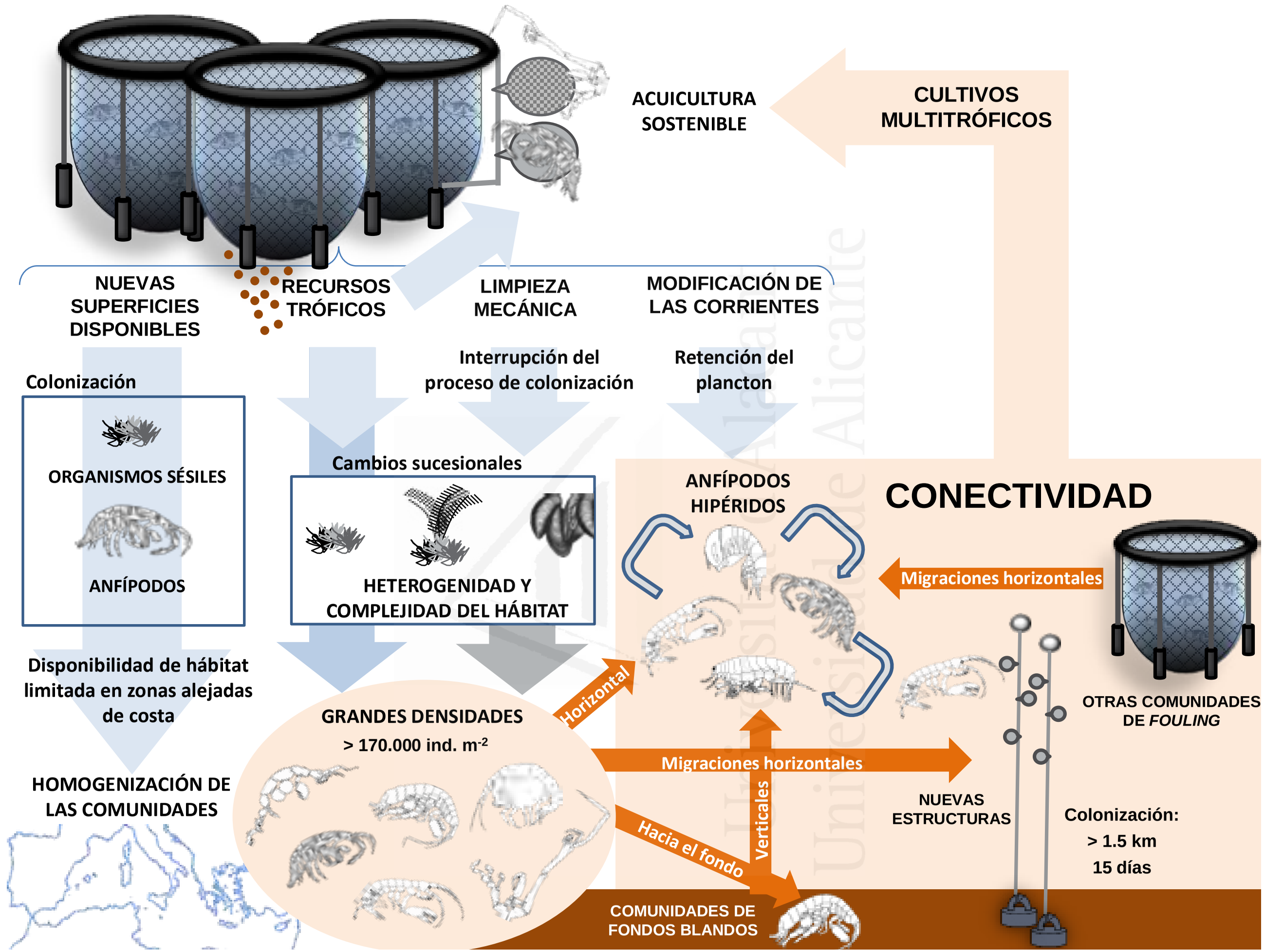



**Figura R.4.** Modelo conceptual de los factores relacionados con la acuicultura que afectan a las comunidades de fouling y de las interacciones ecológicas entre las poblaciones de anfípodos detectadas en esta tesis, así como sus posibles aplicaciones.

establecimiento de grandes densidades de anfípodos en las instalaciones de acuicultura del mar Mediterráneo. La complejidad y la heterogeneidad de los organismos sésiles que crecen en las estructuras de las instalaciones tienen una gran influencia en la abundancia y en la composición de las poblaciones de anfípodos, fomentada también por la continua interrupción de la sucesión ecológica debido a las labores de limpieza del *fouling*.

Además, la presencia de las piscifactorías en las áreas costeras provoca cambios en el comportamiento migratorio de los anfípodos, promoviendo una gran conectividad entre las diferentes subpoblaciones determinada, en primer lugar, por la retención de anfípodos planctónicos, del fondo y de las comunidades de *fouling* en la columna de agua dentro de las instalaciones y en segundo lugar, por las migraciones debidas a las grandes densidades de anfípodos en el *fouling* que promueven la exportación de individuos hacia el fondo o hacia otros hábitats flotantes. Como resultado, surge una nueva aplicación comercial de la posibilidad de usar los anfípodos del *fouling* como biofiltros, reciclando los residuos de la acuicultura dentro de un sistema de acuicultura multitrófica en mar abierto (Fig. R. 4).

## CONCLUSIONES

1. Las comunidades de *fouling* de las instalaciones de acuicultura del Mar Mediterráneo están compuestas principalmente por bivalvos, algas, hidrozoos y briozoos. La epifauna está dominada mayoritariamente por anfípodos, los cuales representan más de un 80% de la fauna asociada a estos organismos.

2. El *fouling* de las instalaciones de acuicultura en el Mediterráneo está caracterizado por presentar comunidades homogéneas representadas por siete especies de anfípodos frecuentes y abundantes: *Elasmopus rapax*, *Jassa marmorata*, *Jassa slatteryi*, *Ericthonius punctatus*, *Stenothoe tergestina*, *Caprella equilibra* y *Caprella dilatata*.

3. La densidad media de anfípodos observada en el *fouling* de las piscifactorías fue de 176.000 ind./$m^2$ y alcanzó un máximo de más de 1.000.000 ind./$m^2$, superando los valores máximos citados en los ecosistemas más productivos del mundo.

4. Los macrohábitats formados por mejillón *Mytilus galloprovincialis* en los cabos de amarre de las instalaciones albergaron las mayores abundancias de anfípodos. Sin embargo, estas estuvieron directamente relacionadas con los microhábitats creados por las especies epífitas de algas e hidrozoos que crecen sobre las valvas. Así, *E. rapax,* se encontró principalmente en algas Ceramiales cespitosas, mientras que *E. punctatus* y *C. equilibra* estuvieron relacionados con el microhábitat formado por el hidrozoo *Aglaophenia* sp.

5. El segundo macrohábitat más importante se caracteriza por densas colonias del hidrozoo *Pennaria disticha,* que estuvo fuertemente dominado por el caprélido *Caprella dilatata* y secundariamente por el gammárido *Jassa slatteryi.* Este último parece competir por el espacio con su congénere *Jassa marmorata*, el cual coloniza la parte central de todos los macrohábitats estudiados, limitando la distribución de *J. slatteryi* a las zonas más expuestas como las ramas de *P. disticha.*

6. Las jaulas de acuicultura provocan un efecto de retención de los anfípodos planctónicos cerca de las instalaciones, evidenciado por el incremento en las abundancias de hipéridos. El número de anfípodos retenidos que realizan migraciones tanto verticales desde el fondo marino como horizontales desde y hacia las comunidades de *fouling* fue también notable.

7. La presencia nocturna de anfípodos en el área de estudio estuvo relacionada con el ciclo lunar. De forma que los hipéridos, principalmente *Lestrigonus schizogeneios,* parecen estar influenciados por la fase de luna llena, mientras que los anfípodos bentónicos, tanto del sedimento como de las comunidades de *fouling*, fueron más frecuentes en la columna de agua durante las noches de luna de cuarto creciente o menguante.

8. Las grandes densidades de anfípodos en las instalaciones de acuicultura influencian los hábitats circundantes, actuando como fuente de anfípodos que migran hacia el fondo o hacia otros hábitats flotantes.

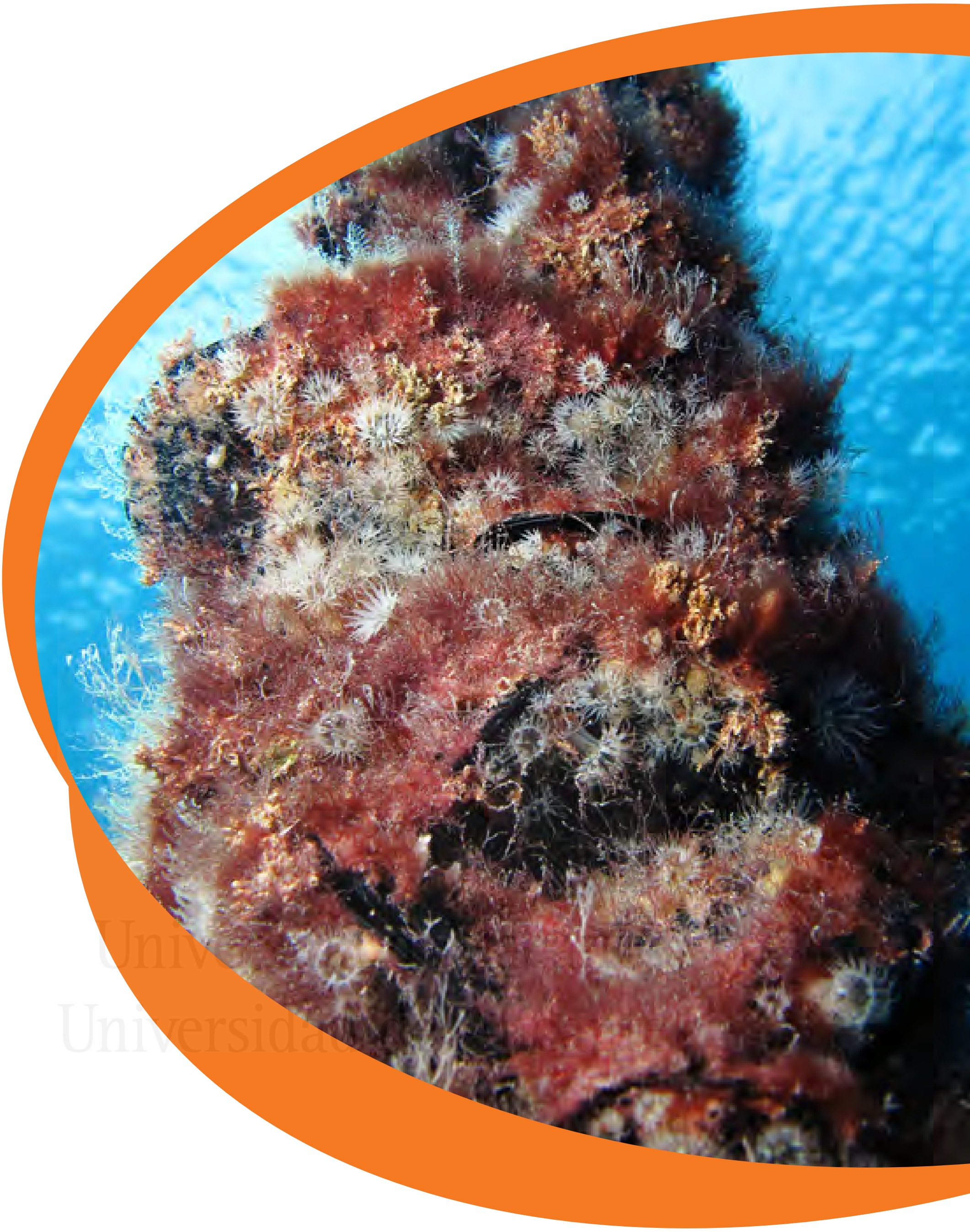
9. Los anfípodos del *fouling* tienen una gran capacidad como primeros colonizadores, principalmente los tubícolas *E. punctatus* y *Jassa* spp., que colonizaron satisfactoriamente tanto sedimentos defaunados como otras comunidades de *fouling,* incluso en estado inicial de colonización.

10. Las instalaciones de acuicultura determinan una gran conectividad entre las poblaciones de anfípodos espacialmente fragmentadas, donde el intercambio de individuos se produce a una escala de cientos de metros en periodos cortos de tiempo. La distancia entre la población fuente y los hábitats receptores, y la posición de estos respecto a la corriente principal son factores determinantes para esta conectividad.

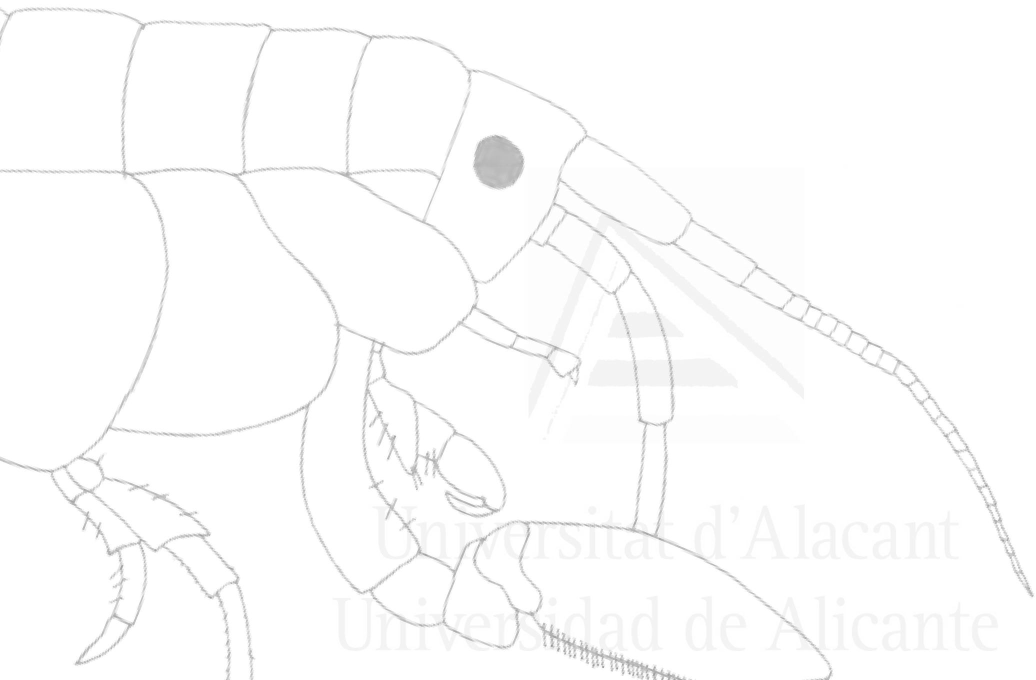
11. Recolectar anfípodos de las instalaciones de acuicultura es factible, siendo una alternativa atractiva para el desarrollo de sistemas de acuicultura multitrófica que permite diversificar las especies cultivables y desarrollar un modelo de acuicultura más sostenible.



12. El valor nutricional del producto de anfípodos obtenido del cultivo multitrófico en mar abierto hace de él un excelente ingrediente natural con prometedoras aplicaciones en el mercado.



# References



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## Taxonomic references

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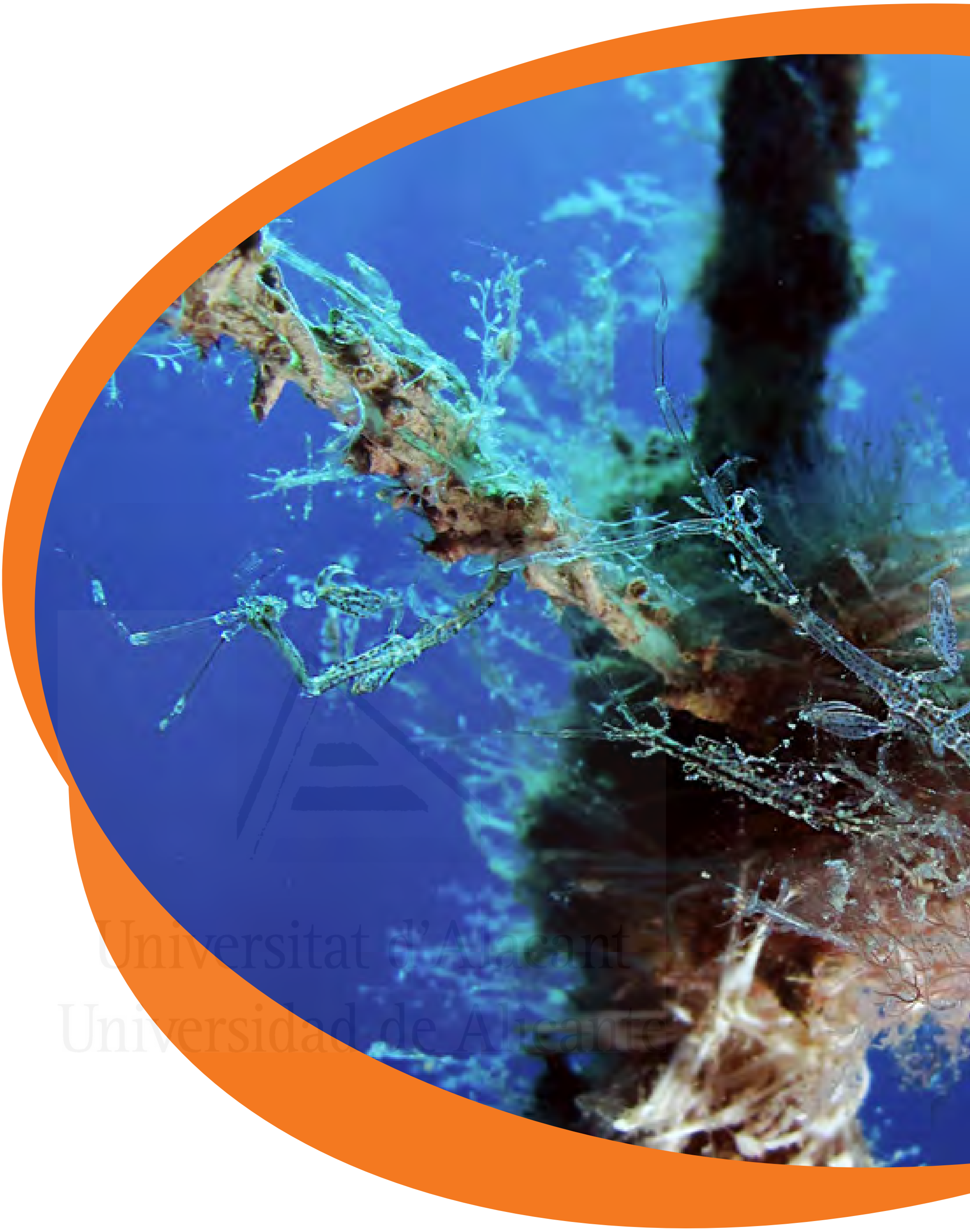
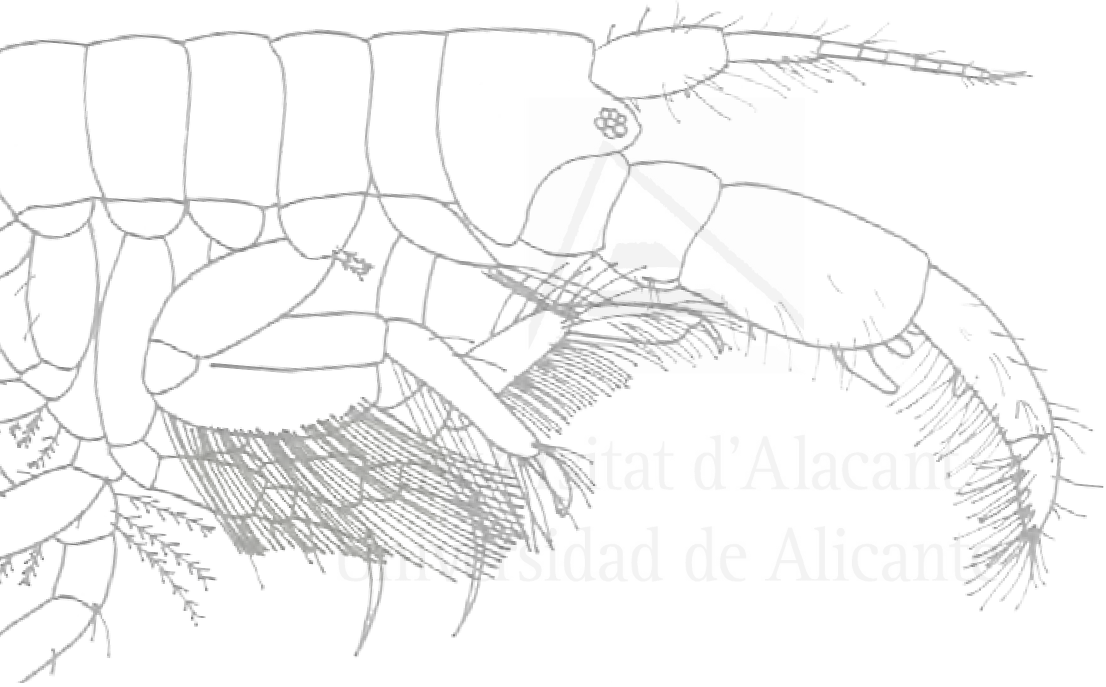




# Annexes



## Taxonomic effort

A complete list of species, including the total number of specimens, families, genera and species identified in this phD thesis is detailed bellow:

- 183,529 amphipods
- 25 families
- 40 genera
- 61 species

| Family | Species |
|---|---|
| Ampeliscidae | *Ampelisca brevicornis* (Costa, 1853) |
| | *Ampelisca diadema* (Costa, 1853) |
| | *Ampelisca intermedia* Bellan-Santini & Diviacco, 1990 |
| | *Ampelisca tenuicornis* Lilljeborg, 1855 |
| | *Ampelisca typica* (Bate, 1856) |
| Amphilochidae | *Amphilochus brunneus* Della Valle, 1893 |
| Ampithoidae | *Ampithoe ramondi* Audouin, 1826 |
| | *Cymadusa filosa* Savigny, 1816 |
| Aoridae | *Aora gracilis* (Bate 1857) |
| | *Aora spinicornis* Afonso, 1976 |
| | *Autonoe karamani* (Myers, 1976) |
| | *Microdeutopus algicola* Della Valle, 1893 |
| Argissidae | *Argissa hamatipes* (Norman, 1869) |
| Atylidae | *Atylus vedlomensis* (Bate & Westwood, 1862) |
| Calliopiidae | *Apherusa chiereghinii* Giordani- Soika, 1949 |
| Caprellidae | *Caprella dilatata* Krøyer, 1843 |
| | *Caprella equilibra* Say, 1818 |
| | Caprella grandimana (Mayer, 1882) |
| | *Caprella scaura* Templeton, 1836 |
| | *Phtisica marina* Slabber, 1769 |
| | *Pseudolirius kroyeri* (Haller, 1879) |
| Cheirocratidae | *Cheirocratus sundevalli* (Rathke, 1843) |

| Family | Species |
|---|---|
| Corophiidae | *Apocorophium acutum* (Chevreux, 1908) |
| | *Leptocheirus mariae* Karaman, 1973 |
| | *Leptocheirus pectinatus* (Norman, 1869) |
| | *Medicorophium aculeatum* (Chevreux, 1908) |
| | *Medicorophium longisetosum* De-La-Ossa-Carretero & Dauvin, 2010 |
| | *Medicorophium runcicorne* (Della Valle, 1893) |
| | *Monocorophium insidiosum* (Crawford, 1937) |
| Dexaminidae | *Dexamine spinosa* (Montagu, 1813) |
| | *Guernea sp.* Chevreux, 1887 |
| Hyalidae | *Hyale perieri* (Lucas, 1849) |
| Ischyroceridae | *Ericthonius punctatus* (Bate, 1857) |
| | *Jassa marmorata* Holmes, 1905 |
| | *Jassa slatteryi* Conlan, 1990 |
| Lestrigonidae | *Lestrigonus schizogeneios* (Stebbing, 1888) |
| Leucothoidae | *Leucothoe incisa* Robertson, 1892 |
| | *Leucothoe lilljeborgi* Boeck, 1861 |
| | *Leucothoe oboa* Karaman, 1971 |
| Maeridae | *Elasmopus rapax* Costa, 1853 |
| Megaluropidae | *Megaluropus massiliensis* Ledoyer, 1976 |
| Oedicerotidae | *Deflexilodes acutipes* (Ledoyer, 1983) |
| | *Deflexilodes griseus* (Della Valle, 1893) |
| | *Perioculodes aequimanus* (Korssman, 1880) |
| | *Perioculodes longimanus* (Bate & Westwood, 1868) |
| | *Synchelidium haplocheles* (Grube, 1864) |
| | *Synchelidium longidigitatum* Ruffo, 1947 |
| Oxycephalidae | *Glossocephalus milneedwardsi* Bovallius, 1887 |
| Photidae | *Gammaropsis maculata* (Johnston, 1828) |
| | *Megamphopus cornutus* Norman, 1869 |
| | *Photis longicaudata* (Bate & Westwood, 1862) |
| | *Photis longipes* (Della Valle, 1893) |
| Phrosinidae | *Anchylomera blossevillei* Milne Edwards, 1830 |
| Phoxocephalidae | *Parametaphoxus fultoni* (Scott, 1890) |
| Stenothoidae | *Stenothoe cattai* Stebbing, 1906 |
| | *Stenothoe georgiana* Bynum & Fox, 1977 |
| | *Stenothoe monoculoides* (Montagu, 1815) |
| | *Stenothoe tergestina* (Nebeski, 1881) |
| | *Stenothoe valida* Dana, 1852 |
| Urothoidae | *Urothoe pulchella* (Costa, 1853) |

## Scientific output of this PhD thesis

*Peer-reviewed journals*

Published papers:

2014 Fernandez-Gonzalez V, Sanchez-Jerez P (2014) First occurrence of Caprella scaura Templeton, 1836 (Crustacea: Amphipoda) on off-coast fish farm cages in the Mediterranean Sea. Helgol Mar Res 68: 375.

2014 Fernandez-Gonzalez V, Fernandez-Jover D, Toledo-Guedes K, Valero-Rodriguez JM, Sanchez-Jerez P (2014) Nocturnal planktonic assemblages of amphipods vary due to the presence of coastal aquaculture cages. Mar Environ Res 101: 22-28.

2016 Fernandez-Gonzalez V, Martinez-Garcia E, Sanchez-Jerez P (2016) Role of fish-farm fouling in recolonisation of nearby soft-bottom habitats affected by coastal aquaculture. J Exp Mar Biol Ecol 474: 210-215.

In press Fernandez-Gonzalez V, Sanchez-Jerez P (in press) Fouling assemblages associated with off-coast aquaculture facilities: an overall assessment on the Mediterranean Sea. Medit Mar Sci. Doi: 10.12681/mms.1806.

Submitted papers:

Fernandez-Gonzalez V, Izquierdo-Gomez D, Sanchez-Jerez P. The importance of macro and microhabitats in holding extremely high densities of amphipods at fish farms.

Papers in preparation:

Fernandez-Gonzalez V, Sanchez-Jerez P. The influence of fish-farm fouling as source population in the maintance of local metapopulations.

Fernandez-Gonzalez V, Toledo-Guedes K, Valero-Rodriguez JM, Agraso MM, Sanchez-Jerez P. Harvesting amphipods within a Integrated Multitrophic Aquaculture (IMTA) concept.

Collaborations:

2016 Fernandez-Leborans G, Fernandez-Gonzalez V, Sanchez-Jerez P and Roura A.(in press) Epibiontic associations between apostomid ciliates *Conidophrys* spp. and amphipods associated with fish farms fouling in the western Mediterranean Sea. Helgol Mar Res 70: 12.

In press Esquete P, Fernandez-Gonzalez V (in press) Description, systematics and ecology of a new tanaidacean (Crustacea, Peracarida) species from Mediterranean fish farms. Helgol Mar Res.

*Patent*

2015 Procedimiento para la obtención de un producto marino a base de anfípodos. Inventors: Sanchez-Jerez P, Fernandez-Gonzalez V, Agraso MM

*Conference Communications*

2011 Amphipods associated with fish-farm fouling: An overview on the Mediterranean Sea (Oral communication). MEB conference: New frontiers for Monitoring European Biodiversity: The role and importance of amphipod crustaceans. Palermo, Italy, 27-29 September 2011.

2012 Anfípodos asociados al *fouling* de las instalaciones de acuicultura en el Mediterráneo Occidental (Poster). XVII Simposio Ibérico de Estudios de Biología Marina (SIEBM). San Sebastián, Spain. 11-14 September 2012.

2013 Changes in nocturnal abundance of amphipods in pelagic system due to aquaculture floating cages (Oral communication).15th International Colloquium on Amphipoda. Szczawnica, Poland, 2-7 September 2013.

2013 Could fish-farm fouling influence the recolonisation of amphipods in adjacent sediments? (Poster). Aquaculture Conference: To the Next 40 Years of Sustainable Global Aquaculture. Gran Canaria, Spain, 3-7 November 2013.

2014 Recolonización de anfípodos en sedimentos afectados por la acuicultura: ¿influye el *fouling*? (Oral communication). XVIII Simposio Ibérico de Estudios de Biología Marina (SIEBM). Gijón, Spain, 2-5 September 2014.

2014 Nuevas estrategias en el aprovechamiento de producción natural: Cultivo de Anfípodos asociados a jaulas de peces (Invited speaker). Cultivos Multitróficos integrados:¿realidad o ficción? Guardamar del Segura, Spain, 28 November 2014.

2015 Dispersal of fouling caprellids around floating aquaculture facilities in the Mediterranean sea.(Oral communication).

First description of the epibiontic associations between apostomid ciliates *Conidophrys* spp. and two amphipods present in fish farms fouling in the western Mediterranean Sea (Poster).

16th International Colloquium on Amphipoda. Aveiro, Portugal, 7-11 September 2015.

2015 ¿Es posible aprovechar la producción natural de *fouling* de las jaulas de acuicultura de dorada y lubina? (Oral communication). XV Congreso Nacional de Acuicultura (CNA) y I Congreso ibérico de Acuicultura (CIA). Huelva, Spain, 13 – 16 October 2015.

2016 Effects of habitat complexity on amphipods colonising fish-farm fouling (Poster).V Simposio Internacional de Ciencias del Mar. Alicante. Spain, 20 – 22 July 2016.

Marine Environmental Research 101 (2014) 22–28

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

# Nocturnal planktonic assemblages of amphipods vary due to the presence of coastal aquaculture cages

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ARTICLE INFO

*Article history:*
Received 23 April 2014
Received in revised form
29 July 2014
Accepted 1 August 2014
Available online 10 August 2014

*Keywords:*
Hyperiids
Gammarids
Caprellids
Light trap
Fish farms
Zooplankton

ABSTRACT

Nocturnal pelagic swimming is common in the daily activity of peracarids in marine ecosystems. Fish farming facilities in coastal areas constitute an optimal artificial habitat for invertebrates such as amphipods, which can reach high abundance and biomass in fouling communities. Additionally, fish farms may modify the local oceanographic conditions and the distribution of pelagic communities. The aim of this study was to determine if nocturnal abundance and species composition of planktonic amphipod assemblages are affected by fish farm structures, using light traps as collecting method. A total of 809 amphipods belonging to 21 species were captured in farm areas, compared to 42 individuals and 11 species captured in control areas. The most important species contributing to the dissimilarity between farms and controls were the pelagic hyperiid *Lestrigonus schizogeneios*, the fouling inhabitants *Ericthonius punctatus*, *Jassa marmorata*, *Stenothoe* sp. and *Caprella equilibra*, and the soft-bottom gammarids *Periculodes aequimanus* and *Urothoe pulchella*. The great concentrations of planktonic amphipods at fish farm facilities is a result of the input of individuals from fouling communities attached to aquaculture facilities, along with the potential retention there of hyperiids normally present in the water column and migrant amphipods from soft sediments. Therefore, in addition to the effects of aquaculture on benthic communities, the presence of fish farms induces major changes in planktonic assemblages of invertebrates such as amphipods.





## 1. Introduction

Nocturnal pelagic swimming is common in the daily activity of many invertebrate organisms in marine ecosystems (Alldredge and King, 1985). A large number of species with a typical diurnal benthic life form part of the zooplankton community at night due to their diel vertical migrations (Watkin, 1939; Armonies, 1988; Kringel et al., 2003). Amphipods, one of the most abundant groups in benthic habitats (Thomas, 1993), characteristically represent this migratory behaviour, ascending from the seabed into the water column and thus frequently appearing during night hours in the pelagic system as members of the zooplankton community (Williams and Bynum, 1972; Macquart-Moulin, 1984; Kaartvedt, 1986). Moreover, holoplanktonic amphipods, the hyperiids, swim up from deeper layers during dark hours towards near-surface waters (Laval, 1980; Pai et al., 2010). Amphipods are an important link in the food web, since they are primary productivity consumers but also predators of larvae and adult organisms at the same time that they constitute a preferential food of small crustacean, polychaetes and many fish species (Bellan-Santini et al., 1998).

Nocturnal movements could have various ecological purposes for these species: to feed in more productive areas, to avoid competition or predation, to promote the colonisation of new habitats, to mate, or to find hosts in the case of parasitoid hyperiids (Mills, 1967; Laval, 1980; Alldredge and King, 1985; Conlan, 1991; Sanchez-Jerez et al., 1999). These migrations can range in extent from centimetres to hundreds of metres (Sanchez-Jerez et al., 1999), increasing the biomass of amphipods in the zooplankton, principally near the surface at night (Watkin, 1939). The driving factors behind these migrations are apparently changes in light intensity such as sunset or sunrise or new and full moon, and also chemical cues (e.g. predator exudates) or food concentration (Ringelberg, 1995). In fact, a relationship between vertical migration patterns of amphipods and the lunar cycle has been detected in several studies (Alldredge and King, 1980; Mcquart-Moulin et al., 1984; Drolet and Barbeau, 2009). All these factors may act as

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http://dx.doi.org/10.1016/j.marenvres.2014.08.001

Journal of Experimental Marine Biology and Ecology 474 (2016) 210–215

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

# Role of fish farm fouling in recolonisation of nearby soft-bottom habitats affected by coastal aquaculture

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ARTICLE INFO

*Article history:*
Received 8 June 2015
Received in revised form 12 October 2015
Accepted 30 October 2015
Available online xxxx

*Keywords:*
Amphipods
Field experiment
Defaunated sediment
Experimental trays
Macrobenthos

ABSTRACT

Organic loading from fish farming constitutes a significant disturbance to marine sediment, normally reducing species abundance and richness and creating disturbed patches in soft-bottom communities. In contrast, floating fish farms harbour a high abundance of invertebrates associated with fouling communities, particularly amphipods. Changes in macrofaunal recolonisation induced by fish farms were researched using amphipod assemblages as a useful representative group. The objectives of this experiment were: (1) to test the effect of fish farms on amphipod colonisation processes in defaunated sediments and (2) to define the influence of surrounding natural and artificial habitats as sources of initial colonisers. Experimental design included 36 plastic trays placed on the sea bottom (25–28 m depth) in fish-farming and control areas and retrieved one month after placement date. Significant differences were found in amphipod assemblage composition in control versus farm sites. While the recolonisation process in control areas depended on the species present in the sediments adjacent to the experimental trays, in fish-farming areas the recolonisation was strongly dependent on the input of amphipods from fouling communities. It is the first time that a spillover effect from fouling communities on floating habitats into the benthos is detected in the coastal areas. If the organic enrichment of aquaculture sediments is moderate, the ecological services of benthic habitats may be balanced, at least partly, by biomass exported from fouling communities on the same fish farms.



## 1. Introduction

High organic loading on the sea bottom is a major anthropogenic disturbance to the marine benthos that constitutes a significant problem in coastal-zone management (Cloern, 2001). Coastal aquaculture perturbations are mainly derived from surplus fish feed and waste products accumulated on marine sediment (Gowen and Bradbury, 1987; Kalantzi and Karakassis, 2006) which cause silting, increased oxygen demand, anoxic sediment generation and toxic gases on the seabed (Wu, 1995; Borja, 2002). These negative effects may defaunate and disturb patches in soft-bottom communities (Berge, 1990; Lu and Wu, 1998; Pereira et al., 2004). Indeed, benthic assemblages are often eliminated or reduced below the cages (Edgar et al., 2005; Tomassetti et al., 2009; Martinez-Garcia et al., 2013). This process maintains spatio-temporal mosaics of affected sediment patches on the sea bottom (Hargrave et al., 1997), which are reflected as a wide variability in benthic communities affected by fish farming, on a scale of metres (Fernandez-Gonzalez et al., 2013).

While benthic fauna in offshore fish-farming areas are negatively affected under the cages, these structures, namely in the nets, ropes and buoys, harbour a high abundance of invertebrates (Fitridge et al., 2012), which are potential colonisers to the neighbouring habitats. Amphipods are numerically dominant organisms among fish-farm fouling epifauna (Greene and Grizzle, 2007; Fernandez-Gonzalez and Sanchez-Jerez, 2014) and are among the most diverse and abundant groups of soft-bottom fauna (Gómez-Gesteira and Dauvin, 2000; De-la-Ossa-Carretero et al., 2010; Carvalho et al., 2012). They constitute an important link in the food web, since they are primary productivity consumers and also predators of larvae and adult organisms, being in turn a preferential prey of small crustaceans, polychaetes and many fish species (Bellan-Santini et al., 1998; Jiménez-Prada et al., 2015). Amphipods lack planktonic larvae so, as in most peracarids, embryos are carried by females in a ventral brood pouch or marsupium, from which fully-developed juveniles emerge (Sainte-Marie, 1991; Thiel, 1999). This impossibility of recruitment by pelagic larvae means that the colonisation must have been by juveniles or adults via crawling or swimming from nearby populations (Guerra-García and García-Gómez, 2006) or via drifting from distant communities (Cummings et al., 1995; Thiel, 2003).

Settlement and colonisation processes are important for soft-bottom benthic species and may be affected by external stressors such as organic enrichment (Snelgrove and Butman, 1994). Some ecological aspects of these processes have been studied through field experiments on artificially defaunated sediment in intertidal (Smith and Brumsickle, 1989; Negrello Filho et al., 2006) and subtidal habitats (Bell and Devlin, 1983;

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http://dx.doi.org/10.1016/j.jembe.2015.10.019
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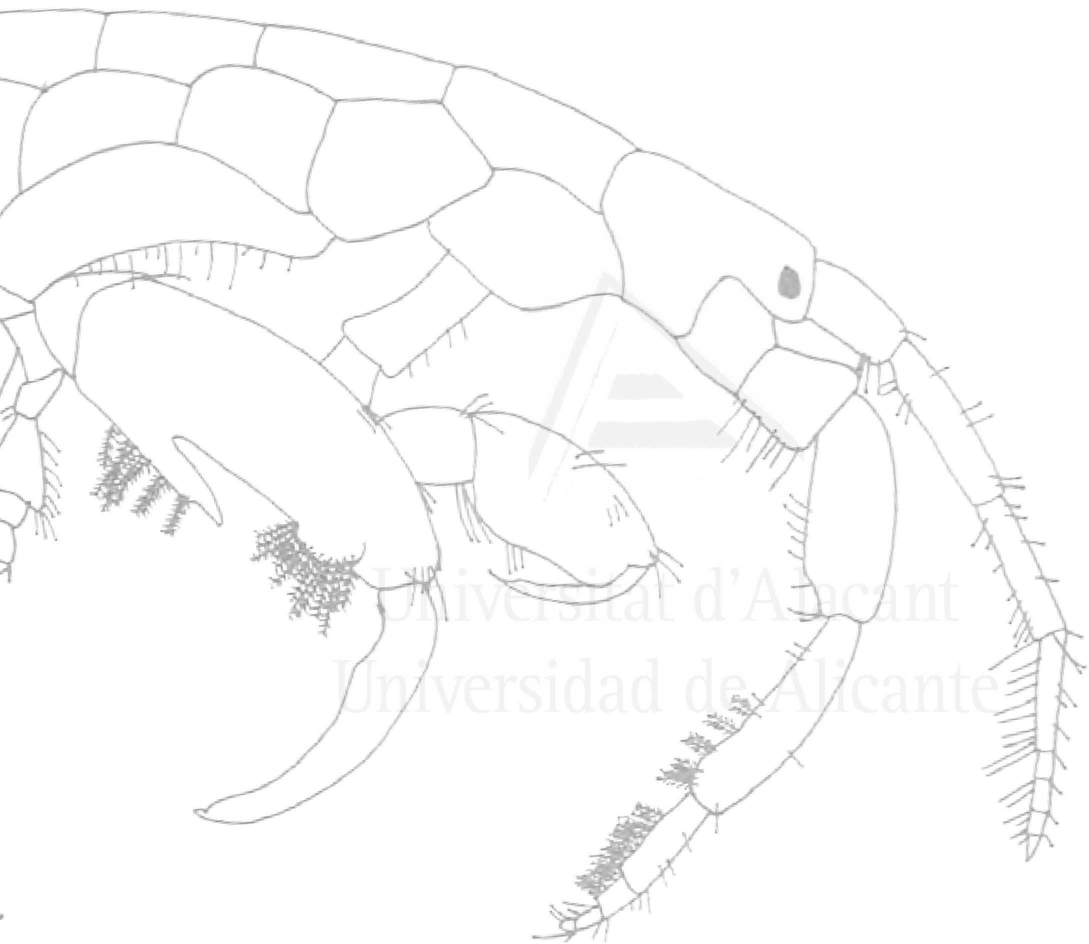
# Agradecimientos/Acknowledgements



¡Por fin llegó el momento!

Desde el día que pensé por primera vez en los agradecimientos de mi tesis (señal inequívoca de que crees que vas a terminar) hasta hoy ha pasado mucho tiempo, tanto que lo que tenía clarísimo en aquel momento, ahora me hace dudar si se me olvidará alguien o no. Espero que la mente no me traicione, que a estas alturas puede ocurrir, y mencionar a las muchísimas personas a las que tengo que agradecer su apoyo y ayuda en todo este tiempo.

Si pienso en cómo he llegado hasta aquí, los primeros que vienen a mi cabeza son mis padres. Sin el ánimo que nos dieron para que eligiéramos un camino y lo persiguiéramos, para ser lo que quisiéramos ser, quizá yo nunca me habría aventurado a ir hacia el mar y a alejarme de Córdoba. Gracias por ser un ejemplo de lucha y superación en el día a día y por inculcarme que siempre hay que esforzarse por hacerlo lo mejor posible.

El siguiente al que debo agradecer haber llegado hasta aquí es Pablo Sánchez, que confió en que sacaría una tesis antes que yo misma me planteara si podía hacerlo. Soy muy consciente de que poca gente puede decir que su director haya estado en todos y cada uno de los momentos de su tesis (¡desde identificar mi primer anfípodo!) y por ello te doy las gracias. Gracias por cada día que te asomaste a mi lupa para ver cómo iba, por tirarte al agua los días que hasta a mí me daba pereza, por hacerme parte de tu grupo y de tu gente, y por preocuparte siempre de buscar financiación para que pudiera acabar tranquila. Pero sobre todo, te agradezco muchísimo esa mezcla ideal entre confianza y supervisión que me ha permitido desarrollarme por mi misma sin sentirme perdida en ningún momento.

Hacer la tesis en la Universidad de Alicante me ha permitido formar parte de un gran equipo (ahora ya equipillo) de los que he podido aprender al máximo todos estos años. Gracias a Dami por ayudarme tanto en los inicios y llenar los momentos de risas. A David, por personalizar tan bien la palabra equipo y emanar cariño y comprensión en los momentos duros de los muestreos. Al todo-terreno Pablo Arechavala, un lobo de mar del que aprender y un grandísimo fotógrafo al que envidiar ¡mil gracias por las todas las maravillosas fotos de esta tesis! A Elena, por poner el punto de cordura (bueno y el de inocencia también…) en los muestreos y por convertirse en mi compañera de alegrías y penas en esta última fase de tesis. Y a Kilian, el último en incorporarse al grupo y el más importante en incorporarse a mi vida. Gracias por haberle dedicado tanto tiempo a esta tesis casi como a la tuya, por acompañarme en todo desde el principio, por ser el revisor más crítico al que tengo que enfrentarme y un ejemplo al que seguir en ciencia. Pero sobre todo por preocuparte de que el engranaje funcione perfectamente y juntos formemos una máquina que funciona mejor día tras día. Como dice mi madre, ¡si hemos sobrevivido a dos tesis podemos sobrevivir a todo!

Muchas gracias también a los compañeros que nos echaron una mano en los muestreos cuando nos hizo falta: Maite (una suerte tener una anfípologa en casa con la que compartir "friquismo"), Ángel, Tito (¡que sabe de buena mano lo que he tenido que sufrir separando!), Lydia y muy especialmente a Juanma, muchísimas gracias por estar siempre dispuesto a ayudarme y trabajar conmigo codo a codo. También agradecer a todos los colaboradores y alumnos que han estado trabajando en el laboratorio por ayudarme con las interminables muestras: Sandra, Fabián, Rubén, Leti, Andrés, Alejandro, María, Rubén C. y Juandi.

Este trabajo no hubiera sido posible sin la colaboración de las instalaciones de acuicultura, gracias especialmente a CULMAR y a Agustín y Jesús Ríos que más allá de permitirnos el acceso a sus instalaciones, cuidaban de nuestros experimentos para que sobrevivieran a las inclemencias del mar. El último experimento fue posible gracias a Mariló López (CULMAREX) y Mª del Mar Agraso (CTAQUA) y al proyecto SUMERGI+DOS, gracias por contar con nosotros. Y a Nieves y Alberto por enseñarme cómo se curra en una empresa y ayudarme tantísimo en el mar.

Thanks to Ivona Mladineo (Institute of Oceanography and Fisheries of Split, Croatia) and Ingebrit Uglem (Norwegian Institute for Nature Research, Trondheim, Norway) for hosting me in their research groups. And also all researchers that kindly provided us Mediterranean fouling samples: Joseph A. Borg (University of Malta), Nikolaos Papandroulakis (Hellenic Centre for Marine Research, Greece), Tanja Segvic (Institute of Oceanography and Fisheries of Split, Croatia), Paolo Tomasseti (ISPRA, Italy), Houssam Hamza (National Agronomic Institute of Tunisia, Tunisia), Felipe Aguado (IMIDA, Spain), Ignasi Gairin (IRTA, Spain) and Pablo Ávila (Junta de Andalucía, Spain).

Al resto de compañeros y profesores del departamento de Ciencias del Mar y Biología Aplicada que de una forma u otra algo han aportado para que llegue hasta aquí: Candela, Esther, Mohamed, Julia, Jose (mi anfipólogo favorito para compartir hallazgos y dudas), Carlos Valle, Santi, Lute, Yolanda, Cristina, Vicent, Javi, Marc (gracias infinitas por ayudarme con las algas), Nuria, Carlos Sanz, Andrés, Irene, Alfonso (gracias por prestarme una lupa con la que seguir identificando cada vez que la mía pasaba por una de sus múltiples averías), Jose Luis, Jose Jacobo, Paqui, Just y Jose Miguel. Y a los compis que dan nombre a "Biología Aplicada (= Patología)" por unirnos aunque fuese al final y luchar por un bien común. Gracias especialmente a Yoana y Aitor, por poder compartir con ellos los pormenores del día a día y ser unos compañeros básicos con los que compartir una copa (venga va Aitor, sí, y por las miles de preguntas de estadística ¡pero eso te lo dice todo el mundo!) y por supuesto a las Anas, por recibirnos siempre con una sonrisa y resolvernos cualquier situación en un periquete.



Gracias a mi gente, a los que siguen sincronizando sus agendas con la mía para aprovechar el tiempo en Córdoba conmigo: Cris, Carlos, Silvia, Javi, Juan, Manuela, Raúl y ahora Álvaro, y por supuesto a mis hermanos y mis sobrinas por esperar el día en el que vuelvo a casa. Hay una canción entre la música que escucho y que define muy bien lo que siento, dice algo así como: "he visto muchos sitios y muchas cosas he probado pero como se está en mi casa no se está ningún lado...". Esté donde esté con vosotros, yo me siento como en casa.

A l@s que me vieron dar mis primeros pasitos por la ciencia y ahora, cada un@ en una parte del mundo, aún siguen viéndome dar mis pasitos por la vida: Carmen, Patri, Fuen, Marta, Adri y Juanma, todo se ve mejor con una cañita y una marinera, ¡ya estoy esperando la próxima!

Bueno, espero no haberme olvidado de nadie, porque ahora sí que sí, puedo decir que: ¡ESTO SE ACABÓ! Espero que estéis cerquita porque estoy deseando celebrarlo con vosotros.

Un besazo.

Vicky



*"La meva terra és la mar"*
*-- Lax'n'Busto --*

benthic · coastal · *Jassa* · organisms · algae · caprellids · ecology · migrations · retention · juveniles · Aquaculture · communities · study · floating · Fish-Farm · abundances · hydroids · production · populations · macrohabitats · Fouling · off-coast · adults · mussels · connectivity · source · Amphipods · species ·sea· facilities · densities · colonisation · *Stenothoe* · females · dispersal · Mediterranean · marine · IMTA · swimming · artificial · biomass · crustaceans · cages · microhabitats · pelagic · gammarids · brooding · sediment · distribution · complexity · *Caprella* · assemblages · current · ropes · environmental · behaviour · males