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Indirect interactions among predators: role of positive and antagonistic feeding behaviors in marine systems

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1 ECOLOGICAL INTERACTIONS

1.1 Brief overview of direct and indirect interactions and their effects

Species interactions represent one the most powerful driving forces of ecological processes (Trussell *et al.*, 2004). Predation, and in particular the effects of multiple predators, are a key factor in structuring communities (Sih *et al.*, 1998). In the study of species interaction a distinction is made between direct and indirect interactions, and direct and indirect effects (Krivtsov, 2004). Is now over twenty years that this discipline is being investigated and the discussion on this subject has reached a certain level of complexity. Like usually happens in ecology we face a plethora of definitions and it may be useful to "tidy up" a little bit. *Direct interactions* are those in which species physically interact (Wootton, 1994b). Instead *indirect interactions* are those effects of one species on another that do not involve physical interaction (Wootton, 1994b). Strong (1997) explains how indirect interactions happen when interspecific influences are changed by interactions between other species. Thus is pretty clear that is convenient to consider the occurring of physical contact as the factor for defining an interaction. From interactions both direct and indirect effects can arise. A species, the initiator, has a direct effect on another, the receiver, if a change in some properties of the initiator species produces a change in a property of the receiver, and this change does not require a change in any property of the receiver species (Abrams, 1995). According to Wootton (1994c) the direct effects are those that arise as a result of a physical interaction between two species. In order to clear things out, from a direct interaction arise direct effects. For example, a decrease of prey population can occur from predation. Through years, this superficial and partial approach has been slowly taken over with the understanding of the importance of indirect effects (Kovalenko *et al.*, 2010). So from direct interactions can also arise indirect effects. Many different authors worked towards a definition of *indirect effects*. According to Menge (1995) a species can, through its direct interactions with some species, indirectly alter the abundance of other species with which it does not interact directly. Abrams (1995), using again the receiver-initiator terminology, defines effects as indirect if a change in some property of another species, transmitter, are caused by the change in the initiator's property and are required to produce the change in the property of the receiver species. Probably the simpler definition is given by Hamilton (2000) according to whom indirect effects are those effects of one species on another with which it does not physically interact. Werner (1992) states that indirect effects arise in food webs of three or more species and may be defined as the effects of one species on the interaction between two others. In general indirect effects are defined as depending on the presence of a species that interact with other two, modifying the expected interaction between the first two species (Strauss, 1991; Wootton, 2002). Strauss (1991) organized the different types of indirect effects in four categories (Table 1).

Table 1 Types of indirect effect: how the relationship between focal species A and B is affected by a third species, C. (Strauss, 1991).

	Type of indirect effect	Effect of sp. C	Response of focal sp. A
1.	Abundance	Change in abundance of sp. B through predation, competion or facilitation	Change in abundance, per capita growth rate, demography or genotype via change in sp. B
2.	Behavioral, morphological, chemical or physiological	Change in behavior, morphology, chemistry or physiology, but not necessarily abundance, of sp. B	Change in abundance, per capita growth rate, demography or genotype via change in sp. B
3.	Environmental	Change in quality of abiotic resource	Change in abundance, per capita growth rate, demography or genotype via change in shared resource
4.	Response	None	Change in abundance, per capita growth rate, demography or genotype as a result of altered response of sp. A to sp. B caused by the presence of sp. C

Menge (1995), based on the same work, defines four types of indirect effects as follows: *trophic linkage* (ecological or abundance) *indirect effects* are mediated through changes in abundance; *behavioral indirect effects* are mediated through changes in behavior independent of abundance; *environmental indirect effects* are mediated through the alteration of abiotic conditions; *chemical response indirect effects* are mediated through chemical pathways. The concepts of *Interaction Chain* and

Interaction Modification, from which indirect effects arise (Wootton, 1993; Wootton, 1994c), play a key role in the dissertation of this subject. *Interaction chains* are a series of direct interactions between species pairs from which indirect effects result. The interaction between two species (A and B) is altered by the presence of a third species (C) that modifies the abundance of one of the other two species. *Interaction modifications* are instead indirect effects that result when a species directly affect the interaction between two species rather than the abundance of another species. *Interaction chains* and *Interaction modifications* resemble the definition of the first two types of indirect effects listed by Menge, trophic linkage and behavioral. They can indeed be considered the developing forms of what now are known as *Density Mediated Indirect Interactions* (*DMII*) and *Trait Mediated Indirect Interaction* (*TMII*) (Wooton, 2002). *DMII* can be for example the direct predation on intermediate predators (Freeman & Hamer, 2009). The first author that talked about “traits that transmit effects” was Abrams (1995). *TMII* (with their effects; Peacor & Werner, 1997; Bernot & Turner, 2001; Trussell *et al.*, 2002 and 2003; Werner and Peacor, 2003; Canning, 2005; Freeman, 2006; Okuyama & Bolker, 2007; Stalling, 2008; Freeman and Hamer, 2009; Utsumi *et al.*, 2010a and 2010b) occur when a trait (e.g. behavior), rather than the density, of the intermediate species changes in the presence of another species, causing the abundance of a third species to be modified (Siddon & Witman, 2004). According to Trussell *et al.* (2003), *TMII* describe how a predator affects a trait of a second species, which in turn affects the interaction of the second species with a third species. Okuyama & Bolker (2007) explain pretty simply how predators both kill foragers (density effects) and induce antipredator behavior in foragers (trait effects), in both cases reducing the absolute rate at which forager population consumes resources. Introducing the idea of *DMII* and *TMII* in the trophic cascade concept (Schmitz *et al.*, 1997; Schmitz & Suttle, 2001), we can see that two different mechanisms exist by which apex predator control the abundance of mesopredators; (1) through direct lethal encounters and (2) through adjustments in behavior and distribution made by mesopredators to avoid direct encounters with apex predators, and motivated by fear of apex predators (Ritchie & Johnson, 2009).

The importance and key role of indirect interactions and indirect effects in ecological studies is thus pretty clear and is what pushed me toward deepening the knowledge and investigate new models and interactions.

1.1.1 Positive interactions. Facilitation

The study of the relationships that exist between organisms is a key point for understanding the ecology of both single species and ecosystem functioning (Sutherland, 1996). Regarding the present work I focus the attention especially on positive interactions within which also exist several interaction not yet taken fully into account in ecological dissertations.

Generally speaking, two opposite interactions may occur. Competition, the most common case, is characterized by a reduced predation rate for each component (Huang & Sih 1991). Conversely, facilitation synergistically enhances predation efficiency. There is a growing body of evidence that commensalism is quite common among predators, for example when a prey is exposed to a predator when it escapes from another predator (Bruno & Cardinale 2008).

Several types of positive interaction exist. As reported by Giangrande & Gravina (2000), if an interaction produces positive effects, for example on growth, for the other species, or both, it is called mutualistic. Within the definition of this general and "big" category, lay a lot of other different interactions of whom is possible give some example also for the marine environment. According to Wootton (1992) its mutualism when: "few or all the participants of an interaction show a direct gaining in the fitness with none having a loss". An example could be the one of the mainland goby, *Psilogobius mainlandi* and a blind shrimp of the *Alpheus* family. This two individuals share the nest dag by the shrimp. *Psilogobius mainlandi* staying close to the entrance of the nest signals the presence of potential dangers and stimulates the shrimp to eventually pull back in the nest where the fish enters right after (Wootton, 1992).

Within positive interactions one of the best known and studied probably is cooperation. This is considered a "good" modality of interaction within a group of two or more organisms in spite of the potential individual costs (Dugatkin & Mesterton-Gibbons, 1996). Cooperation takes place with a coordinate behavior of two or more individuals with benefits for the participants (Mesterton-Gibbons & Dugatkin, 1997). Cooperation was usually thought to be exclusive of more evolved taxa, like for example primates, in association with their social and cognitive skills. However studies have brought to the attention how this are more diffused and common than previously thought. Fish, for example, have shown similar problem solving solutions regarding food exploitment like the one related to the evolution of the big neocortex of primates that is the reason of their cognitive skills (Bshary et., 2002).

According to Alfieri & Dugatkin (2006) exist four categories that origin and maintain cooperation: by-product mutualism, kin selection and trait-group selection. Focusing on by-product mutualism, that can be consider as an accidental mutualism, the definition given by Dugatkin (2002), quoting Brown (1983), is: “In by-product mutualism, each animal must perform a necessary minimum itself that may benefit another individual as a byproduct. These are typically behaviors that a solitary individual must do regardless of the presence of others, such as hunting for food”. By-product mutualism operates in the present, indirectly, through feedback from the environment (Dugatkin & Mesterton-Gibbons, 1996). Base for this cooperative interaction is the so called “harsh environment”, that is an environmental situation that pushes species involved to act together in order to gain better results than what would happen if acting alone. The harsh environment must refer to abiotic features of the environment in order to have by-product mutualism. (Dugatkni & Mesterton-Gibbons, 1996). In few gregarious fish species the territoriality of other species can be considered as the adverse environmental condition that leads to the cooperative strategy, in this case cooperative foraging (Dugatkin & Mesterton-Gibbons, 1996). Several example of fish cooperation exist. Foster (1987) described how the success of *Thalassoma lucasanum* in obtaining embryos of the panamic sergent major *Abudefduf troschelii* as preys was directly correlated to the dimensions of the shoal attacking the preys nests. Shoals with high densities of individuals were never present when *Abudefduf troschelii* weren’t hatching. Groups of thirty or less individuals were not able to successfully reach the resource, while group more numerous (hundreds) had high chances of succeeding in chase away *Abudefduf troschelii* and feed on the embryos. A similar behavior was studied and witnessed in Ustica MPA by Milazzo *et al.* (2006) in relation to touristic presence. The ornate wrasse *Thalassoma pavo* attack the damselfish *Chromis chromis* nests. The male damselfish is able to protect the nest when there are low density of attacking wrasses. Touristic presence and their habit to feed fish conditioned the behavior of *Thalassoma pavo*. The consequence is that wrasses aggregate in big shoals as soon as a diver is in the water and these shoals are then able to successfully attack *Chromis chromis* nests. In this case exist a cooperation within the ornate wrasse but an unintended one (by-product) between divers and *Thalassoma pavo*.

Another important part of positive interaction is the one concerning the role played by facilitation and multiple predators effect (MPe). The definitions of facilitation are diverse and just this could be enough to understand how facilitation has still to become definitely part of the theory of individual interactions. “Modern ecological concepts and theories were well established a decade before the current renaissance of interest in facilitation began, and thus do not consider the importance of a wide variety of facilitative interactions. It is time to bring ecological theory up to date by including facilitation.” (Bruno *et al.* , 2003). In the marine environment the facilitative behavior is basically known in relation to fouling and colonization of solid surface. The first description of a facilitative process, even if not explicitly called like this, dates back to a paper of Charnov *et al.*, (1976). According to the author, the presence of a predator can bring to modifications (“depressions”) in the behavior or use of the environment of the prey. As a result of these changes the prey could result, depends on the case, more or less available at the arrival of an eventual second predator. Then there would eventually be a possible facilitation for the second predator from the first one. Sometimes even solely the presence of a predator can influence the availability of prey for another predator, also of a different species. In general, facilitative, or positive, interactions are definable as encounters between organisms in which at least one of the participants has a benefit and none is damaged (Bruno *et al.*, 2003). Bruno & Bertness (2001) consider “facilitator” those organisms, “modifiers”, that positively influence a close organism. Facilitation can also be seen as a process that increase the quantity of environment that satisfy the necessary niche to a certain species. Using the concept of niche to explain facilitation can be very useful but can also bring to the paradox of having a realized niche bigger than the predicted necessary one (Bruno & Bertness, 2001; Bruno *et al.*, 2003). An example of facilitation is the one between the herons (*Ardea alba*, *Ardea heroides* and *Butorides virescens*) and the smallmouth bass (*Micropterus dolomieu*) in relations to their common fish prey (Steinmetz *et al.*, 2008). When the preys are close to the surface of the water they are preyed and attacked by the herons. When instead they are deeper in the water is the bass that feeds on them. Also a distinction of preys dimensions exists between the two predators, bigger for the herons while small one for the fish. The experiment consisted in presenting or making available preys of different sizes to both the predators or, alternatively, to one of the two. Results showed that when only one of the two predator species was present preys resulted equally available to herons and fish. However when both predators were present an increase in the number of preys captured was recorded. This happened because the presence of the herons facilitated predation by the bass. The fish indeed captured the preys that escaped from the attack of the birds in the surface and moved down to the bottom trying to find shelter The opposite mechanism however, facilitation by the bass for the herons, was not demonstrated.

Within facilitation is necessary to explain and acknowledge the presence of multiple predator effects (MPEs). That is to say, several predators have effects on a shared prey that cannot be predicted simply by adding the effects of single predators (Sih *et al.*, 1998). This effects can show an increase or diminish of the captured preys. If the different predators have among them conflicting interactions, preys would benefit from this and the result would be a lower number of captured preys. In the opposite case of a prey that has an escape response or behavior that, saving it from one predator, put it in the conditions to be preyed upon by another one, the result would be an increase in the rate of captures. However, there is also the chance that a prey would develop escape responses specific for each kind of predator, thus avoiding the potential negative effects caused by the presence of multiple predators (Sih *et al.*, 1998). Again according to Sih *et al.*, (1998): "To identify an emergent MPE, one must compare the observed impacts of multiple predators to an expected effect.". An example of facilitation and MPEs is the one between the southern oyster drill (*Stramonita haemastoma*) and the stone crab (*Menippe adina*) that share the common prey, the eastern oyster (*Crassostrea virginica*) (Fodrie *et al.*, 2008). The peculiar and interesting thing about this interaction is that the stone crab preys also on the other predator, the oyster drill. When both the predators are present, comparing expected and field results, this study demonstrated how crab and oyster drill determine an increase in the predation rate of the oyster (i.e. MPEs). Predation by the crab allows the oyster drill to reach the soft tissues of the oyster more easily, thus having a higher quantity of food source available.

1.2 Objectives

With my PhD I wanted to deepen the knowledge and focus on few different aspects of ecological interactions that arise from food search and its consume, such as predator-prey, predator-predator and in general multiple predators interactions.

My attention was in particular directed towards ecological aspects and interaction usually less investigated and known, such as facilitation and predators interactions. The goal was to take a first step for the Mediterranean toward new and more actual ways to conceive, think and study natural communities, the interaction that drives them. Considering the global scenario of warming waters, overall ecosystem changes and biodiversity loss and species invasion, I wanted also to stress the importance of including indirect interaction in the approach of the ecological issues we are facing.

More precisely I wanted to (1) find new interactions to use as examples towards the understanding of these concepts (2) setting up manipulative experiment both on field and in lab in order to quantify and characterize these interactions from both an ecological and behavioral point of view and (4) understand the ecological scenario where this issues will develop in the next future within the communities web of interactions, cascades and development. This work has indeed its natural breadth and continuation in the general global change frame, biodiversity loss and species invasion.

All the models investigated and the experiments conducted for my Phd and here reported focused on predator-prey interactions of the Western Mediterranean upper subtidal.

2 MUTUALISTIC PREDATION ON SEA URCHIN BY FISH AND STARFISH

2.1 Introduction

Predation is one of the fundamental structuring forces in ecology (Estes *et al.* 2011). Different predator species sharing a prey can establish direct or indirect interactions, which affect the predation efficiency (e.g. Bruno & Cardinale 2008). At the same time mutualistic facilitation during predation is rarer.

Conceivably, opportunities for the establishment of new mutualistic interactions are arising, due to the rapid changes in predator assemblages experienced by most ecosystems worldwide. Depletion of large predators upsets ecosystem structures and provides abundant resources for the remaining secondary predators (Jackson *et al.* 2001, Estes *et al.* 2011). Moreover, recent global climate alterations are causing massive shifts in the biogeographic ranges of species (Harley 2011) providing novel assortments of species with potentially new, unexpected effects on ecosystems (Nogués-Bravo & Rahbek 2011).

In marine systems, the most documented changes on predator’s assemblages are the disappearing of large predators due to the overfishing (Jackson *et al.* 2001) and the inclusion of new exotic predators (Byrnes *et al.* 2007). A compelling key ecological question is how such changes will affect the dynamics of ecosystems and their productivity. A well-known consequence of removal of sea urchin predators in rocky reefs is the shift from productive erect algae forest to the so named sea urchins barrens, due to sea urchin population increase and overgrazing (Estes *et al.* 2011). Barren formation is considered a detrimental process as algal forests magnify secondary production supporting complex food webs and fisheries in coastal zones (Steneck *et al.* 2002). Protection enforcement in marine reserves has been proved to allow the recovery of sea urchins’ predators and the re-establishment of the algal forest state via trophic cascades (Shears & Babcock 2002, 2003, Babcock *et al.* 2010).

This process was demonstrated in protected Mediterranean rocky reefs where the recovery of the sea breams *Diplodus* population, main predators of the sea urchins *Paracentrotus lividus* and *Arbacia lixula*, led to restoration of forest algae (Guidetti 2006). In Ustica marine reserve, however, sea urchin decrease and forest restoration were not accompanied by a parallel increase in *Diplodus* population (Bonaviri *et al.* 2009). Neither exceptionally powerful storms nor mass mortality events justified this event. We hypothesize that a recently established mutualistic interaction between two weak predators of sea urchin, the starfish *Marthasterias glacialis* and the wrasse fish *Thalassoma pavo*, is responsible for the population control of sea urchins at Ustica and, consequently, for forest recovery.

M. glacialis is usually rare in Mediterranean shallow reefs (Bonaviri *et al.* 2009) and it has been generally neglected as predator of sea urchins due to its preference for bivalves (Guidetti 2004). Sea urchins are also able to remotely perceive starfishes (up to 50 cm apart) and successfully escape from them by fleeing away (Urriago *et al.* 2011, Manzur & Navarrete 2011; Urriago *et al.*, 2012). Therefore, the predatory strength of the starfish on sea urchins is usually weak. In Ustica has been observed an unusually high abundance of *M. glacialis* in shallow reef waters (~3 individuals/250mq ±0.3SE, n=60 in 2009) (Di Trapani, 2011). This observation is particularly important since bivalves are scarce in Ustica due to the basaltic nature of the substratum and the low nutrient concentration of water. The importance of the starfish in relation to sea urchin population is also demonstrated by the results of Di Trapani (2011) showing how the diet in the field of the adult individuals consists for the majority of sea urchin.

The wrasse *T. pavo* is known to consume small mollusks and crustaceans and to predate juveniles of sea urchins. However, this small fish is unable to overcome the defense features of adult sea urchins. At Ustica, the wrasse has benefited from the fishing ban (Milazzo *et al.* 2011), and currently the population is thriving.

We repeatedly observed a mutualistic interaction between *M. glacialis* and *T. pavo* in predation on sea urchin at Ustica. In proximity of starfish, sea urchins activate an escape behavior by extending the tube feet, lower the spines and rushing away from the starfish (Jensen 1966). The high abundance of both starfish and urchins at Ustica makes this event quite common. At this point different individuals of the wrasse gathered and precisely and repeatedly bit off the tube feet from the urchins. The extensive occurrence of this behaviour is evidenced by the remarkable presence of sea urchins' tube feet in the stomachs of *T. pavo* collected at Ustica (Badalamenti personal communication).

The goal of this experiment was to describe the interaction, understand and quantify the number of tube feet removed during the attack. I did that through direct observation by both video recording and visual survey. I then proceeded in evaluating the effect on movement ability of tube feet lost within the predator-prey interaction between sea urchin and starfish. To test for this I simulated the effect of the wrasse bite by experimentally removing tube feet from individuals collected in the field and then compared escape and attack speeds.

2.2 Materials and methods

STUDY AREA

The interaction has been observed in the island of Ustica, particularly in the southern zone. Ustica is a volcanic island 67 Km off the northern coast of Sicily, Southwestern Mediterranean. Is characterized by the presence of a Marine Protected Area (MPA) that insists in the entire perimeter of the island. The northern area corresponds to the “no-take zone” of the MPA while the southern one is characterized by partial reinforcement. This area has a length of 7050 m and a total area of 8031ha Here we find the highest density of *Marthasterias glacialis* in Ustica. *Thalassoma pavo* and *Paracentrotus lividus* are widely present too. The bottom is characterized by beds of *Cystoseira* spp. and patches of sea urchin barrens (Bonaviri *et al.*, 2009)

PRE-SURVEY: DESCRIPTION OF THE INTERACTION

The aim was to record, document and evaluate the extent of the indirect interaction between *Marthasterias glacialis*, *Thalassoma pavo*, *Paracentrotus livuds* and *Arbacia Lixula*. We did this by both video recording and scuba dives observations.

We filmed using three camcorders (JVC EVERIO GZ-MG330) with internal hard drive (30GB). Each camera was equipped with a modified waterproof case (Nimar) that allowed us to add and connect to the camera long lasting batteries packs (up to 12hours of recording stamina). Cameras were set on tripods, properly weighted and balanced, and left recording on the bottom. In this way the presence of divers was reduced to the minimum and so were interferences. Several starfish, previously starved, were set free in the area within the visual range of the cameras. The cameras set up was realized in the southern area of Ustica, precisely in Cala Galera. Here the presence of all the three species is diffused and the association has been previously observed.

At the same time we proceeded with our pre-survey observations of the interaction. We observed both the species of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*. We counted the number of bites of *Thalassoma pavo* for each species when *Marthasterias glacialis* was directly attacking and when the starfish was simply moving around the bottom.

PREDATOR-PREY INTERACTION. SPEED COMPARISON AND TUBE FEET REMOVAL

These experiments were also conducted along the southern side of the island described above. Individuals were collected from the same area. To test for attack speed (*Marthasterias glacialis*) and flee speed (*Paracentrotus lividus* and *Arbacia lixula*) we respectively presented a sea urchin to the starfish and a starfish to a sea urchin. In general, after the first movement of the species we were testing, we counted 60s with a stopwatch and measured the distance covered taking in account, at the best possible, the roughness of the substrate. We considered the central disk for *Marthasterias glacialis* and the center (roughly the Aristotele’s lanthern) for *Paracentrotus lividus* and *Arbacia lixula* as points where to measure the distance traveled (spines for sea urchin and arms for starfish can randomly move). Speed were tested in both the substrate states present in Ustica, Erected Macro Algae (EMA) and Barren (BAR). For our experiments we considered EMA substrate as a continuous and thick bed of "soft and easy to bend" algae. The most abundant and present species in these beds was *Cystoseira humilis*.

***Arbacia lixula* and *Paracentrotus lividus* escape speed**. For sea urchins escape speed we collected several individuals of *Marthasterias glacialis*. The size of the individuals chosen (arm height in mm.) depended on the results obtained by the analysis of the diet of the starfish. We used them to trigger the flee. Once a sea urchin was found, the starfish was put close to it and kept that way for 60 seconds. In this way, presenting a constant threat, we can consider to have always registered the fastest escape speed possible. During this procedure the sea urchins were never touched or handled. After the 60 seconds of the experiment the sea urchin was then measured.

***Marthasterias glacialis* attack speed**. Testing for the speed of starfish we collected individuals of *Paracentrotus lividus*. The size of the individuals chosen (test diameter in mm) depended on the results obtained by the analysis of the diet of the starfish. We used them to induce the attack. Once a starfish was found the sea urchin was put right next to it and kept it that way for 60 seconds. In this way, presenting a constant prey, we could avoid losing interest by the starfish during the attack. Starfish were never handled before measuring the distance travelled. After the 60 seconds of the experiment the starfish was then measured.

Effect of tube feet removal on sea urchins escape speed. To test for the effect of tube feet lost we collected individuals of both sea urchins species and brought them to the laboratory (in Ustica). In the laboratory we set up tanks in which we placed one sea urchin per tank. After few minutes the sea urchin were properly attached. Strongly grabbing the sea urchin we were able to rip off the tube feet. We then count the number of tube feet left on the tank walls. Knowing the number of tube feet present on the sea urchin in relation to the test size (Santos & Flammang, 2007) and repeating this operation, we removed 50% and 70% of the tube feet. 70% of tube feet was removed only for *Paracentrotus lividus* because after losing 50% of tube feet we already witnessed a consistent loss of speed in *Arbacia lixula*. After removing the tube feet we brought back the urchins on the field to run the tests. To check for eventual differences between treated and non-treated urchins due to handling or transportation stress, we also run control tests on sea urchins. We harvested urchins, brought them to the laboratory and put in tanks, one urchin for each tank. We left all the individuals in the laboratory the same amount of time needed to rip off the tube feet. They were then brought back to the field and speed tests were run.

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSIS

I designed a 3-way Anova analysis. The three factors were: Species (fixed with 8 levels), Substrate (fixed with 2 levels) and Site (random and nested in Substrate). Species levels were: MG (speed of *Marthasterias glacialis*); PL (speed of *Paracentrotus lividus*); AL (speed of *Arbacia lixula*); PL-50% (speed of *Paracentrotus lividus* with 50% removal of tube feet); AL-50% (speed of *Arbacia lixula* with 50% removal of tube feet); PL-70% (speed of *Paracentrotus lividus* with 70% removal of tube feet); PL CTRL (control test for *Paracentrotus lividus*); AL CTRL (control test for *Arbacia lixula*). Substrate levels were: EMA (Erected Macro Algae state) and BAR (Barren state). We run 6 replicates for each combination of these factors. A total of 192 measurements were taken. The variable used for the speed of the animals tested was cm/s.

Data were collected between June and September 2009 and analyzed with GMAV5 software. To verify the homogeneity of the variance a Cochran's Test war run. An a-posteriori test (SNK - Student-Newman-Keuls) was used to confront averages.

SPECIES

Thalassoma pavo. The ornate wrasse *Thalassoma pavo* is a benthopelagic labrid. Is characteristic of coastal water of the Mediterranean and the Eastern Atlantic Ocean (Portugal, Gabon, Azores). Usually lives in rocky habitats and seaplant meadows, thus shallow and well lighted areas around 25-30m of depth (Bini, 1968; Tortonese, 1975) but can be found even at 100m. Is a subtropical affinity species (Guidetti *et al.*, 2002). In the north-western area of the Mediterranean basin, like the Ligurian Sea, in the past was classified as rare (Tortonese, 1975), but in the last decade we assisted to a northward spreading of this species maybe because of the warming of the Mediterranean waters (Bianchi, 1993; Francour *et al.*, 1994). It then gained increasing attention as a possible candidate as climate change indicator. A series of studies have been carried out on its distribution models and on its ecological charachteristics (Vacchi *et al.*, 1999; Sara & Ugolini, 2001; Guidetti, 2001; Guidetti *et al.,* 2002). Currently even in the north-western basin the ornate wrasse is abundant.

T. pavo presents a quite narrow body, mainly yellow, green and orange with the typical blue stripes on the head. It presents five vertical blue stripes on the body and a black dot between the second and third stripe. The tail is lyred-shaped with the marginal rays that are longer than the rest. In the bigger females that are about to change sex (and progressively reach the terminal color) the dorsal black dot disappear before the other features change or disappear. Juveniles have the body completely green but with the black dot clearly visible on the back.. Is an proteroginic hermaphrodite species. Along the change of sex there is a clear change in color. The blue stripes on the body are totally lost as for the black dot on the back. Only one male protects is spawning site and fecundates several females. Adults males are extremely territorials, while females move in shoals that can reach remarkable size. The ornate wrasse can reach 25cm of length. It is an opportunistic species with the diet principally constituted by small mussels and crustaceans but it’s also able to exploit resources that become temporally superabundant like *Chromis chromis* eggs.

Arbacia lixula, Paracentrotus lividus, Marthasterias glacialis. Echinoderms and water vascular system. All the echinoderms have in common the so called water vascular system that is the body structure for the whole Phylum (Cuénot, 1981; Nichols, 1966) formed by a series of several channels that origin in the coelom and filled with running marine water. Taking for example the system of the *Asteroidea*, there is a central canal (ring canal) that communicates with the external environment with the so called stone canal that terminates in the madreporite. From the ring canal radially depart five radial canals that go through the ambulacral areas and other little canals called the Polian vescicles. These vescicles have to compensate the internal pressure of the animal. The radial canals present regularly two couples of diverticuli, two internal and two external: the internal ones are called ampulla while the external ones are the so called tube feet. The tube feet are mainly used as a locomotion system. The water is veicolated to the ampulla within the system so far described, passes to the tube feet and vice versa. The tube feet are also used to capture preys, as respiratory organ and sensorial one.

Marthsterias glacialis (spiny starfish) is an echinoderm of the class of the *Asteroidea*. As the majority of the species of this class, *M. glacialis* has five arms that, in this case are directly connected without a central disk. The mouth is on the bottom side of the central disk while the anus is in the aboral side. The body is mainly light brown and its covered with spines and vesicles (papulae). This starfish lives in the Mediterranean and in the Eastern Atlantic Ocean. It is the biggest starfish in the Mediterranean reaching 80-85cm of diameter. The habitat usually consists of rocky bottoms but it has no problem to move on basically every type of substrate. The diet is constituted principally by mussels (*Arca noe*) and echinoderms.

Paracentrotus lividus and *Arbacia lixula* are two Echinoderms of the class *Echinoidea*, more precisely regular *Echinoidea*. In the echinoids the shape is globular or discoidal, slightly flatten along the vertical axis. They have an exoskeleton called plate formed by a series of interambulacrals areas and ambulacral grooves (where the tube feet are present) that alternates with a fivefold symmetry. They have moving spines and tube feet. In the skeleton can be distinguished two areas, a basal one and an apical one. The oral zone faces the bottom with the mouth in the center surrounded by plates that form the peristome. In the upper aboral zone there is the anus that is surrounded by plates that form the periprct, here is attached the madreporite. In this area are also found the genital plates with the reproductive organs with the gonopore. On the plates of the test there are the tubercles from which raise the spines. The most peculiar features of the sea urchin is in the mouth and it is called Aristotle’s Lantern. This is an organ with feeding purposes constituted of five teeth supported and moved by muscular tissue. Differences exist between the two species of sea urchin *Paracentrotus lividus* and *Arbacia lixula*. First of all, the color differs from the purple-brown of *P. lividus* to the black of *A. lixula*. The oral apparatus is also quite different, more extended in *A. lixula*. The ambulacral groove is constituted by several pairs of pores from which pass the tube feet in *P. lividus*, while the other species only has three pores that form an arch close to the adjacent interambulacral area. This is also reflected in the different number of tube feet in the two species, with higher numbers for *P. lividus*. Also the spines are different, being longer and more numeorous in *A. lixula*. Both the species are present in the Mediterranean, on the coasts of Scotland and at the Canary Islands. They diet of the two species slightly differs with *P. lividus* preferring to feed on photophilic erected algae and *Posidonia oceanica*, while *A. lixula* feeds more on encrusting algae. A peculiar behavior present *P. lividus* and a key to recognize the two species is the so called covering behavior. The urchin collects pieces of algae, plant or shells and used them to cover its test, in relations to light and UV radiation (Verling *et al.*, 2002). *A. lixula* can reach 6cm of test diameter while *P. lividus* 6cm.

2.3 Results

PRE-SURVEY: DESCRIPTION OF THE INTERACTION

We recorded and documented for the first time this unique interaction between *Marthasterias glacialis*, sea urchins *Paracentrotus lividus* and *Arbacia lixula* and *Thalassoma pavo* (**Fig.1**).

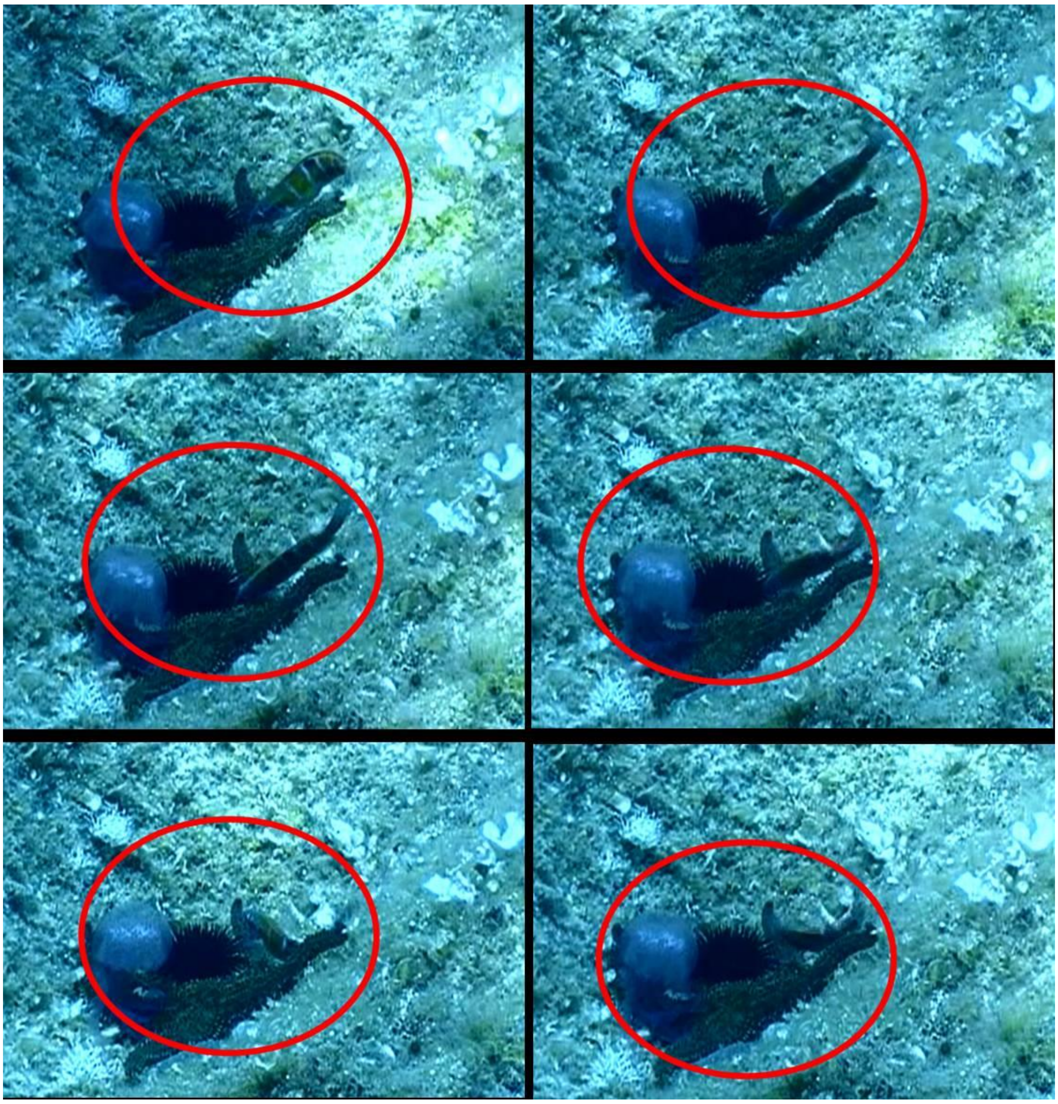

Fig. 1 Tube feet feeding of *Thalassoma pavo* on *Arbacia lixula*.

Despite sometimes seeing, during scuba dives, several *Thalassoma pavo* biting off sea urchin's tube feet simultaneously (Badalementi personal communication), we observed in the videos something different and peculiar. As shown in the sequence (**Fig.2**) we recorded, during the attack on *Arbacia lixula*, an individual of *Thalassoma pavo* (performing the feeding behavior - red circle) chasing away and strongly swimming toward another approaching individual (yellow circle). This suddenly turned and escaped while the first returned to the urchin.

Fig. 2 Chasing behavior of an individual of *Thalassoma pavo*.

From the observations we collected data to better understand the extent of the interaction. Sea urchins performed escape responses and there was the association with *Thalassoma pavo* both when *Marthasterias glacialis* was directly attacking or simply moving.

For both *Arbacia lixula* and *Paracentrotus lividus* the attacks present more the 60 bites. Under this threshold the bites are associated with the starfish moving around the bottom.

For *Arbacia lixula* (**Fig.3**), of the 13 individuals observed, the highest number of bites recorded was 150, the smallest was 6 with a total average of 38.

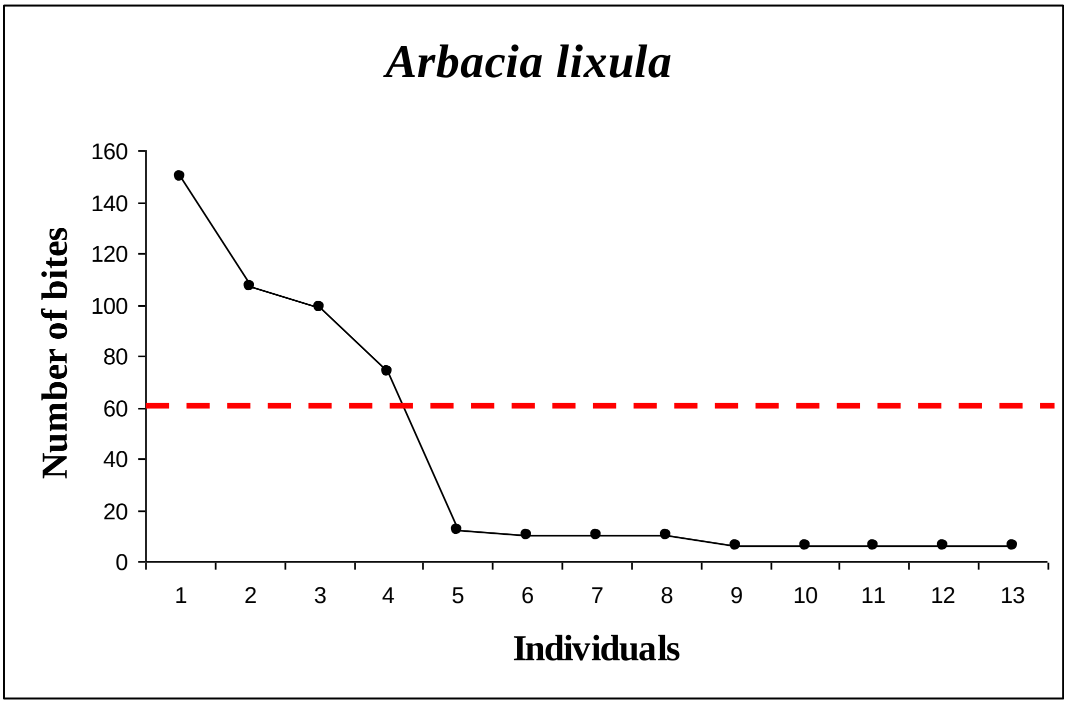

Fig. 3 Number of bites recorded for *A. lixula*.

For *Paracentrotus lividus* (**Fig.4**), of the 13 individuals observed, the highest number of bites recorded was 152, the smallest 5 with a total average of 65.

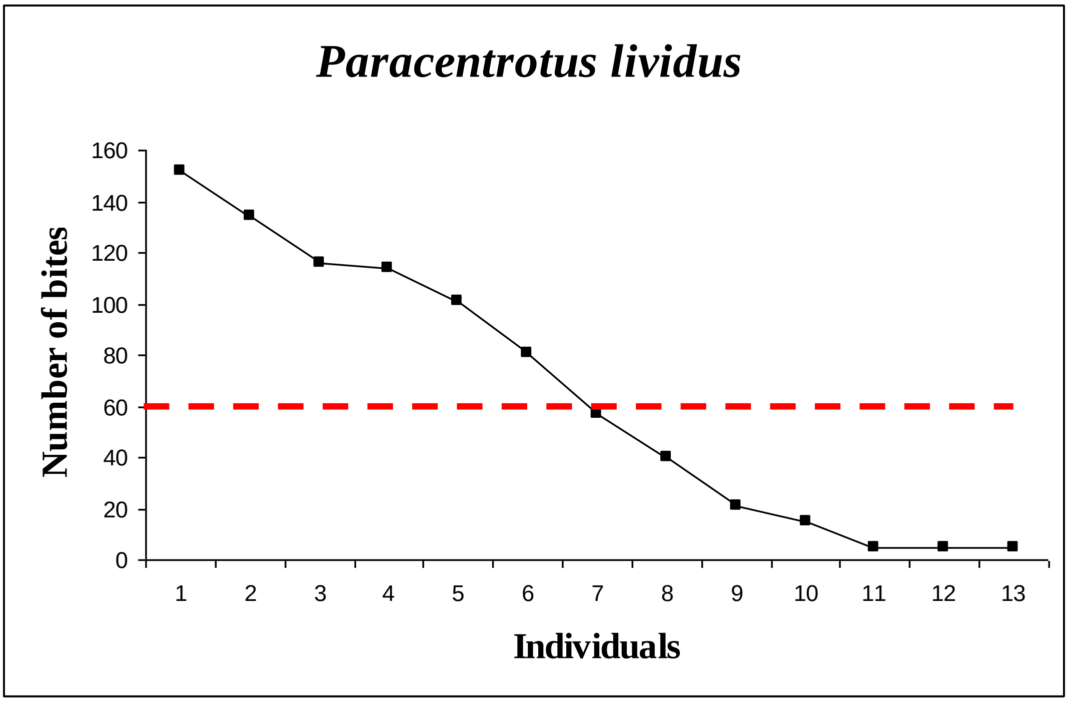

Fig. 4 Number of bites for *P. lividus*.

PREDATOR-PREY INTERACTION. SPEED COMPARISON AND TUBE FEET REMOVAL

The Analysis of the variance showed significant differences in the interaction SpeciesXHabitat (**Table 2**).

Table 2 Anova results for the experiment on attack and prey response speed.

Source	SS	DF	MS	F	P	F versus
Sp	0.7902	7	0.1129	44.65	0	SpXSi(Ha)
Ha	0.0278	1	0.0278	19.63	0.0473	Si(Ha)
Si(Ha)	0.0028	2	0.0014	0.38	0.6835	RES
SpXHa	0.3808	7	0.0544	21.52	0	SpXSi(Ha)
SpXSi(Ha)	0.0354	14	0.0025	0.68	0.7897	RES
RES	0.5932	160	0.0037			
TOT	1.8302	191				

The SNK *a posteriori* test showed that in BARREN state (Fig. 5) the slowest individuals were *Arbacia lixula* with 50% tube feet removal (0,07 cm/s ± 0,01) and *Paracentrotus lividus* with 70% tube feet removal (0,08 cm/s ± 0,01) (P<0.05). There were no significant differences between *Marthasterias glacialis* attack speed (0,14 cm/s ± 0,01), *Arbacia lixula* (handled, 0,16 cm/s ± 0,02; not handled, 0,18 cm/s ± 0,01), *Paracentrotus lividus* (handled, 0,17 cm/sec ± 0,02; not handled, 0,2 cm/sec ± 0,02) and *Paracentrotus lividus* with 50% tube feet removal (0,15 cm/s ± 0,02).

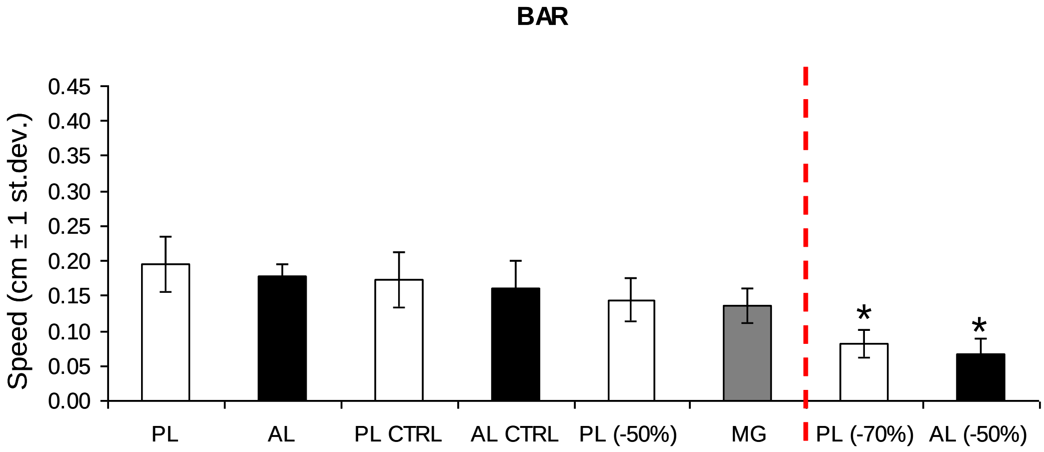

Fig. 5 Speed of all the treatment in barren habitat. *=p<0.05

In EMA state (Fig. 6) *Marthasterias glacialis* resulted significantly faster (0,35 cm/s ± 0,02) (P<0.005) than *Paracentrotus lividus* (not handled, 0,28 cm/s ± 0,03; handled, 0,25 cm/s ± 0,02). Significantly slower (p<0.05) than *Paracentrotus lividus* was *Arbacia lixula* (handled, 0,11 cm/s ± 0,01; not handled, 0,11 cm/s ± 0,01), *Arbacia lixula* with 50% tube feet removal (0,06 cm/s ± 0,01), *Paracentrotus lividus* with 50% (0,1 cm/s ± 0,01) and 70% (0,08 cm/s ± 0,01) tube feet removal.

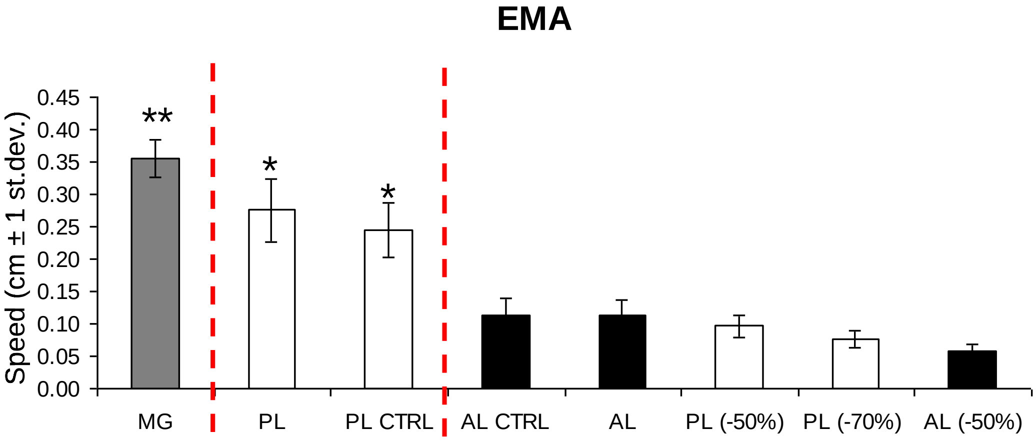

Fig. 6 Speedof all the treatment in erected macroalgae habitat. *=p<0.05, **=p<0.005

See further results in ANNEX A.

2.4 Discussions

My results showed how the attack speed of *Marthasterias glacialis* is similar to the escape speed of both the sea urchin species (i.e., no significative difference in BAR). Thus an external intervention is needed for the attack of the starfish to be successful (Urriago *et al.*, 2011). In our case of study the behavior of *Thalassoma pavo* with the consequent amputation of the tube feet can play this role. Once tested with growing percentage of tube feet removal, the sea urchins were indeed significantly slower (i.e. more catchable).

Noticeably *T. pavo* performs its behavior also when there isn't a direct attack of *M. glacialis*. As a matter of fact my observations showed how the simple movement of the starfish causes the flee of the sea urchin and the associated behavior of *T. pavo*. These interactions are usually characterized by fewer bites. Every attack that doesn't end with the capture and the consumption of the prey, lives indeed on the field one or more crippled sea urchins. These urchins have high chances of encountering again other starfishes and be further disabled by *T. pavo* with the removal of other tube feet. Thus a cumulative effect exists for this behavior with sea urchins more widely and intensely disabled that what my observations could directly show.

The key role played by sea urchin in subtidal communities is well known. With their grazing behavior they operate a control on algae. Thus for different species, studies have been carried out in order to understand density patterns, distribution, movement, anti-predatory behaviors, feeding rate (Bernstein *et al.*, 1981; Dumont *et al.*, 2006; Ebling *et al.*, 1966; James, 2000; Lauzon-Guay & Scheibling, 2007; Lauzon-Guay *et al.*, 2006; Tuya et al, 2004; Campell et al, 2001; Matassa, 2010; Hagen et al, 2002; Pederson & Johnson, 2006; Rosenthal & Johnson, 2006; Vadas & Elner, 2003). When certain densities of sea urchin are reached, barren grounds are created with a shift between different states. For this reason the role played by predators in controlling sea urchin populations is equally important. The presence of proper density of predators species prevents the overcome of sea urchins and the consequent wipeout of algal communities.

In Ustica, densities of sparids species (usual predators of sea urchins) dropped down before the institution of the Marine Protected Area because of professional exploitment and recreational fishing. This caused a bloom of sea urchins and the extended presence of barrens grounds. Nowadays sparids feeding activity is still not sufficient in controlling sea urchins population, not resulting as the main predator of *P. lividus* and *A. lixula* (Bonaviri *et al.*, 2009). This role in Ustica is instead played by the starfish *M. glacialis*. The starfish is usually described mostly as a bivalves consumer. Taking into account the results obtained from the speeds experiment, it is possible to infer that this peculiar diet of *M. glacialis* in Ustica is the direct consequence of the facilitative role played by *T. pavo*. Otherwise, without this indirect interaction, *M. glacialis* won't be able to catch *P. lividus* and *A. lixula*.

Several examples exist of loss of apical or keystone species. When this happens within a community characterized by high biodiversity, an usual consequence can be that another species plays the ecological role of the lost one. What is unique of this interaction is that the "new" predator (*M. glacialis*) is not able to play the role of the "original" one (sparids) by itself. It is instead a guild of predators (*T. pavo* and *M. glacialis* within an indirect interaction) that has the a role in controlling grazers.

This could be considered as the classical example of risk enhancement for a shared prey due to sublethal predation. However properly considering the dynamic and the steps of this interaction it's possible to understand its ecological uniqueness. First of all, *T. pavo* cannot be considered a predator of adult sea urchins performing sublethal predation. Its predatory behavior is always focused only on a part, tube feet, of the body of the prey. Secondly, in a normal risk enhancement interaction, due to sublethal predation, the first predator performs its "attack" alone and despite the presence of the second predator. This one is rather more closely reliant to the presence of the first one. Here, instead, the link between the two species is even tighter. *T. pavo* in fact needs the attack behavior, or at least the presence, of *M. glacialis* in order to perform his sublethal predation (i.e., feeding on the tube feet). Subsequently this facilitates the starfish due to an increased vulnerability for the sea urchin. It could be somehow defined as a mutual facilitation.

Direct observations and videos analysis allowed me to properly demonstrate, document and investigate the presence of this unique behavior and association. Tube feet are known as being sometimes part of the diet of reef fishes. Hubbs (1963 - after personal communications from Limbaugh, 1958 in Randall 1961), reports on the butterflyfish *Forciper* feeding on *Diadema* tube feet. Same behavior is described by the author (after personal communications from Zanveald, 1959) for the longsnout butterflyfish *Prognatodes aculeatus* on different species of echinoids (*Eucidaris tribuloides, Tripneustis esculentus, Lytechinus variegatus, Diadema*). Sakashita (1992) describes how the clingfish *Diademichtys lineatus*, that lives in symbyosis with *Diadema*, feeds also on its tube feet. An example exists also for a wrasse, *Thalassoma noronhaum*, feeding on sea urchin, *Tripneustes ventricosus*, tube feet (Sazima *et al.*, 2005). This food item is usually difficult to reach because hidden between the spines of the urchins. In all the examples above, the different species of fish are described as taking advantage of every chance possible when tube feet were available. However, in none of these, is reported any interaction between the sea urchin and its predator that would induce the escape and thus the availability of the tube feet.

To my knowledge, no examples exist in literature that describe an interaction and a behavior similar to the one we investigated. A slightly similar interaction is the one involving the behavior of groupers that actively seek the help of moray eels during hunting (Bshary et al, 2006). In this case the complementing predation strategies adopted by the two species (open space chasing vs ambush in crevices) prevents the prey escape. The other example (although without the presence of a trigger effect like the one we have with the attack of *M. glacialis*) is the interaction that involves the nipping behavior from fish, mainly flatfish, on the siphons of bivalves (de Goeij., 2001; Cledon & Nunez, 2010. This causes a less deep burial depth for the bivalves making them more available to predator birds with a consequent increase in feeding rate. What is interesting about this interaction is that recent works have assessed the importance of this indirect interaction within the general management scenario (Cledon & Nunez, 2010). The authors underline how all the measures taken for the reassessment of clams stock and the rebalance of densities of this species (i. e., *Mesodesma mactroides* in South America) has been demonstrated to be useless in reducing the constant and irreversible decrease in density. This because it hasn't been taken into account this indirect interaction.

The interaction we investigated can be considered within a similar frame. The facilitation between *T. pavo* and *M. glacialis* is fundamental to understand the drop in sea urchins densities and the shift between EMA and barren states. This would not be possible to understand with a simpler predator-prey interaction model.

To my knowledge, despite the importance of sea urchins within subtidal communities, no experiment with direct comparison of sea urchins escape speed and predator attacking velocity has been done.

However few works testing for sea urchins escape speed exist. I found a general consistence between our results and these experiments. Jensen (1966) found that the speed of *Strongylocentrotus droebachiensis* is similar to what we recorded for *P. lividus* on MAE. While *Psammechinus miliaris* reaches a speed that is similar to what we found in *A. lixula*. Results of the experiment of Vadas & Elner (2003) for *Lytechinus variegatus* and *Tripneustes ventricosus* are comparable to the speed of *A. lixula* we found.

Again, to my knowledge, also no experiment have been conducted to test for the escape speed of *P. lividus* and *A. lixula*. Usually the focus is on the movement (i.e. migrations), the distribution, predation and feeding rate (Dance & Savy, 1987), for *P. lividus* (Ceccherelli *et al.*, 2009), *M. glacialis* (Bell & Turner, 2003) or both (Ebling *et al.*, 1966).

Data exist for *P. lividus* locomotion performance in different substrata (Domenici *et al.*, 2002) although speeds are not comparable with my results due to clear experimental differences.

For the starfish instead, consistent with my findings are the results of Jensen (1966) for *M. glacialis*. Here the speed recorded, both the maximum and the one within the first 60 seconds of attack, are similar to what we measured. Slight differences instead exist with the speed of *M. glacialis* recorded by Mayo & Mackie (1978). In this case the speed tested was however the escape speed and not the attack one.

The significative difference I found between *A. lixula* and *P. lividus* speed in EMA are probably related to the different morphology of the two species. Longer spines in *A. lixula* cause more complex movement and struggle therefore a slower escape then *P. lividus*. Furthermore the difference can reflect the opposite escape behaviors. *A. lixula* relies more on its spines, not investing much energy in escaping while *P. lividus* performs strong escape flee. In this prospective our results contribute in deepening the knowledge on the biology and behavior of these two species.

It is well known how in ecology different factors work together in shaping communities and systems. However it is clear a lack of studies and example in this direction. In this case of study it is possible to see how indirect interactions (associated with peculiar and unique foraging skills), loss of apical species (i.e. fishing of predators), biodiversity effects, global warming and migrations are needed to explain a process, habitat shift, that otherwise would be described in a more simplistic way. There's no doubt that real difficulties exist in approaching this kind of studies, both experimentally and logistically. There's no doubt as well that this is an undeniable mistake that will never let us properly understated ecosystems. The idea of linear interactions between individuals is being slowly put behind the back and a scenario like the one I described is to be considered as a normal ecological system.

More broadly, my study represents an example of ecosystem resilience (Downing & Leibold, 2010), where loss of top-predators is compensated by the establishment of new mutualistic interactions involving species classically considered ecologically unimportant, with cascade effects on ecosystem dynamics and productivity.

3 VISUAL CUES TRIGGER THE RESPONSE OF THE ORNATE WRASSE TO EXTERNAL STIMULI

3.1 Introduction

Almost every ecosystem is usually characterized by some individuals or species that, with their behavior, are capable more than others of exploiting and adapt to the environment they live in. Behavior can be considered based on how an individual collect/filter, process and react to signals and stimuli from the environment through its senses. Senses are what actually allow individuals to properly orientate in their environment (Ridley, 1995).

In all the situations and conditions animals base their responses on sensorial capabilities in order di decode and interpreter the environment they live in. The value of a stimulus depends both on the mean in which it propagates and on the capabilities of the organism to receive it and process it (Kotrshal, 1998). The key for processing external information are the sensorial cells, usually aggregate in sensorial organs.

AUDITIVE STIMULI

Fish live in a mean that is a good driver for sounds (1480 m/s). Of the countless existing species many have evolved different mechanism in order to transduct acoustic stimuli. Not surprising that hearing is one of the principal component for perception in fish cognition (Chase, 2001). Hearing consists in the perception of perturbation in the water. Through experiments Mann (2001) discovered that fish are able to perceive sounds with a frequency between 16 and 7.000 hertz. Physiological abilities of different species in discriminating acoustic signal are quite known (Fay, 1998; Zion *et al.*, 2010). For example studies performed on *Carassius auratus* (goldfish), demonstrated the capability of this fish to discriminate complex auditive stimuli (Fay, 1998). A very unusual experiment to explain frequency discrimination is the one by Chase (2001) with the common carp *Cyprinus carpio*. In an experimental tank fish were given a device to push in response to two stimuli (Sound/Silence). Every time the device was push correctly in response to the sound stimulus, food was deployed as a positive reinforcement. After few trials it was clear how fish were able to deploy the system in response to the Sound stimulus. The same experimental set up was then used to test for three different stimuli (Blues music/Classical music/Silence). After few trials, organisms were able to discriminate classical music from blues. This is because of the different frequency of emission that was recognized and memorized by the fish (Chase, 2001). Both *Carrassius* and *Cyprinus* are considered having specialized hearing system, however also for other species similar results have been obtained (Kawamura, 2002).

CHEMICAL STIMULI

Water contains several chemicals dissolved in it, thus individuals living in this environment have evolved numerous types of chemical reception systems. Fish through chemical substances mediated a variety of key aspects of their lives, like habitat recognition, food research and conspecific identification (Derby & Sorensen, 2008). Mostly this kind of skills are used to locate food even in turbid or deep water. This underlines the ability of fish to detect chemicals associated with food as a partial reason for the evolutionary success of fish in exploiting diverse feeding niches (Moyle & Cech, 2000). Few fish species in particular possess really strong sensibility for chemicals and few examples are worth being cited. The catfish, *Ictalurus punctatus* is an animal mainly nocturnal with really poor visual capabilities. However its chemical receptive system is highly developed. This species is indeed able to find food source chemical stimuli using taste buds placed allover its body. Caprio (1975) surgically damaged individuals of *Ictalurus punctatus* with the taste buds losing their functionality from from one side of the body. The fish was able to overcome the difficulties in finding food, only by bending in a way that would exposed the side where the taste buds were still intact. Fish have therefore the capability to recognize and learn natural chemical stimuli and the most common and fascinating example is the one concerning the salmon *Oncorhynchus spp* (Dittman *et al.*, 1996). These fish are able to migrate toward the ocean and learn the odors associated to their birth site. During their migration they cross several different environment like ocean, lakes and rivers, each one with chemical peculiarities. Thanks to this memory they are able to perform the so-called “homing behavior”, that means going back to the place they first left from. Homing presuppose the ability to orientate in the space and this is done thorough processing chemical stimuli underlying once again their importance within fish realm.

VISUAL STIMULI

In many fish species the most important sense is vision. An indirect proof of the importance of vision are the intense colors of several fish species. Even more, a lot of fish show the capability of changing colors in precise moments of theirs lives (Young, 1962). The visual channel is undoubtedly a fast and efficient way for transmitting signals. All the time in which visual communication is possible, chromatic signals are immediately received by the observing individuals. In order to verify this several experiments have been set up. An example could be the amputation of the dorsal fin in *Pristella riddlei* (Keenleyside, 1995). This disablement was done to determine if the conspicuous black band that covered the fin was an important visual sign in developing the schooling behavior (i.e., the behavior of aggregation of juvenile individuals). Even with swimming capabilities not undermined the individuals without the dorsal fin were able to aggregate less the then untouched conspecific. The explanation is that the amputation made the fish less “attractive” to the other individuals. Similar is the result obtained by Patfield (cited in Guthrie 1986) on the European perch *Perca fluviatilis*. In this case aggregation response was greater in normal perch then in those whose dorsal fin spot had been surgically removed. Thus is easy to understand how the behavior was highly influenced by vision (Swan 1962 in Rowland, 1999). These experiments underlined how vision is important in determining responses and consequentially the behavior of fish. Other experiment, less invasive, have been developed in order to evaluate the sensorial capabilities of fish and their behavior. Several studies have been done to investigate vision and the relation with sexual behavior, reproduction and change in color during courtship. Studies around this subject dates back in decades with findings also by Tinbergen. Precisely the work was focused on the sexual behavior of the three-spined stickleback, *Gasterosteus aculeatus*, considerably influenced by colors. During the reproductive period the stomach turns to a bright red as a signal to females of the availability for mating. At the same time this bright color is used against other males. Tinbergen (1951) studied the importance of this coloration. Placing a female of three-spined stickleback next to a red object, the individual behaved exactly as she would have done next to male stickleback. Similarly the male of the three-spined stickleback react at the sight of all red shape showing aggressive behavior and chases. When mating season is over *G. aculeatus* assumes a mimetic dark grey coloration spending time on caring the eggs in the nest. Interesting to notice how in some population of this species where males don’t change color during reproduction and remain plain grey, they encounter higher difficulties in pushing females toward the nest. This however is compensated by a diminished predation pressure by trout that spot them more difficultly compared to the red conspecific. Vision and sight are not solely related to colors and the implications of its changes. Movements also play a key role. A peculiar behavior is the one by the guppy *Poecilia reticolata* during courtship. Some movements and actions of the male are followed by corresponding movements by the female and again by the male in a sort of “chained response”. To verify the existence of a relationship between the different movements Noble (1958) anesthetized the female that therefore wasn’t anymore able to answer to the male’s movements. As a consequence the male interrupt is courtship display. This experiment is an example of the importance of the vision of a movement in order to obtain a proper response. As shown so far color and movements are important in determining the importance of visual skills and capabilities. Nonetheless also spatial visual stimuli are important, expecially for fish living in complex environments. Typical experiment to investigate for this are the ones involving mazes. Hughes & Blight (1999) studied the ability of the corking wrasse, *Symphodus melops*, in associating spatial visual stimuli to food source in a maze. This consisted of 4 arms in which alternatively food sources were placed. The color of the entrance of each arm was associated with the presence or absence of food. For each trial new food was added. Proceeding with the experiment the accuracy of the choices by the fish increased. This was because the individuals began to associate a given color to the presence of food, thus memorizing useful information to maximize foraging efficiency. In several behavioral situation, from courtship to foraging efficiency and mechanisms characterizing predator-prey interactions, vision results to be a sense of basic and fundamental importance that used in different species according to their lifestyles.

Who behaves more intelligently then others are those that have a better "understanding" of what there is and happens around them and how respond to that (Krebs & Davies, 1984). This capability has been generally associated with cognition, and in particular foraging skills, spatial skills and social intelligence.

For decades all these features were considered uniquely as a trait of primates. Their intelligence has been usually explained with their abilities in modifying and "using" the environment, their complex social structures, all consequences of their brain size. All of these are very human-like attitudes and behaviors, thus thought and considered as a trait of intelligence (Bshary, 2002).

However in the last years attention has grown on how intelligence and cognition are indeed more widespread and present in diverse and different species at several taxonomic levels. Fish as well have been recognized having this kind of skills and capabilities (Laland *et al.*, 2003; 2011).

Proofs, through observations of peculiar behavior, of fish cognition and intelligence are present in literature since the '50s. With the years however the awareness that these were the consequences of real cognitive skills have grown to the point of somehow comparing them to primate's one.

A typical example, given by Brown (2011), is tool using (van Lawick-Goodall, 1970). Beside the argument of what actually "tool use" is, it's clear how this practice is more common than previously thought, particularly in fish. This has been witnessed in several different species. Coyer (1995) in the western tropical Atlantic observed the yellowhead wrasse, *Halichoeres garnoti* using a terrigenous rock as an anvil. The wrasse smashed a scallop against it in order to break it into smaller pieces and feed on it. Within the same note the author mentions the tool-using behavior noted by Heiser (1981) for *Thalassoma lutescens* and other *Thalassoma* in the tropical Pacific. A similar behavior was recorded by Pasko (2010) for the sixbar wrasse, *Thalassoma hardwicke*. This fish was able to properly size, with a rock used as an anvil, food pellets too big to swallow into a food source it could feed from. Widening the span of this behavior, there’s also the observation made by Jones (2011) on the blackspot tuskfish, *Choerodon schoenleii* in the Great Barrier Reef. The wrasse catches a shell in its jaws pounding it against the rock until opened. Thus the works of Brown and Bshary () and all the other examples given above clearly give firm proves of how widespread are developed cognitive skills in fish.

Cognitive skills are considered to be directly linked to the lifestyle of the individual, direct consequence itself of the complexity of the environment and the related “signals” it conveys (Laland *et al.*, 2011).

Natural systems are indeed characterized by numerous stimuli (chemical, visual, etc.). Aquatic systems are no exception with upper subtidal reef/rocky zones usually cumbersome, noisy, crowded, etc. thus to consider complex. Complexity can also be considered from different points of view. First of all, this areas are usually characterized by high densities and diversity. These belong to several different taxa at different trophic levels, thus creating a perfect scenario for an environment full of conspecifics, competitors, predators, preys, food source, that eventually lead to interactions of different kinds like social behaviors, predation, etc. All these “send” different cues/stimuli/information that need to be captured, processed and eventually responded to. So rocky subtidal can primarily be considered complex from an interactional (interaction) and biological point of view. Moreover this rocky areas are complex also from a “structural” (shape) point of view. Holes, crevasses, caves and cavities in general, big rocks and all the others typical structures of this area contribute in making it even more demanding/exacting/complicate to live in. All the features in fact can act like sensorial barriers, blocking or hiding visual and chemical stimuli that could be coming from a predator or a food source. Thus in general a plethora of information need to be processed. Species that are able to do it and develop behaviors toward proper adaptation and resource exploitment must be considered as characterized by high cognitive skills. In this zone, the families of fish that are probably the most adapted and thrives throughout the oceans are wrasses (Labridae) and triggerfish. Within fish realm, this families represents also one of the most promising family for the study of cognitive skills, in particular feeding ones (Bshary *et al.*, 2002). It is present in the majority of the basins of the earth and it’s characteristic of subtidal reef zones. Several examples exist of foraging skills for this family (Bshary *et al.*, 2002) usually concerning feeding techniques on sea urchins. One of the most interesting example of advanced feeding technique is probably the one observed in the blue triggerfish *Pseudobalistes fuscus*. This species has developed peculiar skills in order to feed on sea urchin and other invertebrates. Once it finds out possible preys is able to move and remove obstacle that are in way. This also demonstrates deeply developed spatial intelligence (Fricke, 1975b). Bshary *et al.* (2002), reporting on Fricke (1971) observation, explains how in Eilat five different individuals of *Balistapus undulatus* were able to hunt on sea urchin breaking its spines. Once this first attack was completed they were able to catch them and bring them closer to the surface. Here they began to feed on the oral, unprotected, side of the urchin, while it was slowly falling to the bottom. The same author refers also of individuals of the same species blowing water stream under the urchins thus they would detach and turn upside down becoming in this way available as preys.

Labrids represent another family of marine fish with highly developed cognitive and feeding skills, as seen earlier on “tool-like” behavior. These skills can also be recognized in relation to sea urchin predation. When a sea urchin is too big to be entirely swallowed, but small enough to be held in the mouth, individuals of *Coris julis* and *Thalassoma pavo* are able to carry it toward a rock, smash and open it against it and subsequently feed (Sala, 1997).

In the Mediterranean Sea the most abundant and widespread species of wrasses is the ornate wrasse, *Thalassoma pavo*. This species makes no differences in terms of cognitive, foraging and spatial skills and it has been witnessed foraging on sea urchins using developed feeding skills as manipulation and anvil-like behaviors. As explained in the first experiment reported on this thesis, this species takes part to an indirect interaction that involves the wrasse performing a peculiar feeding behavior. With that in mind I wanted to understand what aspect of the interaction was the one that triggered the behavior in *T. pavo*. Precisely the idea was to understand what the fish could recognize of the interaction between the starfish and the sea urchin and then trigger the feeding behavior. Understanding this would also lead to a better understanding of how *T. pavo* is well adapted in such a demanding area like the upper rocky subtidal. I decided to deepen the knowledge on its behavior considering that the ornate wrasse is a key species both ecologically for the Mediterranean environment and biologically and behaviorally for cognitive studies in general.

I studied how *T. pavo* orientates in the upper subtidal environment in the "Ustica Island" Marine Protected Area (MPA - NW Mediterranean). Here scuba divers and tourist in general, break sea urchins in order to feed and attract fishes during recreational dives. *T. pavo* seems to have learned and recognized this behavior always promptly responding to it. In order to test for the different cues involved and understand which one is the driving force of the response, I "divided" the stimulus known by *T. pavo* (i.e. breaking of a sea urchin by a diver) into its components as follows: acoustic, chemical, visual and their interactions (acoustic and chemical; chemical and visual; acoustic and chemical and visual). We presented them to the fish in the field and counted the number of individuals approaching to each trial.

In my opinion *T. pavo* could represent a perfect model, worth studying, for investigating cognitive skills, behavior and intelligence in fish for the Mediterranean. Even more, being a thermophilic species, *T. pavo*, is spreading northward and increasing in density in the southern areas becoming one of the most present species of the basin. It is thus mandatory to start properly to investigate and understand its biology and behavior.

3.2 Materials and Methods

STUDY AREA

The experiment was conducted in the “Ustica Island” Marine Protected Area (MPA), situated 67 km off the northern coast of Sicily in the Northwestern Mediterranean. Precisely, the study area consisted of the whole south zone (coordinates) where *Thalassoma pavo* is widely present and abundant. Here *T. pavo* responding behavior to the breaking of sea urchins by divers has been often observed. We arbitrarily divided this area in the two sites used for the manipulative experiment (Site 1: point to point coordinates; Site 2: point to point coordinates).

PRE-SURVEY. DENSITY OF *THALASSOMA PAVO*

In order to test for differences in distribution of *T. pavo* within the two experimental sites, we proceeded with the measurement of the density within the two sites. Density were measured randomly through linear transects (25x5m) parallel to the coast. A depth range between 1 and 5 meters (same depth range of the experiments and “most suitable” habitat for *T. pavo* in Ustica; see section below) have been chosen. Individuals were divided into three categories, Large (L), Medium (M) and Small (S) (sizes…).

MANIPULATIVE EXPERIMENT. RESPONSE TO STIMULI

Eight different stimuli were presented:

1) ALL (a scuba diver in the act of breaking a sea urchin)
2) Acoustic Stimulus (A)
3) Visual Stimulus (V)
4) Chemical Stimulus (C)
5) A + V Stimulus
6) V + C Stimulus
7) A + C Stimulus
8) A + C + V Stimulus

All the stimuli were presented by the scuba divers in a depth range between 1 and 5 meters. When the stimulus was deployed the operator would count the number of individuals that immediately approached in response to the stimulus.

From a preliminary survey we calculated that two minutes are enough for *T. pavo* individuals to lose interest in new objects or divers (not moving or performing particular behaviors). Thus before every treatment the operator waited an average of two minutes before presenting the stimulus.

The combination of stimuli (A + V; V + C; A + C; A + C + V) consisted of two or more stimuli presented simultaneously.

Every stimulus or combination of stimuli lasted an average of 10-15 seconds (*i.e.*, the equivalent time needed to break open a sea urchin).

All. This treatment consisted on the actual breaking of a sea urchin with a knife by a scuba diver.

Acoustic stimulus. The acoustic stimulus consisted on the reproduction of an audio file. The audio file has been previously recorded underwater with the sound of the breaking of a sea urchin with a knife. The whole emitting apparatus consisted of an underwater loudspeaker, placed on the reef, a transformer, the battery pack and a mp3 player. These last two were placed on the boat. One operator was needed underwater to deploy the loudspeaker and count the number of *T. pavo*. A second one on the boat would instead play the file once received a signal from the scuba diver (*i.e.* a red buoy released from underwater). The scuba diver, after placing the loudspeaker reached a distance far enough to be able to count the individuals but not to interfere with the experiment.

For this treatment we arranged two controls. One was needed to verify any “physical/mechanical” attraction caused by the loudspeaker. To test for this case we left the object on the bottom turned off (no sound emission) for the same amount of time of the audio file. The other one was needed to verify if any generic sound would have attracted the animals instead of the specific sound of the breaking of a sea urchin. In this case, using the same set up of the normal treatment, we instead played a generic swipe signal (frequency between 100 and 10000 KHz, audible by fish).

Visual stimulus. Once on the bottom the scuba diver simulated, holding only a knife, the breaking of a sea urchin. We considered the presence of a scuba diver not moving as the control for this treatment.

Chemical stimulus. This treatment consisted of the deployment, through a syringe, of a mixture containing all the parts of a sea urchin previously broken in a bowl with seawater. At the far end/tip of the syringe was attached a soft plastic tube (about 2 meters long) with a weight on the end in order to have it as much as flat on the bottom as possible. This allowed the scuba diver to be far enough to not interfere with the experiment but be able to see and count the individuals responding to the stimulus.

Also in this case we arranged two controls. For the first one an empty syringe (with the whole apparatus) was left on the bottom, in order to test for any physical attractiveness of the syringe itself. Instead for testing any bias caused by the color of the guts and other parts of the urchins, a mixture, equal in color and consistence to the one of the urchins, was deployed.

A + V, ***V + C***, ***A + C*** and ***A + C + V*** stimuli were deployed simultaneously as a sum of the previous methodology.

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSIS.

Density. We designed a 2-way Anova. The two factors were Size, fixed, with three levels (Small, Medium and Large) and Site, random, with two levels (Site 1 and Site 2). 18 replicates in two dates have been performed for a total of 72 measures in the two sites during July 2010.

Data have been analyzed with the GMAV 5 Software. To verify the homogeneity of the variance a Cochran’s Test was run and data have been Sqrt(X+1) transformed. An a posteriori test (SNK – Student-Newman-Keuls) was used to confront averages.

Manipulative experiment. We designed a 3-way Anova analysis. The three factors were: (1) Stimulus, fixed with eight levels; (2) Size, fixed and nested with three levels; (3) Site, random and nested with two levels.

The eight levels of the factor Stimulus were: All, Acoustic, Visual, Chemical, U + V, V + C, U + C, U + C + V. Size levels were: Small, Medium and Large. Site levels were Site 1 and Site 2.

The variable used was the number of *Thalassoma pavo* individuals of the different sizes that approached within few second (immediate response) the stimulus presented.

Three replicates for each level of the factor Stimulus have been run per each site with a total of 48 measures. Data were collected all in similar weather and current conditions between July and September 2010.

Data have been analyzed with the GMAV 5 Sotware with “significatività” at P=0.05. To verify the homogeneity of the variance a Cochran's Test was run. An a-posteriori test (SNK - Student-Newman-Keuls) was used to confront averages. Data have been ln transformed.

3.3 Results

PRE-SURVEY. DENSITY OF *THALASSOMA PAVO*

No significant difference resulted from the analysis of variance of the density between the two sites (Table 1).

Table 3 Results for the Anova analysis for density data. No significant difference within sites or within the interaction Size-Site.

Source	SS	DF	MS	F	P	F versus
Size	145.1462	2	72.5731	106.12	0.0093	SizeXSite
Site	0.0362	1	0.0362	0.06	0.8045	RES
SizeXSite	1.3677	2	0.6839	1.16	0.3155	RES
RES	123.7915	210	0.5895			
TOT	270.3416	215				

The individuals in the southern area of the island result divided in sizes as follows: 50% Medium, 42% Small, 8% Large (Fig.7).

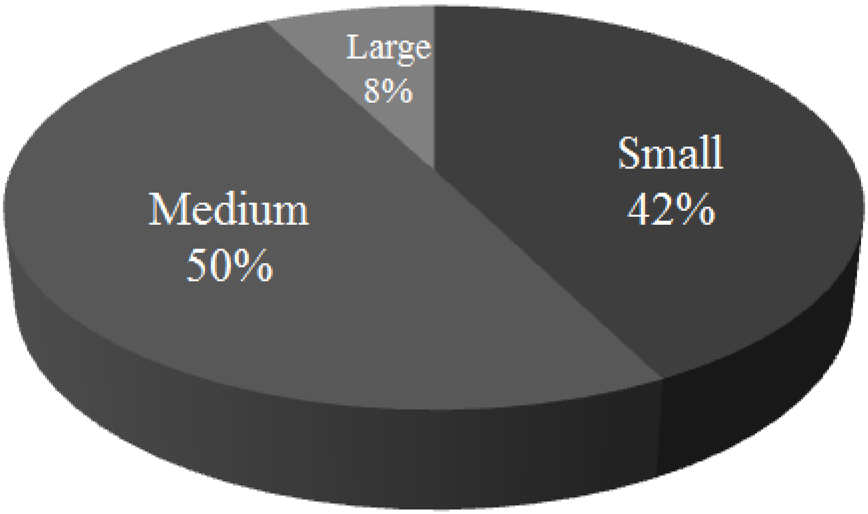

Fig. 7 Percentage of Small, Medium and Large individuals of *Thalassoma pavo* in the southern zone of the Ustica MPA.

MANIPULATIVE EXPERIMENT. RESPONSE TO STIMULI.

Significant differences have been found in the interaction StimulusXSize (Table 2). All controls showed a non-significant number of individuals approaching the stimuli.

Table 4 3-way Anova analysis results for the experiment on the response of *Thalassoma pavo* to external stimuli.

Source	SS	DF	MS	F	P	F versus
Stimulus	39.0605	7	5.5801	22.3	0.0003	StimulusXSite
Size	18.1852	2	9.0926	123.48	0.008	SizeXSite
Site	0.1225	1	0.1225	0.61	0.4381	RES
StimulusXSize	10.7239	14	0.766	4.24	0.0054	StimulusXSizeXSite
StimulusXSite	1.7514	7	0.2502	1.24	0.2895	RES
SizeXSite	0.1473	2	0.0736	0.36	0.6955	RES
StimulusXSizeXSite	2.5315	14	0.1808	0.9	0.5665	RES
RES	19.3935	96	0.202			
TOT	91.9158	143				

In the Small individuals the SNK analysis showed significant differences between all the stimuli that presented the visual component and the ones that didn’t (Fig. 8). These last resulted definitely less attractive than the others (P<0.05). The highest number of individuals was attracted by the C + V stimulus (7.33 ± 1.63 st. dev.), while the least one was the C stimulus (0 ± 0 st. dev.).

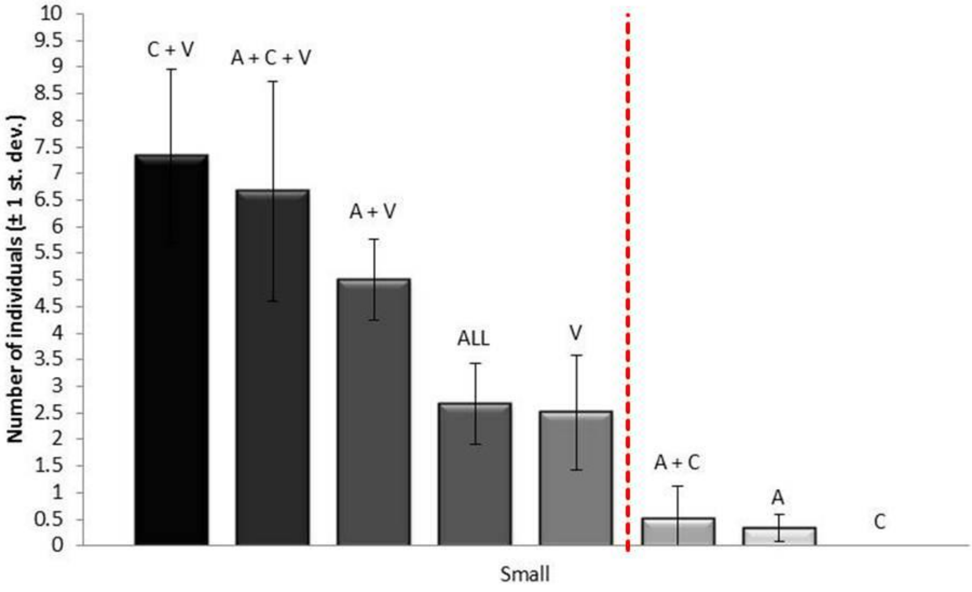

Fig. 8 Number of Small individuals responding to all the different stimuli (± 1 standard deviation). (C + V =7.33 ± 1.63; A + C + V =6.66 ± 2.06; A + V =5 ± 1.2; ALL = 2.66 ± 0.75; V =2.5 ± 1; A + C =0.5 ± 0.6; A =0.33 ± 0.25; C = 0 ± 0)

The same situation resulted from the SNK analysis of the Medium sized individuals. High significant difference exist again between stimuli with the visual component and the ones without it (P<<0.05) (Fig.9).

The highest number of individuals was attracted by the ALL stimulus (6.16 ± 1.59 st. dev.), while the least one was the C stimulus (0.5 ± 0.41 st. dev.).

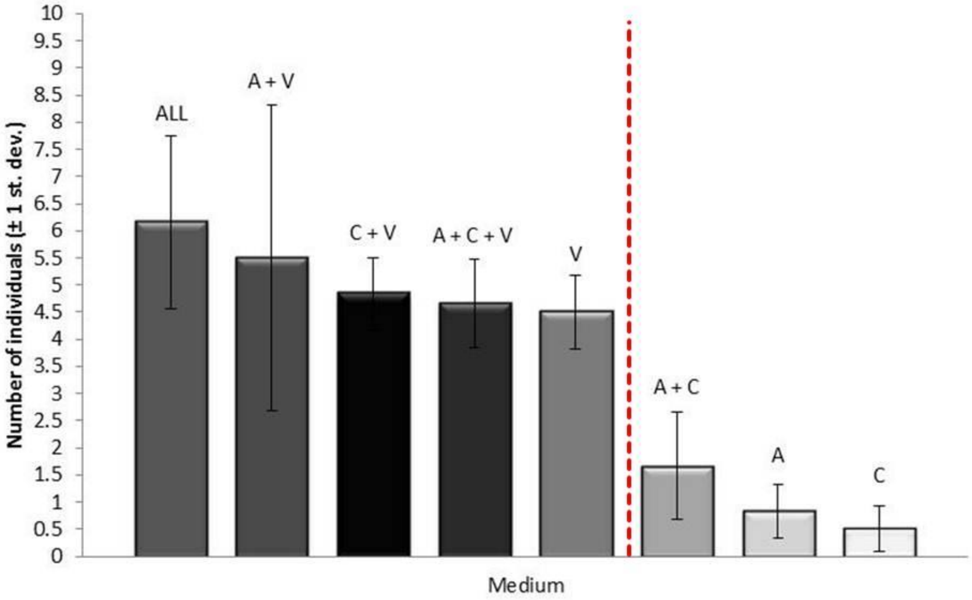

Fig. 9 Number of Medium individuals responding to all the different stimuli (± 1 standard deviation). (ALL =6.16 ± 1.59; A + V =5.5 ± 2.8; C + V =4.8 ± 0.66; A + C + V =4.6 ± 0.8; V =4.5 ± 0.68; A + C =1.66 ± 0.98; A =0.88 ± 0.49; C =0.5 ± 0.41)

For the Large individuals instead no significant differences exist between stimuli (Fig.10).

The highest number of individuals was attracted by the C + V stimulus (1.83 ± 0.8 st. dev.), while the least one was the C stimulus (0.16 ± 0.2 st. dev.).

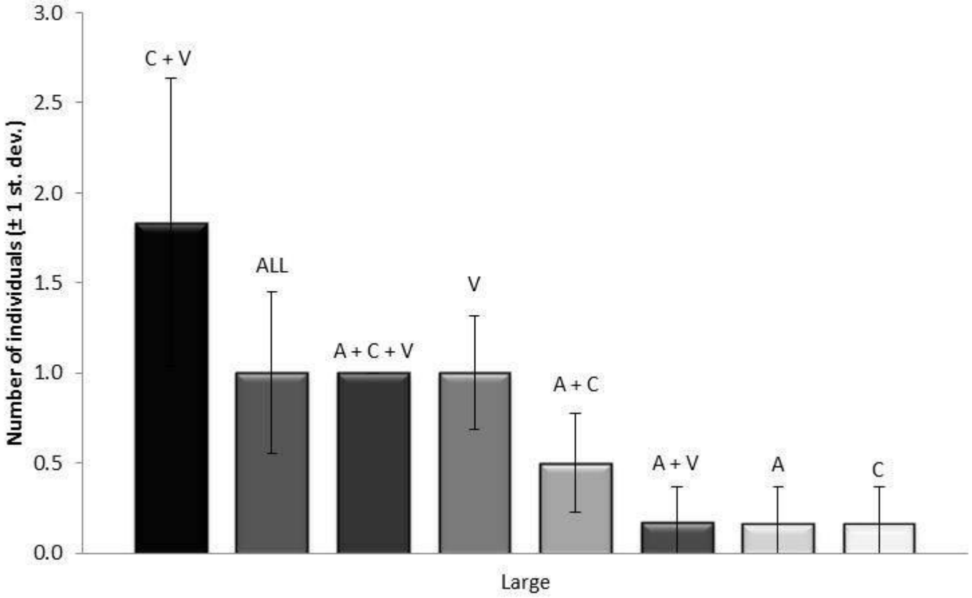

Fig. 10 Number of Large individuals responding to all the different stimuli (± 1 standard deviation). (C + V =1.83 ± 0.8; ALL =1 ± 0.44; A + C + V =1 ± 0; V =1 ± 0.31; A + C =0.5 ± 0.27; A + V =0.16 ± 0.2; A =0.16 ± 0.2;C =0.16 ± 0.2).

For Small and Medium sized individuals all the stimuli that present the visual component resulted significantly more attractive. There are no differences if this stimulus is presented alone or associated with others components.

3.4 Discussions

My experiment clearly demonstrated how *T. pavo* individuals respond and are more attracted to visual stimuli. According to our results their relying on visual inputs is so strong that we found no significant differences between the visual stimulus by itself and when it's presented in association with all the others (including the actual breaking of a sea urchin). Every individual acquires information from the environment it lives in. This can be done through different channels according to the senses used and the cues present. Despite what I found in this experiment, a lot of times cues can work additively allowing a better "understanding" of the overall information and eventually lead to a stronger response (both positive or negative, e.g. food source or predator) (Ward & Menher, 2010). McCormick & Manassa (2008) demonstrated how the antipredator response of *Asterropteryx semipunctatus* to alarm cues was stronger when chemicals and visual ones were presented together. Similar results has been obtained by Mikheev *et al.* (2006), *Perca fluvialis*, and Smith & Belk (2001), mosquitofish, with individuals relying on a multiple sensory modality in an additive way for antipredator behavior. Similar with what we found are instead the results obtained by Utne-Palm (2001) for the *Gobiusculus flavescens*. In this case visual stimuli where much stronger then odour ones in escaping from predator cues. Hughes & Blight (2000) found as well a leading role of visual stimuli in the reef fish corkwing wrasse, *Crenilabrus melops*, in finding food source. Our result, with such a strong importance of visual stimuli, can be considered to be directly linked to the kind of environment *T. pavo* lives in. Low depth subtidal waters are in fact characterized by high visibility, intense solar radiation and bright colors. It has been demonstrated how visual communication mediates several behaviors for reef fish (and wrasses in particular) that live in this type of environment. Also well-known is the role played by colors, of both environment and fish, and their recognition. This has been demonstrated in terms of the importance of contrast between individuals and surroundings, within intra and inter specific interactions and understanding the capability of fish to discriminate between colors and shapes. All this creates a pretty clear scenario that underlines the importance of vision for reef fish. Wrasses make no difference and also for this family there are studies that investigate and demonstrate the importance of vision. An experiment on several species of wrasses (*T. duperrey*, *T. lunare*, etc.) showed how they rely on their colors and how colors are important in "distinguishing" from the environment, for cleaning behavior and the key role played by spectral sensitivity and visual communication in wrasses communities. According to

Siebeck & Marshall (2000) wrasses visual system is also related to the high variability of their behaviors. *T. pavo* is a sequential hermaphrodite (protogyny). Associated with sexual inversion is an evident change in colors, giving another hint and underlying the importance of colors, and vision in general, for this species.

The total absence of an additive effect and a minimal importance of the all the sensorial channels for this species, beside vision, may be due to several reason.

Our experiment was designed not to understand the general orientation capabilities/characteristics of this species but what would drive/trigger (few seconds) a sudden response/behavior/interest. With this perspective is easy to understand why, first of all, chemical cues didn't turn out to be so important. Chemical stimuli can be considered has a firm proof of the presence of something nearby (e.g., food source, predator, conspecific, etc.). Works by Zimmer-Faust *et al.* (2006), on lobster and crab, and McCormick & Larson (2007), with coral reef fish, demonstrated how both for predators, the former, and for preys, the latter, chemical cues drive behaviors. However chemicals propagating in the water can be considered a "slow" messenger of information. Individuals far from the source of stimuli would acknowledge its presence, in absence of a strong current, after a certain amount of time. Our results are a clear example of this scenario. Once the chemical stimulus spread far enough, a consistent number of individuals then approached the area of the trial in a sort of feeding frenzy.

Secondly, the southern area of the Ustica island can be considered "noisy". Sound production and hearing are well developed in various reef species, used for different tasks at different life stages (Popper & Fay, 2011). For example Maruska *et al.* (2007) investigated sound production in sergeant damselfish during social interactions. They found both context depended sounds and hearing abilities that match the frequency characteristics. Simpson *et al.* (2004, 2005) demonstrated attraction to reef sound by settlement stage coral reef fish and how noisy patch reef attract more settler then silent ones. Mann *et al.* (2007), on their note on larval fish and sound attraction, reports the hypothesis that fishes are able to listen for sounds indicating the location of coral reefs and then swim towards them for settlement (Tolimieri *et al.*, 2000, 2004; Higgs, 2005; Simpson *et al.*, 2005a). Also juvenile stages reef fish (Simpson *et al.*, 2008) use sound for orientation in order to migrate and locate to new habitat. As for wrasses, Boyle & Cox (2009) found and examined the use of courtship sound to attract mates in *Thalassoma duperrey*. Thus, based on all these works, we can speculate that *T. pavo* individuals present developed hearing capabilities but that the noisy conditions of the environment of the southern area of Ustica changed their hearing habits. In this area it’s actually placed the port with the ferry service to and from the mainland. The majority of diving sites are present on this side of the island with a consequent heavy traffic of divers rafts and boats, especially in the summer months (july-september, like the time span of our trials). All the small and medium fishermen insist in this same area with their fishing activities. All this situation might have brought this population to not rely so much on sounds as we could have expected. Obviously this is only a speculation and to confirm this hypothesis a replica in another area is needed. Particularly interesting is the difference in results between Small/Medium individuals and Large ones. This finding likely reflect the differences in terms of behavior between large males and the others. These large individuals spend a lot of energy and time patrolling their territory especially for mating purposes (Sara *et al.*, 2005). Is very common to see them chasing away smaller individuals from, for example, food source. The absence of significant differences and the low number of large individuals can thus be related to, first of all, the low density of large individual and, secondly, the fact that they might not “follow” random or “not sure” stimuli being more experienced and less naïve individuals.

Our experiment is one of the few steps made towards a deeper knowledge of one of the behaviorally and cognitively most interesting fish species in the Mediterranean. Only few other works have been done on *T. pavo*, investigating mating behavior (Sara *et al.*, 2005) and distribution (Guidetti *et al.*, 2002).

Our findings can lead the way toward other interesting discovery. It would be key, for example, to confirm a real adaptation of this species to the noisy environment characteristics of southern Ustica. More in general, the focus could be on understanding how our findings relate to other tasks this fish has to deal with (predators, conspecifics, prey, mating, etc.). A plethora of behavior and cognitive skills has still to be discovered, understood and then investigated. The ornate wrasse can represent a perfect model for behavioral and cognition studies like ours, even more now that the species is spreading northward in the basin due to increasing temperature (Guidetti, etc.). High densities of this species make it also easy to find and use it for experiment both in lab and on the field.

Considering also the ecological implications that behaviors by high cognitive skilled species can have (Coyer, 1995) we find that the big lack of information on *Thalassoma pavo* must be slowly filled with works like the one I began with part of my PhD thesis.

4 MULTIPLE PREDATOR EFFECTS. INVESTIGATING LOBSTERS INTERACTION WHILE PREDATING ON SEA URCHIN

4.1 Introduction

According to Soluk & Collins (1988) there are three types of interactions between predators in case of additive interactions: neutral (where predators do not affect one another’s rates of prey consumption), negative (prey consumption is less than neutral values; risk reduction), and positive (prey consumption is greater than neutral values; risk enhancement). However in case of facilitation or interference the interactions might also be non-additive. Removal of predatory species would then affect the overall outcome of predator-prey interactions thus the effects on preys population. Risk reduction generally occurs when a) there are negative interactions between predators, b) occur changes in prey microhabitats or c) preys have behavior in response to one or both the predators. Vance-Chalcraft & Soluk (2005) investigated and considered the effect of prey density within the multiple predators effect and risk reduction scenario. They studied hellgrammites (*Corydalus cornutus*), greenside darters (*Etheostoma blennioides*) and creek chub (*Semotilus atromaculatus*) preying on mayfly larvae and other benthic invertebrates. They found out risk reduction at all levels of prey density, proving the presence of trait mediated interactions, probably caused by predators interferences, thus apparently with no effect of prey density. Sometimes however is the design of the experiment that might alter the outcome of an interaction. Carey & Wahl (2010) experiment on largemouth bass (*Micropterus salmoides*) and muskellunge (*Esox maaquinongy*) preying upon bluegill sunfish (*Lepomis macrochirus*) showed how the result of the multiple predators interaction depended on the experimental design. More precisely, a risk-reducing effect was found with the additive experimental design while a risk-enhancing one arose from the substitution design. Additive and substitution designs are used to investigate multiple predator interactions when there are different species of predators. In the additive design, individual predator densities are kept equal in both single-species and multiple-species treatments (Goldberg & Scheiner, 1993). In the substitution design predators are held constant across multiple predator treatments (Griffen, 2006). Usually substitutive design is used to prove the hypothesis of predator species being in some degree substitutable on to another (Sokol-Hessner & Scmitz, 2002). Sometimes can also be the habitat that produces different outcomes with the same species involved. Siddon & Witman (2004) studied crab (*Cancer borealis*) predation on the sea urchin *Strongylocentrotus droebachiensis* while interacting with the other predator, the lobster *Homarus americanus* in three different habitats: *Codium fragile* algal beds, barren and mussel beds. Results showed a significant risk reduction occurred for urchin in *Codium* and barren habitats when the two predators where simultaneously present. No difference instead where found for mussel habitat. According to the authors, this can be considered a case of predator-predator interference and intraguild predation (Polis & Holt, 1992; Sih *et al.*, 1998; Griffen & Byers, 2006). When instead an anti-predator behavior caused by the presence, or the active predation, of a predator provokes a higher exposure to a functionally diverse one (slightly similar to my first case of study involving *M. glacialis, T. pavo, P. lividus* and *A. lixula*) the usual outcome is risk enhancement. Van Son & Thiel (2006) studied the effect of the interaction between the nemertean *Amphiporus nelsoni*, the shrimp, *Betaeus truncates* and the juveniles of a fish, *Girella laevifrons,* (all with different foraging mode), preying upon the amphipod *Hyale marourbe*. Strong risk enhancement was found in the treatments where shrimps and fish predators preyed simultaneously upon the amphipods.

Consumption rates might also vary in a non-additive way in the case of multiple prey species sharing the same predator. This leads to a risk enhancement scenario when agonistic interactions are performed between those prey species (Toscano *et al.*, 2000). As stated by Griffen (2006; reporting Beddington, 1975 and Hassel, 1978) non-additive predation can also occur when multiple predators of the same species forage together. My case of study follows on this path.

Precisely, I used as experimental model the interactions between individuals of the European spiny lobster *Palinurus elephas*, interacting as predators of the sea urchin *Paracentrotus lividus* setting up a preliminary investigation on these species.

Predatory capabilities of lobsters (Langlois *et al.*, 2006) and their effect in controlling urchins populations are known and have been studied (Tegner & Dayton, 1981; Haley et al., 2011). Predation of lobsters on sea urchins have been studied and demonstrated for several species and in different habitats. Hagen & Mann (1992) investigated the rate of predation of the American lobster (*Homarus americanus*) on the sea urchin *Strongylocentrotus droebachiensis* at different prey densities, sizes and other treatments. Predation on sea urchin was recorded and the lobster showed functional response to increasing urchins abundances as the number of successful attacks increased with increasing densities. A similar work by Pederson & Johnson (2006) showed how the rock lobster *Jasus edwardsii* was the most important predator of the sea urchin *Heliocidaris erythrogramma* in a no-take zone of a Tasmanian Marine Protected Area. Examples of the importance of lobster in predating sea urchins and consequentially controlling their populations also exist within the *Palinuridae* family. Lafferty (2004) demonstrated how the controlling effect operated through predation by the spiny lobster, *Panulirus interruptus* on the sea urchin *Strongylocentrotus purpuratus* populations, prevented from the spreading of diseases and enhance mortality in these populations. Tegner & Levin (1983) in their work on predation and prey choice by the spiny lobster *Panuliris interruptus* on the sea urchins *Strngylocentrotus franciscanus* and *Strongylocentrotus purpuratus* give one of the first description of the feeding technique of the lobsters on sea urchins. The authors demonstrated how small lobsters (juveniles) were able to handle only small-sized urchins, medium-sized lobsters handled only medium urchins while large lobsters had the capability of handling all size of sea urchins. Furthermore they discovered that small urchins were eaten as a whole and with increasing size of urchin larger amount of test was left unconsumed. Methods of consumption changed following urchin sizes. These vary from test fractured into pieces, to removal of spines, peristomial membrane and oral opening widen, and peristomial membrane removed but spines and test untouched. Examples of consumption and handling are given by the authors. They explain how the lobster would put the urchin “directly into its mandibles” with the “initial bite out of a lateral surface with the entire urchin subsequently consumed”. For a slightly larger prey the attack was through the peristomial membrane. Walking legs and third pair of maxillipeds were used to pass the soft tissue of the urchin to the lobster’s mandibles. A clear evidence that lobsters of the *Palinuridae* family are strong and active predators of sea urchins is also given by the presence of non-consumptive predator effects. Lobsters can effectively elicit antipredator behavior on sea urchins just because of their presence (Matassa, 2010). Sea urchin *Strongylocentrotus purpuratus* reduces grazing as a response to risk cues of the spiny lobster *Panulirus interruptus* while not such effect was recorded in the presence of damaged conspecific cues. Similar results have been obtained by Green (2012) with *Panulirus interruptus* and *Strongylocentrotus purpuratus*. In this case the author found also a correlation with the presence of a refuge in urchins grazing behavior, underlying once more the predatory role played by the lobster.

For the European spiny lobster *P. elephas* and the urchin *P. lividus*, to my knowledge, there are not empirical evidence on lobsters preying abilities. Sala *et al.*, (1998) on their review on trophic cascades, reporting the works of Vasserot (1964) and Campillo & Amadei (1978), place *P. elephas* as predators of the urchins *A. lixula* and *P. lividus*. However they state that these species "have almost non-overlapping distributions, with the sea urchins inhabiting shallower waters and lobsters inhabiting deeper communities. Furthermore, predation by lobsters on sea urchins has never been observed in the field". Similarly Guidetti (2004) enlists *P. elephas* as a possible crustacean predator of *P. lividus* although he stressed once more the difference of depth distribution between the two species and focused on fishes as principal urchin consumers. However, Goñi *et al.* (2001) studying the diet of *P. elephas* (size range between 45-167mm) in the Columbretes Islands Marine Reserve (north-western Mediterranean) found that echinoids were an important prey item throughout the whole live cycle of lobsters. Thus *P. elephas* can be considered as a natural predator of sea urchins.

Lobsters are known to live periods of their life cycle together with conspecific, especially juvenile and sub-adults. Thus interactive behaviors, both positive and negative, among these animals exist and in some species some of those have been studied. Cooperative behaviors in palinurids are known to exist in association with antipredator ones. Dolan & Butler (2006) investigated the causes of aggregation and den sharing in juvenile Caribbean spiny lobster *Panulirus argus*. They tried to understand if the main reasons for social behavior was group benefit or a side effect of guide effect (i.e. the mechanism by which shelter is found). The model developed by the authors suggested that the guide effect alone was inadequate to explain social aggregation. This implies reciprocal attraction between lobsters individuals of this species. A step forward to better understand aggregation and den sharing in lobster was made by Briones-Fourzán & Lozano-Álvarez (2008) adding also *Panulirus guttulatus* as study species. The experiments showed how this last species was more willing to aggregate and how this behavior changed in both species in correlation to size. "Aggregation confers more than one antipredator benefit, which may further differ between reef zones" (Briones-Fourzán & Lozano-Álvarez, 2008).

Collective defense in palinurids is well known and encompasses several behaviors (queuing, resting, radial formation) (Herrnkind *et al.*, 2001). One of the more distinctive characteristic of lobsters individuals consist in "assembling" into a rosette-like formation where all the individuals are in contact and face outward toward the predator (Lavalli & Herrnkind, 2009). Buscaino *et al.*, (2011) studied the predator-prey interactions between the European spiny lobster *P. elephas* and its predators *Octopus vulgaris* and *Conger conger*. Although the authors underlined, also in this case, the importance of assembling and proximity among lobsters, no precise reference was made to the phalanx-like formation or any similar grouping formation or cooperative defense strategy. To my knowledge there are no evidence of cooperative or facilitative behavior among individuals of *P. elephas*.

Interactions between lobsters, and crustacean in general, can also be negative and aggressive (Kravitz & Huber, 2003). Shelters are very important in the life of lobster. However sheltering does not solely elicit cooperative defensive behaviors. For example, defending and entering the den can be the cause for aggressive interactions (Bushman & Atema, 1994). An example of aggressive behavior in crustacean within conspecifics is given by Ayres-Peres *et al.*, (2011). The authors studied *Aegla longirostri* giving the precise description of the acts involved in the aggressive behavior like the strong use of antennae and chelipeds. Combats were an escalation, they began with simple approach and reached touching and holding the opponent. Crayfishes among crustacean are well known as aggressive animals. An indirect strong evidence of their aggressive nature is given by the presence of ritualized behaviors for submission. These have the aim of avoiding the aggressive displays and the eventual consequent interactions that can lead to armful contacts. Usually these behaviors consist of pseudocopulatory behaviors toward both females and males (Issa & Edwards, 2006). Aggression is a consistent part of the life of crayfishes and the outcome of these encounters can change because of various aspects, like isolation (Hemsworth *et al.*, 2007). A key role in individual recognition and thus regulating behaviors and aggressive encounters might be vision (Gherardi *et al.*, 2010).

An example of aggressive behavior within palinurids is reported by Shabani *et al.*, (2009) for the Caribbean spiny lobster *Panulirus argus*. This species uses two types of agonistic behavior (urine-born chemical signaling and physical aggressive behavior) to influence the behavior and social status of the eventual subordinate animal.

To my knowledge again there are no information nor studies regarding *P.elephas* and its interaction among conspecific.

A growing concern exists about multiple predators interactions and the unexpected effects they can have on preys populations, cascading down and affecting the whole community level (Soluk & Collins, 1988; Krupa & Sih, 1998; Griffen, 2006). The idea that the presence of more than one predator, of different or same species, can change the predicted outcome of an interaction obviously complicates the situation, but it is necessary to include behavioral interaction in order to properly predict the effects of predators on prey populations (Soluk, 1993).

With the idea of adding a new example for this subject in the Mediterranean, the main objective of my experiment was make a first step in assessing which kind of interspecific interaction sub-adult individual of *P. elephas* would have during predation on the sea urchin *P. lividus*.

Precedent personal observations seemed to show cooperation among young lobsters in capturing and handling adult *P. lividus*. Thus, the main hypothesis was that sub-adult *P. elephas* would cooperate in presence of adult *P. lividus*. Because no prior straightforward knowledge existed about predation of *P. elephas* (especially sub-adult individuals) on *P. lividus*, the first step was to preliminary investigate, characterize and somehow quantify this interaction. More precisely, the objective was to find which was the largest size of *P. lividus* that a single sub-adult *P. elephas* was able to handle and consume. Once found the maximum size, the second objective of the experiment was to understand if coupled individuals of sub-adult *P. elephas* were able to consume the size not consumed in the previous experiment. The third goal was to make a first step and start exploring with preliminary investigations the predator behavior of both single and coupled lobster against urchin and the interaction among predators.

4.2 Materials and Methods

SPECIES

Palinurus elephas. The European spiny lobster *Palinurus Elephas* is a decapod crustacean of the *Malacostraca* class. Is the most abundant and accessible lobster species and had traditionally been the preferred target of fisheries in Ireland, UK, France, Italy, Spain, Portugal, Greece, Tunisia, Morocco and in general in the adjacent waters of the Mediterranean (Goñi & Latrouite, 2005).

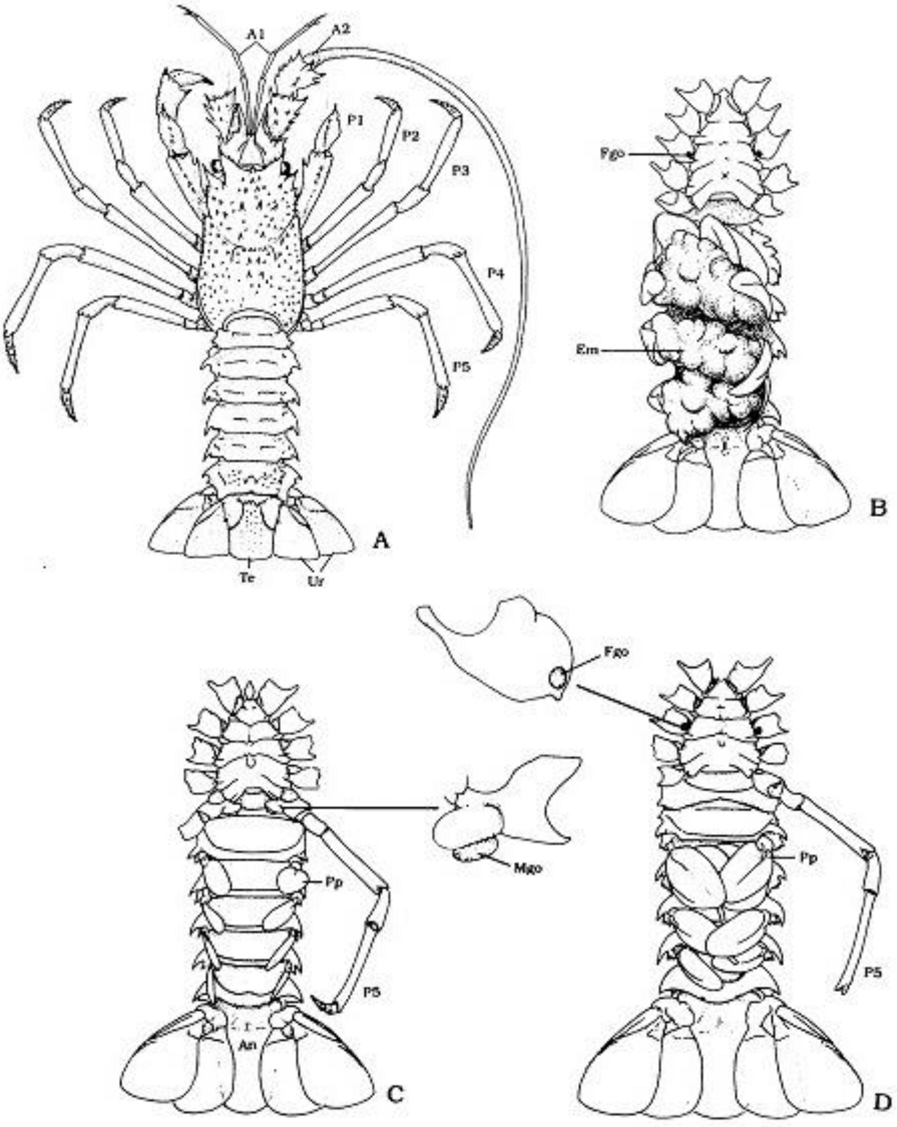

Fig. 11 External morphology of adult *Palinurus elephas*. A, dorsal view; B, female carrying eggs, ventral view; C, male, ventral view; D, female, ventral view. A_1, antennule; A_2, antenna; An, anus; Em, egg mass; Fgo, female genital opening; Mgo, male genital opening; P_1-P_5, pereiopods 1-5; Pp, pleopod; Te, telson; Ur, uropod.

The body of the lobster is divided 19-20 segmnents. Cephalon (head) has two, with sensorial and feeding purpose. Pereion (thorax) has eight, used for movement. Pleon (abdomen) with six and contains guts and is used to swim. Finally the Telson that is the postanal segment of the pleon. Head and thorax form an unique region called cephalothorax. The cephalon is not recognizable from the pereion because from its posterior margin departs a calcified plate, the Carapace, that covers the whole thorax and sides of the pereion. The head has an even number of appendix that are distinguished in antennules, longer and thicker, and antennas, that are movable structures that are used as sensorial organs to capture signals from the environment. There are then the Mandibles, used to chew and grind food, and the I and II Jaws used for manipulation that all together form the buccal appendices. The Pereiopods are appendices located within the eight segments that constitute the pereion. The first three pairs are called Maxellipeds and associated with the mouth while the two posteriors one have the gills. All the others have locomotory functions. The Pleopods are the appendices of the of the six segments present in the pleon while the telson is constituted of Uropodes that form the caudal fin used for swimming and eggs protection.

The majority of information on the biology and ecology of this species are reviewed in Goñi & Latroutte (2005) and in Hunter (1999) and are generated from studies and data of lobster fisheries. *Palinurus elephas* is not deeply studied because of its difficulties to catch and its high costs. The species is distributed in the Eastern Atlantic from Norway to Morocco and in the Mediterranean with the exception of the far eastern areas. It is also present in the Canaray Islands, Azores and probably Madeira Islands (Ceccaldi & Latrouite, 2000). The coloration is red and brown with a white underside but variations can occur. Typical of this species are also two large symmetrical white dots on the tergites of somites 1-5 with a single, centrally located dot, on the final segment. Two other symmetrical dots are present on the telson (Hunter, 1999). *P. elephas* lives between the shore and 200m of depth with the adults that live solitary, in pairs or small groups preferentially at the base of rock or boulders over gravel beds (Goñi & Latrouite, 2005). The late juveniles can be found over *Posidonia oceanica* meadows (Jimenez *et al.*, 1996; Marin, 1987) or in crevices (Mercer, 1973), that live at night for feeding purposes. *P. elephas* undertakes migrations before the reproduction period toward internal waters in spring while in late autumn, after reproduction, accomplish the opposite one (Mercer, 1973; Ansell & Robb, 1977; Goñi *et al.*, 2000; 2001b). This movement are also regulated by the availability of food and necessity of new shelters (Follesa, 2011). Studies have shown how the distances travelled are between 5 and 20km within a 1 to 8 years span (Hepper, 1967; 1970; Marin, 1987; Goñi *et al.*, 2001b). Preys of *P. elephas* are various and it is described as generalist opportunistic feeder that changes is food preferences according to benthic organisms availability. Generally feeds on mussels, echinoderms and other small crustaceans(Goñi & Latrouite, 2005). *P. elephas* undergo the moulting process, usually twice a year. However the number and the period of the moults change according to sex, age, distribution area, temperature and if inviduals are in captivity or in the field (Karlovac, 1965; Corral, 1968; Mercer, 1973; Marin, 1987; Cuccu, 1999; Cuccu *et al.*, 1999; Hunter, 1999; Goñi & Latrouite, 2005; Follesa, 2011). Mating of *P. elephas* has being described by Mercer (1973). Males are attracted by the stridulating sounds produced by females. Once they are spotted by the males, courtship begins. This consists of an initial contact with the antennas that proceeds with a more insisted and continuous rubbing of antennas and antennules. The final stimulus, that determines the actual mating, seems to be a reaction to a pheromones release by the female. At this point the male turns the female upside down, laying down two spermatophores below the gonophores. The external fecundation takes place when the female scratches and open the spermatophores with the fifth pair of pereiopod.

Total length of *P. elephas*, from the tip of the rostrum (in the head, between the eyes) to the posterior end of the telson is the usual length measures taken (Goñi & Lacrouite, 2005). More recently this measurement has been replaced by the distance between the tip of the rostrum and the posterior margin of the cephalothorax. Sexual maturity for female is reached around an average size of 76-77cm, while for male is 82.5cm (Goñi *et al.*, 2003a).

ORGANISM COLLECTION AND LABORATORY SETTING

All the individuals of *Palinurus elephas* were collected, by fisherman as by-catch, in two localities of the north-western Sicily, Isola delle Femmine (PA) and Castellammare del Golfo (TP). *Paracentrotus lividus* were instead collected in the Marine Protected Area of “Capo Gallo – Isola delle Femmine” by divers during scuba dives.

Individuals of both species were hosted, separately, in tanks of 225 liters of volume (90cmX50cmX50cm), equipped with filtration system, air pumps with air stones, refrigerator and shelters (for lobsters) at the University of Palermo’s laboratories. Salinity was constantly checked with a refractometer (Milwaukee Mod. MR100ATC) and kept around the Mediterranean average, 38‰-39‰. Temperature, set with the refrigerators, was around 18°C (or similar to the temperature of the water according to the period). Sea urchins were regularly fed on sea algae (mainly *Cystoseria spp*.) while lobsters were fed ad libitum on frozen mussels and shrimp (defrosted before using).

Lobsters were kept, after the catch, at least for ten days for acclimation. They were never used for the experiments if they were not active or fed actively and regularly. Before the experiment, they were not fed for four days and the last day they were kept in isolation in the experimental tank for acclimation.

The experimental tank was a bigger tank of 262 liters of volume (90cmX95cmX30cm), similarly equipped but without the shelters for the lobsters. This tank was dived into four compartments through bakelite panels. Three of those were used for the experiments while the fourth one was used to collect all the pipes and tubes of water and air pumps.

All the tanks walls were covered from the outside with plastic opaque panels. This was done to avoid stress for the animals and continuous interactions with the visitors of the lab.

Lobsters are known to be active nocturnal predators (Jones & Shulman, 2008). Thus we decided to perform our experiments in the twelve hours of night of the twelve hours day-night cycle of the laboratory. This also allowed us to completely avoid the problem of external interference from visitors of the lab during the experiments.

Camcorder (JVC EVERIO GZ -MG330) with internal hard drive of 30GB, were placed on tripods in front of the experimental tank, were connected to the power line and were left recording in continuum for the whole 12 hours of the experiment. In order to allow visibility for video analysis we placed a red light above the tank. This indeed permitted clear visibility during video analysis and its known to not cause alteration to lobsters behavior (Weiss *et al.*, 2006).

PREDATION OF LOBSTERS ON SEA URCHINS: MAX SIZE CONSUMED

In order to test for the maximum size consumed by lobsters I designed an experiment based on Silva *et al.* (2010a, 2010b). In each of the three sections of the experimental tank a lobster with three sea urchins was placed per trial. Each trial consisted of sea urchins of one singular size. Size classes were of 5mm each, from ≤10mm diameter up (Table 5). I choose the smallest size interval possible in order to obtain a more precise result.

Table 5 Size classes of *P. lividus* used for the experiment.

Class	Size (mm)
1	≤10
2	10.1-15
3	15.1-20
4	20.1-25
5	25.1-30
6	30.1-35
7	35.1-40
8	40.1-45
9	45.1-50
10	50.1-55
11	55.1-60
12	>60

A size class was considered consumed when at least one sea urchin was eaten by at least two different lobsters within the twelve hours of the experiment.

Since no previous knowledge exists, I wanted to make preliminary observations and description of the feeding and handling techniques used by the lobsters for feeding on sea urchin (*sensu* Tegner & Levin, 1983). For this purposes the experiments were recorded for further video analysis. Two of the three compartments were recorded per size trial. For the analysis of the feeding behavior of single lobster, two random size classes of consumed sea urchin were chosen (i.e. 2° and 4°) for further testing through video analysis. The videos from both compartments were analyzed thus obtaining two replicates for each of the above mentioned size.

Video Analysis with behaviors quantification were performed with the freeware software Etholog2.25© for transcription and timing of behavioral observation sessions (Ottoni, 2000). The observation focused on the first urchin to be consumed and ended at the completion of this first predatory event (obviously only trials with the consumption of urchins were considered). Behaviors were divided into Events (i.e. number of time a specific behavior occurred) and States (i.e. period of time a specific behavior occurred).

The response variable was the proportion of time during which a behavior was observed on the total of observation time.

COUPLED LOBSTERS: PREDATION ON SEA URCHINS

Once the maximum size of sea urchins consumed by sub-adult lobster was found I proceeded by presenting the unconsumed size class to a couple of lobsters. This to test for eventual cooperation or positive interaction and the eventual exploitation of the common prey. For each one of the three compartments of the experimental tank two lobsters were placed with three individuals of *P. lividus* of the unconsumed size. This treatment was replicated two times.

Because no previous knowledge exists, I wanted to preliminarily identify and quantify the most important lobster behaviors of both predation and interaction among predators. For this purpose the experiments were recorded for further video analysis. All three compartments were instead simultaneously recorded. For the analysis of the interactive and feeding behavior among two lobsters all the available videos (videos of the consumption of sea urchins) have been analyzed.

Video Analysis with behaviors quantification were performed with the freeware software Etholog2.25© for transcription and timing of behavioral observation sessions (Ottoni, 2000). The observation focused on the first urchin to be consumed and ended at the completion of this first predatory event (obviously only trials with the consumption of urchins were considered). Behaviors were divided into Events (i.e. number of time a specific behavior occurred) and States (i.e. period of time a specific behavior occurred).

For the analysis of the interaction between lobsters, the State “Interaction” has been separately analyzed and dived in further categories (States).

The response variable was the proportion of time during which a behavior was observed on the total of observation time.

STATISTICAL ANALYSIS

Two statistical approaches were used for these experiments, MDS (MultiDimensional Scaling) and 1-way ANOVA (ANalysis Of VAriance). All data have been standardized for the time of observation.

In detail, a MDS (data square root transformed) was performed with both Events and States grouped together for analyzing the feeding behavior during the experiment of the max size of *P. lividus* consumed by *P. elephas*. This was done to understand what behavior would explain the majority of variability during predation. Data have been distnguished between the two size tested (i.e. 2° and 4°).

I then designed a series of 1-way ANOVAs (1 Factor ‘Behavior’ with different Levels depending on the analysis) to test for differences in behaviors (both States and Events) in the coupled lobsters experiment. An *a posteriori* SNK (Student-Newman-Keuls test) test was used to confront the means. Before running the analysis the homogeneity of variance was verified using the Cochran’s test (Winer, 1971).

4.3 Results

PREDATION OF LOBSTERS ON SEA URCHINS: MAX SIZE CONSUMED

Table 6 Number of *Paracentrotus lividus* consumed by solitary *Palinurus elephas* in each compartment.

Size Classes	N° of *P. lividus* eaten
1	3
	3
	3
2	3
	3
	3
3	2
	2
	0
4	1
	1
	1
5	1
	0
	2
6	**0**
	0
	0

In the first experiment the maximum class size consumed was the 5th . For the 6th none of the three sea urchins available was eaten.

COUPLED LOBSTERS: PREDATION ON SEA URCHINS

When presented with three sea urchins the 6 coupled lobsters consumed 1.4±0.5 urchins (mean±st.err.) (Table 7) proving this time the consumption of the 6th size class of *P. lividus*. During video analysis no direct cooperative interaction has been observed.

Table 7 Number of sea urchins of the 6th size class consumed by coupled lobsters

	1st Replicate	*2nd Replicate*
1st couple of lobsters	2	2
2nd couple of lobsters	0	3
3rd couple of lobsters	0	3

VIDEO ANALYSIS: LOBSTERS INTERACTION AND PREDATION ON SEA URCHINS

General description of the predator-prey interactions and feeding technique.

As soon as an urchin is introduced in the compartment the lobster always begins with an initial approach usually with the antennas to start sensing the presence of the prey.

After the presence of *P. lividus* is acknowledged, the lobster gets closer to the prey, increasing the number of contacts with it, especially with the pereiopods. Usually these are also used to detach the urchin, anchored to the substratum, and begin feeding. This behavior however depends according to the size. Smaller sea urchins are more easily detached while for the bigger ones is needed more effort and time (see further details on ANOVA results and ANNEX A).

The lobster then puts the urchin close to the maxellipeds always keeping it within the range of its mouth. The manipulation of the urchin depends again on the size. For the first three size classes of *P. lividus* manipulation consists of keeping close to the mouth of the lobster the peristomial area of the urchin. In this case *P. elephas* used the maxellipeds as tweezers directly cut the urchin open. In this way the lobster is indeed capable of breaking the urchin in two pieces and feed on them. This kind of manipulation did not need long time (see details on further results). Manipulation and handling of the 4th and 5th classes is instead longer and trickier. The first behavior consists in cutting the spines of sea urchin, while constantly holding it between the maxellipeds and turning along is longitudinal side. Once the area around the Aristotele’s lantern is free of spines (and the aboral side has noticeably shorter spines as well) the lobster begins hitting against the membrane in order to reach the inner soft parts and start consuming the prey.

In all the size classes (including the sixth) the size urchins were consumed as whole with nothing left on the tank. Sometimes also the fallen spines were collected and eaten by the lobsters.

Behaviors and time allocation.

I defined the following behaviors:

STATES

- Feeding: the act of handling and consuming the urchin by the lobster
- Touching sea urchin (touch urch): the lobster makes contact with pereipods with the urchin
- Resting: the lobster does not move around the tank
- Walking: the lobster moves around the tank using the pereiopods
- Detaching: time needed by the lobster to detach the sea urchin from the bottom of the tank
- <u>Interaction</u> (6th size class): all the behaviors that include lobsters interacting with each other. Further divided in:
    - Antenna touch (antouch): the lobster touches the other one with the antenna
    - Push Away: the lobster pushes the other individual away
    - Bodytouch: The lobster comes in contact with the other lobster with its body
    - Under: The lobster is standing still, not moving, under the other lobster
    - Walkaway: the lobster (usually after pushaway) moves away from the conspecific

EVENTS

- Antenna point (ant point) (for 2nd and 4th class): the lobster points its antennae at the urchin
- Antenna up (ant up): the lobster points the antenna up
- Leave: the lobster leaves the urchin it was consuming
- Point urchin (pointer) (for 6th class): the lobster points the urchin with the antenna
- Point lobster (pointl): the lobster points the antenna at the other lobster
- Parry: the lobster uses the antenna to push the other lobster away

2nd and 4th SIZE CLASS MDS ANALYSIS

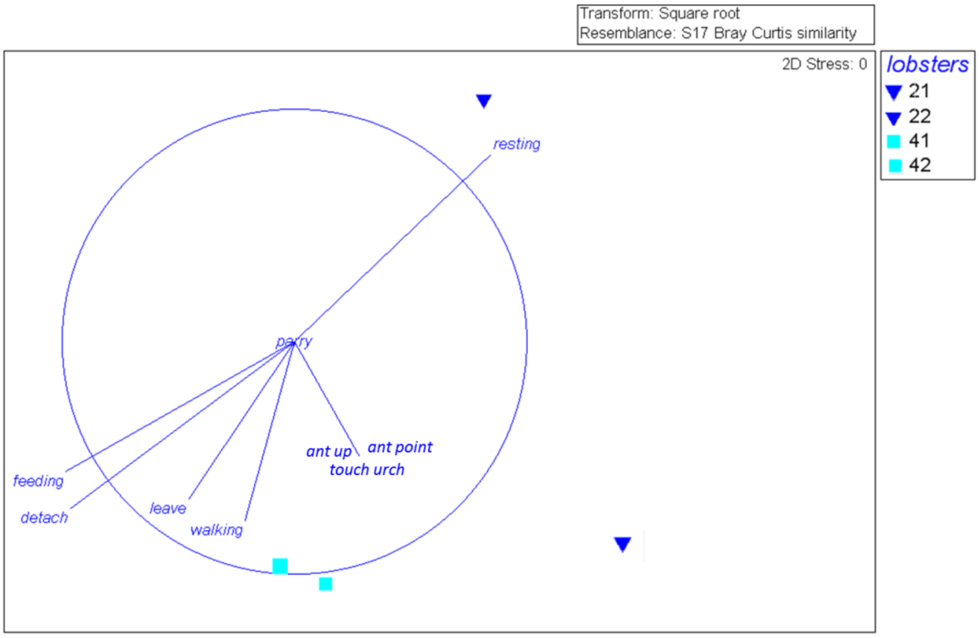

Fig. 12 MDS analysis results on the 2nd and 4th size class. Blue triangles are the two individual of the 2nd size class (21, 22). Light blue squares are the two individuals of the 4th class (41 42)

Both States and Events have been plotted together in the MDS analysis (Fig.12). The analysis shows a correlation between both the sizes and behaviors related to urchin consumptiona and presence (ant point, touch urch) and movement (walking). One of the individuals of the 2nd size class shows a strong correlation toward resting. The two replicates of the 4th size class seem to show a pretty consistence behavior within each other.

6th SIZE CLASS ANOVA ANALYSIS

Behavioral States.

Significant differences exist between behaviors considering all the behavioral States and the interactive behavioral States (Table 8).

Table 8 1-way Anova analysis results for the experiment on the interaction of *Palinurus elephas* individuals and predation on sea urchin. All behavioral States and Interaction behavioral States were considered. Data have been Ln(X+1). (N=4; Levels=10; detach, walkaway, pushaway, under, bodytouch, resting, feeding, antouch, touchurch, walking).

Source	SS	DF	MS	F	P	F versus
Be	64.7498	9	7.1944	21.7	0.000	RES
RES	9.944	30	0.3315			
TOT	74.6938	39				

The SNK a posteriori test showed significant difference (Fig.13) between feeding (66% of time on total time of observation) and all the other behaviors ($p<0.005$).

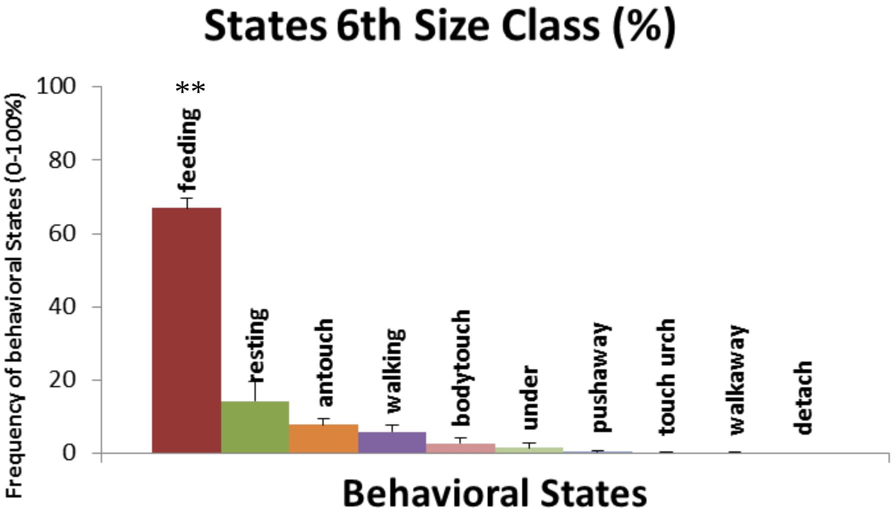

Fig. 13. Percentage of time spent by lobsters engaging in a Behavioral State in relation to total time of observation. All the Behavioral States are considered including the interactional ones (antouch, bodytouch, under, pushaway, walkaway)

Significative differences exist as well when considering all the Behavioral States together (Table 9)

Table 9 1-way Anova analysis results for the experiment on the interaction of *Palinurus elephas* individuals and predation on sea urchin. All behavioral States. Data have been Ln(X). N=4; Levels=6. Detach, feeding, interaction, resting, walking, touchurch.

Source	SS	DF	MS	F	P	F versus
Be	136.7075	5	27.3415	33.9	0.0000	RES
RES	14.5164	18	0.8065			
TOT	151.2239	23				

The SNK a posteriori test showed significant difference (Fig.14) between feeding (66% of time on total time of observation), walking (6%), resting (14%) and interaction (12.5%) ($p<0.005$). These last result significantly different ($p<<0.005$) then detach (0.1%) and touchurch (0.3%).

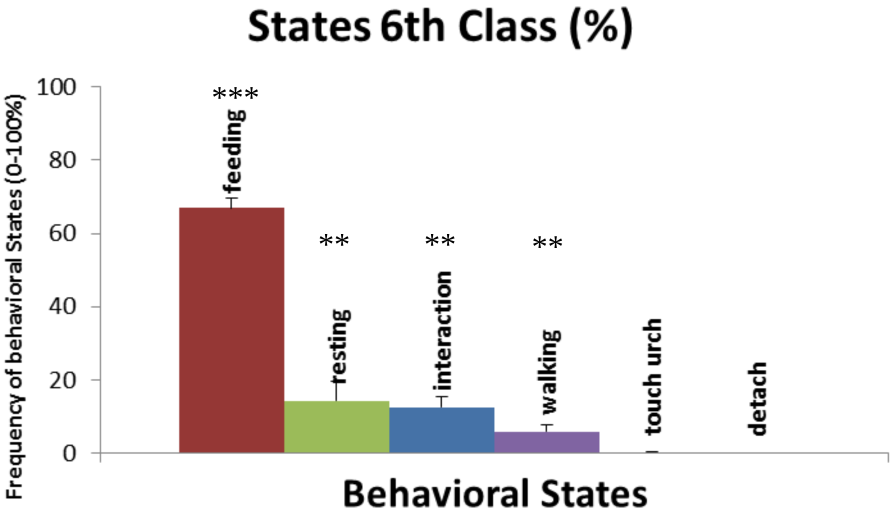

Fig. 14. Percentage of time spent by lobsters engaging in Behavioral States in relation to total time of observation. All the Interactional Behavioral States (antouch, bodytouch, under, pushaway, walkaway) are grouped together as "Interaction" (blue bar).

Significant differences exist as well when analyzing only the Interactional Behavioral States (Table 10)

Table 10 1-way Anova analysis results for the experiment on the interaction of *Palinurus elephas* individuals. N=4; Levels=5. Antouch,under, pushaway, walkaway, bodytouch.

Source	SS	DF	MS	F	P	F versus
be	11584.5	4	2896.124	14.52	0.0000	RES
RES	2992.45	15	199.4967			
TOT	14576.95	19				

The a posteriori SNK test showed (Fig.15) significant differences (p<<0.005) between anotuch (7.8%) and all the other behaviors

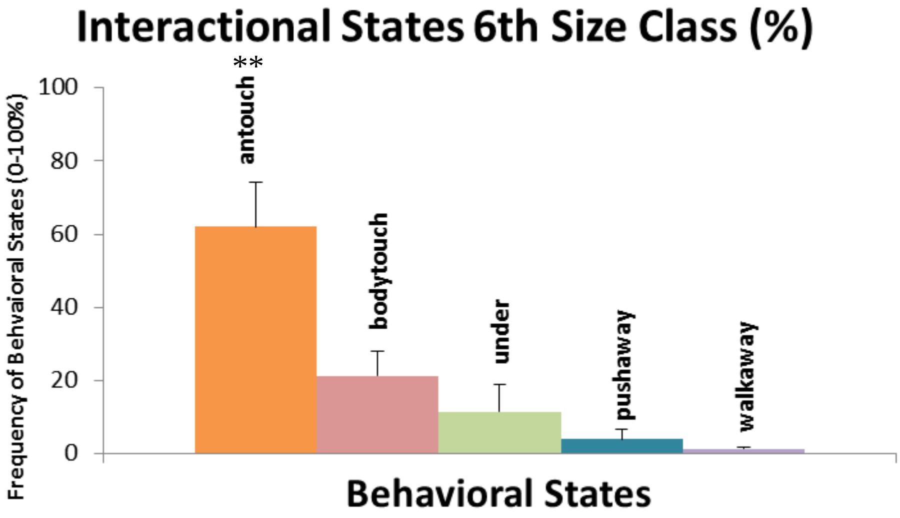

Fig. 15. Percentage of time spent by lobsters engaging in Interactional Behavioral States in relation to total time of observation. In this figure frequency of behaviors is considered in relation to “Interaction” total time, not the total time of observation.

Behavioral Events. Significative differences (Table 11) exist between the 2behavioral events.

Table 11 1-way Anova analysis results for the experiment on behavioral events in the interaction between *Palinurus elephas* individuals,. N=4; Levels=5. pointl,leave,pointur, parry, antup. Data have been Ln (X+1) transformed

Source	SS	DF	MS	F	P	F versus
Be	29.5823	4	7.3956	8.62	0.0008	RES
RES	12.8721	15	0.8581			
TOT	42.4543	19				

The a posteriori SNK test showed (Fig.16) that pointl (% 1.15 events per time of observation) is significantly more frequent than the other behaviors (p<0.05).

Fig. 16. Number of Behavioral Events done by lobsters in relation to total time of observation. In this figure frequency of "parry" (light blue bar) and "pointl" (green bar) are considered separetely. (see further results in ANNEX B; analysis run with "pointl" and "parry" grouped together as "interaction").

4.4 Discussion

This experiment provided, for the first time, firm and direct proofs of European spiny lobster *P. elephas* feeding and handling capabilities on individuals of different sizes of the sea urchin *P. lividus*. The individuals used for my experiment most likely never preyed upon sea urchins in nature (however some habitat overlap is possible beside depths differences) but nevertheless they were able to prey on them. Indeed the bathymetric range of these two species doesn't overlap. But until the '70s, *P. elephas* would insist in shallower waters, as confirmed by fishermen captures, with fishing pressure pushing them slowly but inexorably downward in deeper waters changing both preferential habitat and trophic web (Gristina, personal communication). Nevertheless lobsters also showed adapted and peculiar predatory techniques for the different sizes presented. The technique used to consume the larger individuals of *P. lividus* can be considered similar to the one described by Tegner & Levin (1983), with the spines shorten and then consumption beginning in the oral zone. Similarly the smaller sea urchins were consumed, as in my case of study, completely and directly cracking them open. However, important differences can be underlined. First of all, in all my trials (considering also many hours of observations before the actual experiments) the sea urchins were consumed as a whole with none of the soft or hard tissue left in the tank. This sometimes can be related to a just occurred moult, because of the needing of the individual for calcium carbonate. However, since I have never used individuals that underwent moulting process this can be considered as a peculiar feeding behavioral pattern. It is also important to notice how in my case of study, unlike the findings of the other authors, sub-adult individuals of lobsters were able to consume adult sea urchins.

Considering the possibility that this sub-adult individuals of *P. elephas* never came across sea urchins on the field, the capability of consuming them could be considered as an indirect proof of an innate predatory behavior. Mery & Burns (2010) give the following definition for innate behavioral response, defining it as occurring "when the modification of behaviour in response to environmental factors is the result of the evolution at the population scale over multiple generations; that is, a predetermined phenotypic trait is produced in response to a predetermined environmental stimulus". In my case lobsters responded to sea urchins presence not through a learnt new process (that is a modification of a behavior produced by the experience within lifetime of an individual, Mery & Burns, 2010) but because of a knowledge "acquired during evolution and multiple generations time of the species".

Some examples of innate behaviors can be made for water species. Dalesman *et al.*, (2007) studied the freshwater gastropod *Lymnaea stagnalis* avoidance response. The individuals of this species resulted having anti-predator behaviors even if they did not experience fish predation in their lifetime. This indicated that the populations were still able to recognize the predation threat even responding with appropriate behaviors. Also on marine species studies on innate behavior have been done. Heupel *et al.* (2012) tested blacktip sharks (*Carcharhinus limbatus*) movements patterns. Their results showed how the values of all movement metrics examined were consistent across years despite the presence of naïve cohorts in each year. Thus suggesting that habitat use patterns and ontogenetic shifts in habitat use were innate. To some extent my results can be considered in this prospective showing innate feeding behavior on sea urchins by *P. elephas*.

Giving a general qualitative assessment of my results it is possible to notice that during the predatory behavior for single lobsters on sea urchins, feeding is actually the most time consuming behavioral Event (considering the high value of resting for the 2nd size class being probably an outlier). Looking at the time is also noticeable how it increases between the 2nd and 4th size class. This shows clearly increasing difficulties in handling and consumption of the prey. Although this experiment does not take in account prey selection analysis, the result might also been seen from this perspective. Lobsters, and animals in general, mainly feed on preys that are selected according usually on size (Langlois *et al.*, 2006). Thus by presenting them preys bigger than what they would actually choose and easily manipulate, they engage in more time costing behaviors (however succeeding). Lobsters although proved capable of preying on even bigger urchins.

From preliminary and qualitative examination of behavioral Events, antenna are clearly the most commonly used part of the lobster body. Interesting to notice is while the attention of the solitary lobsters seems to be solely toward the urchins, when two lobsters are simultaneously in the tank, the movements of the antenna aim mainly to the conspecific. In general for the coupled lobsters the majority of events are related to the presence of the conspecific.

When coupled lobsters are tested for predatory capabilities on the previously unconsumed urchins size, they prove to be able to eat them. However no positive interactions between the predators has never been observed. This opens a quite peculiar scenario giving once again the opportunity for indirect positive interactions to emerge.

The presence of a conspecific actually results in time spent in competitive behaviors (see further ANOVA results). However the overall final outcome is the consumption of the urchin size otherwise solitarily not eaten. Thus this dual result, somehow comparable to a MPE, shows how in one way the presence of a competitor produces negative outcomes, as competition and aggressive behaviors, but on the other end seems to trigger an otherwise soothed predatory behavior. It might be concluded that sub-adult individuals of the European spiny lobster *P. elephas* consider the presence of a conspecific as a threat for food source gaining and in any way a reason for cooperative behavior. However this works as a stimulus toward predation.

The MDS analysis shows in general for all the individuals of *P. elephas* analyzed of both classes, how during the predator-prey interaction they all engage in behaviors, living the “resting” behavior only to one individual. Strong correlation seems to exist between the individuals feeding on the 4th size class of sea urchin and all the behaviors concerning interaction with the urchin (from “feeding” to “touch urchin” and “antenna point”). This might underline, how sub-adult individuals of European spiny lobster strongly recognize the sea urchins *P. lividus* as a prey even if chances of no prior encounters between the two species exist. Furthermore, antenna prove to be the most important organ through which sub-adult European spiny lobsters recognize and deal with prey.

The ANOVAs run to analyze the coupled lobsters feeding behavior and the interaction among predators, give other interesting insights into this decapod interactive and feeding processes. The analysis of all the States and the “interactional” States together, shows significant differences among the behaviors. In the *a posteriori* SNK test “feeding” indeed results having significant differences with all the others behaviors. Considering that the experimental set up has the general aim of investigating the feeding behavior of *P. elephas* (observations ended at the end of the consumption of the first sea urchin) this result could be easily understood from this experimental set up prospective. On the other hand, the long time needed to completely feed on an urchin of the 6th size class can also reflect mechanical and physical issues for consumption of adult individuals by sub-adult predators. Grouping together all the interactional behavioral States, the ANOVA shows again significant differences among the different levels. The “feeding” behavior again results the most time consuming State, confirming what just explained. This furthermore shows significant differences with “walking”, “resting” and “interactions”. These in turns resulted having significant differences with “touch urchin” and “detach urchin” behaviors. Through this analysis, it becomes clearer how interactions considered as a whole are indeed time consuming behaviors. This can be seen as the proof that despite being able to consume sea urchins of the 6th size class, the lobsters engage in long competitive and aggressive behaviors. Usually this kind of scenario leads to an absence of prey consumption or at least to a diminishing of preys capture. In the end this can be considered as a direct proof of the unique dual trait of this interaction previously discussed.

From the analysis of the behavioral Events is even more clear how the interaction among lobster has a key importance during the predator-prey interaction. Previously the MDS analysis showed the importance of lobsters antenna in pointing and interacting with the prey. However the results of the ANOVA analysis on Event, show that as soon as another predator is added into the picture the attention is almost totally turned and is focused on the conspecific. Indeed the *a posteriori* test shows how “pointing lobster” is significantly the most common behavior among the Events. Furthermore I analyzed and run an ANOVA, adding together all the Events that can be considered as interactional behaviors (i.e. ,“parry” and “point lobster”). The results of this analysis shows significative differences among “interaction” and “point urchin”. This in turn shows significantive difference with the other behaviors. Two main conclusions can be drawn by this last results. First of all, this can be considered as another evidence of the importance of antenna for lobsters *P. elephas* as sensorial organs. Secondly that when presented with both conspecific and prey, sub-adult individuals of *P. elephas* engage more in interactive behaviors then in predatory ones.

No evidence of violent interactions has never been observed during my experiments. Previous work on lobsters anti-predator behaviors in the presence of predators (Lavalli & Herrnkind, 2009; Buscaino *et al.*, 2011) underlined the importance of antenna as a defensive weapon, considering it the most important. This result is partly confirmed by my work. More precisely, no “whipe” behavior (i.e., a strong stroke with the antenna toward the opponent), has ever occurred. However antenna demonstrated to be the tool used by the lobster both for interacting with sea urchins and, even more, with conspecific. As well no strong “tail flip” escapes (i.e. strong contraction of the telson) have ever been recorded. These differences, with the lack of previously observed vigorous aggressive behaviors, might be due to the opposite aims of the works and the two different scenarios investigated. In one case the lobster experienced extremely dangerous predator encounters while in my experiment the aggressive behaviors were toward less dangerous conspecific, competing for the same food source.

For sure sub-adult individuals of *P. elephas* demonstrated to be strong predators of different size of *P.* *lividus* showing peculiar and adapted feeding techniques. As well lobsters showed strong interactive predisposition towards conspecific competition. In general the importance of antenna in both feeding and interactive behaviors have been found.

5 GENERAL DISCUSSION AND CONCLUSIONS

The objective of this thesis was to demonstrate and confirm how communities are characterized and shaped by various interactions existing among individuals, especially indirect interactions. These arise from different kinds of behaviors, can concern individuals of the same or of different species, and can be both direct and indirect (Molis & Gama, 2009). Moreover, the results of my experiments can be used as example to lead the path for an higher concern about manipulative and experimental works.

It is then possible to speculate around the fact that complex webs of interactions arise in ecosystems with high number of species (i.e. high biodiversity) (Duffy *et al.*, 2007), having investigated myself interactions within high species diversity communities. The findings of the first experiment lay on this scenario. A guild of predators, *M. glacialis* and *T. pavo*, demonstrated to successfully substitute the functional role of prey populations (i.e. sparids), the abundance of which has dramatically decreased due to human impact, in controlling grazers populations. A high number of species can indeed affect ecosystem features, stability and processes or can buffer the ecosystem functions. (Hector & Bagchi, 2007; Ives & Carpenter, 2007; Thébault & Loreau, 2005). Biodiversity ecosystem functioning (BEF) is becoming largely debated also in the marine environment (Solan *et al.*, 2006; Stachowicz *et al.*, 2007; Bruno *et al.*, 2008), and can be generally considered as the effect of multiple species on ecosystem properties, goods or services (Hooper *et al.*, 2005), thus with possible final outcome that directly insist on socio-economic grounds (Diaz *et al.*, 2006; Midgley 2012). The general idea is that within the same community charactherized by high biodiversity, there might be species playing the same ecological role with systems that can: (1) have particular species with important traits that influence ecosystem function, “the sampling effect”; (2) lead to more efficient use of resources, “the niche complementarity effect”; (3) provide “biological insurance” against ecosystem processes in case of species loss; (4) have more species playing the same role (i.e. redundancy) (Duffy *et al.*, 2001; Finke & Snyder, 2010). Having species that, in case of some loss, can functionally substitute some others, as said, also leads to the idea of insuring more stability to the system (i.e. “insurance hypothesis”, Yachi & Loreau, 1999; Loreau, 2001; Griffin & Silliman, 2011). In my case it was possible to indirectly demonstrate how a community with high biodiversity can buffer changes. In particular, and uniquely, substituting a species with a functionally similar guild of predators through mutual indirect facilitation.

The vast majority of the work carried out on redundancy and complementarity, ecological functioning and biodiversity, is mainly based on modeling and theoretical work rather than empirical. As the aim of my thesis was also to focus on experimental studies, it is possible to underline the undeniable difficulties and eventual flaws that can be part of this approach. However it's clear from my point of view and experience that these approach is necessary in order to draw a realistic scenario of ecological communities, especially marine ones. For instance, the empirical approach for the multiple predators experiment with *P. elephas* has demonstrated to be fundamental. In my opinion only thank to this set up we have been able to scratch the surface of this indirect relationship among multiple preying lobsters. Any other kind of approach, numerical or theoretical, would have lead me, in my opinion, to an incomplete information or to a completely misleading one, lacking the intrinsic complexity of the system I was investigating.

Indeed, as I demonstrated with the present thesis, ecological scenarios can be complex and involve several processes to trigger otherwise unpredictable (or not properly understandable) results, with predators behaviors usually playing key roles. It is thus necessary to add predator-prey interactions (PPI) and the indirect interactions among predators (MPEs), also in the BEF framework in order to describe more accurately the consumer-resource systems (Ives *et al.*, 2005). This in my opinion cannot be done without manipulative and experimental approach, both in field and in lab.

This goes hand in hand with the central role played by behavior and consequentially the central role that has to be played by behavioral studies. In this thesis work I proved how necessary is the study of the behavior for the proper knowledge of species. *T. pavo* for example, is a keen species able to consume diverse type of food source, properly exploit resources and adapt in complex and demanding environments. It is spreading northward due to increasing temperature thus insisting in new communities. With my experiment I was again able to preliminary understand the behavior of this species, paving the way to a better understanding of an undoubtedly interesting animal. Similarly *P. elephas* is a really important species in the Mediterranean, especially for its economic value and fisheries related interest. Thus, investigating and begin with preliminary studies and experiments like the one I set up for this PhD thesis, is the only way to finally approach ecological and species knowledge in a profound way. This, in turn, can prove the deep complexity of species interactions and species themselves leading then to proper management rules.

My study strongly supports the complexity existing among communities structures and in intra/inter-specific interactions. This complex communities, food webs, the biodiversity that characterizes them and the effects of biodiversity functioning that arise from them, have been threaten and modified by anthropic impacts (Strong & Frank, 2010). These impacts can be grouped in three mayor categories, tightly connected and consequent one to another: **global change** (global warming) (Landsberg, 1970; Broecker, 1975; Graham & Grimm, 1990; Hooper *et al*. 2005; Moritz *et al*. 2008; Montoya & Raffaelli, 2010; Woodward *et al*., 2010; Kordas *et al*., 2011; Philippart *et al*., 2011; Wernberg *et al*., 2011), **loss of biodiversity** (loss of key species) (Bellwood *et al*., 2003; O'Connor & Crowe, 2005; Cardinale *et al*., 2006; Zhang & Zhang 2007; O'Connor *et al*. 2008) and **species invasion** (Schreiber *et al*., 2002; Rossong *et al*., 2006; White *et al*., 2006; Williams *et al*., 2006; Rodriguez, 2006; Bystrom *et al*., 2007; Byrnes & Stachowicz, 2009; Brenneis *et al*. 2011; Hudina *et al*. 2011; Strecker *et al*., 2011). All this is alter the biogeographic ranges of species (Harley 2011) providing novel assortments of species with potentially new, unexpected effects on ecosystems (Nogués-Bravo & Rahbek 2011).

Biodiversity functioning, species interactions, community complexity, invasive species, indirect interactions, etc. are all interconnected, dependent and consequences one of the other. Considering the tight link between the various aspects here discussed and the undoubted ecological services that affect human life (Worm *et al*., 2006) is key to build up the proper knowledge leading to good management solutions aimed at the understanding and buffer of the current global issues.

For example, quantifying direct and indirect effects, that is measuring the interaction strength, gained importance (Menge, 1995; Laska & Wootton, 1998; Abrams, 2001; Kokkoris *et al.*, 2002; Berlow *et al.*, 2004; Christianou & Ebenman, 2005; Wootton & Emmerson, 2005; Hernandez, 2009; Montoya *et al.*, 2009; O'Gorman, 2010). This insight brought out, for instance, the fact that indirect effects can be stronger then direct ones (Menge, 1997; Webster & Almany, 2002; Borrett *et al.*, 2010), especially in the aquatic environment (Kovalenko, 2010). This is strongly correlated to the proofs that the not proper understanding of the ecological processes so far (e.g. stock reassessment management actions) lead to unexpected results and expensive and costly managerial failures (Nystrom *et al.*, 2001; Dulvy *et al.*, 2004; Mills *et al.*, 2004; Myers et al, 2007; Stalling, 2008; Kovalenko *et al.*, 2010; Madin *et al.*, 2010).

The further steps must be toward the recovery of depletion of biodiversity and the mitigation of damaged areas (restoration) (Simenstad *et al.*, 2006). Obviously in the recovery process (active or passive) all the ecological characteristics and processes of the system must be taken into account thus results like the one in my PhD work are fundamental in order to achieve a proper recovery along the same trajectory of decline (Elliott *et al.*, 2007). A key way to preserve or cure habitats is the establishment of protected areas. The typical example in the marine environment are Marine Protected Areas (MPA). MPAs, as in my work, can be even more important from the research point of view because they can be treated as actual field laboratory. The importance of ecological functioning has lately been taken in account also in their management (Frid *et al.*, 2008). Also in this perspective the scenario discussed and investigated in this thesis, both ecologically and behaviorally, is key for defining proper management measures and controls in order to secure the future of biodiversity and ecosystem processes.

In conclusion, during the work developed for my PhD thesis I focused on interactional ecological aspects that nowadays are resulting fundamental both for ecological knowledge and in order to face and positively respond to environmental issues. The interactional models I investigated are examples of what actually lays within indirect interaction and predator-prey interactions subject. With my results I made the first steps toward a more real understanding of complex ecological marine communities. In the perspective of gaining knowledge and understanding ecological functioning it is now largely emphasized the need for empirical works. My work thus walks in this path of assuring proper understanding largely unconsidered processes that however can drive major changes. Nevertheless behavioral studies must be a part of this process, giving solid and essential ground to build up proper understanding of communities. Although difficulties in this kind of approach are undeniable, in my and largely shared opinion, the need is toward empirical work deepening the knowledge on species interactions.

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8 ANNEX A

Plotting the results for *Paracentrotus lividus* (Fig. 17A) without controls (no significant differences in both states) we can see how in BAR the 70% tube feet removal represent the slowest speed (0,08 cm/s ± 0,01). In EMA both the 50% (0,1 cm/s ± 0,01) and the 70% (0,08 cm/s ± 0,01) tube feet removal had significant differences against non treated individuals. There was no significant difference between them.

Considering also *Marthasterias glacialis* (Fig. 17B), in BAR (0,14 cm/s ± 0,01) the starfish is significantly faster ($p<0.05$) only of the *Paracentrotus lividus* with the 70% removal of tube feet. In EMA *Marthasterias glacialis* (0,35 cm/s ± 0,02) is significantly faster ($p<0.05$) than *Paracentrotus lividus* not treated (0,28 cm/s ± 0,03) that is itself significantly faster ($p<0.005$) than *Paracentrotus lividus* with the 50% (0,1 cm/s ± 0,01) and 70% (0,08 cm/s ± 0,01) tube feet removal.

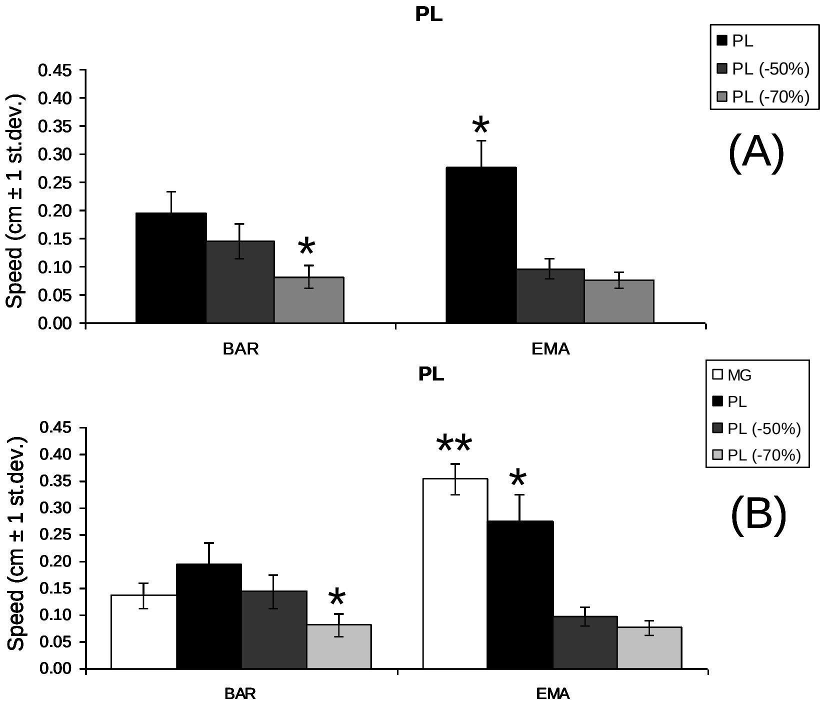

Fig. 17 Speed for all treatments of *P. lividus* in barren and erected macroalgae habitat without (A) and with (B) *M. glacialis* speed. *=p<0.05, **=p<0.005.

Plotting the results for *Arbacia lixula* (Fig. 18A) without controls (no significant differences in both states, Fig. 5 and 6) we found in BAR significant differences (p<0.05) between non treated (0,18 cm/s ± 0,01) and individuals with the 50% removal of tube feet (0,07 cm/s ± 0,01). In EMA no significant differences were recorded (non treated, 0,11 cm/s ± 0,01; 50% removal, 0,06 cm/s ± 0,01).

Marthasterias glacialis (Fig.18B) in BAR is significantly faster (p<0.05) (0,14 cm/s ± 0,01) than the individuals with the 50% removal of tube feet (0,07 cm/s ± 0,01). No significant differences were found between *Marthasterias glacialis* and the non treated *Arbacia lixula*. In EMA *Marthasterias glacialis* is significantly faster (p<0.005) than both the non treated *Arbacia lixula* (0,11 cm/s ± 0,01) and the *Arbacia lixula* with 50% removal of tube feet (0,06 cm/s ± 0,01).

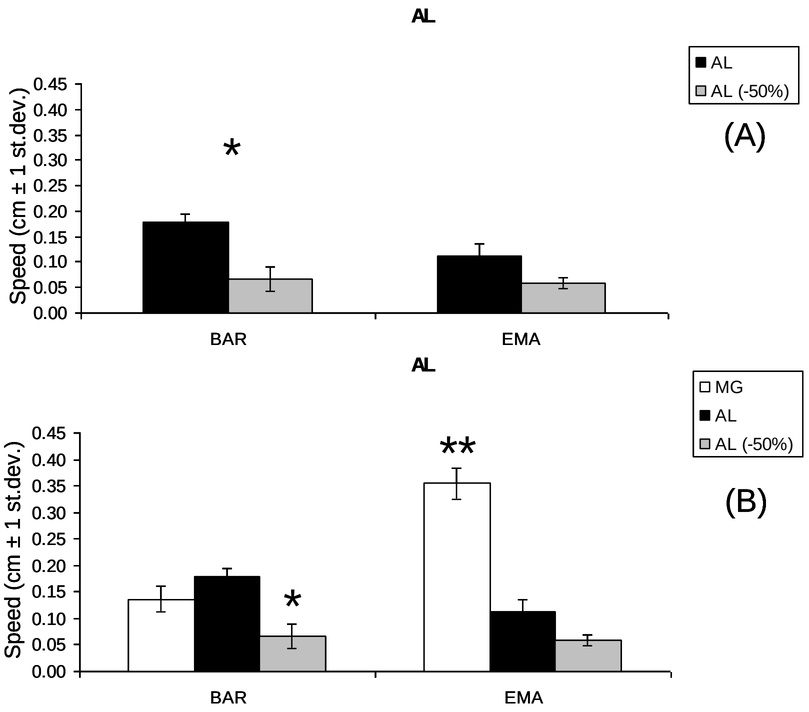

Fig. 18~~19~~ Speed for all treatments of *A. lixula* in barren and erected macroalgae habitat without (A) and with (B) *M. glacialis* speed. *=p<0.05, **=p<0.005.

For *Paracentrotus lividus* (Fig.19) with all the tube feet, speed is significantly higher (P<0.005) in EMA (0,28 cm/s ± 0,03) than in BAR (0,2 cm/s ± 0,02). With 50% removal, *Paracentrotus lividus* is significantly (P<0.05) faster in BAR (0,15 cm/s ± 0,02) then in EMA (0,1 cm/s ± 0,01). When the removal is at 70% there are no significant differences between BAR (0,08 cm/s ± 0,01) and EMA (0,08 cm/s ± 0,01).

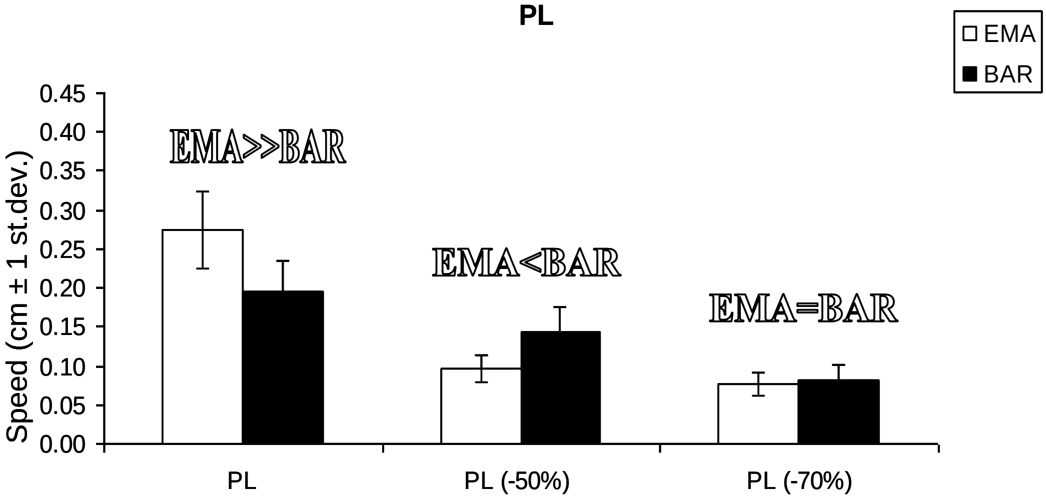

Fig. 19 Comparison of speed in EMA and BAR for *P. lividus*.

For *Arbacia lixula* (Fig.20) with all the tube feet, there are no significant differences between BAR (0,18 cm/s ± 0,01) and EMA (0,11 cm/s ± 0,01). At 50% tube feet removal data showed how *Arbacia lixula* is significantly faster (P<0.005) in BAR (0,07 cm/s ± 0,01) than in EMA (0,06 cm/s ± 0,01).

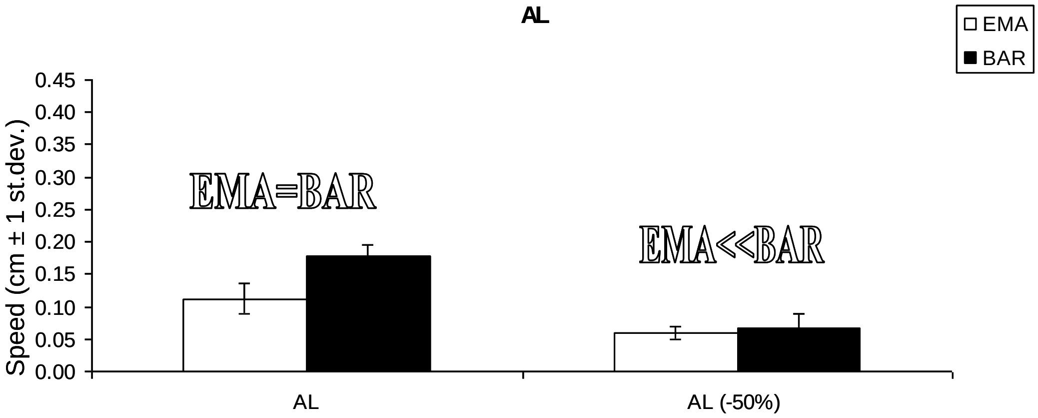

Fig. 20 Comparison of speed in EMA and BAR for *A. lixula*.

9 ANNEX B

SINGLE LOBSTER EXPERIMENT

For a qualitative analysis of the feeding behavior I considered the time used for each behavior in the different size classes investigated.

For the 2nd class (Fig.21) the most frequent behavioral state was resting (66% of observation time) followed by feeding (26%), walking (7%) and touch urchin (1%).

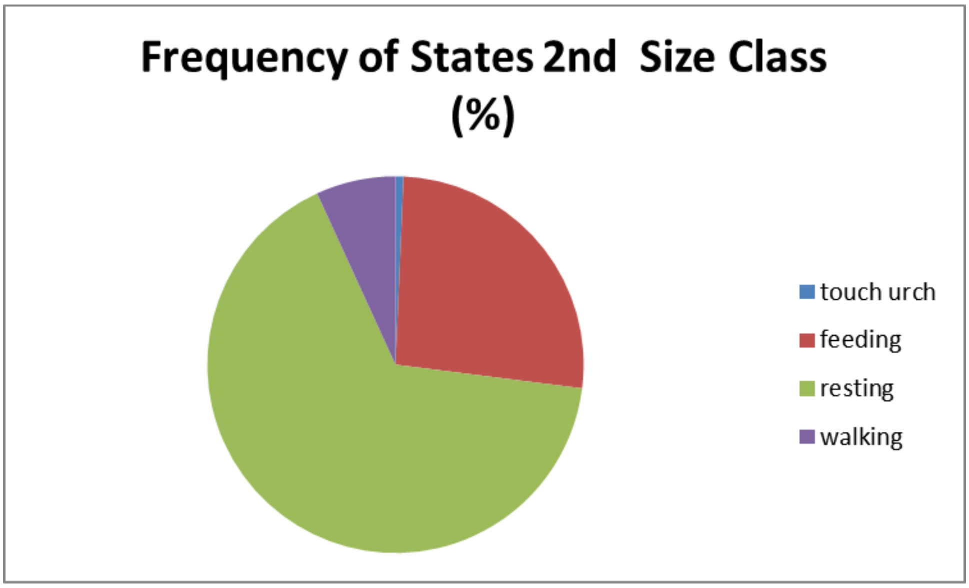

Fig. 21 Percentage of time for each State behavior in the 2nd size class

In the 4th class (Fig.22) the most common behavioral state was feeding (89%), followed by walking (8%), resting (2%), detach (0.5%) and touch urchin (0.5%).

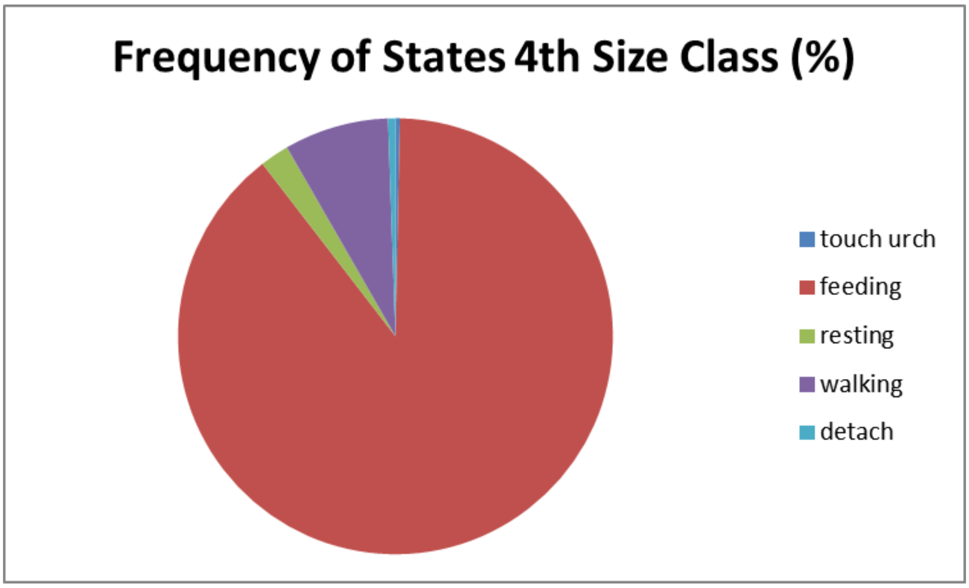

Fig. 22 Percentage of time for each State behavior in the 4th size class

Comparing all the three classes analyzed (Fig. 23-24) feeding results to be the most time requesting behavior.

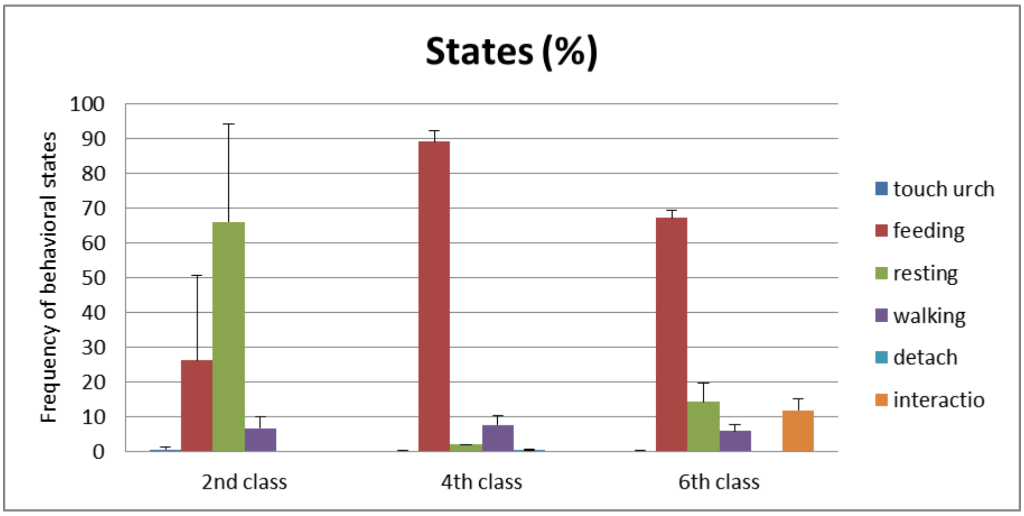

Fig. 23 Comparison of behavioral States (%) between all the classes analyzed.

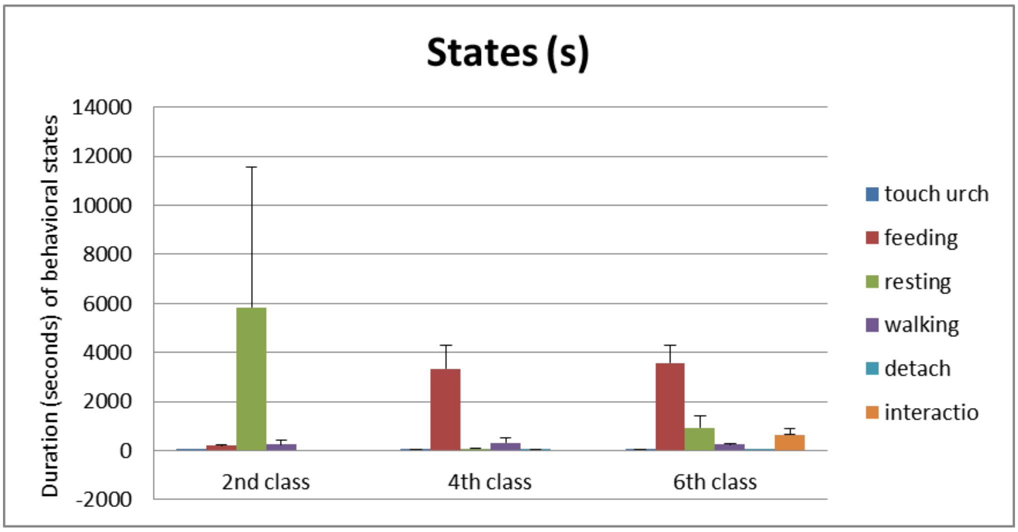

Fig. 24 Comparison of behavioral States (s) between all the classes analyzed.

For the behavioral events in the 2^{nd} size class (Fig.25) Antenna pointing results to be the most frequent behavior (1.9 times per time of observation) with Antenna up strongly less frequent (0.6).

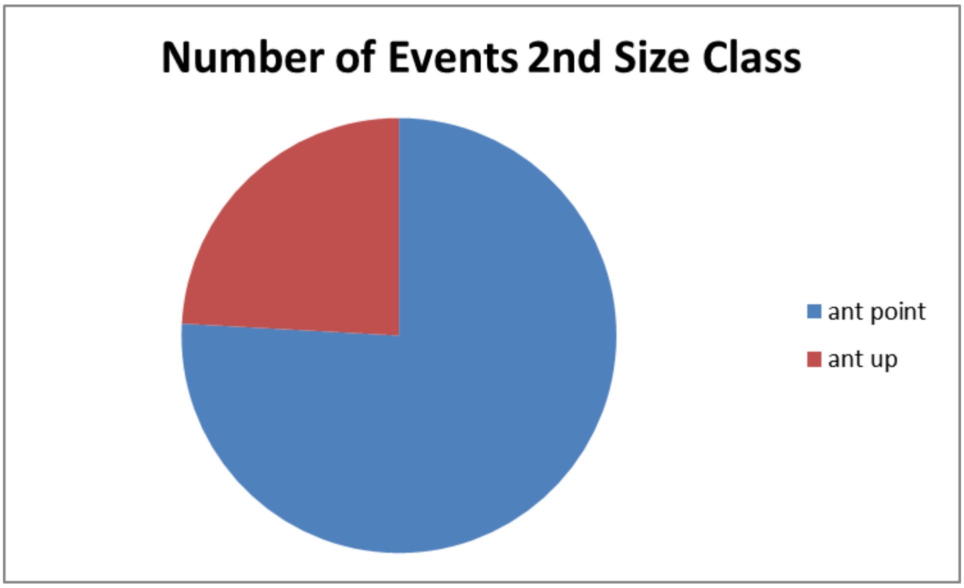

Fig. 25 Number of events per total time of observation for the 2nd size behavioral events.

In the 4th size class (Fig.26) again antenna point is the most common behavior (0.26 times per time of observation) followed by antenna up (0.08) and leave (0.01).

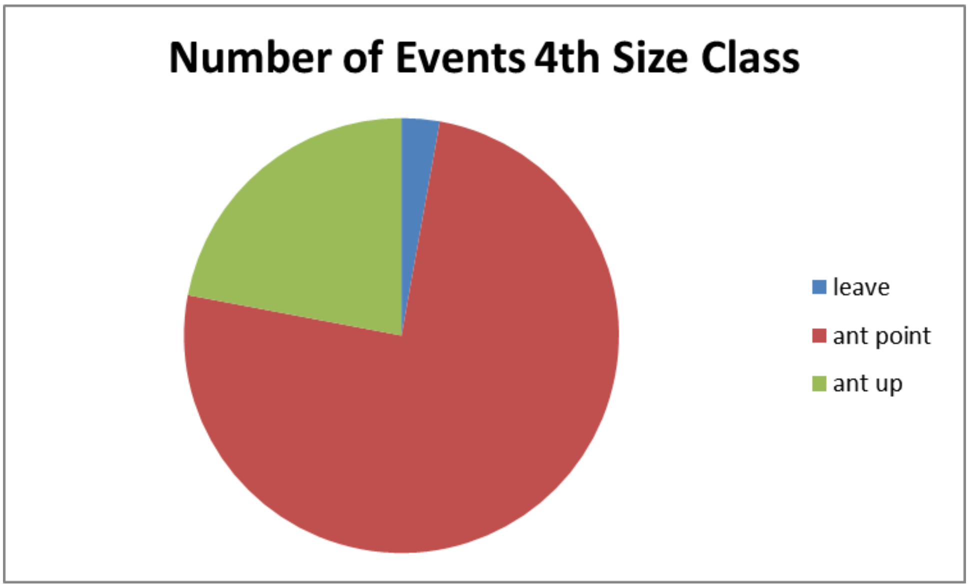

Fig. 26 Number of events per total time of observation for the 4th size behavioral events.

Comparing all the three classes analyzed (Fig. 27-28) antenna point results to be the most commmon behavior for the first two class while Point lobster is the most common behavioral event for the 6th size class.

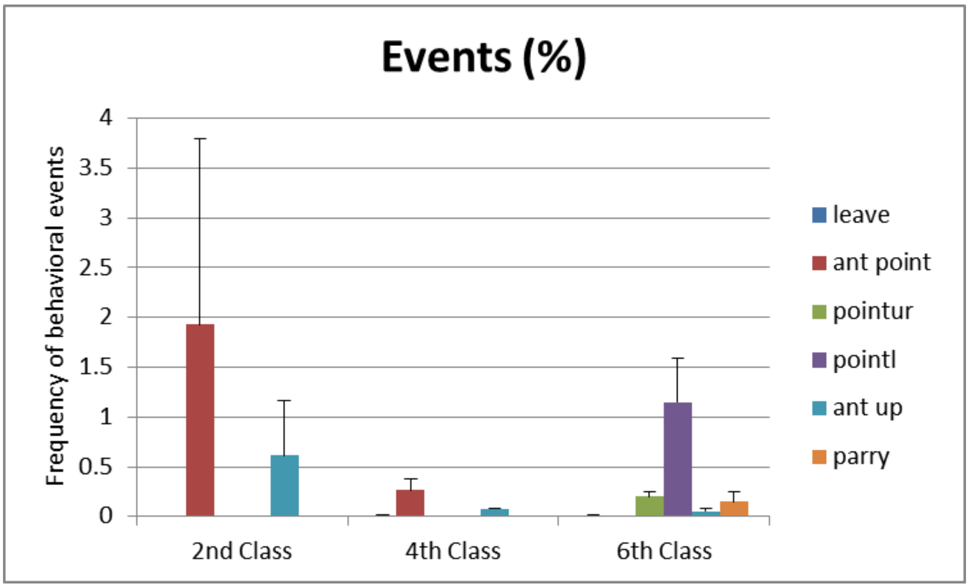

Fig. 27 Comparison of behavioral Events (times per time of observation) between all the classes analyzed

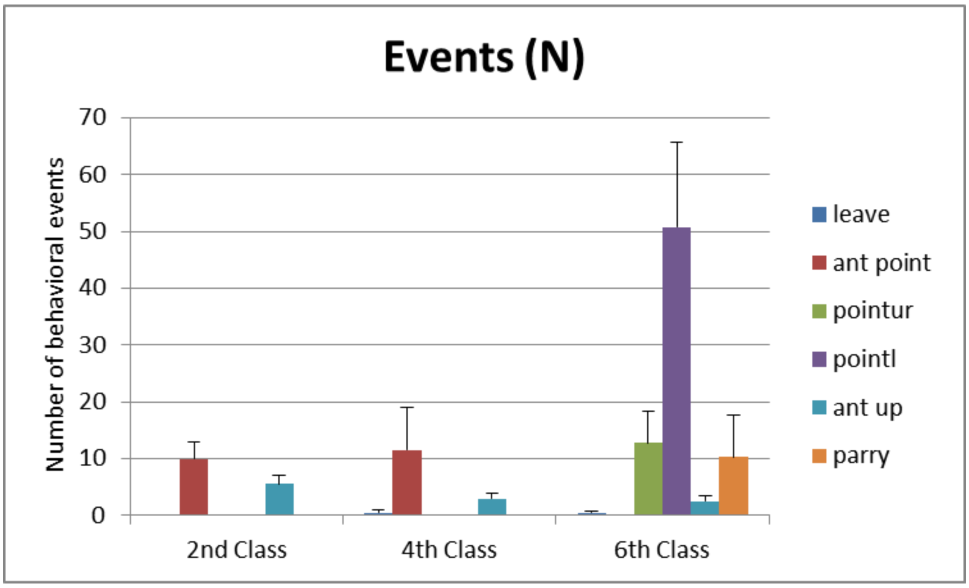

Fig. 28 Comparison of behavioral Events (N) between all the classes analyzed

COUPLED LOBSTERS EXPERIMENT

For the coupled lobsters experiment I also grouped together all the interactional behvaioral events. Significative differnecse are also found (Table 12).

Table 12 1-way Anova analysis results for the experiment on behavioral events (with interactional events grouped together) in the interaction between *Palinurus elephas* individuals,. N=4; Levels=4. Antup, leave, interaction, pointur. Data have been Ln (X+1) transformed

Source	SS	DF	MS	F	P	F versus
Be	34.5637	3	11.5212	27.41	0.0000	RES
RES	5.0435	12	0.4203			
TOT	39.6072	15				

A posteriori test showed significative differences (Fig.29) between interaction (1.3 events per time of observations) and pointur (p<0.005) and between pointur (0.2) and leave (0.01) and antup (0.05) (p<0.05)

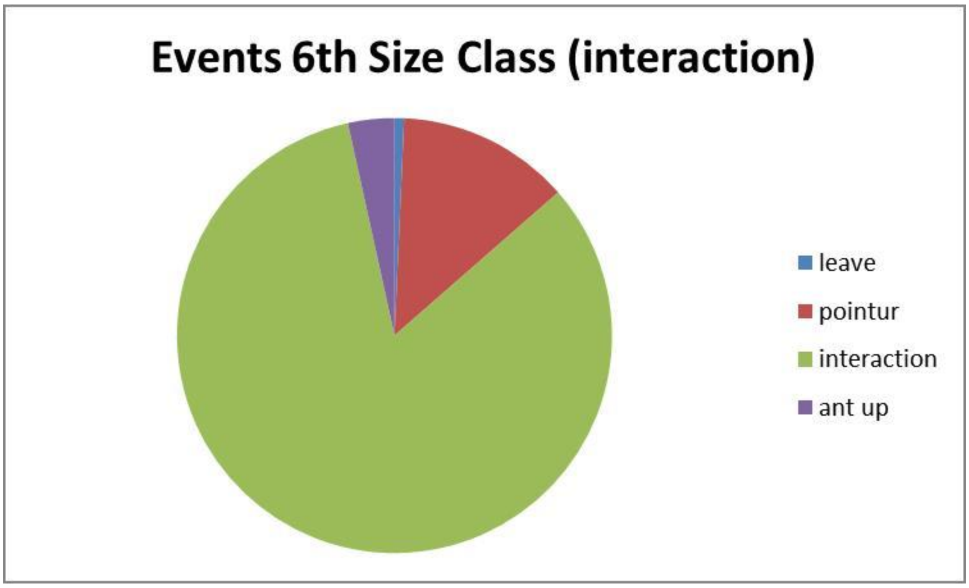

Fig. 29 Behavioral events in sixth class with interaction events grouped together. Leave = antup < pointur << interaction