Community structure and distribution of *Paracentrotus lividus* and *Arbacia lixula* following the 2012 storm at STARESO, Corsica, France

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Abstract

Disturbances like storms can significantly alter intertidal communities, making it imperative that these populations evolve adaptations to survive. Populations may then modify their habitats, facilitating the introduction of less competitive species. We investigated the distribution of two Mediterranean urchins, *Arbacia lixula* and *Paracentrotus lividus*, following a 2012 storm that struck the Station de Recherches Sous Marine et Oceanographique (STARESO) harbor, Corsica, France. Our goals were to study the population and distribution of both species; to determine which mechanisms may have led to *A. lixula* being more abundant than *P. lividus* in STARESO harbor; and to see how the two species may affect their environment. First, we used a spring scale to test both species’ attachment tenacity during intense wave action. Next, we conducted removal experiments to test the species’ competitiveness, and surveyed the harbor’s north wall to determine whether urchins associate with encrusting coralline algae. Our results indicate that *A. lixula* has a greater attachment tenacity than *P. lividus*; that inter- and intraspecific competition occur; and that both species associate strongly with coralline algae over turfy algae. This study demonstrates the relationship between disturbances and intra- and interspecific interactions in an intertidal community, which is crucial for predicting ecosystems’ health.

Introduction

Strong interspecific and intraspecific interactions can significantly influence the structure of biotic communities within an ecosystem. Interspecific competition occurs when individuals of one species suffer a reduction in fecundity, survivorship, or growth as a result of resource exploitation or interference by individuals of a second species. Intraspecific competition occurs when individuals of the same species compete for limiting resources because they have very similar resource requirements. Communities limited by resources such as space and food often exhibit distinct habitat partitioning between different species (Hallacher & Roberts 1985). For instance, competition can drive behavioral and/or morphological adaptations, better suiting competitors to capitalize on limited resources (Hallacher & Roberts 1985). These adaptations can lead to zonation and influence which species are more likely to survive disturbances such as intense wave action and climate change (Chelazzi et al 1997).

Organisms can also physically modify their environment and influence the settlement of other, less competitive species. Some, like the mussel *Mytilus californianus*, out-compete other species and dominate their target habitat, lowering the local species diversity until predation mitigates their effect (Paine 1966). Other organisms may facilitate the introduction of other, less competitive species by altering their habitat (Connell & Slatyer 1977). Therefore, population level adaptations or behaviors may strongly influence community level interactions. Having a comprehensive understanding of how interspecific and intraspecific interactions affect community structure is crucial for predicting the effects disturbances may have on an ecosystem’s health.
For our study, we studied *Paracentrotus lividus* and *Arbacia lixula*, two species of urchins commonly found in shallow subtidal Mediterranean reefs. While other studies have recorded other food preferences, Privitera et al 2008 suggests that *P. lividus*, the purple urchin, prefers to graze on erect foliose algae while *A. lixula*, the black urchin, grazes on encrusting coralline algae. Still, it is possible that they compete for space since research suggests that they exhibit spatial overlap in other habitats (Tuya et al 2007).

Here, we focused on inter- and intraspecific competition between *P. lividus* and *A. lixula* in Station de Recherches Sous Marine et Oceanographique (STARESO) harbor, Corsica, France. Prior to a storm in 2012, *P. lividus* outnumbered *A. lixula* within the harbor (McHugh & Elsmore 2012). Upon surveying the entire harbor to determine whether the population and distribution of the two species had changed, we found that *A. lixula* individuals outnumbered *P. lividus* individuals. Our goals were to determine the distribution of the two species, to identify the general mechanisms (such as attachment tenacity) that may have led to *A. lixula* being more abundant than *P. lividus*, and determine whether urchins associate with coralline algae patches. We hypothesized that *A. lixula* would have greater attachment tenacity than *P. lividus*; that *A. lixula* would be more competitive than *P. lividus*; that *A. lixula* and *P. lividus* would compete for resources; and that both species of urchins would associate with coralline habitats. We tested our hypotheses by measuring differences in attachment tenacity between species, removal experiments, and habitat association through the following experiments:

1. To test our hypothesis that *A. lixula* has stronger attachment tenacity, we used a spring scale to apply a force X to *P. lividus* and *A. lixula* individuals to simulate intense wave action during a storm. We predicted that *A. lixula* would be less susceptible to being torn from substrate than *P. lividus*.

2. To determine whether *A. lixula* was out-competing *P. lividus* individuals, we removed *A. lixula* from a 1m x 1m quadrat at 2.5m depth from the north harbor in replicate. We compared the results with the control where we did not remove either species, and expected to see the population in the removal quadrats to rise more quickly than that of the control quadrats.

3. To determine whether *A. lixula* and *P. lividus* compete for limited resources, we removed *A. lixula* and *P. lividus* from a 1m x 1m quadrat at 2.5m depth from the north harbor in replicate. We compared the results with the control quadrats and *A. lixula* removal quadrats. We expected the population in the quadrats where both species were removed to rise more quickly than the control quadrats and *A. lixula* removal quadrats.

4. Lastly, we placed quadrats against the north harbor wall to determine whether the urchins associated with “patchy” coralline habitats. We hypothesized that urchins would associate more with coralline red algae than with turfy algae habitats. We compared the coralline patches with patches of turfy algae as a control.

We found that *A. lixula* has significantly greater attachment tenacity than *P. lividus*; that the two species likely compete and suppress each other’s numbers; and that the urchins associate strongly with “patches” of coralline algae interspersed throughout erect algae cover.
Materials and Methods

Species Description

*A. lixula* and *P. lividus* share shallow subtidal habitats in the Mediterranean and north-east Atlantic (Bulleri et al 1999; Privitera et al 2008). However, *A. lixula* is more abundant in shallow water and on vertical substrates with high wave action, while *P. lividus* occurs on horizontal substrates and in between crevices (Bulleri et al 1999; Privitera et al 2008). *P. lividus*, found to be purple, brown, or olive green, has a circular, flattened test that is densely covered in long spines. *A. lixula*, the black urchin, has an oval test with a flat bottom. *P. lividus* feeds primarily on fleshy algae and suspended organic particles, while *A. lixula* feeds primarily on encrusting coralline algae (Privitera et al 2008). Both species are more active at night, specifically in regards to feeding.

Sea urchins’ gonads are internal and next to the anus. Urchins reproduce through spawning events, during which they release gametes into the water column. Because urchins’ gonads are a popular dish in France and Spain, urchins are harvested and exploited, resulting in fluctuations within populations and creating a more diverse and complex algal community (Guidetti et al 2004).

Site Description

We conducted this study at Station de Recherches Sous Marine et Oceanographique (STARESO), Pointe Revellata, Calvi, France throughout October 2014. The STARESO harbor contained an abundance of rocky crevices, diverse substrates, and areas of a dense algal coverage. The different types of substrate within the harbor include boulders, bedrock, cement walls, and cobble. We exploited this variable habitat to study community structure and distribution of *P. lividus* and *A. lixula*.

Methods

Initial Harbor Survey

To test our hypothesis that population density and distribution of *A. lixula* and *P. lividus* have changed drastically due to a storm in Calvi, Corsica in 2012, we conducted a thorough survey of the entire harbor for four consecutive nights, recording each urchin. The survey was done on snorkel from depths of 0 meters to 5.5 meters, and depths greater than 5.5 meters were surveyed with the help of SCUBA divers.

A separate team of students placed a permanent transect line from the entry ladder down the middle of the harbor. The permanent transect line ran for 50 meters in a straight line, essentially dividing the harbor into north and south. We tied flagging tape to the permanent transect line every 5 meters (20m, 25m, 30m, etc.) up to the 50m mark. Our survey transects ran perpendicular from the permanent transect line along the bottom of the harbor until it reached the harbor’s outer edge, or an obstacle such as a boulder near the edge (Fig. 1). We created ten transects on both the southern and northern sides, recording each *A. lixula* and *P. lividus* within each transect.

Once the transects were set up, we divided the survey into sections of depth. These sections started at the water surface (0
meters deep) to the bottom of the harbor ranging all the way to 7.4 meters at the deepest. Skin divers focused on each meter of depth while counting, for the ten total transects in the north and south. Once the depth exceeded 5.5 meters, two SCUBA divers assisted us by laying out the perpendicular transect tape and counting the urchins at depths of 5.5 meters to 7.4 meters.

**Attachment Tenacity During Wave Disturbance**

**Hypothesis 1:** If we use a spring scale to apply a force X to *P. lividus* and *A. lixula* individuals, the *A. lixula* individuals will have greater attachment strength and would be less susceptible to being torn from substrate than *P. lividus*.

We used a spring scale to recreate the effect that the 2012 storm may have had on populations of *A. lixula* and *P. lividus*. This experiment tested which urchin species had greater attachment tenacity to withstand force from wave disturbance. For the spring scale trials, three types of rocky substrates were collected for the urchins to attach to before applying force: rock covered in coralline algae, turfy algae, or completely bare. We predicted that *A. lixula* would be harder to remove than *P. lividus* and bare rock would be the toughest surface for removal. The expectations were based on the fact that *A. lixula* has flatter tests, allowing the urchin to cover more surface area with their tube feet as opposed to *P. lividus*, whose test is spherical.

First, six *A. lixula*—approximately eight centimeters in diameter and six *P. lividus* approximately nine centimeters in diameter—were collected from the harbor on snorkel. Then, the urchins were brought into the wet lab and put in a tank so they could get acclimated to the new environment. After letting them adjust to the water for two hours, we collected various bare rocks and created a rocky habitat in the tank for the urchins to settle on. Three purple and three black urchins then went into six “goodie bags” made of fish net and string. The urchins placed their podia through the net and onto the substrate, giving us the opportunity to attach the spring scale to the end of the string (Fig. 2). The extra urchins that were not being tested remained in a separate tank.

At the beginning of each trial, we applied 100 grams of force to the scale for every second that passed (ex: 5 sec. pass, spring scale shows 500g). This allowed us to calculate the total amount of force necessary for a given urchin to be torn from the substrate. We gave the urchins fifteen minutes to attach themselves to the rocks and conducted eight trials for the black urchins and eight trials for the purple urchins in total.

Once bare rock testing finished, we replaced the bare rocks with turfy algae-covered rocks. Since the bare rock urchins had lost some of their podia during the trials, a new batch of purple and black urchins were collected from the harbor to test their strength against turfy algae substrate. The same process from the bare rock trials was repeated using the turfy algae. To stay consistent, six to eight more urchins of both purple and black were collected in order to test the last substrate: coralline algae. We repeated the process again with rock covered in coralline algae, and came up with nine successful trials for both species.

After conducting the spring scale tests, JMP 11 was used to execute a one-way analysis of the data via Means/ANOVA/Pooled t. This allowed us to individually analyze the urchins’ attachment strength on the following substrate: bare rock, rock covered in turfy algae, and rock covered in coralline algae. Using this one-way analysis, we were able to view a distribution of forces each urchin was able to withstand. For all statistical analyses we accepted a critical p-value of 0.05.

**Competition Observed Through Urchin Removal**
Hypothesis 2: After removing *A. lixula* from a 1m x 1m quadrat at 2.5m depth from the north harbor in replicate, we expect *P. lividus* to populate the 1m x 1m quadrat where *A. lixula* used to be. Then, we will compare the results with the control where we did not remove either species, and expect to see the population in the removal quadrats to rise more quickly than that of the control quadrats.

Hypothesis 3: After removing *A. lixula* and *P. lividus* from a 1m x 1m quadrat at 2.5m depth from the north harbor in replicate, we expect both species to recolonize the 1m x 1m quadrat. Then, we will compare the results with the control quadrats and *A. lixula* removal quadrats. We expect the population in the quadrats where both species were removed to rise more quickly than the control quadrats and *A. lixula* removal quadrats.

To study the competitive nature of *A. lixula* and *P. lividus*, twelve quadrats, 1 meter by 1 meter each, were set up on a rocky substrate. We color-coded the quadrats with flagging tape and divided them into sets of three (Fig. 3). Color organization allowed categorization of the quadrats into a control (red), removal of black urchins (yellow), and removal of both species (silver).

![Fig. 3: Quadrat one had red flagging tape on the stakes, quadrat two had yellow tape, and quadrat 3 had silver tape.](image)

We chose a region in the north end of the harbor with a variety of both purple and black urchins at a depth between two and three meters. First, a row of six quadrats was set up with the colored stakes that ran parallel to the north wall. Directly below that row, we arranged two rows each containing three 1m x 1m quadrats (Fig. 4) The 1m x 1m quadrats were created by using a PVC pipe square with dimensions of 1m x 1m as a stencil, enabling us to place the stakes at each corner.

![Fig. 4: Exact layout of 12 quadrats in north harbor for quadrat experiment](image)

An initial survey of the urchins in each square was taken for comparison. After the first night, we dove for seven consecutive nights at 8:00 pm on snorkel. The second night of the experiment, we removed urchins from the corresponding quadrats. All four red quadrats were considered “controls” and left alone regardless of the number of urchins that migrated in and out. All four yellow quadrats had black urchins removed and all four silver quadrats had both purple and black urchins removed. Each of the initial urchins that were removed lived in the tanks outside the wet lab. Every night after the first night of removal, the number of urchins in all of the quadrats were recorded to show which urchins moved in and where. As the trials continued,
we would continually remove the black urchins from all yellow quadrats, however, the silver quadrats were left alone.

After removing *A. lixula* from the yellow 1m x 1m quadrats and removing *A. lixula* and *P. lividus* from silver 1m x 1m quadrats, the data was entered into Graph Builder using JMP 11 to picture the rate of population growth by day. This enabled us to picture the slope of the population growth in the control quadrats, the quadrats in which *A. lixula* were removed, and the quadrats in which *P. lividus* and *A. lixula* were removed.

**Wall Community Classification and Observation**

*Hypothesis 4:* We will place quadrats against the north harbor wall to determine whether the urchins associated with “patchy” coralline habitats. We hypothesize that urchins would associate more with coralline red algae than with turfy algae habitats. Then, we will compare the coralline patches with patches of turfy algae as a control.

In order to determine whether urchins associate with coralline “patches” in their environment, our team used a meter tape to trace a chalk line across the north harbor wall. We then used chalk to mark (above the water line) where the urchins were at night, and delineated “patches” of coralline algae vs. turfy algae. Next, we characterized those habitats by placing 50 cm x 50 cm quadrats against the wall and counting the number of erect and coralline algae, rock, film (of green algae), limpets, snails, sea stars, sponge, and urchins we found. Following this, for 5 consecutive nights, team members counted the number and species of urchins present in the coralline patches. This experiment was done entirely on snorkel. Overall, there were 6 patches of coralline algae, along with 6 replicate control “patches” where erect algae dominated. After conducting the urchin swaths along the north wall of the harbor, our data was entered into JMP 11 to view the relationship between urchin abundance and coralline vs. control patches. If the density of urchins within the coralline patches was much higher than that in the control patches, we will conclude that urchin grazing creates “patchiness” in the habitat and may facilitate the presence of other species.

**Results**

*Initial Harbor Survey*

We found *A. lixula* abundance to not be significantly different between North and South Harbor throughout the survey (Fig. 5, P=0.1030). *P. lividus* appeared almost exclusively in North Harbor, with very few individuals found in South Harbor (Fig. 5, P=0.0001). We found a difference in urchin distribution in the two portions of the harbor (Fig. 5, P=0.0005). The highest urchin abundance for both species occurred in the shallow 0-5m transect and decreased with distance from the 0-5m transect (Fig. 6, P=0.0082).
Attachment Tenacity During Wave Disturbance

The spring scale experiments conducted using *A. lixula* and *P. lividus* on bare rock, turfy algae, and encrusted coralline algae, determined each species’ attachment tenacity to the rock surface. On bare rock, *A. lixula* required an average of 2043.75 grams of force from a spring scale experiment.
dynamometer to be removed from the rock, *P. lividus* required an average of 406.25 grams of force. Our results indicate that *A. lixula* may have a higher tenacity than *P. lividus* while attaching to bare rock (Fig. 7, *P*=0.014). Using coralline algae, *A. lixula* required an average of 950 grams of force to be removed from the substrate, whereas *P. lividus* required an average of 372.22 grams of force. *A. lixula* exhibited higher tenacity on coralline algae than *P. lividus* (Fig. 7, *P*=0.0021). While attaching to a rock covered in turfy algae, *A. lixula* required an average of 493.75 grams of force for removal, which was significantly more than *P. lividus*, which required 197.5 grams of force (Fig. 7, *P*=0.0055). Overall, a significantly different amount of force was required to remove urchins from the varying substrates (Fig. 7, *P*=0.0220).

![Force required to remove urchins](image)

Figure 7: Force required to remove *A. lixula* and *P. lividus* from bare rock, coralline algae, and turfy algae. *A. lixula* demonstrated stronger attachment tenacity than *P. lividus* in each substrate tested, with the greatest force required to remove black urchins from bare rock.

**Competition Observed Through Urchin Removal**

On the first night of quadrat observations, we conducted a preliminary survey. After the survey, four red quadrats were placed as controls in areas of relatively similar urchin populations to the treatment quadrats. 14 *A. lixula* were removed from the four yellow quadrats so they were completely void of *A. lixula*. All urchins (7 *A. lixula* and 18 *P. lividus*) were removed from the silver quadrats. Over the seven nights of observation, urchin populations fluctuated at different rates within the twelve manipulated quadrats (Fig. 8, *P*=0.0075). The control quadrat populations rose by an average of 2.0 individuals after seven days. The *P. lividus* population in the quadrats where only *A. lixula* were removed rose by an average of 2.75 individuals over the seven days. The urchin populations in the quadrats where both *A. lixula* and *P. lividus* were removed rose by an average of 5.0 individuals of both species combined over the seven days.
Figure 8: Change in population per day in quadrats where both *A. lixula* and *P. lividus* were removed, quadrats where only *A. lixula* was removed, and quadrats where no urchins were removed. Observations of population change began the day following initial manipulations (i.e. removal). The populations with both species removed recovered at a faster rate than the controls and the populations with only *A. lixula* removed.

Wall Community Classification and Observation

The initial surveys conducted along the harbor wall showed variation in substrate abundances between control (turfy algae) and treatment (coralline algae) patches (Fig. 9). Control “patches” showed less variation in substrate than the treatment “patches” since they were dominated by erect algae (Fig. 9). The urchin swaths showed low urchin abundance in the turfy algae sections of the wall (control) and high urchin abundance in coralline algae regions of the wall (treatment). This demonstrates a significant relationship between the presence of urchins and encrusting coralline algae (Fig. 10, P<0.0001).
Figure 9: Turfy and coralline algal community compositions along the walls of STARESO harbor. We estimated abundance of coralline algae, erect algae, film, and rock by counting points on 50 cm x 50 cm quadrats. Each error bar represents one standard error.

Figure 10: Urchin swaths on turfy (control) and coralline (treatment) algae. The density of urchins is greater in the treatment habitats than in the control habitats. Error bars represent one standard error.

**Discussion**

Initial Harbor Survey

Our initial urchin surveys conflicted with results from a similar survey done in 2012 that previously found *P. lividus* was more abundant in STARESO harbor (McHugh & Elsmore 2012). Our data suggests that this is no longer the case. In particular, South Harbor was inundated with *A. lixula* (85% of urchins present in the South, 49% of urchins in North Harbor).
This could be due to the fact that South Harbor is exposed to strong wave action, while North Harbor is more protected.

A study done on Mediterranean reef assemblages found that densities of *A. lixula* were higher on the windward side of the study island than on the leeward side, where *P. lividus* was more populous (Micheli et al 2005). This could coincide with our results from the spring scale experiment showing that *A. lixula* has greater attachment tenacity than *P. lividus*. This survey allowed us to notice a change in *A. lixula* and *P. lividus* abundances and provided a record for future urchin studies in STARESO harbor.

**Attachment Tenacity During Wave Disturbance**

*A. lixula* required more force to be removed from the substrates tested -- bare rock, turfy algae, and coralline algae -- than *P. lividus*, so we accept our hypothesis. Our results suggest that *A. lixula* is less affected than *P. lividus* by physical perturbations, such as wave action during storms. Although we initially proposed using a flow tank to test urchins’ attachment tenacity, the spring scale allowed us to test tenacity regardless of wave direction.

Both urchin species were able to withstand more force when attached to bare rock than when attached to rocks covered in coralline algae or turfy algae. This indicates that urchins may be less able to attach to algae. Also, *A. lixula*’s test has a flatter shape than *P. lividus*, potentially giving it a more hydrodynamic form. As previous research shows, having a high adhesion-surface to body height ratio can reduce the risk of dislodgment from a substrate by wave action (Rilov et al 2005). A separate study demonstrated that *A. lixula* has a higher adhesion-surface to body height ratio than *P. lividus* (Tuya et al 2007). Therefore, it is possible that the shape of *A. lixula*’s test gives it stronger attachment tenacity than *P. lividus*.

Our results provide evidence that *A. lixula* has greater attachment tenacity regardless of the attachment substrate, and may provide an explanation for the abundance of *A. lixula* in South Harbor, STARESO. When storms hit STARESO, the southern side is more exposed to powerful waves, therefore crushing the intertidal and subtidal zone where urchins live. However, the north side is shaped like a protected pocket facing away from the majority of incoming waves. By the time waves reach the north wall, a portion of the energy may have dissipated. Our data suggest that *P. lividus* have a weaker tenacity than *A. lixula* and may prefer areas with less wave disturbance. This is potentially the cause of the pattern we found during the harbor survey with a low abundance of *P. lividus* in the south side. *A. lixula*’s likely stronger attachment tenacity may have allowed it to better survive the 2012 storm than *P. lividus*.

Little research has been done to examine the relationship between strong wave action and the reproductive health of *A. lixula*; this has been studied in *P. lividus*. Gianguzza et al 2013 showed that *P. lividus*’ gonad mass was lower in areas with high hydrodynamism. Studying the reproductive health of *A. lixula* in the context of disturbances could further our understanding of the mechanisms that drive a species’ reproductive success.

**Competition Observed Through Urchin Removal**

The *P. lividus* population in the *A. lixula* removal quadrats grew at a slower rate than the quadrats where both species were removed, but more quickly than the control quadrats, allowing us to accept our hypothesis. This may be due to the intraspecific competition between the already present urchins, although interspecific competition was removed. The quadrats with both species removed were repopulated at the highest rate because both inter- and intraspecific competition were removed, allowing us to accept our hypothesis.
Research suggests that *A. lixula* is more abundant on shallow, vertical substrate exposed to wave action, than *P. lividus* (Bulleri et al 1999). In context with our results, this may imply that the two species are spatially competitive, leading to zonation patterns. In contrast, Bulleri et al 1999 also conducted removal experiments and did not find strong evidence for interspecific competition between *A. lixula* and *P. lividus*. This led the researchers to suggest that factors other than competition may have affected the current zonation patterns.

Our removal experiments had the benefit of showing us the direct effects intra- and interspecific competition have on a population. An increased duration and larger study area would have strengthened this experiment. Due to spatial constraints on the study area, the quadrats were within close proximity to each other. We expected the urchin populations in the control quadrats to remain relatively similar over time, but the populations rose instead. The control quadrats contained few *A. lixula*, possibly resulting in a population change resembling that of the quadrats where *A. lixula* was removed.

Wall Community Classification and Observation

We accept our hypothesis that urchins associate with the coralline patches. Our results demonstrate a significant relationship between the presence of *A. lixula* and *P. lividus* and patches of crustose coralline algae (P = <0.0001). Studies have shown that urchin herbivory suppresses the growth of fleshy algae, allowing coralline algae and other organisms to colonize barrens (Bulleri et al 1999). Specifically, urchin herbivory may facilitate the introduction of the endangered Mediterranean *Patella sp.* limpets by preventing erect algae from dominating the substrate (Bulleri et al 1999). Thus, urchin herbivory may indirectly affect the available substrates and diversity of algal communities.

Privitera et al 2008 has shown that *A. lixula* prefers to consume encrusting coralline algae and *P. lividus* prefers to graze on erect turfy algae. It is possible that *P. lividus* may have a stronger influence on the maintenance of these patches, but more research is required. Our study contributes evidence to urchins’ association with coralline red algae; however, its weaknesses lie in the brief duration of our study. With more time, we may have been able to design a study demonstrating that urchin herbivory suppresses fleshy algae growth and facilitates the introduction of coralline algae.

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Literature Cited


