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UPPER AND LOWER LIMITS OF ROCKY SHORE ORGANISMS AT DIFFERENT SPATIAL SCALES AND WAVE EXPOSURE (ISLAS CÍES, NW SPAIN)

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Key words: intertidal zonation, temperate coast, rocky shores, lichen, algae, sessile invertebrate, digital image analysis, linear mixed effects models.

ABSTRACT

A photographically sampling was conducted at Islas Cíes, NW, Spain with the goal of determinate the upper and lower limits of vertical distribution of sessile organisms on the intertidal rocky shore of this National Park. The response of the species to different Atlantic Ocean exposure was tested at west coast (exposed) and east coast (sheltered) of Islas Cíes. The sampling was made following a hierarchical spatial design. The contribution in the variation around the mean of the intertidal limits of each organism at diverse spatial scales in the rocky shore was estimated with Linear Mixed Effects Model with software R. The majority of the species were found to increase their upper limits in the exposed coast of the two islands. Several intertidal algae, mainly the fucoids, were absent at the exposed shore and this pattern could be influenced by excessive turbulence. The variation at large spatial scales was related to changes in the degree of exposure between islands. Physical characteristics and biological interactions accounted for the variability observed on the intertidal. The spatial heterogeneity introduces variability from very small to mid spatial scale. The species presented in the low intertidal have more variation at small scale (meter to tens of meters), and the organisms in the high intertidal vary their limits at medium scale (tens to hundreds of meters). The life cycle, adaptations, ecology and natural history of the intertidal organisms described in previous studies of Galician, Portuguese, and the British shores may explain the patterns found in Islas Cíes.

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INTRODUCTION

The upper limits of the vertical distribution of intertidal organisms are determined by increased desiccation, higher temperatures, or stronger solar radiation. In the life cycle of the organisms, the first stages and in some cases the adults, are less tolerant to increasing desiccation. The upper and lower limits of the distribution of common intertidal organisms on a rocky shore are most frequently located near the critical levels environmental parameters (Connell, 1972). The abundance of crevices and other types of spatial heterogeneities allow the expansion of the upper limits of distribution to higher levels than on plain surfaces (Menge, 1976).

Biological interactions have an important role on determining the lower limits of distribution and relative abundance of a species. Typical examples are the competition for space among barnacles, the presence of sea stars predators (known as keystone species), and herbivorous species at low intertidal levels (Connell, 1972). Moreover, oceanographic factors as wave exposure, currents, and upwelling can influence the geographical distribution of the species and the composition of the rocky communities in several ways. These factors change the values for abundance, coverage, patchiness, or the vertical intertidal limits (Little & Kitching, 1996; Menge *et al*, 1997; Schiel, 2004).

Underwood (2000) indicated that intertidal snails change more in their density at centimeters to meters scale influenced by local topography, food availability, and micro-climates. The magnitude of change decreased at higher scales due to biological interactions, recruitment success, and the magnitude of physical disturbances. Finally, the density varies less due to wave-action and storms between localities spaced at hundreds of meters to km (Underwood 2000). On the other hand, Denny *et al.* (2004), sampled along an intertidal shore and found higher variation in the diversity of intertidal species at large scale (334 m long transect), than at a small scale

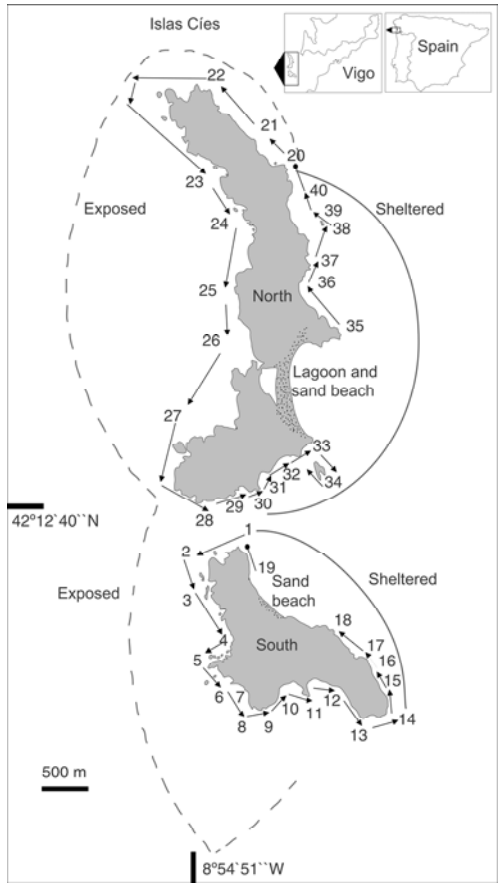


Figure 1:
Distribution of coast line sections between and their exposure conditions in each island of the National Park Islas Cíes, NW Spain. 2009. Exposure lines based in Acuña-Castroviejo et al. 1984b

(44 m long transect). They used a transect sampling and the close quadrats (-0.5-m intervals) were more similar than the more spaced (-3.4-m intervals). Denny *et al.* (2004) criticized that Underwood and Chapman (1996) had localities matched and that the variability at large scale was removed by the sampling design. Denny *et al.* (2004) sampled without replicates for each observation point within each transect, contrary to Undewood & Chapman (1996) that had more replicates per site. In the present study, the intertidal limits of the organisms of a rocky shore were measured as continually was possible. The

sampling design was hierarchical, with measures at different nested spatial scales. Using this method, the contribution of each spatial scale in explaining the variation of intertidal limits of the organisms was separated at Islas Cíes of the Galician coast, Spain.

The Galician coastline is composed manly granite rocky shores. In this region coastal upwelling during summer and water temperatures around 14 ºC, produce environmental conditions similar to those found at more northerly latitudes. The algal flora has more affinities with floras of northern European latitudes (Arrontes, 2002). However, few ecological studies have been made on the ecology of these rocky intertidal communities. Perez-Cirera (1975) point out the difficulty of collecting algal specimens on the cliffs of NW Spain. Niell (1977) sampled along vertical profiles of the zonation patterns in the Ría de Vigo, and found the expected pattern of change according with the ocean exposure. Recently, Olabarria *et al.* (2009) studied the dynamics of exposed rocky shores of the Ría de Vigo.

The National Park of Islas Cíes is located outside of the Ría de Vigo estuary and play a role as natural barrier between the Ría and the Atlantic Ocean (Figure 1). The communities in this rocky archipelago have not been adequately sampled at the present time. Acuña-Castroviejo *et al.* (1984a) mentioned that the littoral of Islas Cíes was only used as an algae and invertebrate collecting station. The only intertidal sites studied quantitatively in Islas Cíes were at the sheltered shore of the North Island (Figure 1) during April and May of 2003, as part of a survey to quantify the impacts of the Prestige oil spill. The rocky intertidal walls were sampled with 40 x 40 cm quadrats and photographs of each one were used to estimate the mean species cover by digital image analysis (Besteiro-Rodríguez, 2004). The West Coast of the Islas Cíes is directly exposed to the Atlantic Ocean and to wind influence (Acuña-Castroviejo *et al.*, 1984b), and their intertidal cliffs are under the impact of heavy waves and were never sampled before.

Mettam (1994) sampled the Bristol Channel and Servern Estuary rock cliffs photographically and produce vertical profiles of the dominant species. Sibaja-Cordero (2008) sampled the cliffs of the Cocos Island, Costa Rica (5º30'N and 87º03'W) with digital photography and studied the upper limits of sessile species. With these photographic methods Mettam (1994) and Sibaja-Cordero (2008) were able to show the variation in the limits of intertidal species in rocky shores at different latitudes. Using similar methods, the present study provides a description of the distribution of algae, lichens, mussels, and barnacles, along the rocky coast line of Islas Cíes by their presence or absence in the North or South Islands and the eastern or western faces of the archipelago. For each organism, the heights of the upper or lower limit of distribution above the low tide level were estimated. The effect of ocean exposure on these limits is tested by comparison between the eastern faces (sheltered) with the western faces (exposed). The variability of the intertidal limits of the benthic organisms at these different scales: centimeter to meters, meters to tens of meters, tens to hundreds of meters, or the whole faces of the islands, is also evaluated.

MATERIALS AND METHODS

The rocky shore of the South and North Islands of the National Park Islas Cíes, N.W. Spain, were sampled at low spring tide on 28 of February and 14 of March 2009, respectively when the sea was "calm". The rock walls of the coast around the islands were surveyed photographically from a boat equipped with 75 HP outboard motor. The coast line at each island (South and North) was divided in two: a western face (exposed to ocean influence) and eastern face (sheltered). Within each island face several transects were made and the rocky coast line was divided into a total of 40 sections (Figure 1). The geographic coordinates of start-end of each one of these sections were obtained with a GPS (Table 1). In each section several pictures (7 megapixels) were taken with a digital camera (Table 1). A total of 482 images were

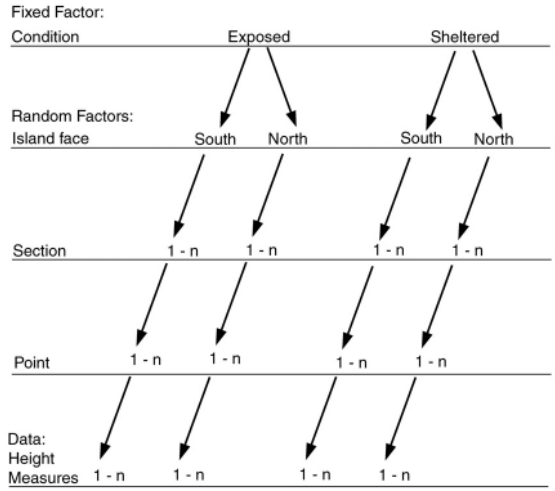


Figure 2:
Hierarchical spatial design used to study the rocky coast organisms of Isla Cíes, NW Spain. The random factors Section, Point and the repeat measures of height in each point were unbalanced at the n-th level

taken, each one from an independent point of the rocky shore wall. Each picture showed the complete rock wall from the water level to the limit of vascular vegetation.

The height (~35 cm) of the gull, *Larus cachinans* captured on first plane in each picture was used for calibrating the spatial scale of images and convert the x-y pixels coordinates to a metric scale. In this way the height (y axis of the image) above the low tide sea level of each sessile organism was estimate in centimeters by digital image analysis, with the "point" command of the UTHSCSA Image Tool, developed by the University of Texas Health Science Center, San Antonio, Texas (http://ddsdx.uthscsa.edu/dig). For each image a sequence of points was used to mark the limit of the bands, fringes or patches of each organism (Sibaja-Cordero 2008). The height represents the upper and/or the lower limits for marine organisms: algae, mussels, barnacles, and lichens, and the lower limit of terrestrial lichens and vascular vegetation.

Data analysis

The oceanic exposure condition (exposed or sheltered) is an informative fixed factor (Figure 2), that could have an effect on the mean height above low tide sea level of the populations of organisms (Little & Kitching, 1996). Within each condition, the sampling design is a hierarchical spatial division of the coast (Figure 1 and 2), with two replicates (island face South and the North), and within each island face are nested the sections, and points (pictures) of the rocky shore. The goal is measuring the effect of these random factors (spatial scales), on the variance around the mean height above sea level in each organism. Similar hierarchical designs were used in other rocky intertidal studies (Underwood, 2000).

The number of sections by island face is unbalanced, because the islands differ in outline of the coast line, and within each island the western and eastern faces are also different (Figure 1).

The number of images is also unbalanced. Some distorted pictures caused by the boat movements were discarded. Finally, within each of the 482 images used the number of height measures varies because the bands, fringes, or patches of each organism were interrupted by other organisms or bare rock. The sampling design was unbalanced and has different levels of spatial pseudoreplication. To overcome this problem with the data matrix, Crawley (2007), recommend using a Linear Mixed-Effects model (LME), instead of Analysis of Variance. Therefore, a LME model was carried out for each organism using software R (R Development Core Team, 2008), with the function lmer that is part of the lme4 package created by Bates *et al.* (2008). To construct the LME models the steps by Crawley (2007) and Rodríguez (2007) were utilized, as well as the implementation instructions of lme4 (Bates *et al.*, 2008). The initial estimate model for the sampling design in Figure 2, was calculated in R as follows:

Height ~ condition + (1 | condition/island face/ section/point)

The response variable (height) is specified to the left of the tilde ~ and the fixed factor (condition) on the right (Crawley, 2007). The random part of the model is enclosed in parentheses. Following the plus sign, and to the right of the symbol | the random factors are showed from largest to smallest scale (island face, section and point), nested in each level of the fixed factor (Crawley, 2007). Bates & DebRoy (2004) discuss the extended notation of the LME models.

The model assumptions of homoscedasticity (variance do not increases with the mean) and normality distribution of the residuals, were checking with the plot of residuals as a function of the fitted values and the QQ plots, respectively (Crawley, 2007; Quinn & Keough, 2003). When the assumptions were violated (Figure 3), the Box-Cox transformation of height by condition (fixed factor) was used as guide to found the appropriate power transformation and the model was corrected and run again (Figure 3), (Crawley, 2007). Finally, the non pseudoreplicate degrees of freedom (d.f) for the fixed factor are 2 = 4 – 1 – 1, by four island face (replicates), two level of condition (exposed-sheltered) less one, and less one estimate parameter (Crawley, 2007). However, the t value in the output of LME does not follow a Student's T distribution, with unbalanced data and large number of groups and observations (Bates *et al.*, 2008). The p value do not be calculate in usual way (Bates *et al.*, 2008), and the decision rule are all $|t| > 2$ are significant ($p < 0.05$), (Crawley, 2007; Bates *et al.*, 2008).

RESULTS

Organisms in bands

The infralittoral zone of the Archipelago showed a dense band of species of Rhodophyta. The upper limit of this band increased from 80cm in sheltered condition to 168cm in the exposed condition (t: -5.24, $p<0.05$) (Figure 4). The variation around the mean was lower between islands (Table 2), but exposed faces presented more change than sheltered coast (more stable height mean) (Figure 4). The variation produced by sections account for 20% and was more marked in the exposed condition (Figure 4). The mayor source of variation was present in small scale (61%), by changes of height from point to point of the shore within each section (Table 2). The higher standard deviations at section scale were present in exposed condition of both islands (Figure 4). Differences between measures were of 18% (Table 2).

The band of the mussels, *Mytilus galloprovincialis* was presented in sheltered condition from the infralittoral to 190 cm above the low tide, and reached above 262 cm in the exposed condition (t: -3.31, $p<0.05$). The mean of the upper limit varied low within each condition between North and South Islands (Table 2; Figure 4). The variation between sections was of 23% (higher in exposed coast), and in the same way the variation inner sections (62%)

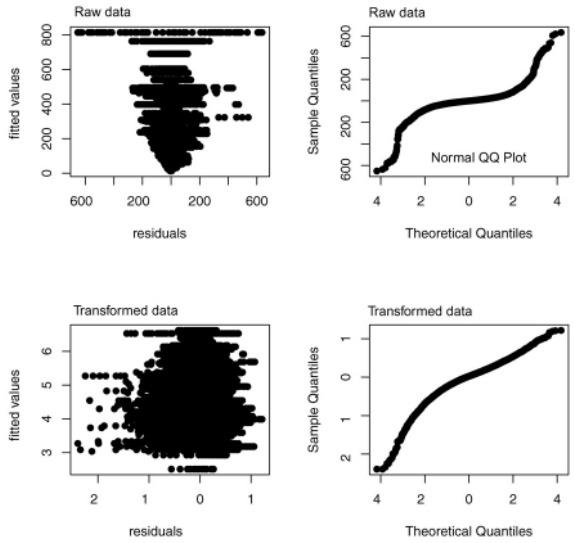


Figure 3:
Graph checking of the assumption of homoscedasticity and normality of the residuals in Linear Mixed Effects models of height above tidal level for raw and transformed (Ln) data. With the transformation the fan-shaped pattern in the raw data residuals vrs. fitted values (heteroscedasticity) was corrected and the residuals are reasonably close to normally distributed.

(Table 2, Figure 4). During the sampling, white patches of dead *Balanus* barnacles were found in sheltered sites at both islands (Figure 5). The patches were immersed in the band of mussels and follow a similar distribution.

The species of barnacles (Cirripedia) showed a trend to increase in their upper limit from 245 cm in sheltered coast to 324 cm in exposed condition, but the variation at larger scale accounts to only 9% (Table 2), with more change between sheltered faces (Figure 4) resulting in a non significant ocean exposure effect (t: -1.38, $p>0.05$). Similar to that found for the red algae and mussels, the variance around the condition means have more change in the exposed conditions. Variation between sections (23%) was lower than within sections (58%), but less change was found between measures (9.8%), (Table 2).

The upper limit of the black lichen, *Verrucaria maura* increased higher from sheltered coast (5m) to exposed condition (11.8m), (t: -6.20, $p<0.05$). In comparison with the previous organisms the source of variation (Table 2) increased in sections (42%) and decreased between sections (44%). *V. maura* presented higher internal changes in their upper limit in the exposed condition (Figure 4).

The lower limit above low tide of the orange lichen, *Caloplaca marina* was of 5m in sheltered coast and increased to 15.7m at exposed condition (t: -4.54, $p<0.05$). The variation at larger scale was of 8% (Table 2). Between the exposed faces (North and South), *C. marina* presented a difference of 8.9m between their lower limit (Figure 4). On the other hand, between sheltered faces this species has low change (Figure 4). The variation between sections was higher (54%) and more abrupt in the exposed North face. The deviation within sections decreased to 31%. The sheltered coast presented the lowest variation (Figure 4).

Vascular vegetation colonized at a lower height

(5.3m) in the sheltered condition than in exposed shore, where the plants appear at 12.9m above low tide level (t: -5.95, $p<0.05$). The contribution in the variation by the faces was low (Table 2), but exposed faces presented variation of 3.5m around the mean height (Figure 4). The remaining of the variation was distributed similarly to the orange lichen, *C. marina* (Table 2).

Organisms with interrupted fringes or patches

The red algae, *Asparagopsis armata* was present mainly in sheltered faces. The upper limit was well defined in this condition, with low variation between islands (Table 2, Figure 5), but alternated between patches or fringes of the rest of red algae species. The observed scenario introduces variation at small and very small spatial scales (Table 2). Moreover, the species occurs in patches in some exposed sections and an increased in the variation at larger scale occurs (22%). *A. arnata* did not show a difference in upper limit height when found either in exposed coast or sheltered condition (t= -1.565, $p>0.05$).

Around the rocky shore of North and South Islands black patches or less defined fringes of *Mastocarpus stellatus* in their tetrasporophyte crust phase "*Petrocelis*" were found. This organism occurred from the infralittoral to a height of 163cm in sheltered conditions, and reached 318cm in exposed condition (t=-2.51, $p<0.05$). The exposed face presented variation in this upper limit more than sheltered faces (Table 2, Figure 6). The rest of variation decreased from medium scale to very small scale (Table 2).

Fucus spiralis was present mainly in sheltered faces formed a fringe. It was found in sections 10 and 11 of exposed coast of South Island, resulting in high variability at large scale level (Table 2), However, no difference between ocean conditions was found in the lower limit (t=-0.098, $p>0.05$) and the upper limit (t=0.084, $p>0.05$) above low tidal level (Figure 5). The fringe of *F. spiralis* varies highly between points inner sections, but varies less at very small scale (Table 2). Above or below of *F. spiralis* several small patches of *Pelvetia canaliculata* were found in sheltered coast (Figure 5). A film fringe of algae was present in sheltered faces in the high littoral (2.5m), but occurred in sections 10-12 at 4m, with higher variation and no difference in upper limit height was found (t=-0.424, $p>0.05$). Film showed similar distribution of their variation as *F. spiralis* (Table 2).

Above the mussels, barnacles and fucoid algae were found a fringe of bare rock that concluded in the lower limit of lichen *V. maura*. The height of the upper limit (Figure 5) was higher at exposed condition (t=-2.3, $p<0.05$). No variation was found between islands, and the sections vary higher in exposed coast (Figure 5). The bare space was wider in exposed condition than in sheltered (Figure 5) where the fringe was repeatedly interrupted by the organisms.

Organisms in patches

The infralittoral has a cover of the green algae *Ulva rigida*. The algae was nearly absent in North exposed face (Figure 6). In the exposed shore of South Island it reaches a high of its upper limit (>1.8m) than in sheltered condition with 1m above low tide (t=-5.4, $p<0.05$). Other algae *Bifurcaria bifurcata* was present mainly in sheltered faces (Figure 6). *B. bifurcata* also form patches in some sections of exposed shore and occurred with similar height than in sheltered condition (t=-0.361, $p>0.05$). In the high littoral patches of the green algae *Ulva intestinalis* sporadically occurs and showed a difference in the upper limit height. The limit was high in exposed South face than in the sheltered sections (t=-5.4, $p<0.05$). The biofilm of cianobacteria occurs also sporadically in the high littoral and not showed a difference in height between exposed or sheltered conditions (t=-1.964, $p>0.05$). This group of sessile organism that occurs in patches has most variation at small scale and increased with the height on the intertidal. Finally, isolated patches of red algae were found in some crevices of the sheltered South face (Figure 6).

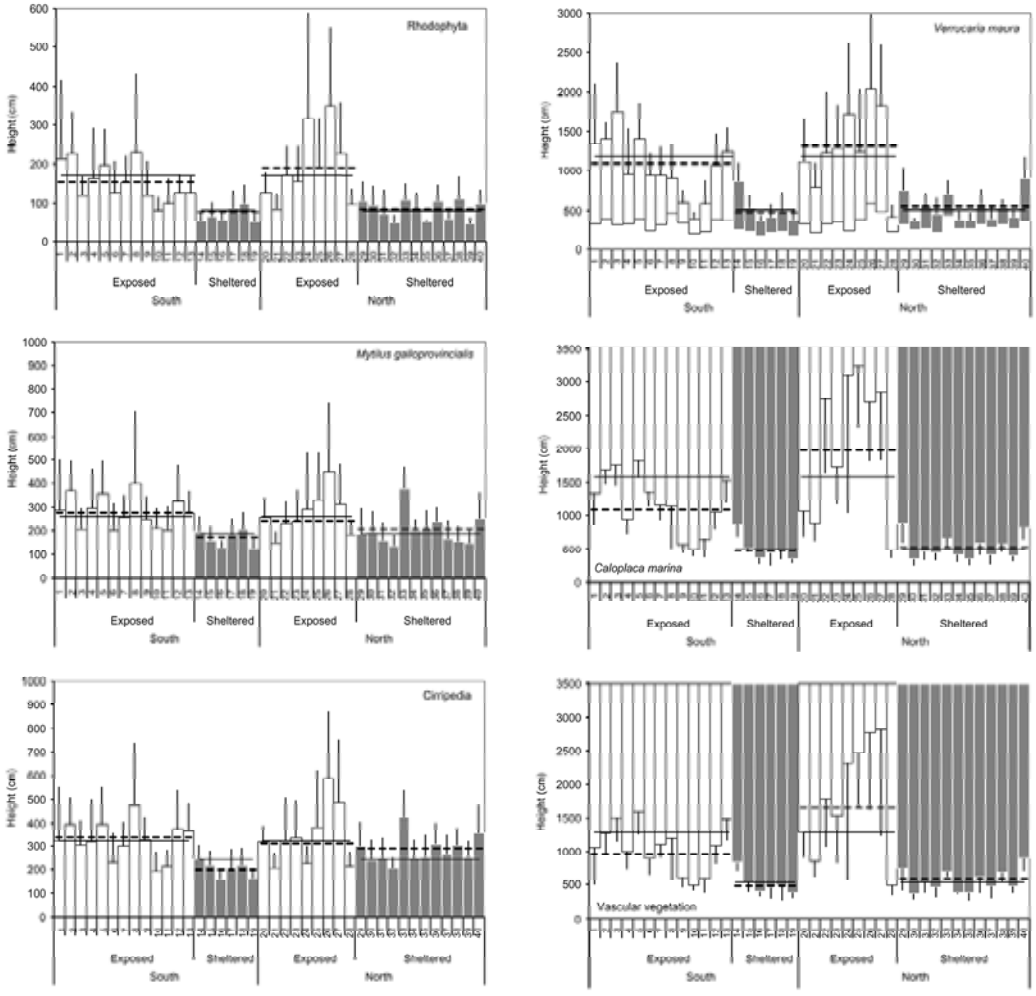


Figure 4:
Upper and lower limits of rocky coast organisms of Islas Cíes, NW Spain. Bars: height mean (cm) above low tide for section of the coast, with their standard deviation. Line in scripts: height mean above low tide for each face in each island. Straight line: general height mean above low tide for the exposed or sheltered condition to Atlantic Ocean influence

DISCUSSION

The variation at mid scale (tens to hundreds of meters) in the intertidal limits of the organisms in Islas Cíes was less for species in low littoral and increased for species living at higher levels. Underwood (2000) point out that the variation in gastropod abundance at this scale could be attributable by changes in recruitment or physical disturbances due to weather. At Islas Cíes the mainly source of variation for the intertidal limits of the sessile organisms was the geographical accidents that increased the extension of the splash zone. Other cause may be the differences in the ranges of the tidal cycle along the year, that may bring larvae and propagules of marine species to higher height, or reduce the presence of terrestrial organisms up in the intertidal. The sessile species that live in low intertidal presented a greater variation at

small scale (meter to tens of meters), that could be related to the inclination and orientation of the rock (Menconi *et al.*, 1999). The hard substrate presented a changing desiccation time and in this way the variation decreased for species that live up in the intertidal (best adapted to the desiccation). The low variation at very small spatial scale (centimeter-meters) is attributable to the heterogeneity of the topography caused by crevices (Underwood, 2000). Several patterns occur for each space scale according to the differences in the natural history of each species (Menconi *et al.*, 1999) that they also are reflected in the response of these organisms to the wave exposure.

Red algae

The basal stratum in the very wave beaten shores of Galicia is dominated by *Corallina elongata* and *Lithophyllum incrustans* (Cremades-Ugarte *et al.*, 2006). The belt of red algaes (Rhodophyta) in the present study increased on the exposed shore and was found with low variation between islands. The oscillation around the mean was more marked at the exposed condition. In the cliffs of NW, Spain the communities between 0.5-3m above the low tide level are composed by cespitoses and brown-blackish color algae (*Ceramium*, *Callithamnion* and others), but bellow the 0.8m in exposed localities dominated the corallines. The algae belt of Islas Cíes was in pink color by the high contribution of *Corallina officinalis*, *L. incrustans* and *Chondrus* (Perez-Cicera, 1978). Other algae common in the Galician low littoral is *Gelidium sesquipedale*, present in localities of North and South of Vigo (Besteiro-Rodríguez, 2004). The change in dominance of species above the 0.8m made raise the belt in the exposed faces of the Archipelago. Leigh *et al.* (1987) found that on exposed shores the wave energy enhance productivity of resident algae, by increase the capacity for acquire nutrients and protect they from grazers species.

The variation between sections in Islas Cíes accounts 20% (higher in exposed condition). Changes in physical factors may also affect recruitment, growth, and mortality of macroalgae, producing spatial variability at mid to large scales (Menconi *et al.*, 1999). Araújo *et al.* (2005) found in N Portugal that the dominance in each assemblage is usually attributable to particular species with high cover. In the present study, the dominant coralline belt was interrupted in the sheltered faces by fringes or patches dominated by, *Asparagopsys armata*. Besteiro-Rodríguez (2004) previously found *A. armata*, and *Ceramium cilliatum* at this level in Islas Cíes. Across transects at the same height level, large variability occurs also on the composition of algae in North Portugal rocky shores (Araújo *et al.*, 2005).

The small scale variation of red algae in Islas Cíes (between points of the shore) was 61%, more evident in the exposed condition. Underwood (1980) found that the upper limit of frondose macroalgae in Australia increased in absence of herbivorous. His results demonstrate that the exclusion of grazers from mid-shore levels led to colonization by frondose algae above the normal upper limit of their distribution. After the colonization of the bare rock in the mid littoral, the physical factors controlled the upper limit of algae (Boaventura *et al.*, 2002). These effects suggest that the upper limits of algae belt are given by physical stress and grazing (Underwood, 1980). Ortega (1987) found that the variation of grazer's abundance could be due by the orientation of the rock from point to point in the shore. The measures of the upper limit of the algae belt in Islas Cíes had a variation of 18% due to the heterogeneity and inclination of substratum and their influence on the establishment of benthic organisms (Menconi *et al.*, 1999).

The allien rodophyte, *A. armata* was introduced to Europe in the early years of the XXth century. This species was reported at the same time at several localities on Atlantic and Mediterranean shores around 1940 (Rindi & Guiry, 2004; Bárbara *et al.*, 2005). *A. armata* occurs mainly in sheltered coast of Islas Cíes, but appears also in the cove of the exposed face of the South Island (points 9-12) at similar

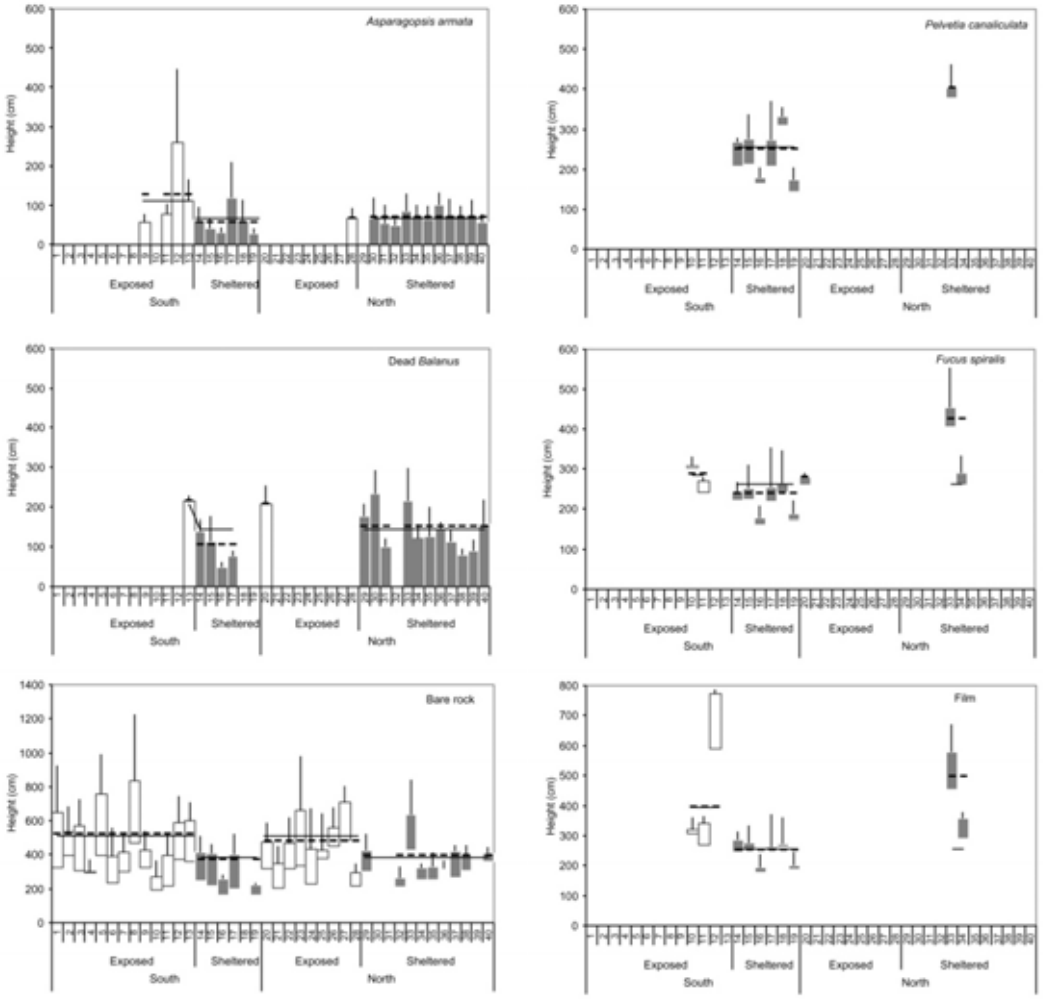


Figure 5:
Upper and lower limits of intertidal organisms and bare rock of Islas Cíes, NW Spain. Bars: height mean (cm) above low tide for section of the coast, with their standard deviation. Line in scripts: height mean above low tide for each face in each 28 island. Straight line: general height mean above low tide for the exposed or sheltered condition to Atlantic Ocean influence

height on the intertidal, because it only can grow well in sheltered zones. The higher variation occurs in scale of a few meters or centimeters, because the patch dominates by *A. armata* was interrupted by other algae or mussels. In the Azores this species covers less than the 10% of the infralittoral zone (Wallenstein & Neto, 2006) and continues subtidally with higher cover coexisting with other frondose algae and articulated corallines (Neto, 2000).

Another red algae, *Mastocarpus stellatus* was found forming a crust fringe that increased their upper limit on the exposed faces of the Islas Cíes. The crust phase in North Portugal predominates in areas

of high disturbance or stress and the higher cover of the "*Petrocelis*" phase was found on emerged rock than in intertidal pools (Araújo *et al.,* 2006), but the fronds phase occurred mainly in sheltered infralittoral (Araújo *et al.,* 2005). Bartsch & Tittley (2004) found an opposite scenario at Helgoland island (North Sea), where the frond phase was more common in exposed sites. The ecology and physiology of tetrasporophytic crust stage of most species of *Mastocarpus* are still unknown (Dudgeon *et al.,* 1995). For example, the tetrasporophytes can cover great rock area, moreover the crust grow below frond phase in Galicia (Besteiro-Rodríguez, 2004), but in the coast of Maine (Atlantic, USA), their distribution within the intertidal zone differs and the crust dominated bellow 0.25 m and at the fronds at 0.75 m above the mean low tide level (Dudgeon *et al.,* 1995). This can explain why in the Islas Cíes the crust fringe has more variation between and within the sections, similar to other sites of Galicia (Besteiro-Rodríguez, 2004), where *M. stellatus* occurs at mid littoral with the possibility of extend to high o lower intertidal levels.

The oscillation of cover in the crust phase is results of varying limpet densities (Hawkins & Hartnoll, 1983). Besteiro-Rodríguez (2004) reported that the abundance of limpet, *Patella vulgata* was 200 ind/m^2 in the Islas Cíes. Little & Kitching (1996) point out that the algae crust are enhanced by grazers that remove epiphytes. The crust stage had high grazer resistance and is long lived (Hawkins & Hartnoll, 1983; Dudgeon *et al.,* 1995). In the present study (end of the winter) no conspicuous patches of *M. stellatus* fronds was found. The frond phase of *M. stellatus* is annuals and recruits in spring and autumn (Little & Kitching, 1996). By these reasons at the time of the present sampling the crust phase of *M. stellatus* was common around the Islas Cíes.

Brown algae

Galician coast have a spring tides up 3.8 m and the low water temperature during the upwelling determining the development of the Northern cold temperate species, *Fucus spiralis* and *Pelvetia canaliculata* (Bárbara *et al.,* 2005). In Islas Cíes both species occurs in the high littoral. *F. spiralis* and *P. canaliculata* are present in semiexposed to sheltered littoral of the Ría de Vigo (Perez-Cicera, 1975). In sheltered coast of Galicia *F. spiralis* was found above of *P. canaliculata* (Niell, 1977). *P. canaliculata* occurred above or below of *F. spiralis* in Islas Cíes. Moreover, *P. canaliculata* was found with low cover and continuity when are compared with *F. spiralis* fringe in Islas Cíes. Similar situation occurs in North Wales and Isle of Cumbrae, UK, where *F. spiralis* presented more cover because to their fast growth in comparison to P. canaliculata, when both are at same level of the intertidal (Schonbeck & Norton, 1980).

The grown of *P. canaliculata* above *F. spiralis* in Islas Cíes could be related to its tolerance to desiccation above in the intertidal. The possibly cause of this variation in the upper limit of both species in Islas Cíes is that in drying days of neap tide the fringes of both species could be 'pruned back' by the absence of water and spray, similarly as others European rocky shores (Schonbeck & Norton, 1978; Dring & Brown, 1982). In contrast, the lower limits of the *P. canaliculata* and *F. spiralis* are not determined by physical environmental conditions. The lower limit of recruitment of *P. canaliculata* near the neap high tide level is established by grazing effect (Pyefinch, 1943; Schonbeck & Norton, 1980), but reduction in light incidence decayed transplanted individuals of *F. spiralis* and *P. canaliculata* to low intertidal level in Isle of Cumbrae, UK (Schonbeck & Norton, 1980). This pattern was also found in natural populations in shores or pools with constant submergence (Connell, 1972; Niell, 1977; Araújo *et al.,* 2006). The combination of both factors could modify the lower limits in Islas Cíes.

F. spiralis was found in sheltered coast of the Islas Cíes and in the cove of the exposed shore of South Island at the same height. Hawkins & Hartnoll (1983) showed that *Patella vulgata* occurs joins fucoids in more sheltered sites of North Spain. At high exposure

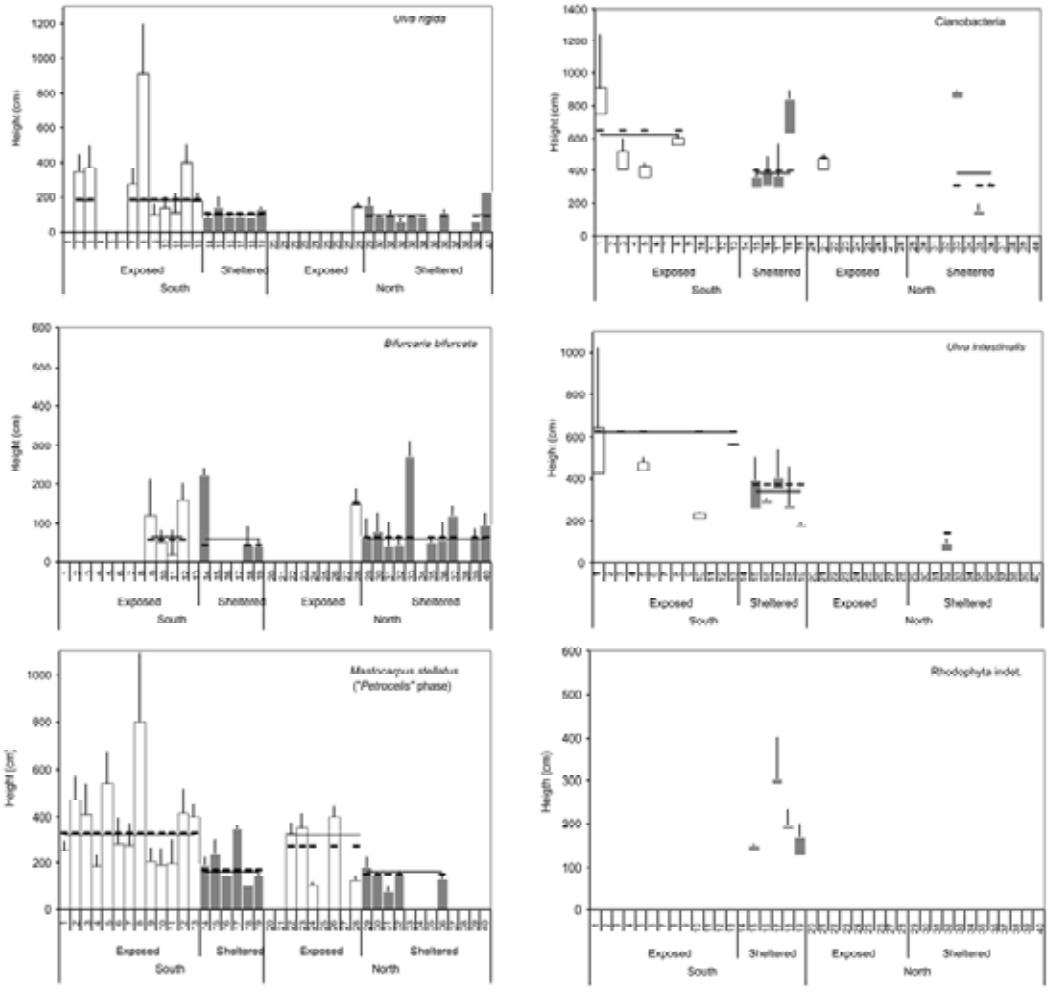


Figure 6:
Upper and lower limits of intertidal organisms of Islas Cíes, NW Spain. Bars: height mean (cm) above low tide for section of the coast, with their standard deviation. Line in scripts: height mean above low tide for each face in each island. Straight line: general height mean above low tide for the exposed or sheltered condition to Atlantic Ocean influence

P. vulgata change by *Patella depresa* and *Patella lusitanica,* and fucoids are absent of the shore. In Norway *P. vulgata* (exposed sites) showed contrary distribution than fucoids (sheltered sites) and *F. spiralis* have they the lower limit fixed by the limpet grazing. *F. spiralis* is common in Galician semiexposed shores, but in exposed sites disappear (Niell, 1977).

Within the sheltered shore low variation was detected between measures of the upper limit of *F. spiralis*, possibly the crevices has no influence in this species. Higher variation occurred from point to point of the shore of the shore and a possibly cause is the rock inclination. Niell (1977) found that the upper limit *F. spiralis* in Canido, Vigo was raised

by the physical characteristics of the coast and in sheltered shore form a fringe of 30 cm wide at 280 cm above low tide level. *F. spiralis* tolerate less than *P. canaliculata* the high wave exposure and this last species is present only as scattered plants in these sites (Jones & Demetropoulos, 1968). But in Islas Cíes, *P. canaliculata* only was found in sheltered shores of South Island and in fewer patches in the sheltered coast of North Island. Contrary with Jones & Demetropoulos (1968), the studies of Connell (1972) and Niell (1977) point out that *Pelvetia* can grow in shores with high turbulence but not directly exposed to the waves and North winds. The crevices raise the upper limit of *P. canaliculata* and the species wins continuity in their fringe inner in the Ría de Vigo (Niell, 1977). The algae film above *P. canaliculata* was found in the sheltered shore and the exposed cove of the South Island, where it presented uniformity in their upper limit. The film layer may be a mix in of *Porphyra linearis*, *Bangia fuscopurpurea,* and the lichen, *Lichina pygmanea*, as in other places of the Ría the Vigo (Niell, 1977).

The third Ochrophyta in Islas Cíes was *Bifurcaria bifurcata*, found in the low littoral of sheltered shore and the cove in South Island, below 1m of the low tide level. This algae presented high variation between sections and points of the coast. This endemic lusitanic algae (Bárbara *et al.,* 2005), was found in the North of Portugal shores near of Galicia with high cover only on intertidal pools below 1 m low tide level and was absent in exposed shore (Araújo *et al.,* 2005; 2006). In Islas Cíes was found with few patches in each point. The studies in Galician coast determined that in the range between 0.6 to 0.9 m, *B. bifurcaria* has low cover in the semiexposed shores of Vigo with a cover peak on winter (Fernández *et al.,* 1983; Olabarria *et al.,* 2009). This algae prefer the low inclined rock and borders of intertidal pools (Besteiro-Rodríguez, 2004).

Green algae and biofilms

Ulva rigida enhanced their upper limit in the exposed face of the South Island. In the sheltered shore of the North Island only few patches was found in the low intertidal. *U. rigida* is a common algae in Galicia (Niell, 1978; Bárbara *et al.,* 2005), for example was present in semiexposed to sheltered coast of the Ría de Cedeira (Perez-Cicera, 1975). This species only can grow in exposed shores of Galicia in form of small patches (Cremades-Ugarte *et al.,* 2006). *U. rigida* presented low cover (<10%) in Monte Lourido, Vigo in the first months of the year (Olabarria *et al.,* 2009). *U. rigida* covered 20 to 22 % at the low intertidal of North Island of Islas Cíes between April and May 2003 (Besteiro-Rodríguez, 2004). The low cover results in the patchy distribution found in the present study and may explain the higher variation at small and very small scale (meters to centimeters). Moreover, *U. rigida* can cover around 40% in spring in Monte Lourido (Olabarria *et al.,* 2009). Other Chlorophyta, *Ulva intestinalis* showed higher upper limit in the South exposed face than in the sheltered shore. *U. intestinalis* also have low presence in North Island. This species has higher values of variation at small and very small scale. *U. intestinalis* grow better in crevices with freshwater flow in Galicia (Niell, 1977), similarly to the cliffs of Helgoland (Bartsch & Tittley, 2004). *U. intestinalis* occurs in few sites in the intertidal of Islas Cíes, similarly with Iceland shores (Espinosa & Guerra-García, 2005).

The epilithic biofilm found in Islas Cíes in the high littoral presented higher variation at smaller spatial scale. The majority of Galician shores have films of cianobacteria in the supralittoral with irregular distribution that change by the crevices and waters flow (Niell, 1977). The diatoms dominate over cianobacteria species on epilithic biofilms on temperate shores (Mak & Williams, 1999), this explain the spatial variation found. The epilithic biofilms on rocky shores are regulated by physical factors, growth, recruitment and grazing (Stafford & Davies, 2005). The result is the early colonization of bare rock by bacteria and/or diatoms (MacLulich, 1986). Similar process can occurs in rock walls of Islas Cíes. The bare rock was more constant in the

Table 1:
Samples sections, number of images and the mean height and coast line of Islas Cíes, N.W. Spain

Island	Condition	Section	Latitude	Longitude	No. Point	Coast Line (m)	Mean Height (m)
South	Exposed	1	44º12.52	8º54.435	17	435.5	18.75
		2	42º12.345	08º54.901	8	191.3	20.32
		3	42º12.185	08º54.825	10	308.7	21.28
		4	42º11.87	8º54.608	9	175.7	14.48
		5	42º11.764	8º54.82	14	340.8	19.74
		6	42º11.649	8º54.599	11	184.5	14.42
		7	42º11.537	8º54.492	9	143.7	13.67
		8	42º11.48	8º54.491	10	179.1	13.82
		9	42º11.492	8º54.314	11	152.1	11.04
		10	42º11.561	8º54.183	6	109.1	8.57
		11	42º11.532	8º53.936	14	206.5	11.56
		12	42º11.557	8º53.708	9	182.2	15.80
		13	42º11.389	8º53.552	11	224.9	16.34
South	Sheltered	14	42º11.47	8º53.356	10	122.7	10.30
		15	42º11.583	8º53.356	19	170.5	6.71
		16	42º11.728	8º53.46	11	71.1	4.72
		17	42º11.823	8º53.52	28	291.2	6.44
		18	42º11.954	8º53.765	22	216.3	7.29
		19	43º12.254	8º54.415	16	107.3	4.76
North	Exposed	20	42º14.618	08º54.123	11	335.3	21.83
		21	42º14.772	08º54.348	16	303.2	14.19
		22	42º15.059	08º54.704	12	872.8	43.04
		23	42º14.516	08º54.724	10	364.0	28.50
		24	42º14.288	08º54.525	12	923.4	57.04
		25	42º13.820	08º54.719	9	588.9	58.00
		26	42º13.551	08º54.652	10	866.9	51.54
		27	42º13.156	08º54.977	12	1084.1	64.18
		28	42º12.642	08º54.705	9	156.9	11.71
North	Sheltered	29	42º12.687	08.54.486	7	151.8	17.13
		30	42º12.732	08º54.347	10	114.3	4.45
		31	42º12.825	08º54.310	15	174.4	7.10
		32	42º12.928	08º54.102	13	135.3	5.82
		33	42º12.925	08º53.961	17	233.2	9.15
		34	42º12.847	08º53.824	15	145.9	5.33
		35	42º13.609	08º53.726	16	189.4	4.94
		36	42º13.938	08º54.014	7	148.1	8.29
		37	42º14.025	08º53.914	8	226.9	6.08
		38	42º14.178	08º53.806	7	358.7	8.43
		39	42º14.330	08º54.040	10	150.2	6.22
		40	42º14.401	08º54.072	11	235.6	13.61

exposed face, but was interrupted by organisms and biofilms in sheltered shore of the archipelago. In this way, the variation occurs at small and mid scale. In the semiexposed shores of Galician at mid level several places showed a bare rock space, possibly associated by the absence of *Ascophyllum nodosum* at this latitude (Niell, 1977). Moreover, the mainly species on the intertidal reach their upper limits near mean neap high tide and produced an upper denuded midshore (Schonbeck & Norton, 1980).

Sessile invertebrates

The mussel's band increased their upper limit in exposed shore without important variation between islands. Wave exposure has been demonstrated to extend upper intertidal limits (Blanchette & Gaines, 2007). In the external sites of the Rías Baixas of Galicia, the seed banks of mussels occurs in moderate or exposed rocks to waves. The distribution of this species ranges from the intertidal to 15 m depth (Besteiro-Rodríguez, 2004). Blanchette *et al.* (2007) found that *M. galloprovincialis* grew faster and better at moderately exposed than at sheltered sites. However, at extremely exposed sites were diminished. Across different wave exposures condition on the South Island, New Zeland, the mussels *M. galloprovincialis* are only found commonly on sheltered shores behind headlands, and mid intertidal zone with wave force of 40–60 Newtons (Schiel, 2004). In Islas Cíes the exposed shore showed higher upper limits of this mussel, but these bivalves not form extended beds as in the sheltered shore. *M. galloprovincialis* is less resistant to wave action (Zardi *et al.,* 2008), by this reason the variation among sections in Islas Cíes was moderate but more marked in exposed condition. *M. galloprovincialis* grow faster in areas of high water circulation related to greater food availability (Blanchette *et al.,* 2007).

In Islas Cíes the change in the height of the upper limit from point to point of the shore was higher in exposed faces. Perez-Cicera (1978) says that the mussel *Mytilus* in Galicia can occur in any horizon of the littoral zone, and would be introduced at upper levels with the help humidity over the rock. In some points the mussel had patches at two levels. This situation introduced part of the variation at small scale. Mettam (1994) found similar two peaks distribution for *Mytilus edulis* in some sections of the Severn Estuary. The mussels *M. galloprovincialis* have various recruitment peaks from April-May to September in the exterior of the Ría de Vigo (Caceres-Martinez *et al.,* 1993). The oceanographic conditions would be change the level in that larvae can recruit in the intertidal along the year. The variation was 14% between measures of the upper limit. Menge (1976) indicated that structural heterogeneities such as crevices extend more than 2.5m the vertical range of mussel species to higher than usual levels. The adults may move short distance within the mussel's bed and recruit faster the free space in wave beaten shores (Zairdi *et al.,* 2008). Its important point out that the dead *Balanus* patches were found only inner the mussel's band of the sheltered shore of Islas Cíes. These patches in the National Park were produced by illegal mussel's extraction. The exploitation of this bivalve occurs at the zone of tidal balance (Besteiro-Rodríguez, 2004).

Besteiro-Rodríguez (2004) reported for the mid littoral of Islas Cíes two barnacles: *Balanus perforatus* in the mussel's zone and above this *Chthamalus montagui*. This pattern occurs with other species of the same genera in North America, where *Balanus* win over *Chthamalus* in the low littoral, but at high littoral, *Chthamalus* can tolerance the desiccation more than *Balanus* (Connell, 1972). In the Islas Cíes was found a non significant increased in upper limit of barnacles (Cirripedia) in spite of the increased trend that the barnacles showed in the exposed faces. The higher variation between island faces (9%) was more marked in sheltered faces and obscures the trend. The barnacle's band could be enhanced their height inner in the Ría de Vigo. Previous studies indicate that differences in patterns of circulation of water, availability of food and type of substratum,

Table 2:
Contribution (%) of the random effects in explaining variance in height above tidal level of the upper limits (*) or lower limits (º) in rocky coast organism and bare rock. Islas Cíes, N.W. Spain. 2009

Organisms and bare rock	Random effects: Larger scale (Whole faces)	Residual: Medium scale (tens to hundreds of meters)	Small scale (meters to tens of meters)	Very small scale (centimeter to meters)
Bands	Island face	Sections	Points	Measures
Rhodophyta*	0.57	19.97	61.12	18.34
Mytillus galloprovincialis *	0.00	23.33	62.12	14.55
Cirripedia *	9.15	23.08	58.02	9.76
Verrucaria maura *	0.00	41.67	43.95	14.38
Caloplaca marina º	8.71	53.84	31.02	6.43
Vascular vegetation º	0.00	55.78	35.46	8.75
Fringes and patches	Island face	Sections	Points	Measures
Asparagopsis armata *	22.15	0.00	56.18	21.67
Mastocarpus stellatus ("*Petrocelis*" phase)*	5.87	54.44	32.52	7.17
Fucus spiralis º	50.48	0.00	47.13	2.39
F. spiralis *	41.90	8.46	47.00	2.64
Film*	65.63	3.24	29.78	1.36
Bare rock *	0.00	32.92	52.67	14.41
Patches	Island face	Sections	Points	Measures
*Ulva rigida**	0.00	13.86	60.53	25.61
*Bifurcaria bifurcata**	0.00	42.98	40.93	16.09
*Ulva intestinalis**	0.00	13.86	60.53	25.61
Cianobacteria*	0.00	0.00	91.57	8.43

may have important effects on the demography and structure of populations of barnacles at higher spatial scale (Menconi *et al.,* 1999). In this way, more variation was found in barnacles at the sections level than the organisms of the low intertidal, but point to point of the intertidal the variation was reduced. In both spatial scales the exposed shores vary more than the sheltered. The barnacle's band showed between measures of the upper limit less variation than the mussels or the red algae. Transplants experiments proved information that the adults can live at higher level, but juveniles die (Connell, 1972), this cause that the upper limit was best defined than in other organisms.

Littoral lichens

The black lichen, *Verrucaria maura* occurs higher in the rock walls of the exposed faces of both islands. This lichen dramatically may enhance from few meters in sheltered sites to 30 m in exposed shores of UK (Little & Kitching, 1996). The black lichen can become well established only in the upper littoral where the effects of wave action are minimal (Flecher, 1973). The variation between island faces of Islas Cíes at same exposure condition was no relevant. *V. maura*, occurring associated with "dry" conditions but need some input of seawater (Flecher, 1973). In Islas Cíes most variation between sections was found

on exposed faces than in sheltered. The higher wave-splash over the accidents of the exposed coast provides the necessary seawater to the higher cliffs where *V. maura* grown. The black lichen as well as reported higher in the intertidal in the North Atlantic shores, where produces a tar crust in the spray zone, near the cliff base to the top, including the seaward faces (Hall *et al.,* 2008; Little & Kitching, 1996). On extremely sheltered shores, *V. maura* usually are the only lichen representatives of the littoral zone (Flecher, 1973). In the sheltered sites in North Portugal sampled by Araújo *et al*. (2005), *V. maura* do not occurs above the 4m with difference to the exposed sites. The variation between points in Islas Cíes was low for this intertidal organism in comparison with the mid and low littoral species. The upper limit of *V. maura* was used to fix the upper limit of the 'littoral fringe' and this zone can be submerged only on very sheltered shores (Flecher, 1973). The horizon of *V. maura* in some cases may be has their lower limit in the high midlittoral of Galicia (Niell, 1977). In Islas Cíes variation between measures of their upper limit of this lichen only account a 14%. The upper limit was imposed by the terrestrial vegetation and others lichens.

The orange lichen, *Caloplaca marina* appears higher in exposed faces of Islas Cíes. On the other hand this lichen in very sheltered sites of the Ría de Vigo (Sotoxusto) can colonize the rock wall with an inferior limit at 4.4m above the chart datum (Niell, 1977). *C. marina* varies enough between the islands on the exposed shore. In Shetland, Scotland quickly colonizes relatively sheltered surfaces on cliffs, but this lichen is absent from rock surfaces with greater exposure (Hall *et al.,* 2008). Variation between sections was greater in exposed faces of Islas Cíes. The orange lichen form colonies on surfaces irregularly covered by water or heavy spray (Hall *et al.,* 2008). *C. marina* was located in the Ría de Vigo in the sunny coast and with strong exposure (Niell, 1977). The less variation between points was found in the exposed face in the Western shore of the North Island. Wootton (1991) found that *C. marina* increased the width of their band in presence of guano, in sites with not guano was at 1.2-3.6m above *Balanus* band and in zones with guano at 11.6-17.3m. Moreover, guano inhibits the abundance of *Verrucaria* in the splash zone (Wootton, 1991). The Islas Cíes have a nesting population of Yellow-legged Gulls numbering around 25.000 breeding pairs that build nests on high cliffs on the West coast (Alonso-Alvarez & Velando, 2003). This factor introducing part of the variation observed in the lichens of Islas Cíes.

To conclude, the difference in the presence or absence of algae species between exposed or sheltered faces of the Islas Cíes, could be influenced by the excessive turbulence (Connell, 1972). Physical characteristics and biological interactions accounted the variability observed from one part of the intertidal to another (Menconi *et al.,* 1999). Wave-exposure produced the change in the intertidal limits of the organisms at larger spatial scales. The spatial heterogeneity (coast accidents to crevices) made oscillate these intertidal limits at mid to very small-scale. Structural complexity may reduce environmental stress of intertidal at low tide (Araújo *et al.,* 2005). Menconi *et al*. (1999) mentioned that patchiness is promoted by substratum heterogeneity and the inclination of the rock influence in some grade the recruitment, growth and mortality of organisms.

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