



DISTRIBUTION AND POPULATION STRUCTURE OF *PATELLA VULGATA* LINNAEUS, 1758 (GASTROPODA: PATELLIDAE) ON INTERTIDAL SEAWALLS AND ROCKY SHORES IN THE RÍA DE FERROL (GALICIA, NW IBERIAN PENINSULA)

GUILLERMO DÍAZ-AGRAS⁽¹⁾, JUAN MOREIRA⁽¹⁾, RAMIRO TATO⁽¹⁾, XANDRO GARCÍA-REGUEIRA⁽¹⁾ & VICTORIANO URGORRI^(1,2,3)

Key words: *Patella vulgata*; Gastropoda; artificial; seawall; rocky shore; intertidal; population; distribution; Ría de Ferrol; Iberian Peninsula; Atlantic Ocean

ABSTRACT

Intertidal seawalls are a common feature on the shoreline of many urbanized coastal areas. In the Ría de Ferrol (Galicia, NW Iberian Peninsula), many seawalls are built vertically and have replaced or fragmented most of the natural horizontal rocky shores. Grazing gastropods, including the limpet, *Patella vulgata* Linnaeus, 1758, play an important role in the structuring of the assemblages of intertidal organisms,

by affecting the distribution and abundance of algae, sessile and mobile invertebrates. In order to compare patterns of abundance and population structure of *P. vulgata* on intertidal horizontal rocky shores and vertical seawalls in the Ría de Ferrol, four sampling stations were selected at the middle part of the ria, corresponding to semi-exposed areas. At each station, two rocky shores and two seawalls extensive enough for the intended sampling were selected and two sites separated by 5-10 m were visually sampled at each seawall/rocky shore. There were no clear differences regarding abundance, frequency of occurrence and population structure between the two studied habitats. Differences were found between sites (at the scale of metres) within any given seawall or rocky shore. Nevertheless, at some stations maximal sizes of limpets were greater on rocky shores than on seawalls. These results need to be further explored by manipulative experiments in order to understand whether seawalls constitute a surrogate habitat for limpets.

(1) Estación de Bioloxía Mariña da Graña, Universidade de Santiago de Compostela, Casa do Hórreo, Rúa da Ribeira 1, E-15590, A Graña, Ferrol, Spain.
e-mail: guillermo.diaz@usc.es

(2)Departamento de Zooloxía e Antropoloxía Física, Universidade de Santiago de Compostela,

Campus Sur, E-15782, Santiago de Compostela, Spain.

(3)Instituto de Acuicultura, Universidade de Santiago de Compostela,

Campus Sur, E-15782, Santiago de Compostela, Spain.

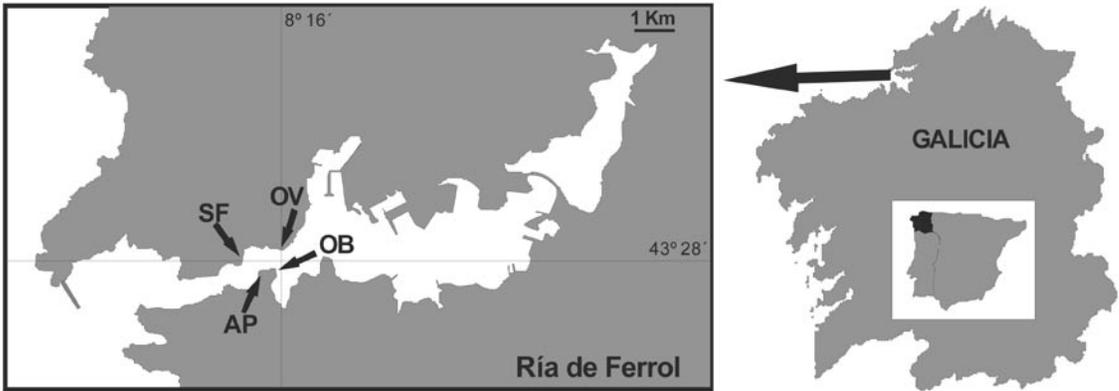


Figure 1:
Location of the Ría de Ferrol and of sampling stations. AP, A Palma; SF, San Felipe; OB, O Baño; OV, O Vispón.

INTRODUCTION

The continuous town-planning development associated to the constant growing of human population makes the urbanized areas have a greater and greater impact on the natural ecosystems (Carroll *et al.*, 2004). It has been estimated that approximately between 30 and 40% of the human population live at present in coastal areas or next to them (Small & Nicholls, 2002) and it is foreseen that this percentage will grow up to 60% towards the year 2030 (Pickett *et al.*, 2001). This means a proliferation of artificial structures as jetties, breakwaters, groynes, pilings, pontoons and seawalls, which destroy and fragment the natural habitats and add new structures to the marine ecosystems (McDonnell & Pickett, 1990; Glasby & Connell, 1999). These new structures differ from the natural ones in composition, orientation and texture of the surface as well as in the diversity and characteristics of the microhabitats they host (Chapman & Bulleri, 2003). Although previous work suggests that these new structures provide with new habitats and might be surrogates for natural rocky shores (Thompson *et al.*, 2002), recent studies have shown that the greater differences between intertidal seawalls and natural rocky areas are not only in the composition of biological assemblages but also in the relative abundance of common species (Chapman,

2003; Chapman & Bulleri, 2003; Bulleri & Chapman, 2004). Understanding how these new structures affect the processes and the assemblages they host, is the key to try to mitigate the effects they have on the natural habitats to enable the design of artificial structures that have a lower impact on the coastal ecosystems and allow to host a diversity of organisms similar to the present on natural rocky shores.

To date, numerous studies have been carried out on the contamination level of water and sediment or on the effects of different pollutants on marine organisms (Thomas, 1999; Biselli *et al.*, 2000; Diez *et al.*, 2002). However, very few studies have been carried out on the impact that the artificial structures that replace the natural rocky areas have on the assemblages of intertidal organisms. In general, these studies have been done in very specific areas around the world as Australia (Chapman, 2003) and Italy (Bulleri & Chapman, 2004), where the tidal ranges vary between 1 and 2 metres. The intertidal zone of the Galician rias (NW Iberian Peninsula) has a tidal range of up to 4 m and a large diversity of natural habitats inhabited by a rich and diverse benthic fauna (e.g. Junoy & Viéitez, 1990; Troncoso & Urgorri, 1991). The shoreline of the rias is nowadays highly urbanized because of the concentration of population in coastal areas; many natural areas have been replaced or fragmented by

the construction of vertical seawalls, marinas and a number of harbour facilities. To date, no study has been done on the impact of the artificial structures on the intertidal assemblages of the rias.

In the Galician rias, intertidal seawalls are usually built vertically and made of granite, which is the material making up most of the natural shores. In many areas, seawalls are extensive and constitute the most common artificial habitat. Preliminary observations show that intertidal seawalls are colonized by a series of algae and invertebrates, including several species of limpets and snails. The Mollusca, sessile and vagile, are an important and varied component of the natural populations of invertebrates on the Galician coasts. For example, the bivalve, *Mytilus galloprovincialis* Lamarck, 1819, is very frequent on natural rocky shores and intertidal seawalls where it constitutes extensive belts at mid-tidal levels; on natural shores, mussel beds also provide with habitat to a large suite of organisms. Among the intertidal molluscs, grazing gastropods also play an important role in the intertidal assemblages (Underwood *et al.*, 1983), for example, controlling the growth and distribution of algae (Underwood, 1980; 1998; Underwood & Jerkanoff, 1981) and ‘bulldozing’ small sessile specimens (Denley & Underwood, 1979). Among these grazers, the limpet, *Patella vulgata* Linnaeus, 1758, is one of the most common and numerous on natural habitats of the Galician coasts and is also present on intertidal vertical seawalls. This limpet mostly grazes on diatoms, settling stages of algae and filamentous and blue green algae growing on the rock surface and shows homing behaviour (Evans & Williams, 1991). Previous studies done on other limpets in other parts of the world (Chapman, 2006) show that the populations of some species inhabiting intertidal natural rocky shores and seawalls are similar as regards presence and frequency of appearance. However, there are differences in behaviour and performance between natural and artificial habitats, for example, as regards nourishing and mobility habits (Bulleri *et al.*, 2004), sizes and reproductive output (Moreira *et al.*, 2006).

Previous observations indicate that *P. vulgata* is a common species on intertidal seawalls. However, it is not known whether there are differences in abundance and population structure among natural rocky shores and seawalls. If they were found, this would mean that seawalls do not make up a suitable habitat for the populations of *P. vulgata* and therefore, they could not be considered as surrogate for natural habitats.

In this paper, we present a comparison of abundance, frequency of occurrence and population size-structure of the limpet, *P. vulgata*, among intertidal seawalls made of granite blocks and natural granitic rocky shores, located at a highly urbanized ria, i.e., the Ría de Ferrol.

MATERIALS AND METHODS

Study sites and sampling

Sampling was done in four stations in the middle area of the Ría de Ferrol (Galicia, NW Iberian Peninsula; Figure 1) because the shoreline has vertical seawalls and horizontal rocky shores which are extensive enough to do the intended sampling. Inner areas of the ria were not sampled because the adequate rocky shores were not available; similarly, the outer ria has no seawalls extensive enough for the same purpose. Sampling was done in summer 2008 (August) and winter 2009 (February); at each station, two seawalls and two rocky shores (locations) were sampled. On each location (seawall or rocky shore) three heights representing different assemblages of organisms were chosen to examine the abundance, frequency of occurrence and sizes of *Patella vulgata*: 3-3.5 m (highshore), 2-2.5 m (midshore) and 1.5-2 m (lowshore); heights varied slightly depending on the place. Tidal level below 1.5 m was not sampled because it was not available in each location. The sampling design did not eliminate potential sources of confounding due to intrinsic characteristics of locations, but was a sensible scheme on the fragmented shoreline of the Ría de Ferrol. All stations were, however, located in the semi-exposed

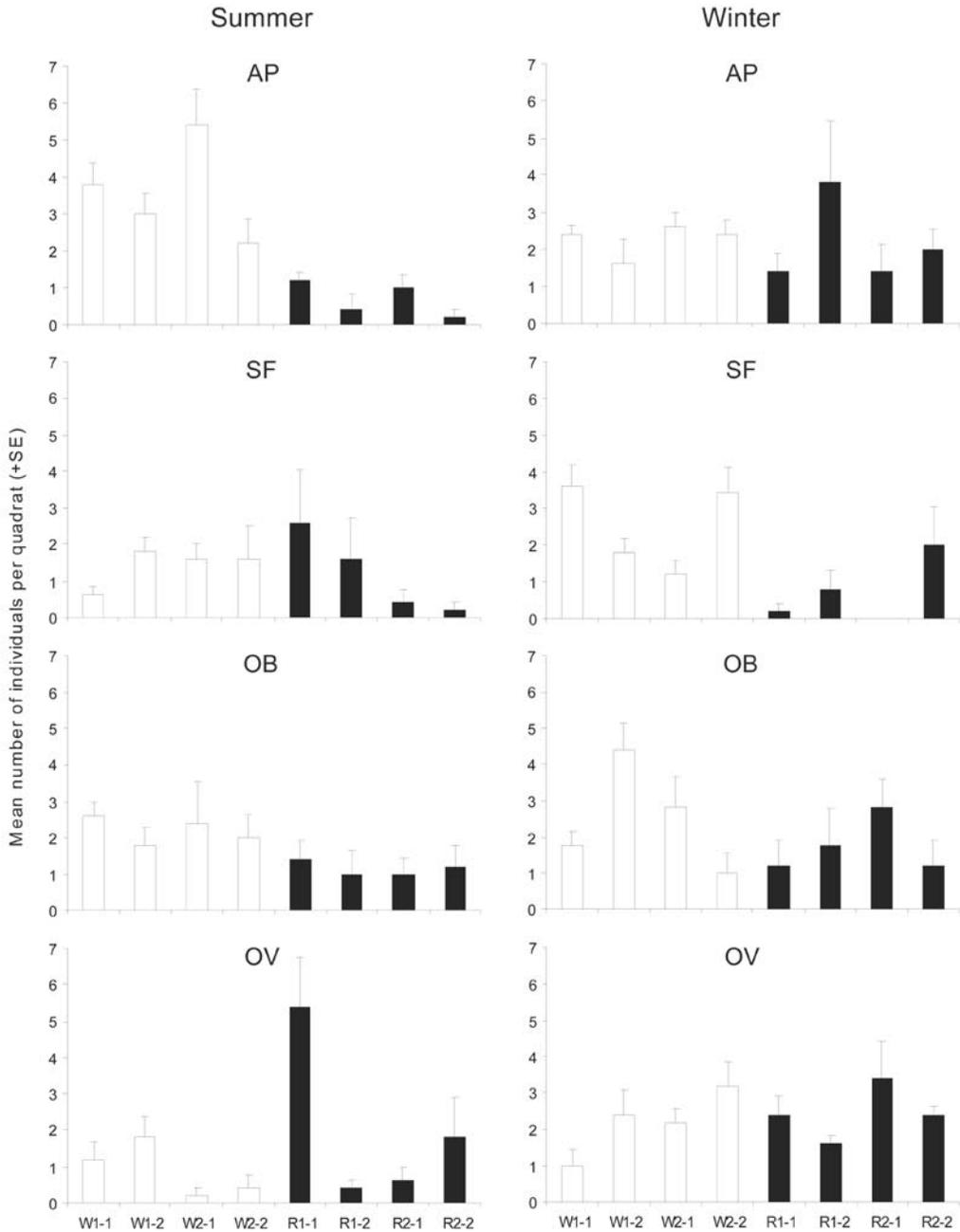


Figure 2:

Densities of *Patella vulgata* (mean number per quadrat + SE) for midshore at each site on seawalls and rocky shores at each station. AP, A Palma; SF, San Felipe; OB, O Baño; OV, O Vispón. Legend for sites: W1-1, seawall 1 - site 1; R1-1, rocky shore 1 - site 1

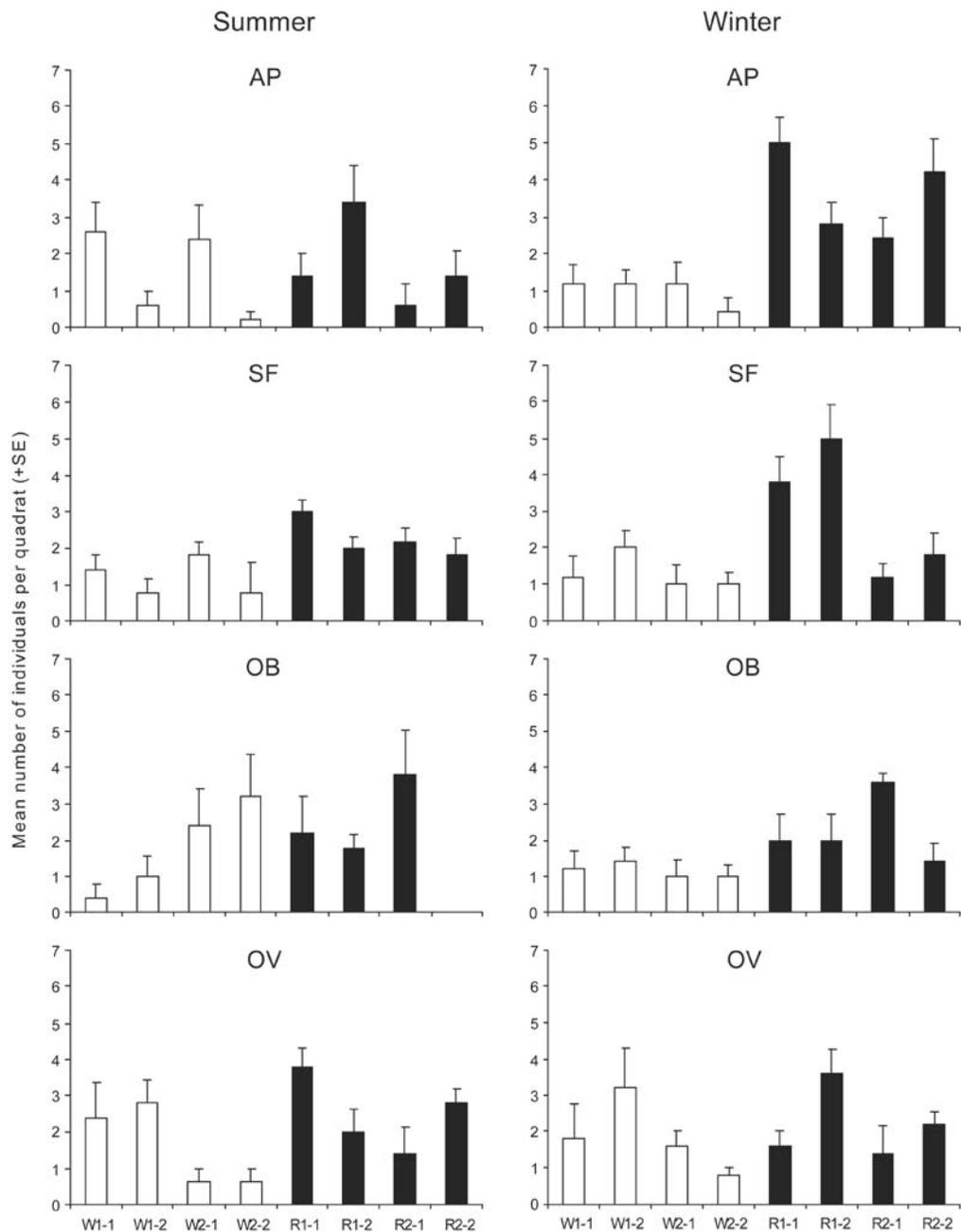


Figure 3:

Densities of *Patella vulgata* (mean number per quadrat + SE) for lowshore at each site on seawalls and rocky shores at each station. AP, A Palma; SF, San Felipe; OB, O Baño; OV, O Vispón. Legend for sites: W1-1, seawall 1 - site 1; R1-1, rocky shore 1 - site 1.

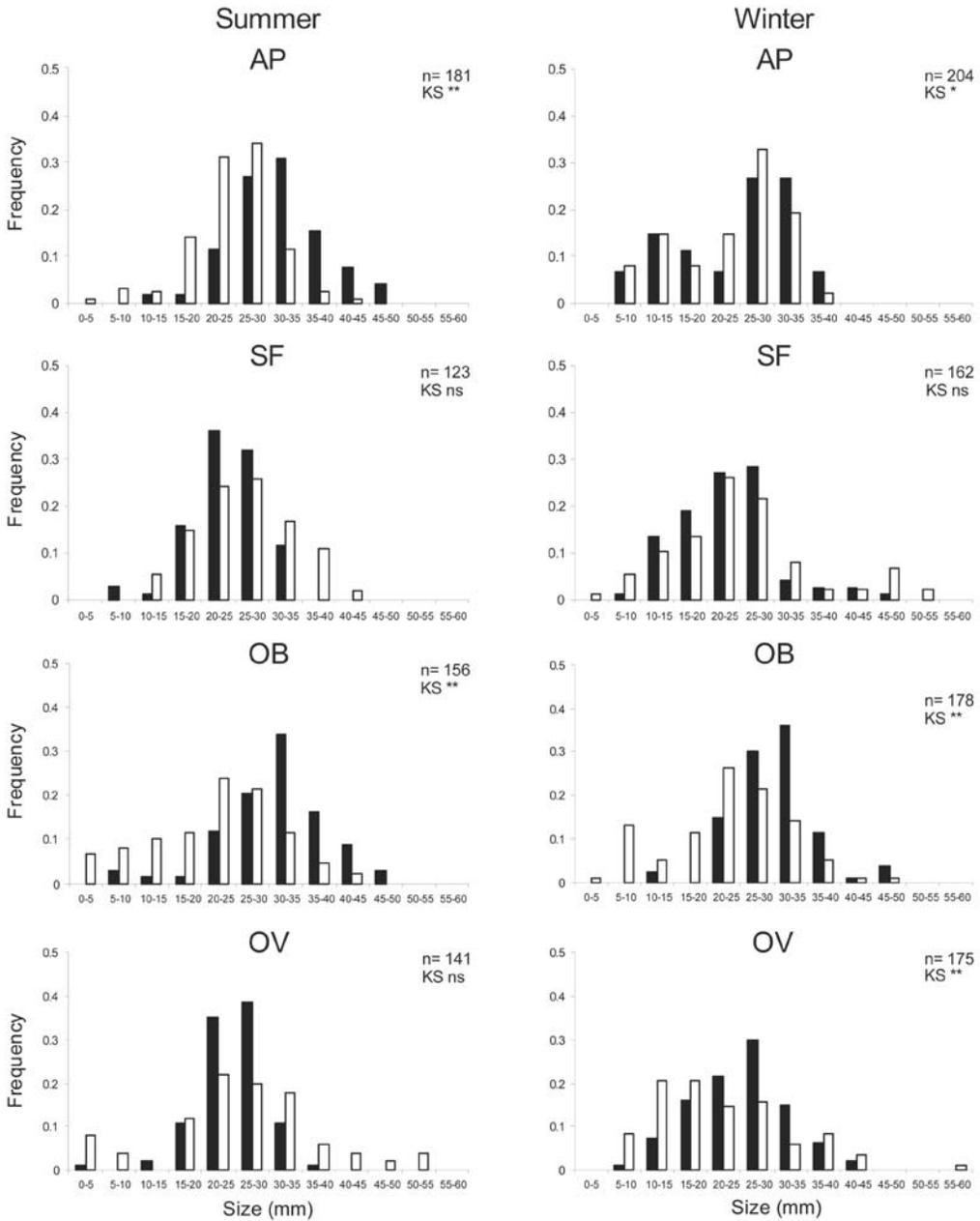


Figure 4:

Length-frequency distribution of *Patella vulgata* on seawalls and rocky shores at each station in summer and winter. Black bars, rocky shores; white bars, seawalls; n, total number of individuals measured; AP, A Palma; SF, San Felipe; OB, O Baño; OV, O Vispón. Results of KS tests are shown.

zone of the Ría de Ferrol and apparently experienced similar wave-wash due to the intense maritime traffic. In addition, because seawalls were built vertically and are not gently sloped, comparisons among seawalls of different slope were not possible. Furthermore, patches of vertical rocky shores are not present in the Ría de Ferrol and therefore could not be sampled for comparisons.

Two replicate sites, approximately 5 m long and separated by 5-10 m were selected at each tidal level at each seawall and rocky shore. Five replicate quadrats (20 x 20 cm each) were randomly positioned in each site. Quadrats within the same site were separated by at least 50 cm. On seawalls and rocky shores, quadrats were placed at least 10 cm away from crevices. Numbers and sizes (shell length) of *P. vulgata* were counted and measured respectively in each quadrat.

Analysis of data

Abundances of *P. vulgata* were compared between habitats (seawall vs rocky shore) for each tidal level at each station by means of analysis of variance (three-factor ANOVA), to test for effects of habitat (fixed), location (nested in habitat) and site (nested in habitat and location). Analyses were done separately for summer and winter. Homogeneity of variances was checked using Cochran's test before analysis and data were transformed when appropriate. Data were analyzed untransformed when homogeneity of variances could not be achieved. ANOVA is a robust analysis despite heterogeneous variances when there are many independent replicates and sizes of samples are equal (Underwood, 1997).

To compare the frequency of occurrence of *P. vulgata* between habitats at each station regardless of actual densities, counts of presence/absence were added for each tidal level and habitat (Chapman, 2006); frequencies were compared through χ^2 contingency tests separately for summer and winter.

For each station, the length-frequency distribution of limpets on seawalls and rocky shores were compared by means of Kolmogorov-Smirnov tests (KS). To achieve that, frequency distributions were constructed by considering all limpets present at the three tidal levels at the two seawalls and the two rocky shores.

RESULTS

Comparisons of abundance of *Patella vulgata* among seawalls and rocky shores did not show a clear pattern for midshore and lowshore (Tables 1, 2). Analyses were not done for highshore because of the low numbers of limpets there. When there were differences between habitats, those were not consistent between summer and winter. For example, at midshore level at A Palma and O Baño, there were more limpets on the seawalls than on the rocky shores in summer and there were no significant differences in winter (Figures 2-3). In general, there were no differences between seawalls or rocky shores at the same location apart from both rocky shores at lowshore at San Felipe in winter. On the contrary, significant differences were common between sites within the same seawall or rocky shore for both midshore and lowshore.

Frequencies of occurrence of *P. vulgata* were compared between habitats for each station through χ^2 contingency tests, adding all the counts of presence/absence across either seawalls or rocky shores for each tidal level and sampling period. When there were significant differences (San Felipe and A Palma), limpets tended to be more frequent on seawalls than on rocky shores for midshore and the opposite pattern was found for lowshore, i.e. limpets were more frequent on rocky shores (Table 3). At O Baño and O Vispón there were no significant differences between habitats.

Kolmogorov-Smirnov tests showed that there were significant differences in sizes of limpets in summer and winter at A Palma and O Baño and in winter at O

Table 1

| | df | A Palma | | | | San Felipe | | | |
|---------------------|----|---------|-----------|---------|---------|------------|---------|--------|----------|
| | | Summer | | Winter | | Summer | | Winter | |
| | | MS | F | MS | F | MS | F | MS | F |
| Habitat = Ha | 1 | 84.10 | 168.20 ** | 0.21 | 0.90 ns | 0.40 | 0.05 ns | 30.62 | 29.88 ns |
| Location = Lo (Ha) | 2 | 0.50 | 0.07 ns | 0.24 | 0.57 ns | 8.50 | 5.48 ns | 1.02 | 0.13 ns |
| Site = Si (Ha x Lo) | 4 | 7.60 | 5.11 ** | 0.41 | 1.58 ns | 1.55 | 0.52 ns | 7.77 | 4.82 ** |
| Residual | 32 | 1.49 | | 0.26 | | 2.96 | | 1.61 | |
| Total | 39 | | | | | | | | |
| Cochran's test | | 0.40 * | | 0.24 ns | | 0.43 * | | 0.42* | |

Table 2

| | df | A Palma | | | | San Felipe | | | |
|---------------------|----|---------|---------|---------|---------|------------|----------|---------|---------|
| | | Summer | | Winter | | Summer | | Winter | |
| | | MS | F | MS | F | MS | F | MS | F |
| Habitat = Ha | 1 | 0.62 | 0.12 ns | 67.60 | 52.00 * | 11.02 | 15.21 ns | 25.60 | 1.25 ns |
| Location = Lo (Ha) | 2 | 5.12 | 0.61 ns | 1.30 | 0.24 ns | 0.72 | 0.46 ns | 20.50 | 16.40 * |
| Site = Si (Ha x Lo) | 4 | 8.42 | 3.40 * | 5.45 | 2.99 * | 1.57 | 1.52 ns | 1.25 | 0.80 ns |
| Residual | 32 | 2.47 | | 1.82 | | 1.04 | | 1.56 | |
| Total | 39 | | | | | | | | |
| Cochran's test | | 0.26 ns | | 0.29 ns | | 0.38 ns | | 0.25 ns | |

Vispón (Figure 4). In general, limpets longer than 30 mm tended to be more frequent on rocky shores than on seawalls although this was not true for San Felipe and in summer at O Vispón.

DISCUSSION

There were no consistent differences across stations on abundance and frequency of occurrence among populations of *Patella vulgata* on seawalls and rocky shores at the Ría de Ferrol. Similar patterns of abundance were observed for other limpets, namely *Patelloida alticostata*, *P. latistrigata* and *Siphonaria denticulata*, on seawalls and rocky shores at Sydney

Harbour (Chapman, 2006; Moreira *et al.*, 2006). On the contrary, other limpets such as *Cellana tramoserica*, *Patella aspera* and *P. rustica* showed greater densities on rocky shores than on seawalls (Bulleri & Chapman, 2004; Bulleri *et al.*, 2004). Furthermore, Guerra-García *et al.* (2004) found greater numbers of *Patella ferruginea* in artificial breakwaters than on natural shores. In general, when differences are observed those have been suggested to be related to the very nature of the habitat, i.e. seawalls provide a different habitat because they are vertical and lack microhabitats such as crevices and tidal pools (Chapman, 2006). Indeed, the physical characteristics of the habitat may have

| O Baño | | | | O Vispón | | | |
|---------|-----------|---------|---------|----------|----------|--------|---------|
| Summer | | Winter | | Summer | | Winter | |
| MS | F | MS | F | MS | F | MS | F |
| 11.02 | 441.00 ** | 5.62 | 1.33 ns | 13.22 | 1.22 ns | 0.62 | 0.14 ns |
| 0.02 | 0.04 ns | 4.22 | 0.52 ns | 10.82 | 0.65 ns | 4.52 | 1.57 ns |
| 0.62 | 0.31 ns | 8.07 | 2.94 * | 16.77 | 6.55 *** | 2.87 | 1.72 ns |
| 2.04 | | 2.75 | | 2.56 | | 1.67 | |
| 0.38 ns | | 0.21 ns | | 0.45 * | | 0.39 * | |

Table 1:
Analyses of densities of *Patella vulgata* at midshore on seawalls and rocky shores at the Ría de Ferrol. ns, not significant ($p > 0.05$); *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

| O Baño | | | | O Vispón | | | |
|---------|---------|---------|----------|----------|---------|---------|---------|
| Summer | | Winter | | Summer | | Winter | |
| MS | F | MS | F | MS | F | MS | F |
| 0.62 | 0.06 ns | 12.10 | 14.24 ns | 8.10 | 0.70 ns | 1.22 | 0.21 ns |
| 10.02 | 1.01 ns | 0.85 | 0.28 ns | 11.60 | 3.46 ns | 5.82 | 1.29 ns |
| 9.97 | 3.03 * | 3.05 | 2.42 ns | 3.35 | 1.75 ns | 4.52 | 1.96 ns |
| 3.29 | | 1.26 | | 1.91 | | 2.31 | |
| 0.29 ns | | 0.24 ns | | 0.31 ns | | 0.33 ns | |

Table 2:
Analyses of densities of *Patella vulgata* at lowshore on seawalls and rocky shores at the Ría de Ferrol. ns, not significant ($p > 0.05$); *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

a great influence in processes such as recruitment, competition and predation, which, in turn, affect the structure of populations (McGuinness, 1989; Underwood & Chapman, 1992).

There was a lack of a consistent pattern in differences in abundance between habitats. In general, differences were found between sites within locations for most of the studied stations. According to the intraspecific variability among populations of *P. vulgata*, these differences might be related to the aggregation of specimens in relation to trophic resources or use of habitat, being indifferent whether they are on rocky shores or seawalls. On natural

rocky shores, *P. vulgata* shows great behavioural plasticity (Hartnoll & Wright, 1977); for example, there are differences in patterns of foraging activity according to inclination of substratum, geographical latitude, topography and cover of sessile organisms (Little *et al.*, 1988; Williams *et al.*, 1999). On the contrary, Santini *et al.* (2004) pointed out that foraging behaviour varies depending on the time of the year rather than substratum being vertical or horizontal; this suggests that populations are very variable. Nevertheless, Bulleri *et al.* (2004) showed that differences in topography among seawalls and rocky shores may translate in differences in patterns of long-term dispersal; thus, many seawalls are made

Table 3:
Summary of contingency tests for comparisons of frequency of occurrence of *Patella vulgata* among seawalls (SW) and rocky shores (RS) at midshore and lowshore levels. ns, not significant ($p > 0.05$); * $p < 0.05$; ** $p < 0.01$.

| Station | Summer | | Winter | |
|------------|----------|----------|----------|----------|
| | Midshore | Lowshore | Midshore | Lowshore |
| A Palma | SW>RS ** | ns | ns | SW<RS ** |
| San Felipe | SW>RS * | SW<RS * | SW>RS ** | ns |
| O Baño | ns | ns | ns | ns |
| O Vispón | ns | ns | ns | ns |

of stone blocks separated by crevices which can be a physical limit for the movement of limpets. In our case, the studied seawalls at the Ría de Ferrol have, in many cases, crevices among blocks but it is not known yet whether this can affect biological performance of *P. vulgata* there, e.g. foraging activity and intra- and interspecific competition.

At some stations, limpets tended to be more frequent at midshore on seawalls than on rocky shores while the opposite pattern was found for lowshore. This fact could be related to differences between habitats in the vertical extent of intertidal space and the cover of sessile organisms. At both habitats, cover of barnacles at midshore was similar while at lowshore mussel beds appeared to be denser on seawalls. In addition, on seawalls the intertidal extent is about 3.0-3.5 m while on the studied rocky shores that is about >10 m; therefore, distances among tidal levels and among different sessile assemblages (i.e. barnacles and mussel beds) are smaller on seawalls. Presence of mussel beds favour recruitment of limpets (Lewis & Bowman, 1975) and thus it is likely that limpets would migrate from those beds to higher on the shore as they grow in size (Hobday, 1995), where space is not occupied by mussels. In addition, because on seawalls mussel beds are relatively close to limpets at midshore (at the scale of tens of centimetres rather than of metres) limpets could set their home

scars close to those and benefit of protection against desiccation (Lewis & Bowman, 1975). Nevertheless, patterns of homing behaviour on seawalls are not yet known and this needs to be further studied. On the other hand, this pattern in frequency of occurrence might just be a consequence of populations of limpets being more crowded on seawalls because of the smaller intertidal extent.

On the other hand, *P. vulgata* shows a high tenacity to the substratum of up to 5.1 kg/cm² which is helped by the production of mucus (Branch & Marsh, 1978). This might explain its common presence on the studied vertical seawalls where the presence of other grazers (i.e. snails) is more sparse; those snails might have more difficulties to stand on vertical surfaces in comparison to limpets (Díaz-Agras, unpublished results). Therefore, this intrinsic ability of this limpet could suppose an advantage in terms of interspecific competition and, in turn, to contribute to a different structuring of intertidal assemblages on seawalls. On the contrary, standing on vertical surfaces might translate in more energy dedicated to attach to the substratum and this can be affect to the biological performance of limpets on seawalls (maximal sizes attained, reproductive output, survival) when compared to those of populations on natural horizontal rocky shores (Branch, 1981).

In fact, there seem to be differences on length-frequency distribution among populations on seawalls and rocky shores. Thus, greater sizes were observed on rocky shores (>30 mm in length) although this pattern was not true for all stations. Moreira *et al.* (2006) showed that populations of the pulmonate limpet, *S. denticulata*, on vertical seawalls are composed by juveniles and small adults and that reproductive output of those are smaller than on populations on rocky shores. In our case, it is not known yet whether the reproductive output of *P. vulgata* differs among natural and artificial habitats. Smaller adults of gastropods in general, and of limpets, in particular, have a smaller reproductive output than larger specimens (Creese, 1980; Valentinsson, 2002; Moreira *et al.*, 2006). This fact has an important implication in maintenance of populations on seawalls. Thus, if animals on seawalls have a smaller reproductive output and produce few larvae, maintenance of their populations in the artificial habitat will depend on the existence of viable populations on natural habitats (Moreira *et al.*, 2006). That way, reduction or fragmenting of rocky shores at expenses of artificial structures could translate in a potential risk for survival of local populations, and, in turn, in the structuring of intertidal assemblages and in a loss of biodiversity. In addition, alterations in composition assemblages may facilitate the spread of invasive species, which in many cases have a negative impact in survival of local species (Vaselli *et al.*, 2008).

In conclusion, further experimental work is needed to test the patterns found here. Furthermore, reproductive output, competitive interactions and grazing behaviour of *P. vulgata* should be studied and compared among natural and artificial habitats in order to understand the value of seawalls as a surrogate habitat for this limpet.

ACKNOWLEDGEMENTS

The authors want to express their gratitude to the staff of the Estación de Biología Mariña da Graña for their help during field work and to J. García-

Carracedo who kindly revised the English version of the manuscript. Two anonymous referees provided useful comments which contributed to improve the final version of the manuscript.

REFERENCES

- Biselli S, Bester K, Huhnerfuss H, Kent K (2000). Concentrations of the antifouling compound Irgarol 1051 and of organotins in waters and sediments of German North and Baltic Sea marinas. *Marine Pollution Bulletin*, 40: 233-243.
- Branch GM (1981). The biology of limpets: Physical factors, energy flow, and ecological interactions. *Oceanography and Marine Biology: an Annual Review*, 19: 235-379.
- Branch GM, Marsh AC (1978). Tenacity and shell shape in six *Patella* species: adaptative features. *Journal of Experimental Marine Biology and Ecology*, 34: 111-130.
- Bulleri F, Chapman MG (2004). Intertidal assemblages on artificial and natural habitats in marinas on the north-west coast of Italy. *Marine Biology*, 145: 381-391.
- Bulleri F, Chapman MG, Underwood AJ (2004). Patterns of movement of the limpet *Cellana tramoserica* on rocky shores and retaining seawalls. *Marine Ecology Progress Series*, 281: 121-129.
- Carroll C, Noss RF, Paquet PC, Schumaker NH (2004). Extinction debt of protected areas in developing landscapes. *Conservation Biology*, 18: 1110-1120.
- Chapman MG (2003). Paucity of mobile species on constructed seawalls: effects of urbanization on biodiversity. *Marine Ecology Progress Series*, 264: 21-29.
- Chapman MG (2006). Intertidal seawalls as habitats for molluscs. *Journal of Molluscan Studies*, 72: 247-257.
- Chapman MG, Bulleri F (2003). Intertidal seawalls – new features of landscape in intertidal environments. *Landscape and Urban Planning*, 2: 159-172.
- Creese RG (1980). Reproductive cycles and fecundities of two species of *Siphonaria* (Mollusca: Pulmonata) in South-eastern Australia. *Australian Journal of Marine and Freshwater Research*, 31: 37-47.
- Denley EJ, Underwood AJ (1979). Experiments on factors influencing settlement, survival and growth of two

- species of barnacles in New South Wales. *Journal of Experimental Marine Biology and Ecology*, 36: 269-293.
- Diez S, Abalos M, Bayona JM (2002). Organotin contamination in sediments from the western Mediterranean enclosures following 10 years of TBT regulation. *Water Research*, 36: 905-918.
- Evans MR, Williams GA (1991). Time partitioning of foraging in the limpet *Patella vulgata*. *Journal of Animal Ecology*, 60: 563-575.
- Glasby TM, Connell SD (1999). Urban structures as marine habitats. *Ambio*, 28: 595-598.
- Guerra-García JM, Corzo J, Espinosa F, García-Gómez JC (2004). Assessing habitat use of the endangered marine mollusc *Patella ferruginea* (Gastropoda, Patellidae) in northern Africa: preliminary results and implications for conservation. *Biological Conservation*, 116: 319-326.
- Hartnoll RG, Wright JR (1977). Foraging movements and homing in the limpet *Patella vulgata* L. *Animal Behaviour*, 25: 806-810.
- Hobday A (1995). Body-size variation exhibited by an intertidal limpet: influence of wave exposure, tidal height and migratory behaviour. *Journal of Experimental Marine Biology and Ecology*, 189: 29-45.
- Junoy J, Viéitez JM (1990). Macrozoobenthic community structure in the Ría de Foz, an intertidal estuary (Galicia, Northwest Spain). *Marine Biology*, 107: 329-339.
- Lewis JR, Bowman RS (1975). Local habitat-induced variations in the population dynamics of *Patella vulgata* L. *Journal of Experimental Marine Biology and Ecology*, 17: 165-203.
- Little C, Williams GA, Morrill D, Perrins JM, Stirling P (1988). Foraging behaviour of *Patella vulgata* L. in an Irish sea-lough. *Journal of Experimental Marine Biology and Ecology*, 120: 1-21.
- McDonnell MJ, Pickett STA (1990). Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology*, 71: 1232-1237.
- McGuinness KA (1989). Effects of some natural and artificial substrata on sessile marine organisms at Galeta Reef, Panama. *Marine Ecology Progress Series*, 52: 21-28.
- Moreira J, Chapman MG, Underwood AJ (2006). Seawalls do not sustain viable populations of limpets. *Marine Ecology Progress Series*, 322: 179-188.
- Pickett STA, Cadenasso ML, Grove JM, Nilon CH, Pouyat RV, Zipperer WC, Constanza R (2001). Urban ecology systems: linking terrestrial, ecological, physical, and socioeconomic components of metropolitan areas. *Annual Review Ecological Systems*, 32: 127-157.
- Santini G, Thompson RC, Tendi C, Hawkins SJ, Hartnoll RG, Chelazzi G (2004). Intra-specific variability in the temporal organisation of foraging activity in the limpet *Patella vulgata*. *Marine Biology*, 144: 1165-1172.
- Small C, Nicholls RJ (2002). A global analysis of human settlement in coastal zones. *Journal of Coastal Research*, 19: 584-599.
- Thomas KV (1999). Determination of the antifouling agent zinc pyrithone in water samples by copper chelate formation and light-performance liquid chromatography-atmospheric ionization mass spectrometry. *Journal of Chromatography*, 833: 105-109.
- Thompson RC, Crowe TP, Hawkins SJ (2002). Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environmental Conservation*, 29: 168-191.
- Troncoso JS, Urgorri V (1991). Los moluscos intermareales de la Ría de Ares y Betanzos (Galicia, España). *Nova Acta Científica Compostelana (Biología)*, 2: 83-89.
- Underwood AJ (1980). The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. *Oecologia*, 46: 201-213.
- Underwood AJ (1997). *Experiments in ecology. Their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, U.K.
- Underwood AJ (1998). Grazing and disturbance: an experimental analysis of patchiness in recovery from a severe storm by the intertidal alga *Hormosira banksii* on rocky shores in New South Wales. *Journal of Experimental Marine Biology and Ecology*, 231: 291-306.
- Underwood AJ, Chapman MG (1992). Experiments on topographic influences on density and dispersion of *Littorina unifasciata* in New South Wales. In: Grahame, J., Mill, P.J. & Reid, D.G. (Eds.), *Proceedings of the*

Third International Symposium on Littorinid Biology.

The Malacological Society of London, London, pp. 181-195.

Underwood AJ, Denley EJ, Moran MJ (1983). Experimental analyses of the structure and dynamics of the midshore intertidal communities in New South Wales. *Oecologia*, 56: 202-219.

Underwood AJ, Jerkanoff P (1981). Effects on interactions between algae and grazing gastropods on the structure of a lowshore algal community. *Oecologia*, 48: 221-233.

Valentinsson D (2002). Reproductive cycle and maternal effects on offspring size and number in the neogastropod *Buccinum undatum* (L.) *Marine Biology*, 140: 1139-1147.

Vaselli S, Bulleri F, Benedetti-Cecchi L (2008). Hard coastal-defence structures as habitats for native and exotic rocky-bottom species. *Marine Environmental Research*, 66: 395-403.

Williams GA, Little C, Morritt D, Stirling P, Teagle L, Miles A, Pilling G, Consalvey M (1999). Foraging in the limpet *Patella vulgata*: The influence of rock slope on the timing of activity. *Journal of the Marine Biological Association of the United Kingdom*, 79: 881-889.

