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The role of shellfish in human subsistence during the Mesolithic of Atlantic Europe: an approach from meat yield estimations

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Abstract

In spite of the increased number of investigations of the Mesolithic period in Atlantic Europe, including studies that have focused on reconstructing human diets, the information about the role of shellfish in human subsistence strategies is still very limited. In this study, an experimental programme to collect modern molluscs was carried out in northern Iberia over a three-year period in order to establish the meat yield of the four main species recovered from archaeological sites in this coastal area. The resulting dataset enabled accurate estimates of the meat yield from the shell remains recovered in the shell midden deposits of El Mazo cave (Asturias, N Spain). Results show that the mollusc meat yield contributed at least 20% of the meat yield obtained from ungulates. This value is notably higher than in previous studies, showing that molluscs had a more important role in human subsistence strategies than previously recognised. The mollusc meat contribution relative to ungulates would be even higher if estimates were based on the number of identified bone remains, instead of the minimum number of individuals, which is a more subjective method and tends to overestimate the amount of mammal meat consumed by human populations. In any case, and independently of the methodology applied, our data show a greater dietary importance of shellfish during the Mesolithic than previously published for Atlantic Europe.

Keywords

Mesolithic, Shell Middens, Atlantic Europe, Subsistence strategies, Molluscs, Meat Yield.

1. Introduction

One of the key issues in relation to subsistence strategies and human behaviour during the Mesolithic along the Atlantic façade of Europe is to determine the role of shellfish in the diet of the last hunter-fisher-gatherers (Arias, 2006; Dupont and Bicho, 2015; Fano et al., 2013; Fontanals-Coll et al., 2014; Marín-Arroyo, 2013). Nevertheless, very few studies have carried out a meat yield reconstruction from mollusc shell remains recovered from archaeological sites. Exceptions are Thomas and Mannino (2017) in England, Dupont and Gruet (2002), Dupont (2003) in France, and Bailey (1978) in Denmark. Here, we examine estimates of meat yields from molluscs and compare them with estimates derived from ungulate remains in the Cantabrian region of northern Iberia (Craighead, 1995; Gutiérrez-Zugasti, 2009; Marín-Arroyo, 2013; Ortea, 1986).

Previous investigations in the Cantabrian region have reached different conclusions as a consequence of the different methodological approaches applied, but in general terms most of them have proposed a low contribution of shellfish to human diets during the Mesolithic, especially when the data are compared with results derived from mammalian fauna. For example, Marín-Arroyo (2013) and Craighead (1995) concluded that meat yield extracted from molluscs represented less than 1% of the total meat yield derived from ungulates. Carbon and nitrogen isotope studies of human bone in the Cantabrian region (Arias, 2006) and elsewhere along the Atlantic façade of Europe (Guiry et al., 2015; Schulting and Richards, 2001) suggest that the protein component of the Mesolithic diet consisted equally of marine and terrestrial resources. However, these studies do not differentiate between the relative contribution of marine molluscs

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and other marine resources such as fish, so that the role of shellfish in human subsistence remains unclear and points to the need for additional investigations.

Here, we reconstruct the meat yield represented by shell remains recovered from the Mesolithic shell midden site of El Mazo cave (N Spain). Mesolithic layers at El Mazo have a time span of at least 1,500 years, providing the opportunity to study long-term changes in coastal resource exploitation patterns. Previous investigations of molluscan meat yield in the Cantabrian region (Gutiérrez-Zugasti, 2009; Marín- Arroyo, 2013) have applied data from modern shells collected at different locations along the Atlantic coast of France (Dupont and Gruet, 2002). In our study, we collected samples of modern molluscs on the Cantabrian coast every 40–50 days over a three-year period for the four species best represented in the Mesolithic middens of the region, the topshell *Phorcus lineatus* (da Costa, 1778) and the limpets *Patella vulgata* Linnaeus 1758, *Patella depressa* Pennant, 1777 and *Patella ulyssiponensis*, Gmelin, 1791 (Álvarez-Fernández, 2011; Gutiérrez-Zugasti, 2009; 2011a). We applied the meat yields obtained from this experimental programme to the shell remains from El Mazo. In addition, we compared these results with the meat yield from ungulate bones recovered from El Mazo previously studied by Andreu-Alarcón (2013).

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2. Materials and methods

2.1 Modern shell collection programme

Modern specimens of *P. vulgata*, *P. depressa*, *P. ulyssiponensis* and *Ph. lineatus* were collected from Langre beach (Ribamontán al Mar, Cantabria), in northern Iberia (Fig. 1). This coastal location exhibits very similar oceanographic and geomorphological conditions to those littoral areas located near El Mazo cave. Mollusc species distribution observed from the archaeomalacological analysis conducted on this shell midden site showed that these littoral areas were characterised by rocky exposed shores (García-Escárzaga, in press). Shell collection events were carried out year-round, at the beginning and during the middle part of each season (Table 1). Topshells *Ph. lineatus* were harvested throughout three different years (from August 2014 to June 2016) in a total of 24 collection events. The three limpet species were collected over the same time span but only during 17 events in the case of *P. vulgata* and *P. depressa*, and 15 events in the case of *P. ulyssiponensis*. These three species were not collected during five events (from August 2015 to March 2016) in order to avoid overexploitation in Langre beach, nor in November 2016 and February 2017 because of environmental conditions that prevented access to the lower intertidal zone. *P. ulyssiponensis* was not harvested during the last two collection events (April and June 2017). In any case, the collection events for these limpet species covered more than two annual cycles, a time span that is notably longer than in previous studies (Dupont and Gruet, 2002; Thomas and Mannino, 2017)

The limpets *P. vulgata* and *P. depressa* inhabit the higher and lower intertidal zones, while the topshell *Ph. lineatus* inhabits mainly the higher zone and the limpet *P. ulyssiponensis*, the lower zone and sometimes rock pools located in the higher intertidal zone. During the period of the study, 40 topshells of *Ph. lineatus*, 50 limpets of *P. vulgata* and *P. depressa* (25 from the lower zone and 25 from the higher zone) and 25 limpets of *P. ulyssiponensis* were recovered in each collection event. After collection, the meat of the molluscs was measured using two different methods, depending on the morphology of each species. In the case of the limpets, where the soft parts of the mollusc can be easily accessed, the mollusc meat was weighed before and after processing, and thus we obtained both wet (live) and dry meat weight. In contrast, in the case of the topshells, cooked the specimens before extracting the mollusc meat is required, and this prevented us from weighing the wet meat weight. Instead, we estimated the wet meat weight of topshells applying the method previously proposed by Thomas and Mannino (2017) (i.e., whole mollusc weight before cooking minus dry shell weight after cooking). Independently of the method applied to weigh the mollusc meat, all specimens were killed by immersion in boiling water for one minute. Finally, all shells were measured and weighed in order to obtain a direct comparison between these two variables and the weight of the mollusc meat.

2.2 Modern shells: calculation of meat yield and relative meat yield

Following the terminology proposed by Thomas and Mannino (2017), meat yield (MY) and relative meat yield (%MY) were calculated. MY values correspond to the weight of the soft part of the mollusc (i.e., meat weight expressed in grams). Depending on whether meat yield is

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calculated from wet or dry meat weight, meat yield is referred to as dry meat yield (DMY) or wet meat yield (WMY). On the other hand, %MY corresponds to the meat extracted per one gram of shell, which was calculated from the ratio between the wet mollusc meat weight and the shell weight. The use of the relative meat yield is crucial to compare the profitability of the four species and also the cost-effectiveness of the higher and lower intertidal zones, since *P. vulgata* and *P. depressa* were collected in both zones.

2.3 Archaeological shells from El Mazo (Asturias, N Iberia)

The archaeological site of El Mazo is located in northern Iberia, in the western area of the Cantabrian region (Fig. 1). The site is situated in a hillside depression near a large doline. The archaeological deposit is located in the rockshelter, which is approximately 18 m long and 7 m deep. The excavation of a test pit close to the walls of the rockshelter produced several stratigraphic units (SUs) composed mainly of shell midden deposits (Gutiérrez-Zugasti et al., 2018). Some of the units were almost entirely composed of a shell matrix, others were dominated by sediments containing smaller amounts of shell, and others corresponded to combustion structures containing shells, sediments, ashes and charcoal (Fig. 2). The radiocarbon dates place the formation of the shell midden during the Early Holocene, between 9,000 and 7,500 cal BP (García-Escárzaga et al., 2019; Gutiérrez-Zugasti and González-Morales, 2013; Gutiérrez-Zugasti et al., 2013; 2018). Furthermore, the archaeomalacological study conducted on the shell remains enabled us to accurately establish the species representation, with a total of 78,723 individuals of *Ph. lineatus* and *Patella* species throughout the sequence (Supplementary Material) (both taxa represent together more than 90% of the total MNI recovered from El Mazo). This number is higher than the one previously employed by Marín-Arroyo (2013) (n = 72,656) to estimate the molluscs contribution to the Mesolithic diet. Therefore, taking into account the time span of the El Mazo shell midden and the large number of specimens recovered from this site, we consider our dataset sufficient representative to accurately establish the subsistence contribution of the molluscs.

2.4 Meat yield (MY) quantification from archaeological samples

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To reconstruct MY, three different, but complementary, methodologies were applied: (1) multiplying the MNI of each species by the average MY obtained for each taxa in the experimental programme (Thomas and Mannino, 2017); (2) applying the regression equation obtained by Dupont and Gruet (2002) from a comparison between shell weight and MY from modern molluscs; and (3) using the regression equation derived from the comparison between shell size (maximum diameter and length in the case of *Ph. lineatus* and *Patella* genus, respectively) and MY for each mollusc harvested during the experimental programme. Information about the *Patella* spp. and *Ph. lineatus* MNI recovered from El Mazo shell midden site and the average shell weight and shell size for each stratigraphic unit are included in the Supplementary Material and in García-Escárzaga´s PhD thesis (García-Escárzaga, in press).

The regression equations applied in this study were successfully tested on modern samples. The MY estimated using these equations was very similar to the real MY obtained from the 40 modern control specimens considered in the study (± 0.1 g). Due to taphonomic processes occurring at El Mazo, not all specimens recovered from this site could be measured and weighed. As a consequence, the average MY derived for each species in each stratigraphic unit from those shells measured and weighed was subsequently multiplied by the MNI obtained for each species in each unit in order to obtain the total MY of each species.

The analysis of the shell assemblage conducted at El Mazo showed that around 40% of the minimum number of limpets recovered were assigned to *Patella* sp. category (Supplementary Material). In order to estimate the MY from these specimens, the MNI corresponding to *Patella* sp. was assigned to each limpet species according to its percentage representation in each unit. For example, if *P. vulgata* represents 50% of the limpets in a given stratigraphic unit, 50% of the individuals classified as *Patella* sp. were assigned to *P. vulgata*. Finally, and taking into account that a recent study has shown that *Ph. lineatus* was mainly collected from late autumn to early spring throughout the shell midden sequence (García-Escárzaga et al., 2019), in this study only the modern values obtained from November to March were used to estimate the MY of this species. The differences between the year-round values and the November to March values are very small, just 250 g for the whole stratigraphic units. Nevertheless, we have used the November to March values for greatest

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accuracy. In contrast, year-round values obtained from modern limpets were used to estimate the MY of these taxa, since *P. vulgata* was harvested year-round in the Cantabrian region (Bailey and Craighead, 2003) and we make the same assumption for *P. depressa* and *P. ulyssiponensis* though we lack information on the season of collection of these two species.

3. Results

3.1 Experimental programme: calculation of meat yield (MY) and relative meat yield (%MY)

The results show that the MY of the limpets decreased around 25–30% after cooking, as a consequence of water loss (Table 2). However, this difference was slightly lower in the case of *Ph. lineatus* (ca. 10%). The results also exhibited a high correlation between dry and wet meat weight for the three species of limpets (Fig. 3a-c; $R^2 > 0.88$; $p < 0.0001$), showing that weight loss affected all specimens in a similar way. Nevertheless, in the case of *Ph. lineatus*, the correlation between dry meat weight and estimated wet meat weight following the method proposed by Thomas and Mannino (2017) is markedly lower, although a moderately-high correlation between both variables can still be observed (Fig. 3d; $R^2 = 0.66$; $p < 0.0001$).

On the other hand, the average MY of the topshells is notably lower than the average MY of the limpets, both before and after cooking (Table 2). The topshells also exhibit a lower %MY and therefore lower profitability than the three species of limpets (Table 3). The results obtained for the three limpet species show a similar %MY for *P. vulgata* and *P. depressa*, while *P. ulyssiponensis* shows a slightly higher yield than the other two taxa. A comparison between both areas of the intertidal zone, using the results from *P. vulgata* and *P. depressa*, show that molluscs harvested in the higher intertidal zone yields larger %MY values than those harvested in the lower zone (Table 3).

Finally, and from a methodological point of view, the results also show a different correlation between shell weight/size and MY depending on whether wet or dry meat yield values are considered. In the case of *Ph. lineatus*, shell weight exhibits a stronger correlation with DMY than with WMY (Fig. 4a-b). A similar result is also obtained for this species if shell

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size is compared with DMY and WMY (Fig. 5a-b). In contrast, the three species of limpets show a stronger correlation between shell weight and WMY (Fig. 4c-h) and between size and WMT (Fig. 5c-h).

3.2 Estimation of meat yield (MY) from archaeological samples

Our results show that estimation of the MY depends on the method applied (Table 4). In all three different methodologies used here, the values for WMY are always higher than those obtained for DMY. On the other hand, the highest values for all four species are obtained by multiplying the MNI by the average MY obtained for each taxa in the experimental programme (Table 4). The application of this method gives a total of ca. 116 and 88 kg for the WMY and DMY, respectively. In contrast, the regression equations derived from the modern samples (Fig. 4 and 5) give a notably lower MY than previously presented applying exclusively the average MY obtained from modern samples (Table 4). Nevertheless, the MY values derived from shell size and shell weight are very similar, although shell size gives slightly lower values.

4. Discussion

4.1 Meat yield (MY) and relative meat yield (%MY) from modern limpets and topshells in Atlantic Europe

The average MY obtained for each species shows that the soft part of the limpets are heavier than those extracted from the topshells, a result that is in agreement with previous studies for the Atlantic façade of Europe (Thomas and Mannino, 2017). Nevertheless, the MY values of *Ph. lineatus* and *P. vulgata* obtained here (Table 2) are notably lower than those previously published by Thomas and Mannino (2017) for southern Britain (1.66 g and 8.03 for *Ph. lineatus* and *P. vulgata*, respectively), although very similar to those reported by Dupont and Gruet (2002) in different locations along the Atlantic shore of France. The differences between northern Iberia and Great Britain are probably due to the larger size of the specimens collected by Thomas and Mannino (2017).

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The results obtained in this study for the %MY confirm that limpets are more profitable in terms of meat yield return in comparison to topshells (Table 3), in agreement with data previously published for these species (Dupont and Gruet, 2002; Thomas and Mannino, 2017). The average MY of *P. vulgata* is 1.6 times larger than that obtained from *Ph. lineatus*, a ratio that is in agreement with the factors 1.4 and 1.7 published by Thomas and Mannino (2017) and Dupont and Gruet (2002), respectively. Likewise, comparison between the topshell and the other two species of limpets also exhibits ratios of 1.6 and 1.9 in favour of *P. depressa* and *P. ulyssiponensis*, respectively.

4.2 Methodological development: mollusc meat yield estimation

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As described above, the experimental programme provided information about the MY before and after mollusc cooking, a comparison that was not considered in previous investigations in Atlantic Europe (Dupont and Gruet, 2002; Thomas and Mannino, 2017). The results show a similar decrease in MY after cooking in the case of the three limpet species, with a strong correlation between DMY and WMY (Fig. 3). However, the topshells showed a lower correlation between DMY and WMY, which could be a consequence of having estimated the WMY for this species. Taking into account that topshells recovered from archaeological sites were probably cooked before they were eaten (shell taphonomy does not suggest any other way to extract the soft parts), in this investigation only the information derived from DMY was used to reconstruct the MY contribution of this species. Therefore, the MY values based on average DMY from modern samples and the equations derived from DMY in comparison with shell weight (Fig. 4a) and shell size (Fig. 5a) were used to discuss the role of *Ph. lineatus* during the Mesolithic (Table 4). In the case of the limpets, available information up to now is not conclusive regarding whether they were cooked before consumption or not. Moreover, the results also show a higher correlation between mollusc MY and shell weight (Fig. 4c-h) and between mollusc MY and shell size (Fig. 5c-h) when the WMY is considered. Consequently, in the case of the three limpet species, WMY based on modern samples are preferred (Table 4).

On the other hand, and after concluding that *Patella* spp. and *Ph. lineatus* MY values should be estimated using WMY and DMY, respectively, the different methodological approaches applied in this investigation give three different estimates of the mollusc meat consumed by Mesolithic inhabitants of El Mazo cave. The highest value derived from this study (ca. 113 kg) was obtained by multiplying the average MY obtained from modern specimens (Table 2) by the MNI assigned to each taxon in each stratigraphic unit, following the method described by Thomas and Mannino (2017). However, this approach does not take into account either shell size or shell weight information. A comparison between shell size and weight from modern samples (Table 2) and archaeological specimens from El Mazo cave (Table 5) shows that modern shells exhibit greater size and weight than archaeological samples, especially in the case of *P. vulgata* and *P. depressa*. Ancient limpet shells are almost 2 g lighter than modern control specimens. Likewise, archaeological limpets and topshells are 10 mm and 2 mm smaller than modern samples, respectively. Consequently, if the MY of modern samples is used to calculate the MY extracted from archaeological shell remains, this would clearly overestimate the meat weight consumed by humans during the Mesolithic. Therefore, equations derived from shell weight (Fig. 4) and shell size (Fig. 5) should be used in order to more accurately reconstruct the MY extracted from ancient remains. The results obtained using equations designed for shell weight and size are very similar (ca. 46–51 kg), and notably lower than the results provided by the MNI method. Considering the limited differences observed between estimates derived from shell weight and shell size, we use figures derived from shell size, since the number of measured specimens is three times higher than the number of weighed specimens, so providing a more representative sample size.

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4.3 The role of shellfish in the Mesolithic diet

As described above, most of the previous investigations carried out in the Cantabrian region with the objective of reconstructing the meat yield derived from mollusc shells have concluded that these resources were not very important in the subsistence strategies of the last hunter-fisher-gatherers. A comparison between MY calculated from MNI obtained for shellfish and ungulates showed that molluscs represented less than 0.8% of the total meat yield estimated from mammalian fauna (Craighead, 1995; Marín-Arroyo 2013) (Table 6).

The estimate of MY from the shell remains recovered in squares X15 and X16 of El Mazo cave gives a total of 46.1 kg of meat consumed, a value that is notably lower than that previously obtained by Andreu-Alarcón (2013) for the ungulates (1,301 kg) using the MNI calculated from bone remains recovered from squares V15 and V16 of the same site (Table 6). However, the remains considered by Andreu-Alarcón were recovered from a much larger volume of sediment excavated (1,764 dm^3) than the shell remains used to estimate the mollusc MY (293.5 dm^3). In order to obtain a direct comparison between the two datasets, the meat yield per one dm^3 of sediment was calculated. The results provide a mollusc MY of 157 g/dm^3, compared to 738 g/dm^3 for ungulates (Table 6). Therefore, mollusc MY represents 21.3% of the total meat yield derived from the mammalian fauna, a value much higher than the value previously published of less than 0.8%, suggesting thus that molluscs had a greater dietary importance than previously argued by other scholars (Craighead, 1995; Marín-Arroyo, 2013).

Moreover, this difference between ungulates and shellfish might be biased by the methodological approach applied to estimate mammalian fauna contributions. As described above, meat yield from ungulates was calculated using the MNI estimated for each stratigraphic unit. However, Gutiérrez-Zugasti (2009) criticized this approach, since a few bones from a given species cannot be used to represent the weight of a whole individual. He proposed the use of bone weight in order to avoid an overestimation of the ungulate meat yield, as the MNI approach does not consider the possible differential transport from the kill sites located elsewhere. He also highlighted the differences between the two methods by calculating the meat yield derived from ungulate and shellfish remains recovered from La Riera and La Fragua caves (Table 6). Results showed that when using the MNI, the contribution of ungulates to the diet was much higher than the molluscs, but when using the bone weight, the results were very similar, and sometimes even favourable to shellfish, as occurs for example at La Fragua cave (Table 6). In this investigation, meat yield derived from the ungulate remains recovered from El Mazo cave and previously studied by Andreu-Alarcón (2013) was calculated using the weight of bones and the percent of usable meat for each species (Clark, 1983; Craighead, 1995). The results obtained showed a total meat yield return of ca. 2 kg, a value that is 600 times lower than the one previously obtained applying the MNI data.

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Marín-Arroyo (2013) argued that using the MNI was a valid method for calculation of the meat yield extracted from mammalian fauna, since normally the number of bone remains that account for an individual is high, especially during the Mesolithic. However, this situation is not observed in the case of the shell midden of El Mazo, where on average just 5.1 identified bones correspond to each minimum individual and where several units exhibit lower representation than 2.5 bone remains per individual (Andreu-Alarcon, 2013). One example that shows how meat yield from ungulates can easily be overestimated when using the MNI method is unit 104 of El Mazo, where one single vertebra of red deer was used to hypothesize a consumption of 100 kg of meat, a value that is far higher than that derived from all mollusc shell remains considered in this investigation. These results suggest that estimating ungulate contribution exclusively from MNI is more subjective as it is not strictly based on the remains recovered from the archaeological site but on a hypothetical extrapolation to a larger number that may not be justified. Similarly, other investigations have also shown a large shellfish consumption in littoral areas (Hausmann et al., 2019; Jazwa et al., 2015). However, as the ecological conditions in these other areas and the methods used cannot be applied to the particular case of El Mazo cave, it is more accurate to calculate the MY exclusively from those remains recovered from the archaeological assemblage. Besides, there are three additional biases that also contribute to the overestimation of the ungulate meat yield in the Marín-Arroyo study (2013). The first is that in many sites all faunal remains recovered from the excavations were studied, while in the case of molluscs, these were exclusively studied using a sample from each level (Álvarez-Fernández, 2011; Gutiérrez-Zugasti, 2009; 2011a). The second bias is that changes in sea level and the position of the sites in relation to the coast were not taken into account and this omission has important implications in the interpretation of the data, since the sites dating to the Late Glacial and very early Holocene, that may contain significant evidence for exploitation of coastal resources, are currently submerged. The third is that Marín-Arroyo (2013) significantly overestimated the ungulate contribution in the particular case of Poza l´Egua cave, since she considered that 64 individuals were recorded at the site (ca. 43% of the total ungulates documented in the Cantabrian region for the Mesolithic). However, the information previously published for this site (Arias et al., 2007) refers to NISP not to MNI.

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On the other hand, and even though a differential preservation between bones and shells could be argued to explain the differences in the relative contribution of these resources to human diet, the meat yield return from ungulates only represents less than 5% of the meat yield derived from molluscs. This difference is, arguably, too large to be explained exclusively by better preservation of shells. Moreover, in this particular case, the taphonomic alterations inferred from the bones (Andreu-Alarcón, 2013) and mollusc shells (García-Escárzaga, in press) recovered from El Mazo, were not very important. Therefore, it can be concluded that (i) previous calculations of ungulate meat yield from northern Iberia are significantly overestimated, especially if they are compared with molluscs, and that (ii) shellfish had a greater dietary importance than previously proposed by most studies in this coastal area.

However, it is not only the cost effectiveness of meat yield that is relevant. Shellfish may also have been relatively important in the diets of last hunter-fisher-gatherers because of their nutritional benefits (Duarte, 2014; Erlandson, 1988; 2001; Henshilwood, 1994), their social value (Gutiérrez-Zugasti et al., 2016) and their potential to stay fresh for a longer time, enabling deferred consumption (Arias, 1991; Fano, 1998; Gutiérrez-Zugasti, 2009; Madariaga, 1964; 1967; 1994; Ortea, 1986).

Although this investigation suggests a more important role of molluscs in the subsistence strategies of the last hunter-fisher-gatherers than previously proposed, shellfish cannot be considered as a principal subsistence resource, but rather, a complementary food within a highly diverse diet (Clark, 1976; 1995; Clark and Straus, 1986; Fano, 1998; González-Morales et al., 2004). In this sense, results of δ^{13}C and δ^{15}N analysis on human remains in the Cantabrian region suggest that most of the marine protein consumed by humans would be obtained from fish, instead of from marine invertebrates (Arias, 2006). This conclusion has also been proposed for other coastal sites in Atlantic Europe, such as for example Téviec and Höedic in Britanny (Schulting and Richards, 2001) and Arapouco and Poças de São Bento in Portugal (Guiry et al., 2015), where δ^{15}N values show that fish was the main source of marine protein. However, although fish was probably an important resource for human populations, available data from archaeological assemblages in the Cantabrian region and also throughout Atlantic Europe is still very limited (Adan et al., 2009; Fano et al., 2013; McQuade and O´Donnell, 2007; Pickard and

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Bonsall, 2004) and further studies are required to accurately establish the role of fish in human diets. Moreover, other resources scarcely represented in the archaeological assemblages must also be considered in further studies to properly understand Mesolithic diets, such as for example cephalopods, recently documented in Portugal (Araújo, 2016), or nuts, which also exhibit a high energy return (Prado-Novoa et al., 2017).

4.4 Coastal resource intensification and intertidal zone profitability

The increasing consumption of coastal resources during the Mesolithic in comparison with previous periods has been traditionally explained by a process of intensification in shellfish exploitation as a result of population increase (Straus and Clark, 1986). According to this interpretation, intensification was demonstrated by a clear decrease in shell size through time (Mannino and Thomas, 2001; Ortea, 1986; Vega del Sella, 1916). However, Bailey and Craighead (2003) highlighted an alternative hypothesis, that decreased shell sizes could have been induced by changes in climatic and environmental conditions. Recently, in order to discriminate between these alternatives, Gutiérrez-Zugasti (2011b) studied both the size and age distributions of marine gastropods (limpets and topshells) from Upper Palaeolithic and Mesolithic sites in northern Iberia. Results revealed a decrease in the mean size and a decrease in mean age of these species. He also found a clear increase in the use of the lower intertidal zone during the Mesolithic in comparison with the Upper Palaeolithic (Gutiérrez-Zugasti, 2010; 2011b). Lower zones are emerged for a shorter period of time and they are continually wave-beaten, shell collection being more difficult and dangerous than in higher intertidal zones, meaning that these zones would not have been priority targets for shell gathering.

Our study has enabled the comparison between limpets collected in the lower and higher zones of the intertidal zones (*P. vulgata* and *P. depressa*) in order to obtain an estimate of the relative profitability of the two areas. The results show that the molluscs gathered from the higher zone exhibit more %MY than those harvested in the lower zone (Table 5), reinforcing the suggestions that increased exploitation of the lower intertidal zones must be considered as a sign of intensification. Consequently, these datasets provide a better understanding of human behaviour and shellfish exploitation patterns during prehistory in the Cantabrian region, since

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increased exploitation of a less profitable intertidal zone is in agreement with the hypothesis of intensification in coastal resource exploitation during the Mesolithic.

5. Conclusion

The results obtained in this study have shown a greater dietary importance of molluscs than previously proposed by other studies (Craighead, 1995; Marín-Arroyo, 2013), although their contribution is probably less than that estimated for the ungulates recovered from El Mazo site (Table 6). Nevertheless, this difference appears to be less than expected according to previous investigations, since the methods traditionally applied to calculate the amount of meat obtained from ungulates overestimate their contribution to human diet. In any case, neither molluscs nor ungulates were by themselves the only contribution to human diet, which seems to have been quite broad, a conclusion supported by carbon and nitrogen isotope analyses in the Cantabrian region (Arias, 2006). This study has shown that terrestrial and marine resources had roughly similar dietary contributions. However, further analyses are required to determine the complete human diet with greater accuracy, since there are food resources not preserved (including vegetables and cephalopods), or poorly preserved (including fish, birds and nuts) in the archaeological record.

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Acknowledgments

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2014							
Winter	**Spring**		**Summer**		**Autumn**		**Winter**
-----	-----	-----	-----	Aug. 11	Sep. 24	Nov. 07	Dec. 23

2015							
Winter	**Spring**		**Summer**		**Autumn**		**Winter**
Feb. 03	Mar. 21	May. 30	Jul. 14	Aug. 25 *	Sep. 24 *	Nov. 27 *	Dec. 28 *

2016							
Winter	**Spring**		**Summer**		**Autumn**		**Winter**
Feb. 08 *	Mar. 11	May. 05	Jun. 19	Aug. 01	Sep. 18	Nov. 27 *	Dec. 27

2017							
Winter	**Spring**		**Summer**		**Autumn**		**Winter**
Feb. 13 *	Mar. 25	Apr. 24 #	Jun. 24 #	-----	-----	-----	-----

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	N samples	Mean shell size (mm)	Mean shell weight (g)	Dry Meat Yield (g)				Wet Meat Yield (g)			
				Mean	±SD	Maximum	Minimum	Mean	±SD	Maximum	Minimum
Ph. lineatus	960	17.6	1.96	0.66	0.20	1.29	0.20	0.73	0.10	1.80	0.20
P. vulgata	850	32.1	3.30	1.41	0.81	6.36	0.20	1.98	1.08	9.00	0.30
P. depressa	850	33.5	3.46	1.47	0.79	6.50	0.20	2.02	1.00	8.20	0.20
P. ulyssiponensis	600	36.1	2.69	1.54	0.68	5.47	0.30	2.02	0.85	7.40	0.40

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	Relative Meat Yield (g)					
	Mean	±SD	Maximum	Minimum	Higher zone mean	Lower zone mean
Ph. lineatus	0.38	0.09	1.20	0.05		
P. vulgata	0.61	0.13	1.13	0.19	0.64	0.56
P. depressa	0.59	0.14	1.11	0.25	0.64	0.54
P. ulyssiponensis	0.71	0.16	1.63	0.32		

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Relative Dry Meat Yield (g)			
Mean	±SD	Maximum	Minimum
0.34	0.06	0.70	0.15
0.43	0.12	0.95	0.12
0.43	0.13	1.13	0.12

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	Phorcus linetus	*Patella vulgata*	*Patella depressa*	*Patella ulyssiponensis*
Wet meat yield (kg)				
From MNI	23.74	57.73	29.49	4.9
From shell weight	21.30	22.06	7.86	2.3
From shell size	17.46	21.74	8.13	1.0
Dry meat yield (kg)				
From MNI	21.46	41.11	21.46	3.78
From shell weight	18.51	16.33	5.09	1.75
From shell size	15.24	15.24	5.41	0.78

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	Mean shell size (mm)	Mean shell weight (g)
Ph. lineatus	15.9	1.4
P. vulgata	23.3	1.5
P. depressa	22.3	1.4
P. ulyssiponensis	33.8	2.0

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	Ungulates (using MNI)		Molluscs		Ungulates (using bones weight)	
	Total weight (kg)	g/dm^3	Total weight (kg)	g/dm^3	Total weight (kg)	g/dm^3
La Riera (29)	711	---	0.6	---	1	---
La Fragua (1)	1,697	---	11.7	---	3	---
Several mesolithic sites	11,945	---	94	---	---	---
El Mazo	1,301	738	46.2	157	2	1.14

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Figure 1. a) Location of the Cantabrian region (white rectangle), b) Langre Beach and intertidal areas where the collection programme was conducted, and c) location of the archaeological site of El Mazo.

Figure 2. a) View of the rockshelter of El Mazo; b) topographic map of the rockshelter showing excavation areas and provenance of the studied samples (shaded squares) and c) stratigraphy of the inner test pit (squares X15 and X16).

Figure 3. Correlation between dry meat yield (DMY) and wet meat yield (WMY) in *Patella vulgata* (a), *Patella depressa* (b), *Patella ulyssiponensis* (b) and *Phorcus lineatus* (d).

Figure 4. Correlation between meat yield (MY) and shell weight in *Phorcus lineatus* (a-b), *Patella vulgata* (c-d), *Patella depressa* (e-f) and *Patella ulyssiponensis* (g-h), considering both dry meat yield (DMY) and wet meat yield (WMY).

Figure 5. Correlation between meat yield (MY) and shell length in *Phorcus lineatus* (a-b), P*atella vulgata* (c-d), *Patella depressa* (e-f) and *Patella ulyssiponensis* (g-h) considering both dry meat yield (DMY) and wet meat yield (WMY).

Table 1. Date of each collection event in Langre Beach during the experimental programme developed in this study. Stars (*) indicate that only *Phorcus lineatus* was harvested in that collection event. Hashes (#) show that *Patella ulyssiponensis* was not captured in that collection event, unlike the other two species of limpets.

Table 2. Mean, maximum and minimum dry meat yield (DMY) and wet meat yield (WMY) from the species harvested from Langre Beach (N Spain) during the collection programme. The shell size show the maximum diameter for *Phorcus lineatus* and maximum length for *Patella* spp.

Table 3. Mean, maximum and minimum relative meat yield (%MY) from the species harvested from Langre Beach (N Spain) during the collection programme. In the case of *Patella vulgata* and *Patella depressa*, the mean relative meat yield extracted from limpets collected on the lower and higher zone of the intertidal is showed.

Table 4. Wet meat yield (WMY) and dry meat yield (DMY) for the four main gastropod species present at the shell midden site of El Mazo. The meat yield was obtained applying the three different methodologies previously explained in detail in section 2.4.

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Table 5. Mean shell size and mean shell weight from *Phorcus lineatus*, *Patella vulgata*, *Patella depressa* and *Patella ulyssiponensis* specimens recovered from the shell midden site of El Mazo cave.

Table 6. Meat yield estimation from molluscs and ungulates from different shell midden sites in the Cantabrian region during the Mesolithic. Meat yield from ungulates have been calculated from MNI and from bone weight. The results are reported as total meat yield and as relative meat yield according to the total volume of sediment excavated. The table was elaborated from data published by Andreu-Alarcon (2013) for El Mazo, Gutiérrez-Zugasti (2009) and Ortea (1986) for La Fragua (level 1) and La Riera (level 29), and Marín-Arroyo (2013) for several mesolithic sites along the Cantabrian region.

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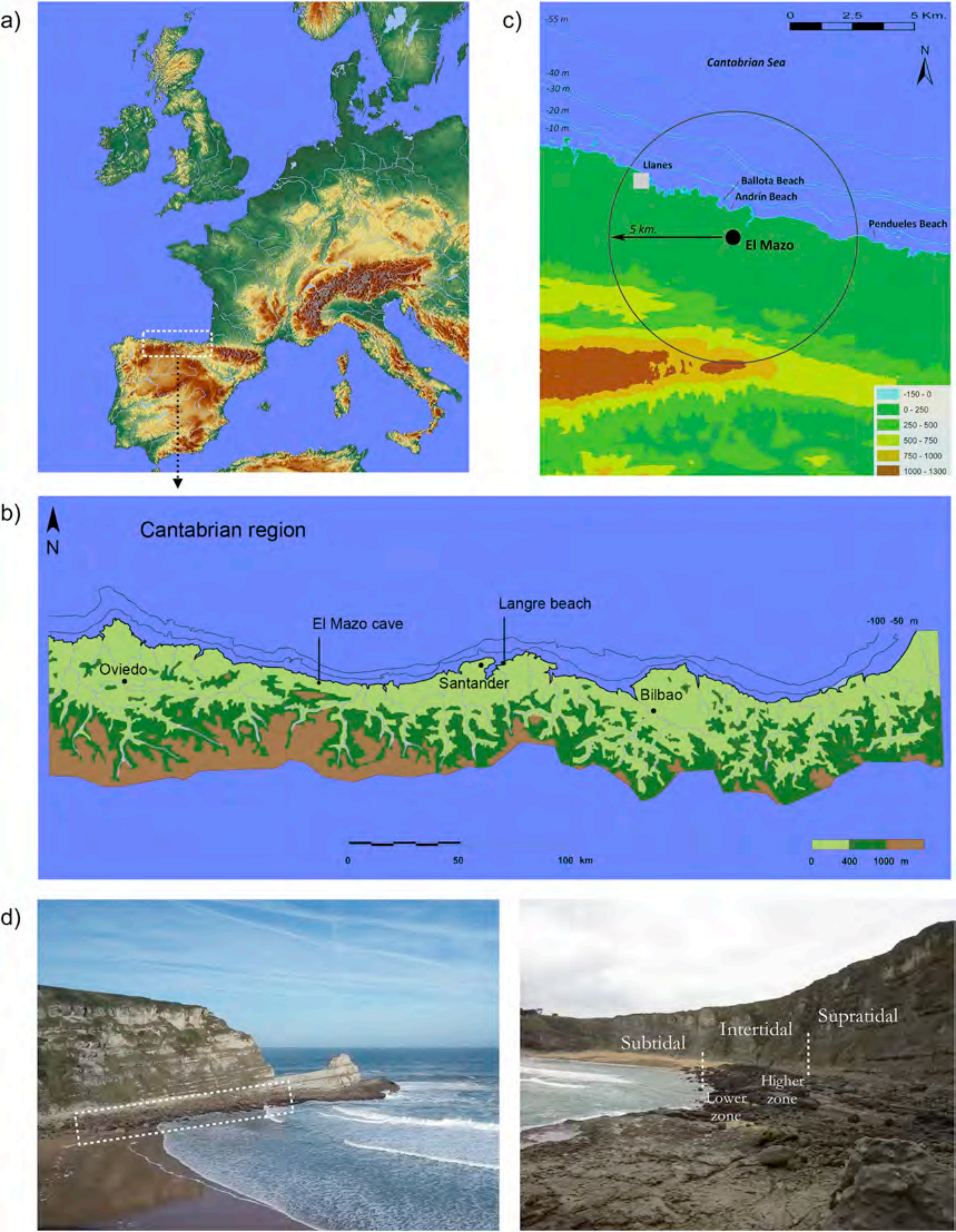
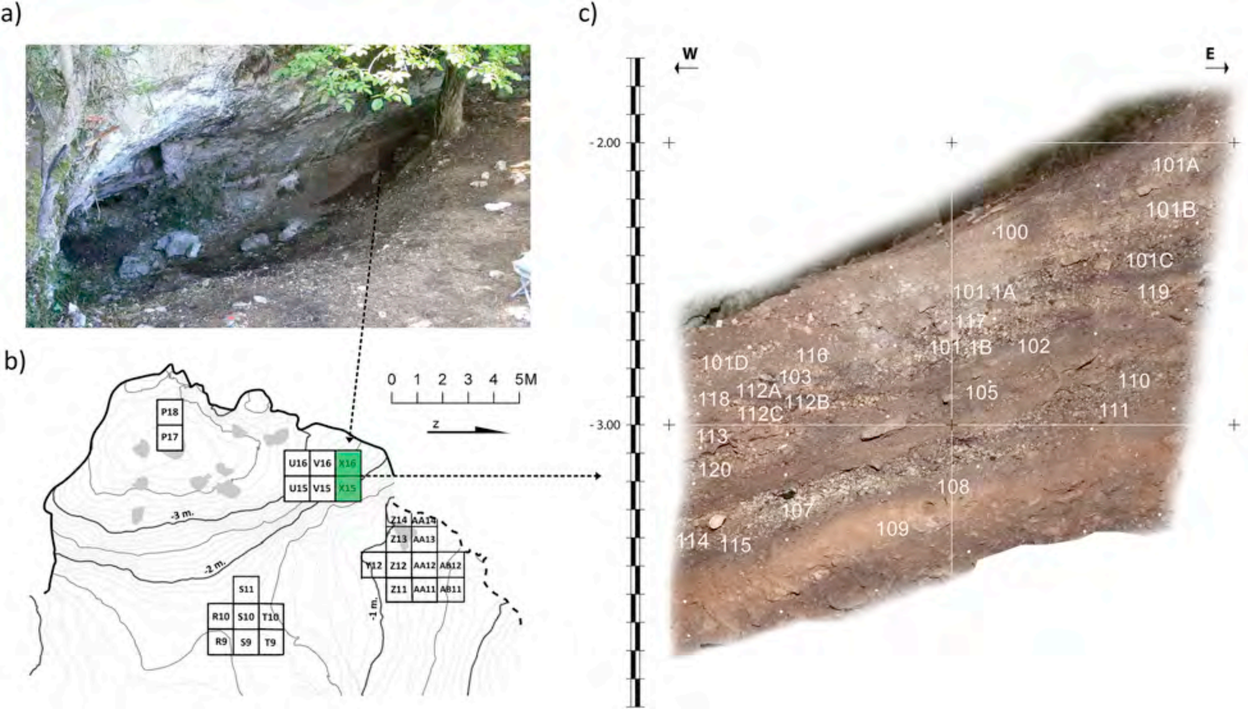
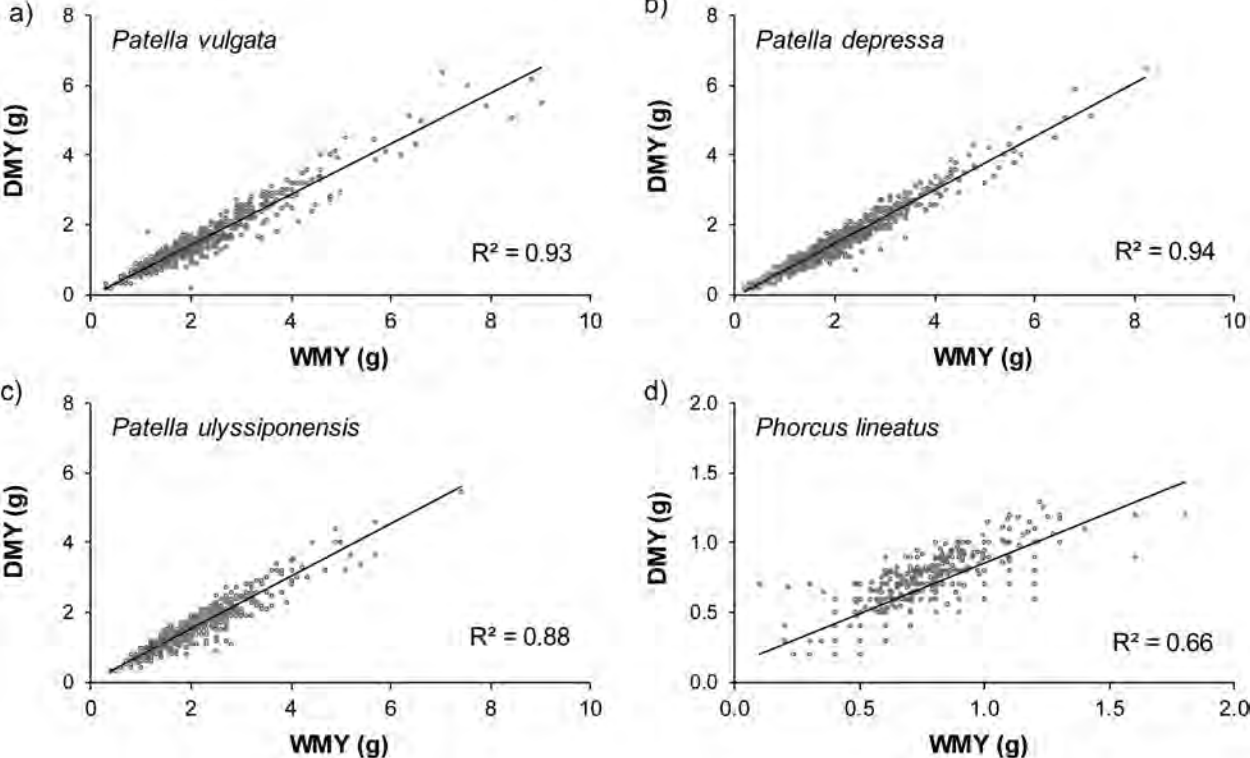
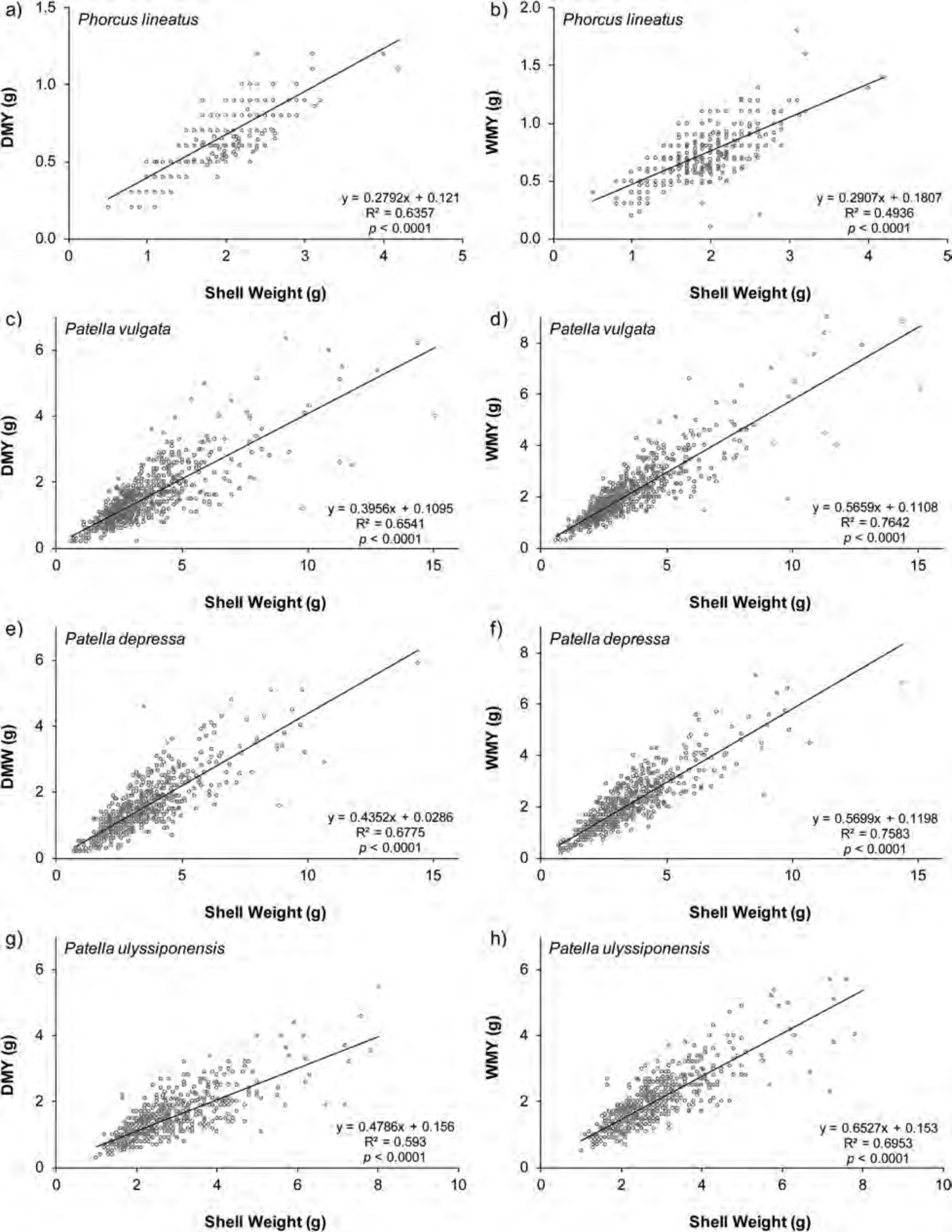
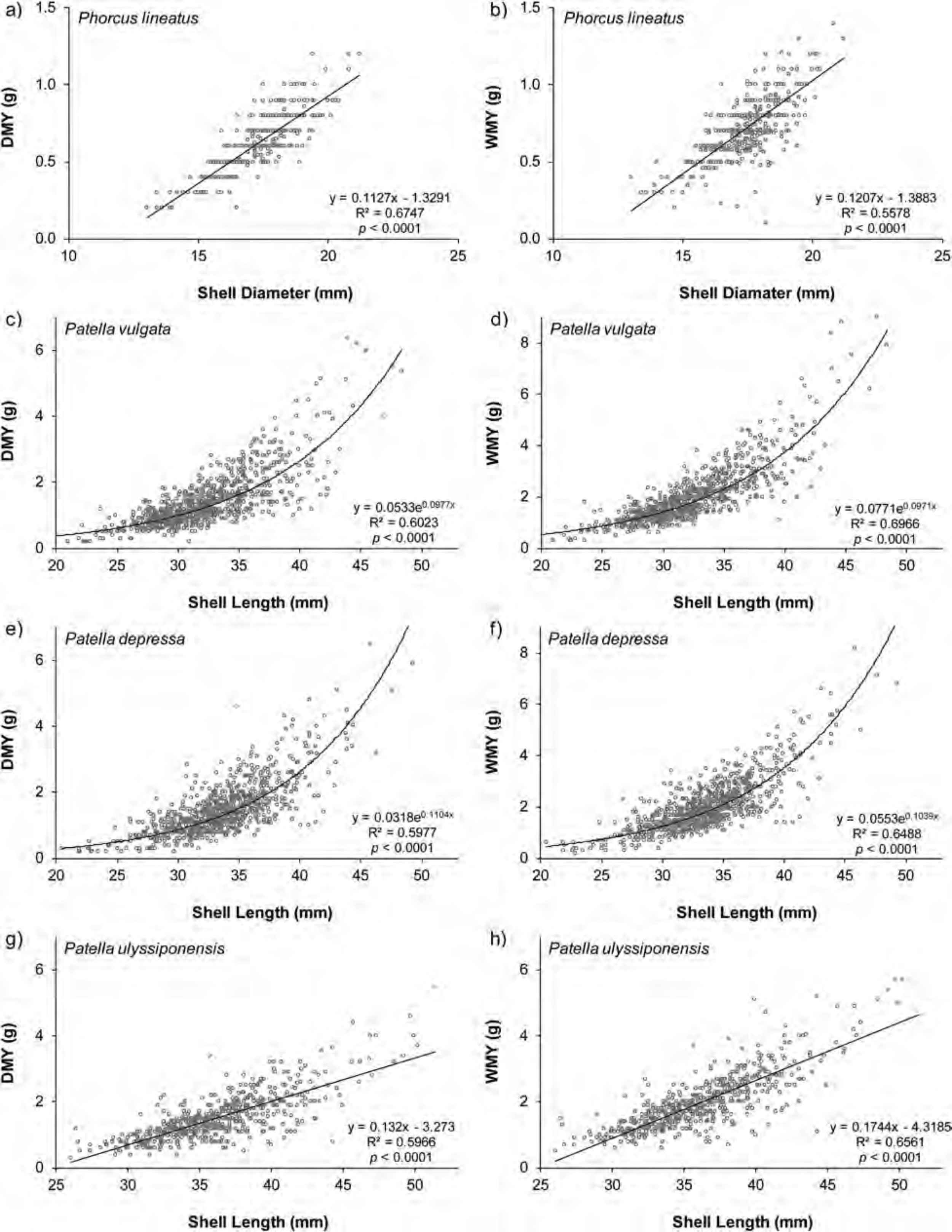

a)
b)
c)
d)
-55 m
0
2,5
5 Km.
Cantabrian Sea
N
-40 m
-30 m
-20 m
-10 m
Llanes
Ballota Beach
Andrín Beach
Pendueles Beach
5 km.
El Mazo
-150 - 0
0 - 250
250 - 500
500 - 750
750 - 1000
1000 - 1300
N
Cantabrian region
Langre beach
El Mazo cave
-100 -50 m
Oviedo
Santander
Bilbao
0
50
100 km
0
400
1000 m
Subtidal
Intertidal
Supratidal
Higher zone
Lower zone


a)
b)
c)
P18
P17
U16
V16
X16
U15
V15
X15
-3 m.
-2 m.
-1 m.
0 1 2 3 4 5M
z
Z14
AA14
Z13
AA13
Y12
Z12
AA12
AB12
Z11
AA11
AB11
S11
R10
S10
T10
R9
S9
T9
W
E
- 2.00
- 3.00
101A
101B
100
101C
101.1A
119
117
101.1B
102
101D
116
103
118
112A
112B
112C
105
110
111
113
120
108
107
109
114
115


a)
Patella vulgata
R² = 0.93
DMY (g)
WMY (g)
0
2
4
6
8
0
2
4
6
8
10
b)
Patella depressa
R² = 0.94
DMY (g)
WMY (g)
0
2
4
6
8
0
2
4
6
8
10
c)
Patella ulyssiponensis
R² = 0.88
DMY (g)
WMY (g)
0
2
4
6
8
0
2
4
6
8
10
d)
Phorcus lineatus
R² = 0.66
DMY (g)
WMY (g)
0.0
0.5
1.0
1.5
2.0
0.0
0.5
1.0
1.5
2.0


a)
Phorcus lineatus
DMY (g)
Shell Weight (g)
y = 0.2792x + 0.121
R² = 0.6357
p < 0.0001
b)
Phorcus lineatus
WMY (g)
Shell Weight (g)
y = 0.2907x + 0.1807
R² = 0.4936
p < 0.0001
c)
Patella vulgata
DMY (g)
Shell Weight (g)
y = 0.3956x + 0.1095
R² = 0.6541
p < 0.0001
d)
Patella vulgata
WMY (g)
Shell Weight (g)
y = 0.5659x + 0.1108
R² = 0.7642
p < 0.0001
e)
Patella depressa
DMW (g)
Shell Weight (g)
y = 0.4352x + 0.0286
R² = 0.6775
p < 0.0001
f)
Patella depressa
WMY (g)
Shell Weight (g)
y = 0.5699x + 0.1198
R² = 0.7583
p < 0.0001
g)
Patella ulyssiponensis
DMY (g)
Shell Weight (g)
y = 0.4786x + 0.156
R² = 0.593
p < 0.0001
h)
Patella ulyssiponensis
WMY (g)
Shell Weight (g)
y = 0.6527x + 0.153
R² = 0.6953
p < 0.0001


a)
Phorcus lineatus
DMY (g)
y = 0.1127x - 1.3291
R² = 0.6747
p < 0.0001
Shell Diameter (mm)
b)
Phorcus lineatus
WMY (g)
y = 0.1207x - 1.3883
R² = 0.5578
p < 0.0001
Shell Diamater (mm)
c)
Patella vulgata
DMY (g)
y = 0.0533e^0.0977x
R² = 0.6023
p < 0.0001
Shell Length (mm)
d)
Patella vulgata
WMY (g)
y = 0.0771e^0.0971x
R² = 0.6966
p < 0.0001
Shell Length (mm)
e)
Patella depressa
DMY (g)
y = 0.0318e^0.1104x
R² = 0.5977
p < 0.0001
Shell Length (mm)
f)
Patella depressa
WMY (g)
y = 0.0553e^0.1039x
R² = 0.6488
p < 0.0001
Shell Length (mm)
g)
Patella ulyssiponensis
DMY (g)
y = 0.132x - 3.273
R² = 0.5966
p < 0.0001
Shell Length (mm)
h)
Patella ulyssiponensis
WMY (g)
y = 0.1744x - 4.3185
R² = 0.6561
p < 0.0001
Shell Length (mm)