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## RELATIVE GROWTH RATES OF THE NOBLE PEN SHELL *PINNA NOBILIS* THROUGHOUT ONTOGENY AROUND THE BALEARIC ISLANDS (WESTERN MEDITERRANEAN, SPAIN)

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**ABSTRACT** In this study, we evaluated the growth of adults and juveniles of the endangered noble pen shell *Pinna nobilis*, calculated the growth rates of newly recruited juveniles, and described relative directional growth during ontogeny. We described growth using posterior adductor muscle scars (PAMS) and fit of the von Bertalanffy growth curve for adult population data at shallow depths (5–10 m) around the Mallorca and Ibiza islands, and compared the parameters with other Mediterranean populations. Populations around Mallorca could be fitted according to the von Bertalanffy function  $L_t = 65.31(1 - e^{-0.11(t + 0.53)})$ , whereas for Ibiza the function was  $L_t = 154.55(1 - e^{-0.03(t + 4.31)})$ . We compared first-year growth rates obtained in the laboratory and from field collections with newly settled individuals. We found that experimentally evaluated growth rates of juveniles in the laboratory of 0.18 mm/day are low compared with minimum values obtained in the field, which range, on average, from 0.28–0.32 mm/day, indicating food availability can limit growth. Furthermore we investigated relative allometric growth patterns during ontogeny using a unique data set ranging from measurements of newly recruited juveniles with shell length less than 1 cm to measurements on adult shells of 69.8 cm length. Fitting a sigmoidal function to our data and solving for the allometric exponent  $b$ , we found 3 distinct growth periods: preferential growth in the length direction up to 5.82 cm in shell length, then widening of the shell up to 14.64 cm, after which the shape of the shell becomes more elongated once again.

**KEY WORDS:** *Pinna nobilis*, pen shell, growth rate, allometric growth, von Bertalanffy growth curve

### INTRODUCTION

The pen shell *Pinna nobilis* (Linnaeus, 1758) is one of the largest mollusc species, reaching total anteroposterior lengths of up to 1.2 m (Zavodnik et al. 1991, Richardson et al. 1999, García-March et al. 2007a). The species is endemic to the Mediterranean Sea, where it typically occurs in association with *Posidonia oceanica* (L.) Delile meadows. Pen shells live partially buried upright in the sand, anchored by their numerous byssus filaments to the rhizomes and shoots of *P. oceanica*. The population numbers of the bivalve *P. nobilis* are currently in decline (Centoducati et al. 2007) and the pen shell is subject to strict protection as an endangered species under European Council Directive 92/43/EEC (EEC 1992). The pen shell *P. nobilis* is long-lived, achieving a life span in excess of 20 y (Butler et al. 1993, Richardson et al. 1999, Galinou-Mitsoudi et al. 2006). The full life cycle of the pen shell is still understudied; for example, the mortality of larvae is unknown and, for juveniles, there is very little information available (Katsanevakis 2007). Butler et al. (1993) state that larvae of the fan mussel have a life span of 5–10 days, and they have, like most bivalve species, a highly variable recruitment (Katsanevakis 2007).

Little is known about growth during the direct period after settlement and metamorphosis, although growth is fast during the first 2–3 y, and much slower thereafter, according to a 10-y study of the growth of *P. nobilis* in the French Mediterranean (Vicente et al. 1980, Moreteau & Vicente 1982).

A disputed method to estimate the age and growth of related *Pinna bicolor* in South Australia relies on the interpretation of putative adductor muscle scars, which represent seasonal migration of the adductor muscle as the length of the shell increases (Butler & Brewster 1979, Butler 1987). These posterior adductor muscle scars (PAMS) represent a year of life, but not all years are discernible as PAMS on the inner surface of the shell (García-March & Marquez-Aliaga 2007b, Garcia-March et al. 2011). The inner shell surfaces of *P. nobilis* from the Spanish Mediterranean also show PAMS. In general, a linear relationship exists between shell growth rate and water temperature (Richardson et al. 1999). After settlement, shell growth is rapid, reaching a maximum rate during the summer high water temperatures. During a similar period of increasing water temperatures in the second year (May and June), shell accretion appears to be marginally slower than at the same time the previous year, and it correlates with the appearance of the “first” ring on the adductor muscle scar. Therefore, the first year is not accounted for by a PAMS, as corroborated with stable isotope data (Richardson et al. 1999). Estimates of the growth rates of the pinnids using adductor muscle scar rings should take into account a missing first-year ring, as well as the fact that not all years are visible as PAMS. However, evaluating PAMS can be useful to make comparisons among populations to explore qualitative differences in growth. During ontogeny, growth is characterized by changes in proportion as well as size, called allometric growth. In pen shell populations on the Tunisian coast, there was a breakpoint at a shell length  $\approx$  18 cm, corresponding to a widening of the shell after which growth became elongated (Rabaoui et al. 2007). Such a change in the growth trajectory might be a useful source of information about life

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history events of the pen shell or a fast ecological change. A comparison with other regions, like the Balearic Islands, might reveal this change in growth pattern as specific for the species or highly regional, connected to local changes.

In this study, our main objectives were (1) to evaluate, for the first time, growth rates of *P. nobilis* ranging the full life span—from newly settled recruits to adults—and (2) to compare differences in growth in *P. nobilis* populations around the Balearic Islands. We used laboratory measurements and field observations of juvenile and adult individuals for this aim. We measured growth of young individuals of younger than 1 mo, 3 mo, and 6 mo of age caught in collectors directly after recruitment. Furthermore, we kept juveniles in aquaria subjected to a known food regime. With our data set, which contains a large size range of shell size, we focus on relative allometric growth throughout ontogeny and evaluate discontinuities in preferential growth direction.

## MATERIALS AND METHODS

### Study Site

We sampled 5 sites around the island of Mallorca (depth, 5–6 m), Magalluf (39°30.1' N, 2°32.36' E), Cala d'Or (39°22.164' N, 3°13.887' E), Es Cargol (39°16.394' N, 3°2.476' E), St. Maria (Cabrera), and Pollença (39°53.792' N, 3°05.523' E; Fig. 1). Additional data for adult valves were obtained by measurements of shells of individuals obtained alive from Ibiza: Talamanca, Esponja, and Espardell (7–25 m), and Dragonera (Mallorca, 7–10 m) by Cabanellas-Reboredo et al. (2009b).

### Age-Size Relationship of Adult *Pinna nobilis*

During 2006 and 2007, we collected 70 valves from dead individuals in the meadows around the Balearic Islands (Fig. 1), consisting out of 2 valves stuck together or without too much epiphyte cover. In addition, from the same meadows, we used the valves of 16 specimen originally collected alive for another study, see Cabanellas-Reboredo et al. (2009b). Shell length ranged from 8.5–69.8 cm. We measured the distance from the posterior end of the anterior adductor muscle scar to the last ring of the PAMS deposited at the leading edge of the dorsal nacre lobe (Fig. 2B in Richardson et al. (1999)).

There is a good linear relationship between shell length and the youngest leading edge of the dorsal nacre lobe (Richardson et al. 1999). Therefore, fitting an equation between these 2 dimensions, it is possible to extrapolate the corresponding shell lengths when each PAMS was deposited. Even if age of individuals cannot be established reliably by counting the number of scars, we relate the number of PAMS to shell length adding 1 for the first year when no scarring occurs to compare growth patterns in Mallorca with other sites in the Mediterranean. We fitted growth curves based on the von Bertalanffy growth function  $L_t = L_\infty (1 - e^{-k(t - t_0)})$  with the FSA package in R (Ogle 2010), where  $L$  is shell length,  $k$  is a rate constant, and  $t$  is the number of PAMS + 1. The von Bertalanffy growth model (von Bertalanffy 1938) is the most commonly applied among length-age models and, although other models have been used, it seems to be the most fitting for growth of *P. nobilis*, as a comparison among models for 5 populations along the Tunisian coast demonstrated (Rabaoui et al. 2007).

### Growth in Juvenile *Pinna nobilis*

#### Field

Recruits were sampled at the same field sites around Mallorca where the adult valves were collected (Fig. 1). Mesh bags, providing a large surface and substratum similar to *P. oceanica* rhizomes, were used to collect recruits. Collectors were adjusted from Type II used in the same area by Cabanellas-Reboredo et al. (2009a). Every collector consisted of a concrete block moored at a 5-m depth in natural sand patches within the seagrass meadow to cause minimal disturbance to the plants. A rope was attached to the blocks, and a subsurface buoy was used to keep the bags afloat and to mark the collector. Three collector bags, each with their own mooring, were suspended at depths of 2–3 m at each site, with approximately 10 m between each mooring. Subsurface buoys were used to avoid hindering navigating ships and unwanted removal by third parties. Polyethylene mesh bags (0.7 × 0.4 m big, with a mesh width of 0.01 × 0.01 m) were attached to the rope at intervals between 0.5 m and 1.0 m. Inside each bag, 13-m-long × 0.1-m-wide thin onion nets with a mesh width of 0.005 × 0.005 m were placed to increase the available recruitment surface.

Starting at the beginning of summer (late June), these bags were changed every month, then frozen until further analysis. One set of bags for each site was left for the full sampling period (3 mo), and at 1 site (Pollença), 15 additional bags were left for 6 mo total. After defrosting, bags were cut in manageable pieces and flushed under tap water using a brush. Organisms were picked out with tweezers. Length and width of visible juveniles were measured with a digital caliper. Small recruits were collected on a 200- $\mu$ m sieve after filtering the processed water. Small postlarvae were isolated and counted under a microscope (Stemi 2000C, Zeiss). Organism size was obtained from calibrated measurements of photos acquired using a stereomicroscopic camera (AxioCam MRc5, Zeiss; with AxioVision 40 V4.3.0, Carl Zeiss Imaging solutions software) and was processed using ImageJ software (ImageJ Java 1.6.010). Samples were preserved on alcohol. From the exact submersion period of the bags and larval size, a minimum growth rate is estimated, assuming that the largest individual in each bag settled on the first submersion day of trap deployment and grew until recollection.

#### Laboratory

To estimate growth rates of juvenile recruits in the laboratory, we submerged collector bags in Pollença (Fig. 1) from June 24 until September 16, 2010 (a total of 85 days). The 63 individuals collected in these field collectors were transferred to a controlled laboratory environment. They were suspended for 13 days in a 100-L tank in small individual mesh bags, keeping them upright but permitting the exchange of water and food. Juveniles were fed daily an equal mixture of *Rhinomonas* and *Tetraselmis* sp., species commonly used in shellfish cultures (Coutteau & Sorgeloos 1992), with a final concentration of 1,000 cells/mL. Temperature was kept constant at 26°C, the average summer (June to October) water temperature around Mallorca and the temperature at the time of collection. Individual shell length and width were measured at the beginning and end of the experiment.

#### Allometric Growth Patterns

The relationship between age and unburied length has little informative value in field studies because the amount of buried

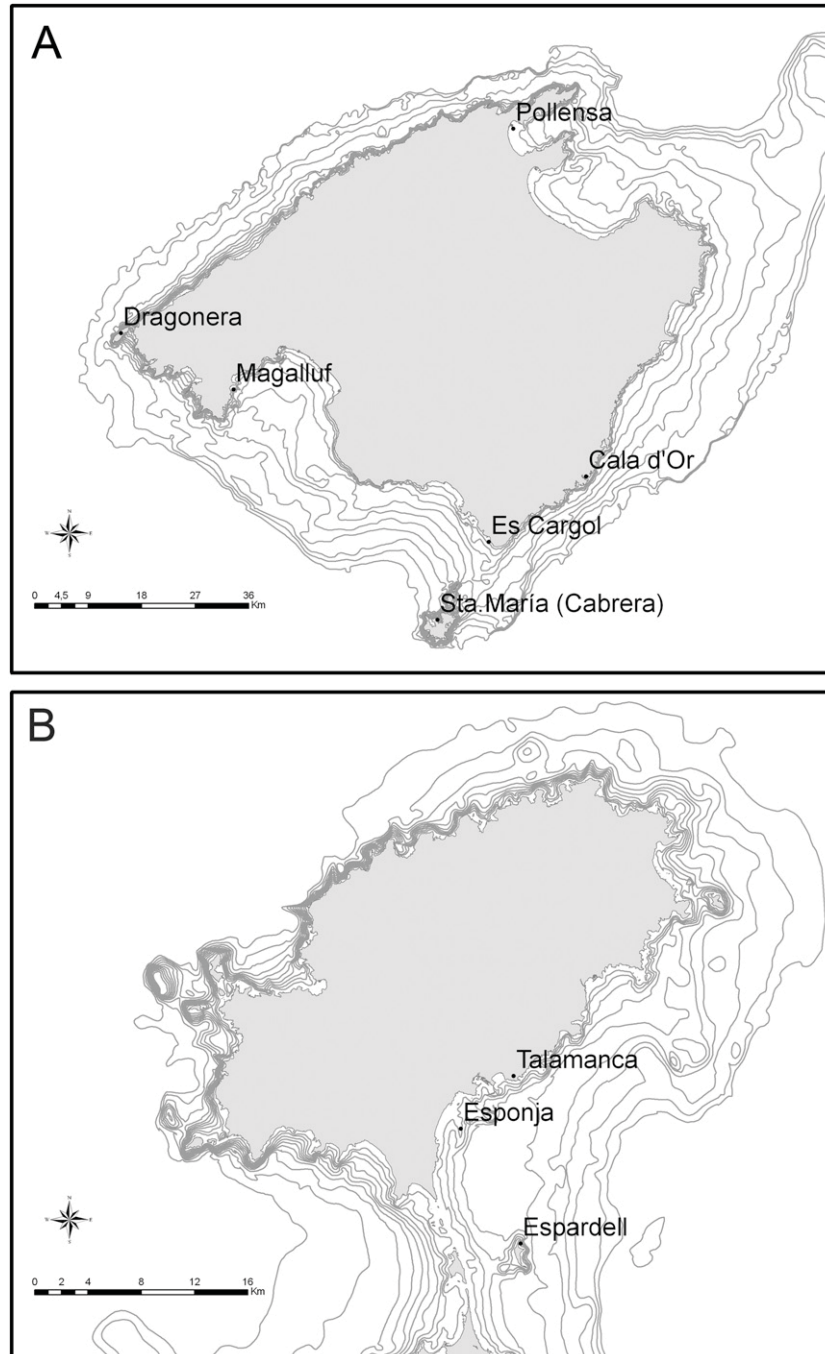


Figure 1. Geographical location and sample sites of the study area in the Balearic Islands (western Mediterranean). (A) Mallorca. (B) Ibiza. Continuous lines show isobaths.

shell is highly variable among individuals. Therefore, we generally use a length–width relationship to back-calculate probable age of individuals measured in the field, unlike García-March et al. (2002), who used a measurement of unburied shell parts together with an estimation of the length of the buried shell using an empirical equation (García-March & Ferrer 1995). It is important to know changes in length–width relationships throughout ontogeny of the organism because this adds accuracy to age estimates of monitored individuals in the field. Because growth is often accompanied by changes in proportion as well as size, the

allometric equation  $W = aL^b$  (Huxley 1932) should be used. In this equation,  $W$  is shell width,  $L$  is shell length, and exponent  $b$  is a measure of the difference in growth rates of the shell parts. However, this classic model fails for pen shell growth because of the existence of a breakpoint in the growth trajectory (Rabaoui et al. 2007), and a more complex model of the form  $\log W = f(\log L)$  should be used (Katsanevakis et al. 2007). We selected the quadratic model, assuming that nonlinearity exists in the relationship of width and length:  $\ln W = a_1 + i_1 \ln L + b_2 (\ln L)^2$ , with the allometric exponent  $b$  calculated as described in

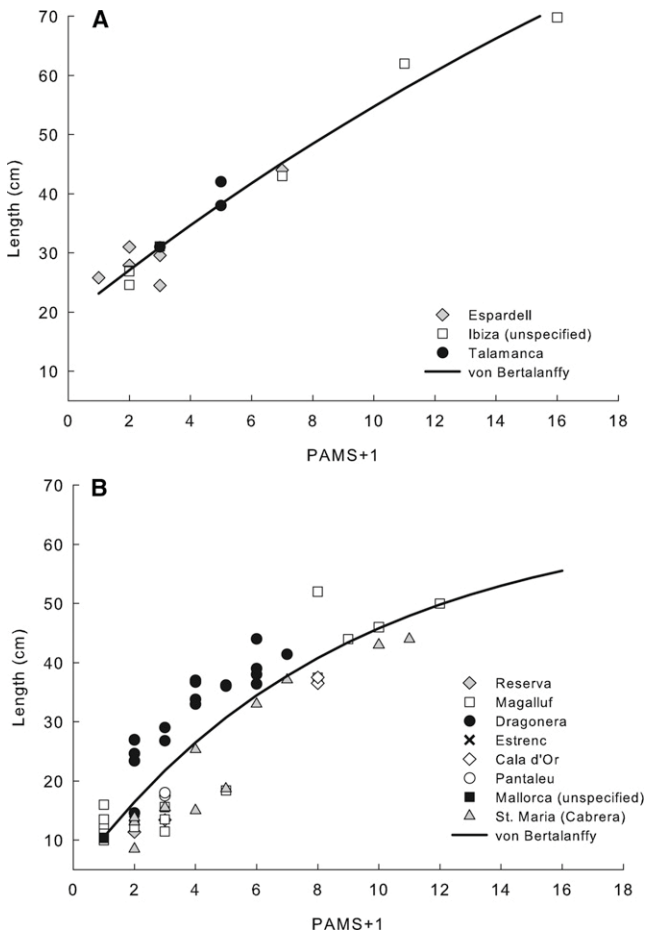


Figure 2. (A, B) Von Bertalanffy growth curve for pinnids around the islands of Mallorca (A) and Ibiza (B). PAMS, posterior adductor muscle scars.

Katsanevakis et al. (2007) as  $b = b_1 + 2b_2 \ln L$ . The exponent  $b$  is a measure of the difference in the growth rates of the 2 parts of the body. When  $b$  is less than 1, the type of growth is described as negative allometric; when  $b$  is greater than 1, growth type is described as positive allometric; when  $b$  equals 1, growth is labeled isometric. However, our data ranges from size measurements of the smallest stages (<1 cm) to very large adults, and the quadratic model, only solve for the allometric exponent  $b$  for 1 discontinuity in allometric growth, and we suspect more than 1 discontinuity. For these reasons, we also explored another model—a sigmoidal function  $f = a/1 + \exp(-(x - x_0)/b_1)$ —and solved for  $b$  numerically (as first derivative of the function) in agreement with Katsanevakis et al. (2007). Measurements from a total of 390 individuals (adults and recruits) were used to fit the model.

## RESULTS

### Adult Growth Rates

A Tukey-Kramer test showed that there was no difference in the relationship between PAMS and shell length for sites around the island of Mallorca; in Ibiza only 3 sites were sampled. The relationship between PAMS and length was different for Ibiza and Mallorca ( $t$ -test,  $t = -4.78$ ,  $P > 0.001$ ). Esponja (depth, 20–25 m) was different from other sampled sites in Ibiza, such as

Talamanca and Espardell (depth, 7–10 m depth), so we excluded the 4 measurements from Esponja. Populations around the island of Ibiza could be fitted according to the von Bertalanffy function  $L_t = 154.55(1 - e^{-0.03t + 4.31})$ , whereas for Mallorca the function was  $L_t = 65.31(1 - e^{-0.11(t + 0.53)})$ ; Fig. 2). Note that the asymptotic length ( $L_\infty$ ) reached by the bivalves is not significant in Ibiza (Table 1) and we probably lack data points for a good estimation of growth in this island.

### Juvenile Growth Rates

At the beginning of the experiment, the smallest *Pinna* in our laboratory setup was 1.41 cm long and the largest measured 5.57 cm. During a period of 13 days, juveniles grew, on average,  $0.18 \pm 0.021$  (SE) mm/day ( $n = 63$ ) in the laboratory. There was no significant relationship between the amount grown and the initial size ( $y = 0.036x + 1.308$ ,  $R^2 = 0.04$ ) as the slope of the regression was not significantly different from 0 ( $a = 0.036 \pm 0.0251$ ,  $t = 1.43$ ,  $P = 0.16$ ,  $n = 56$ ).

*In situ* juvenile minimal growth rates (Table 2) differed considering month of submersion ( $F_{df=2} = 6.70$ ,  $P < 0.01$ ) but not collection site ( $F_{df=4} = 2.26$ ,  $P = 0.11$ ), although Pollença seems to be different from the other sites in parameter estimation ( $t = 2.7$ ,  $P = 0.02$ ). The average monthly minimum growth rate for all sites as inferred from the largest individual in each collector was  $0.32 \pm 0.069$  mm/day ( $n = 34$ ), with a maximum of 0.85 mm/day in September in Pollença. The growth rate of individuals that had been submersed the entire summer (3 mo) was  $0.28 \pm 0.069$  mm/day ( $n = 12$ ).

After 6 mo of submersion, calculated growth rates were similar to the subjective growth estimated from PAMS in adult shells (Fig. 3, inset):  $0.29 \pm 0.008$  mm/day ( $n = 120$ ) versus 0.29 mm/day, as inferred from the von Bertalanffy fit (Fig. 3, Table 1). However, adult growth is subjective because not all years are visible as a PAMS, and therefore the estimated value is an overestimation of the growth rate. Because of the high variability in juvenile growth rates among months, growth rates measured over 1 mo, 3 mo, and 6 mo are not significantly different (Tukey-Kramer HSD), with the highest variation in the first month corresponding to the highest average growth rate.

### Morphometry

The data of the length–width relationship (log transformed) of the pen shells of Mallorca indicate possible breakpoints from

TABLE 1.  
Parameters of the von Bertalanffy fit as performed in R with the FSA package (Ogle 2011).

	Estimate	SE	$t$ Value	$P(> t )$
Mallorca				
$L_\infty$	65.31401	17.92615	3.644	0.00063***
$K$	0.11480	0.05962	1.925	0.05977
$t_0$	-0.52821	0.62637	-0.843	0.40301
Ibiza				
$L_\infty$	154.54687	95.88768	1.612	0.1310
$K$	0.03053	0.02730	1.119	0.2836
$t_0$	-4.31230	1.51107	-2.854	0.0136*

$L$ , length;  $K$ , rate constant;  $t$ , number of posterior adductor muscle scars. \*, indicates a significance of  $P < 0.05$ , \*\*\*,  $P < 0.001$

TABLE 2.

Mean juvenile growth rates (measured in millimeters per day  $\pm$  SD) estimated from field samples directly after recruitment around the island of Mallorca during the summer months.

Month	Pollença	St. Maria	Cala d'Or	Es Cargol	Magalluf
July	0.17 $\pm$ 0.041		0.10 $\pm$ 0.100		
August	0.42 $\pm$ 0.018	0.25		0.33 $\pm$ 0.028	0.19 $\pm$ 0.128
September	0.85		0.38	0.14 $\pm$ 0.010	0.42 $\pm$ 0.043
Summer	0.37 $\pm$ 0.084	0.27 $\pm$ 0.056	0.35	0.21 $\pm$ 0.080	0.19 $\pm$ 0.060

Values for summer are from traps submerged during the full sampling period and are not an average of the values per month. When no value is given, there was no recruitment observed or a sample was missing (e.g., August in Cala d'Or).

juvenile through adult stages (Fig. 4A). Using a quadratic model, the relative growth in width was negative allometric ( $b < 1$ ) up to a length size of  $\approx 20$  cm, and then became positive allometric ( $b > 1$ ) with continuously increasing  $b$  (Fig. 4B). This means that during the first months after metamorphosis, and during the first few years, the organisms invest in growth along the length axis. Only when they reach ca. 20 cm in length growth is preferentially in width. However, through ontogeny the relationship between length and width is not stable, as recently metamorphosed post-larvae of *P. nobilis* do not have the same length-width relationship as adults (Fig. 4C). Using a quadratic relationship clearly means we miss the breakpoint that is visible around 5 cm. Using a sigmoidal function (Fig. 4D) allowed us to estimate 2 discontinuities of the allometric exponent  $b$  by solving the first derivative of the function. Using this model, we find negative allometric growth ( $b < 1$ ) up to 5.82 cm, after which there is a period of positive allometric growth, or preferential widening of the shell, up to 14.64 cm. After this size, the shape becomes more and more elongated.

## DISCUSSION

### Adult Growth Rates

We found no apparent differences in growth rates between the 5 sampled sites around Mallorca, even when they were located

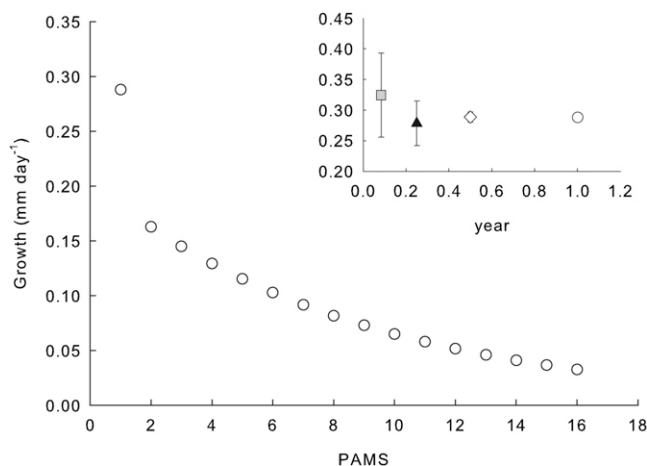
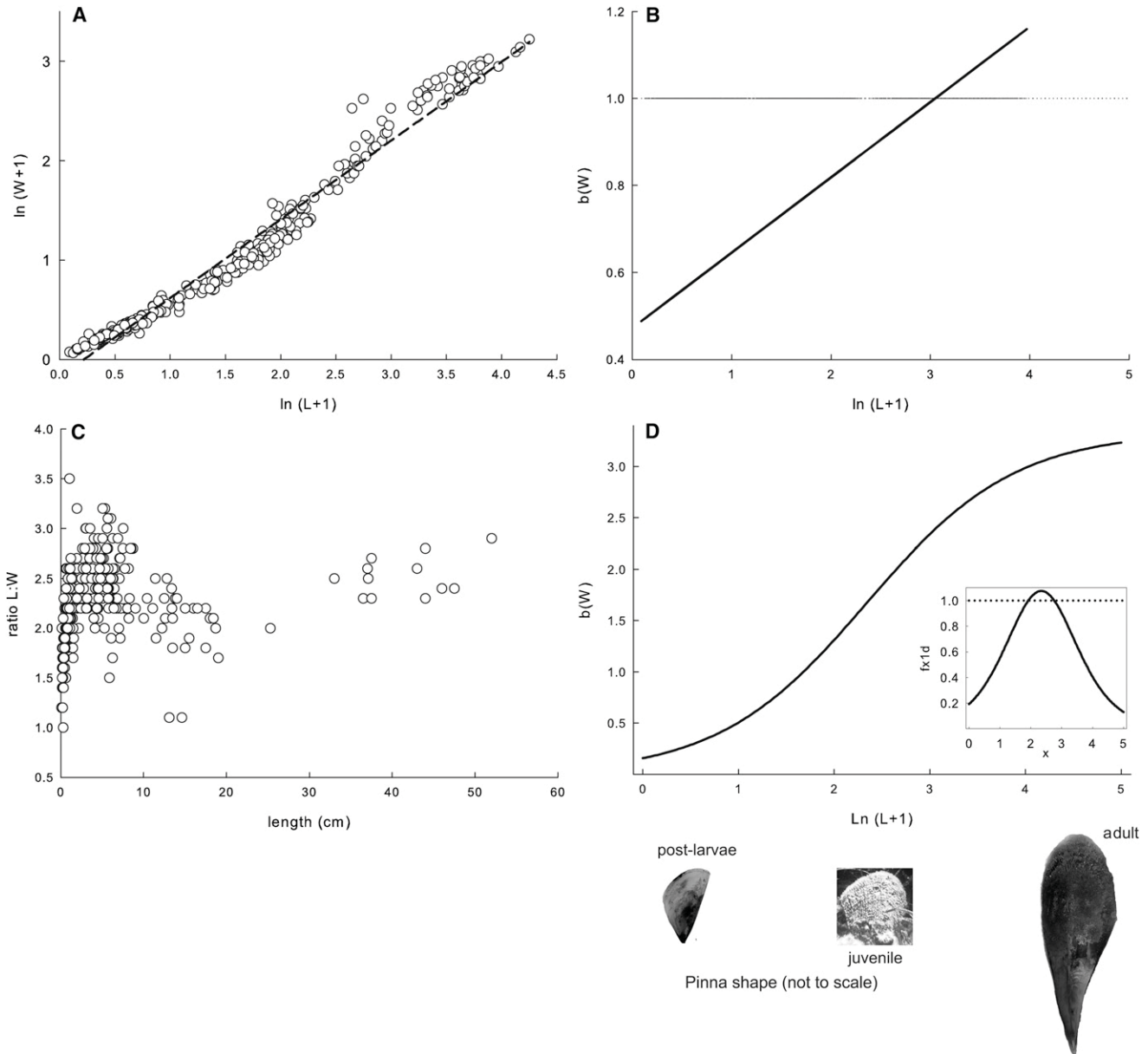


Figure 3. Growth rates for age classes around the island of Mallorca. (Inset) Growth rates for juveniles and the estimate for a 1-y-old specimen from the von Bertalanffy fit (large graph).  $\circ$ , adults;  $\square$ , 1-mo-old juveniles;  $\triangle$ , 3-mo-old organisms;  $\diamond$ , 6-mo-old organisms.

at different sides of the island (north, southeast, southwest, and east). Growth rates of populations of pinnids can be influenced by oceanographic differences among sites. Particle capture by filter feeders, for example, differs considerably among sites because of velocity and organic content of water currents (Shimeta & Jumars 1991). Differences in feeding are reflected in the stable isotopic values of organism tissue. A stable isotope study of *Pinna* tissue (Cabanelas-Reboredo et al. 2009b) around the island of Mallorca showed differences in nitrogen but not in carbon for different sites. Based on these and our results, we assume the differences in food are unimportant among our sampling sites. Another factor influencing growth rate is temperature. Temperatures do differ among depths. In the archipelago of Cabrera, annual mean temperature at a depth of 5 m is  $3.5 \pm 0.65^\circ\text{C}$  warmer than at a depth of 35 m depth (E. Cebrian, pers. comm.; www.t-mednet.org), and growth rates could be influenced by this difference. Even among individuals of the same population, depth-related growth differences in absolute growth are found (García-March et al. 2007a). This might explain the different growth rates in Esponja (depth, 20–25 m; Ibiza), which caused us to exclude data from this site. The other sites in Ibiza were at 7–10 m, whereas the sites in Mallorca were at 5 m. In simultaneous studies using the same sites in Mallorca we never observed differences in summer temperatures at 5 m depth (Hendriks et al. unpubl.), while there are more differences between the sites in Ibiza and Mallorca than depth (2–5 m difference) alone so this factor is probably not the most important.

The maximum estimated size obtained by the bivalves ( $L_\infty$ ) in our study was 65.31 cm for Mallorca and 154.55 cm for Ibiza (Fig. 2). The value for Ibiza was not significant in the model and indeed is disparate compared with literature values for Spanish Mediterranean populations: 37.59 cm for Moraira at a depth of 6 m (García-March et al. 2007a), 49.41 cm at Aguamarga (depth, 3–24 m), 45.27 cm at Rodalquilar (depth, 2–5 m), and 68.98 cm at Carboneras (depth, 4–17 m) (Richardson et al. 1999). Growth parameters of the von Bertalanffy growth curve can be quite imprecise when estimated on a data set without available large sizes close to the asymptotic length (Rabaoui et al. 2007), like their asymptotic length of a Tunisian population ( $L_\infty = 104.3$ ) or our values for Ibiza. The growth rate ( $k$ ) encountered for Mallorca ( $-0.11$ ) is low compared with Southeast Spain ( $-0.2$ ,  $-0.28$ ,  $-0.22$ ) (Richardson et al. 1999), where bivalves tend to reach a maximum length at a younger age. The value calculated for Ibiza ( $-0.03$ ) is very low, so much that we suspect this is an artefact caused by the fact that we have not collected enough data points.



**Figure 4.** (A) Measured width ( $W$ ) in centimeters in relation to shell length ( $L$ ) of juvenile and adult *Pinna nobilis* around the island of Mallorca. Data are transformed as  $\ln(x + 1)$  because the smallest individuals measure less than 1 cm. Regression line:  $y = 0.7914x - 0.1737$  ( $r^2 = 0.98$ ). (B) Allometric exponent  $b$  for the relative growth of shell  $W$  versus  $L$ . (C)  $L:W$  ratio versus Length for juvenile and adult *P. nobilis*. (D) Sigmoidal model and allometric exponent  $b$  based on this model (inset).

#### Juvenile Growth Rates

To our knowledge, this is the first study to measure growth reliably during the first month, first 3 mo, and first half year after recruitment (Table 2). In the literature, growth rates are historically reconstructed by the measurement of dead valves and the assumption of the relationship between growth (length) and PAMS (proxy for age). However, this leads to underestimation of an individual's age (García-March & Marquez-Aliaga 2007b, García-March et al. 2011). Because we can pinpoint the recruitment date, we have a reliable estimate of age to which to couple size. Because growth rate decreases during the life of the bivalves and is high during the first year, we assumed we

would find even greater growth rates during the first months. However, we cannot demonstrate a significant difference in growth rates compared with averages over the first year, although there is an indication that, during the first month, growth rates (0.32 mm/day) are greater compared with those calculated for later dates (0.28 mm/day). The estimate obtained with direct measurements is in agreement with calculations from the von Bertalanffy fit on adult valves (Fig. 3), indicating that the estimate for the first year, when no scar is visible, might be better than for later years. Additional proof should be collected, however, because the method has been criticized for its accuracy and other methods less prone to observer error are available (Richardson et al. 2004).

The laboratory results, when growth was low compared with growth in the field (0.18 mm/day vs. 0.28 mm/day), show that growth is food limited, as during the laboratory experiment, juveniles were fed only 1,000 algal cells/mL daily. The algal densities used commonly in bivalve hatchery production systems are 30–100 times greater, ranging from 30–100 × 10<sup>3</sup> cells/mL (Gosling 2007). Although optimal standard rations should have values between 50–200 × 10<sup>3</sup> cells/mL (Rico-Villa et al. 2006). Several studies confirm that algal densities lower than standard values can compromise juvenile and larval bivalve growth (Cahalan et al. 1989, Coutteau et al. 1994, Kheder et al. 2010).

With a database of measured length–width relationships of *P. nobilis* ranging from very small recruits of <<1 (0.094)–69.8 cm, corresponding to a range of individuals younger than 1 mo old to approximately 14 to 18-y-old organisms, we had a unique set of data to investigate how length–width relationships change over time (Fig. 4). The sigmoidal model was able to resolve the growth patterns observed in young individuals up to ca. 6 cm in length (0.5 y old), which invest in growth along the vertical axis (elongation). From that point on (corresponding to their first spring), proportionally more effort is invested in the horizontal (width) direction until they reach ca. 15 cm length (corresponding to ca. 2 y of age). After that, growth is again proportionally more

important in the vertical direction until a stable relationship of L:W = 2.9 is reached. We hypothesize that this first investment along the vertical axis serves for attachment purposes, as newly recruited *Pinna* during winter surveys are often found buried more than two thirds in the sand between *Posidonia* rhizomes. The results of our sigmoidal model resolve patterns of relative growth from very small recruits onward, whereas the upper limit of change of allometric growth (ca. 15 cm) is slightly smaller than that observed by Rabaoui et al. (2007) at ≈ 18 cm, and Katsanevakis et al. (2007) at ≈ 20 cm. This could be caused by local differences in food supply, hydrodynamics, or predators.

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