

SHELL POLYMORPHISMS IN THE BATHYAL MEDITERRANEAN TOP SNAIL *CLELANDELLA MYRIAMAE* GOFAS, 2005

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Abstract Differences in shell morphology in the gastropod *Clelandella myriamae* Gofas, 2005 were investigated. Observations on a total of 341 empty shells supplemented the original description and allowed the distinction of two morphotypes differing in shell size, shape and wall thickness. The existence of shell variations was also demonstrated by statistical morphometrics. Size-frequency distributions of major parameters are slightly bimodal, suggesting a disruptive selection, which tends to encourage the extreme shell forms. The achievement of larger sizes and the construction of thicker shells was interpreted as a capability of the species to withstand predatory attack, testified by several drills and scars on most shells. The occurrence of the species and the shell size variation were put in relation with other possible environmental causes such as food availability represented in the area by abundant decaying vegetal detritus. The record of *C. myriamae* from the epibathyal of the Gioia Basin is quite far from the first finding in the bathyal Eastern Mediterranean, thus extending bathymetrical and geographical range of the species.

Key words Gastropoda, Trochidae, morphometry, morphotypes, Holocene.

INTRODUCTION

Gastropods are a versatile group of molluscs characterized by an extreme adaptability to different environmental conditions, commonly displaying intraspecific variation in size and shape (Reimchen, 1982). Phenotypic expression of characters may be attributed to both genetic and environmental control (Vermeij, 1980, 1987; Kempt & Bertness, 1984).

Genetic allometries in gastropods (Reid, 1996) are documented to govern shell shape. Some allometric growth variations, such as the apical angle of the shell (O'Loughlin & Aldrich, 1987) and the shell thickness, may co-occur and have been often interpreted as phenotypic variations (Cotton *et al.*, 2004).

However, several studies aiming to define the determinants of biometric variations of gastropod shells agree in recognizing the environment as the main factor inducing shell size variability within a single species (*e.g.* Vermeij, 1973; Trussel, 2000). Particularly, hydrodynamics and predation are currently considered as the main environmental forces which control phenotypic variability in shell morphology (Crothers, 1970; Reimchen, 1982; Boulding *et al.*, 1999): low hydrodynamic energy is thought to favour

smaller and thinner shells with wide apertures, whereas exposure to shell-breakage and drilling predation is thought to select shells with small apertures and increased sizes and thickness (Currey & Hughes, 1982; Boulding *et al.*, 1999).

Clelandella myriamae belongs to a trochid genus that includes a few morphologically-related species typically distributed on seamounts, open sea archipelagos and outer shelf from restricted areas of E Atlantic and in the Mediterranean continental slopes (Gofas, 2005; Vilvens *et al.*, 2011). A sole exception is represented by *C. miliaris*, an outer shelf to shallow slope species, widespread in the Mediterranean and the nearest Atlantic, extending northward and southward of Gibraltar (Gofas, 2005). According to Gofas (2005), *C. myriamae* probably diversified from *C. miliaris*, becoming specialised to colonise deep-water mud volcanoes in the Eastern Mediterranean. A certain intraspecific variation within *Clelandella* species has been documented (see Gofas, 2005).

In the present paper shape changes in a sample of *C. myriamae* shells collected from the Gioia Basin (southeastern Tyrrhenian Sea) are analysed through morphological analysis, morphometrics and statistical treatment. Aims of the study are: 1. to supplement the original description of the



Figure 1 Records of *C. myriamae* in the Mediterranean Sea. Living (solid symbols) and dead (open symbols) specimens. Arrow indicates the location of the sampling site of *C. myriamae*, on the upper slope of the Gioia Basin (Western Mediterranean).

species; 2. to describe the intraspecific variability and mostly the existence of two different morphotypes; 3. to determine if environmental factors can induce the observed shell features variations within this species.

MATERIALS AND METHODS

Sampling site

The specimens here described were sampled in October 2008 by the R/V *Cooperonaut Franca* in the framework of the POR-CAL 2008 project, aimed to investigate benthic environments in the South Tyrrhenian Sea. A Van Veen grab, 0.25m² surface sampling was employed. Samples 1C were carried out on the upper slope of the Gioia Basin (38°19'0240N, 15°44'9990E), 335m depth (Fig. 1).

Bottom sediment consisted of allochthonous gravelly sands, covered by a thin muddy layer. Coarser fraction is metamorphic and pyroclastic in composition, secondarily consisting of invertebrate remains. A large amount of organic remnants rich in fibres and rhizomes of *Posidonia* was also present. Benthic association included *in situ* lower circalittoral to bathyal species, such as the brachiopod *Gryphus vitreus*, the bivalves *Abra longicallus* and *Timoclea ovata*, the gastropods *Alvania cimicoides*, *Jujubinus montagui* and *Putseisia wiseri*. Some allochthonous shallow-shelf species co-occurred. Living assemblages, markedly oligotypic, accounted only juveniles/subadults of two mollusc species, the bivalves *Timoclea ovata*, two specimens, and *Yoldiella philippiana*, one specimen. The steep physiography of the area coupled with tectonic instability has led to down-shelf displacement of isolated shells and debris

flows in the basin as noted by Rosso & Corselli (1996) and Gamberi *et al.* (2011). Instability is also reflected in the benthic community zonation characterized by sublittoral opportunistic filter feeders able to monopolise a highly seasonal supply of autochthonous phytoplanktonic seston associated with imported macro debris and terrigenous components (Cosentino & Giacobbe, 2008).

Morphological investigations

All shells isolated from the washed residue > 1mm from an original sample of 4l, were measured using a stereomicroscope equipped with an Axiocam MRC measuring software. The largest specimens were measured by means of a calliper (precision of 0.1±0.02mm). Low magnification photos were acquired with a Zeiss Discovery V8A stereomicroscope equipped with an Axiovision acquisition system, in order to document shell morphologies and thickness. Some selected shells were examined uncoated under a LMU Tescan Vega Scanning Electron Microscope in Low Vacuum modality. Some shells were broken and coated with gold-palladium to investigate their structure.

Size-frequency distributions were performed on the following shell parameters (Fig. 2) shell height (H); shell width (W); height of aperture (apH); width of aperture (apW); apical angle (α) calculated by modelling the shell as a cone and by using shell height and width in the equation: $\alpha = 2 * \arctan(0.5 * \frac{W}{H})$, $= 2 * \arctan(0.5 * \frac{W}{H})$ (as in Preston & Roberts, 2007); outer area of shell (A²) calculated as follows: $A^2 = \pi * W \sqrt{(0.5 * W)^2 + H^2} = \pi * W \sqrt{(0.5 * W)^2 + H^2}$.

These morphometric data were statistically processed (frequency histograms, linear regression, t-student test) and further by a multivariate analysis, by means of principal component analysis (PCA). This technique verifies if the shells assigned to the different morphotypes are clustered together. Multivariate analyses were run with the R platform (version 3.1.2 for Windows: www.R-project.org; Ihaka & Gentleman, 1996).

Studied material is located in part at the Paleontological Section of the Earth Science Museum at the University of Catania, and in part at the Benthic Ecology Laboratory, Department of Biological and Environmental Sciences, Messina University.

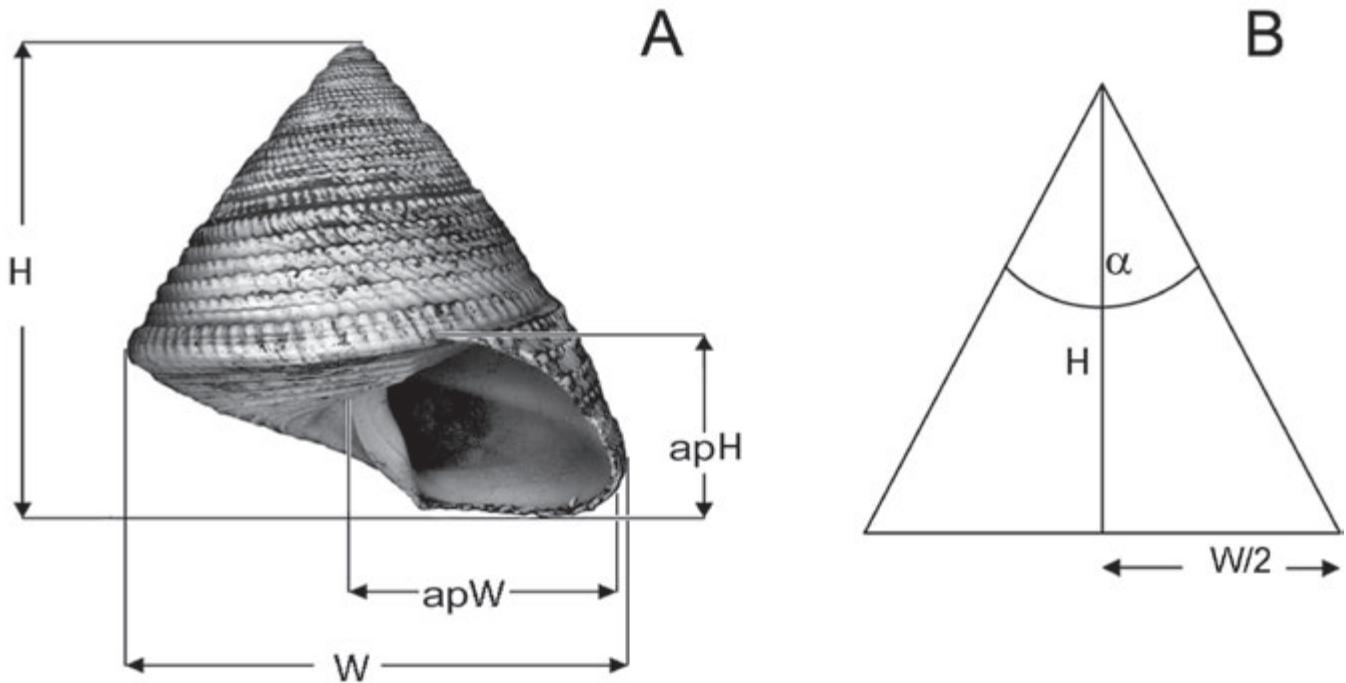


Figure 2 A. *Clelandella* shell parameters: shell height (H); shell width (W); aperture height (apH), aperture width (apW). B. Method of estimation of shell apical angle (α) using shell height (H) and half basal width (W/2).

RESULTS

Morphology

A total of 341 empty shells of a small trochid recognisable as *Clelandella* sp. were obtained. Studied specimens fit well within the description of *C. myriamae*, originally reported by Gofas (2005). The species is distinguishable from the sole Mediterranean congener *C. miliaris* with a broader shell profile, small umbilical chink and not beaded or feebly beaded spiral cords. Minor differences with *C. miryamae* types concern the slightly smaller size and the minor number of whorls (Figs 3, 4). Based on the hundreds of examined specimens some characters were better documented by images (protoconch and details of the sculpture) and others, such as the shape of abapical spiral cords were added supplementing the original description. Shell structure was described for the first time in this genus. A degree of morphological variability, recognised throughout the whole specimen set, allows two morphotypes to be distinguished, culminating in a few specimens that show extreme morphologies (Table 1, Fig. 4A–D, M–P), with respect to the numerically prevalent intermediate forms (Table 1, Fig. 4E–L).

Specimens constituting the whole set, show the following common characters: shell conical,

usually as high as wide (Fig. 4A), with a teleoconch of 5–6 whorls (Fig. 4B) and a smooth protoconch about 180mm wide, of 1 to 1,25 whorls, bordered by a delicate lip (Fig. 4E). Spire sculptured with spiral cords faintly beaded, as wide as interspaces (Fig. 4C). First teleoconch whorl with 3 spiral cords and a fine subsutural thread (Fig. 4E), number of spirals later being 6 (Fig. 4C) and rarely 7–9 by intercalation of additional fine spiral cords on the adapical part of last whorl (Fig. 4F). Shell profile regularly continued from one whorl to another convex only from the first two teleoconch whorls (Fig. 4A). Abapical surface weakly convex, bearing 10–12 smooth spiral cords as wide as interspaces (Fig. 4D). Cords asymmetric in profile with the crest facing to the periphery of the whorl (Fig. 4F). Axis with a narrow umbilical chink, bordered by a columellar edge (Fig. 4D).

Shell composed of aragonite, showing the typically layered structure of gastropods (see Yourdkhani *et al.*, 2011). Outer *prismatic* layer consisting of elongated crystals perpendicular to the external surface, and inner *nacreous* layer with plate-like crystals parallel to the internal surface (Fig. 4G, H). The prismatic layer is the most developed, representing about 90% of the shell thickness.

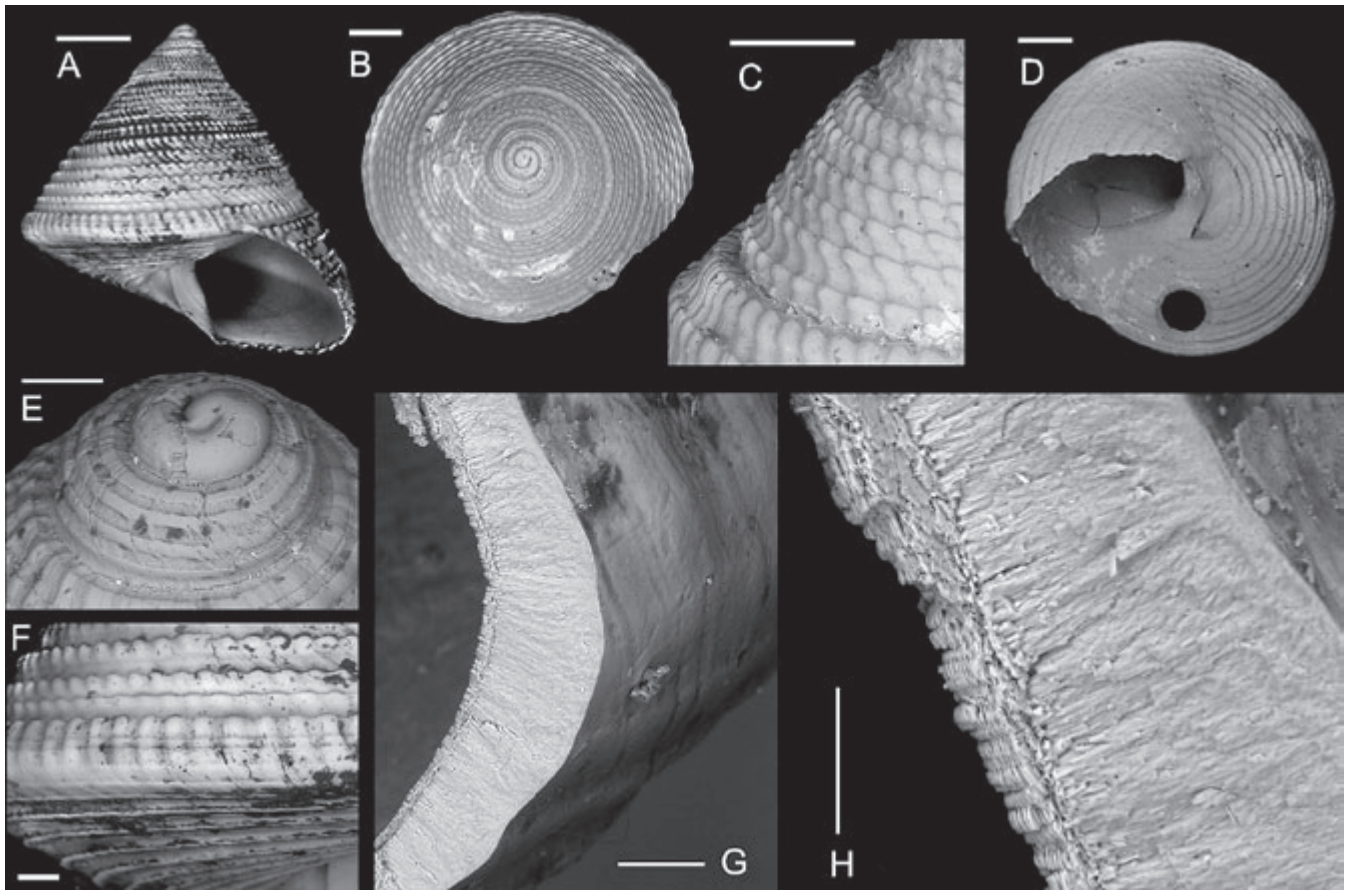


Figure 3 Scanning electron micrographs of *C. myriamae*. A. Conical, as high as wide, shells with a teleoconch of 5–6 whorls and a strongly prosocline aperture. Scale bar=1mm. B. Spire with beaded spiral cords, as wide as interspaces. Scale bar=1mm. C. Detail of the whorl, with 6 beaded spiral cords. Suture underlined by the adapical cord. Scale bar=500 μ m. D. Abapical surface weakly convex, with 10–12 smooth spiral cords, and a narrow umbilical chink, bordered by a columellar edge. Scale bar=1mm. E. Smooth protoconch less than 1 whorl, bordered by a delicate lip, passing to the first teleoconch whorl with 3 not beaded spiral cords. F. Periphery of last whorl with intercalated 2 additional spiral cords. Cords from the abapical surface asymmetric in profile, their crest facing laterally. Scale bar=250 μ m. G. Fractured typically two-layered shell showing an outer, irregularly thick (80 to 150 μ m) layer and an inner uniformly thick (20 μ m) layer. Scale bar=100 μ m. H. Detail of G: inner structure of the wall with an outer prismatic layer (right) made by elongated crystals with the main axis perpendicular to the outer shell surface, and an inner nacreous one (left) made by platy aragonite crystals parallel to the inner shell surface. Scale bar=50 μ m.

The two morphotypes have the following features culminating in extreme forms:

Morphotype A (Figs 3, 4A–D): Shell moderately solid and thin-walled, conical, slightly wider than high, with mean values of 6.07 and 5.60mm, respectively (Table 1). Aperture rhomboidal in outline, with a thin sharp outer lip. Whorls beaded on the adapical surface. Periphery of last whorl forming a blunt angle. Shell colour yellowish to reddish, some specimens nearly without pattern, others with cords articulated by brown or pink-reddish flecks; abapical cords colourless or less intensely coloured than the adapical ones.

Morphotype B (Fig. 4M–P): Shell solid and thick-walled, conical or slightly cyrtocooidal, quite as high as wide, with mean values of 7.32 and 7.44mm, respectively (Table 1). Aperture roundly rhomboidal in outline, inside brightly nacreous and with a thick outer lip. Whorls strongly beaded on the adapical surface. Periphery of last whorl forming a blunt angle, in some cases roundish. Shell colour brown to dark reddish, generally with cords articulated by brown or reddish flecks; flecks aligned to form axial flames; abapical cords equally coloured or less intensely coloured than the adapical.

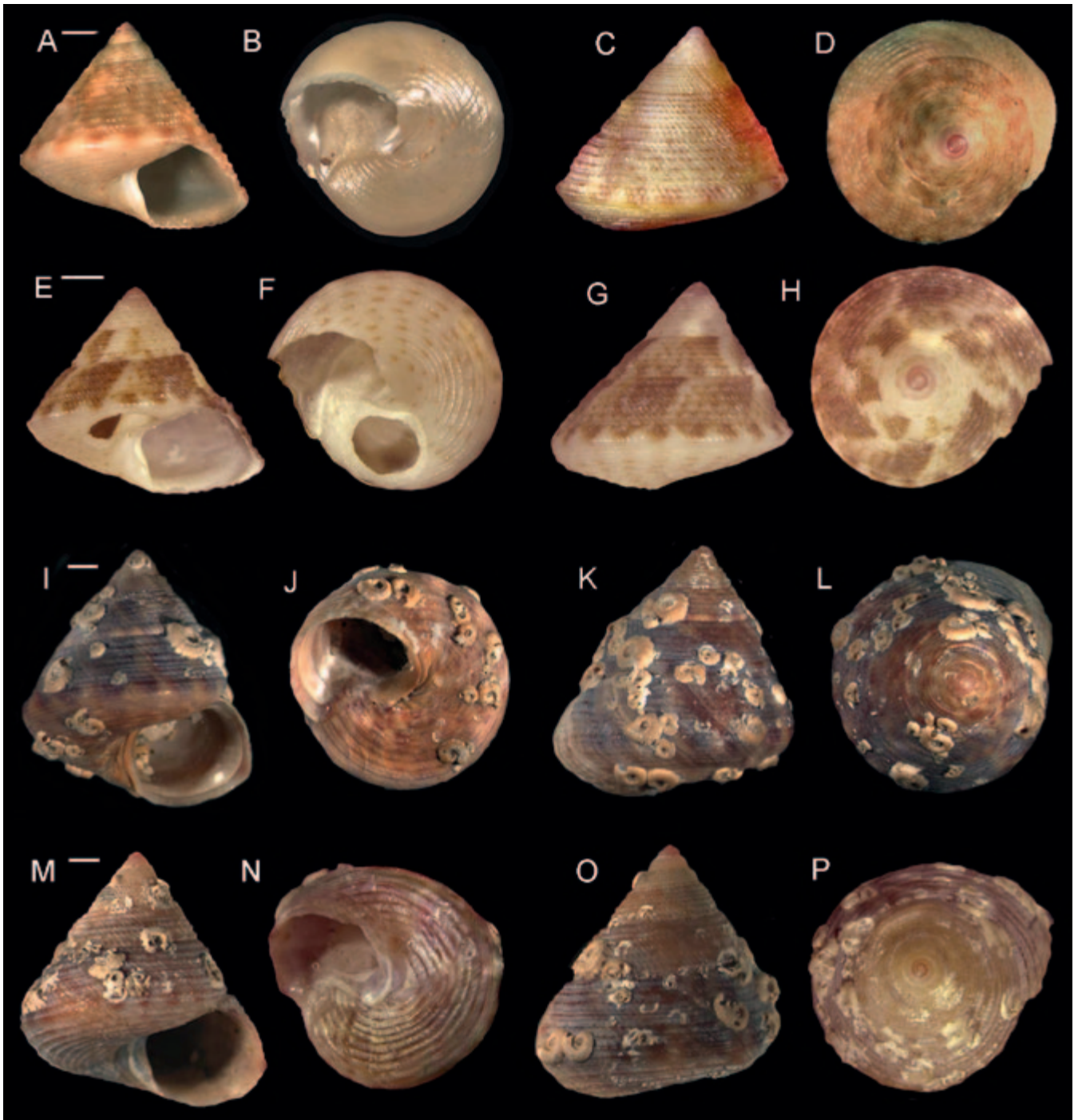


Figure 4 *C. myriamae*. A–D: Shell showing an extreme form of the A morphotype. E–H: Shell showing an intermediate form of the A morphotype. Scale bars=1mm. A, E. Apertural views: shells slightly wider than high, with the last whorl forming a blunt angle. Aperture rhomboidal in outline. B, F. Abapical views: shells with smooth spiral cords; apertures with a thin margin. C, G. Abapertural views: shells triangular in profile, less intensely coloured than adapically. D, H. Adapical views: pink coloured in the apex, theleoconch yellowish to reddish, or with a colour pattern of pinky-reddish flecks. I–L: Shell showing an intermediate form of the B morphotype. M–P: Shell showing an extreme form of the B morphotype. Scale bars=1mm. I, M. Apertural views: shells quite as high as wide thick-walled; periphery of last whorl rounded. Aperture subcircular in outline. J, N. Abapical views: shells with strong spiral cords; apertures with a thick margin. K, O. Abapertural views: shells sub-triangular in profile, uniformly coloured abapically and adapically; whorls slightly rounded. L, P. Adapical views: Shells pinky coloured in the apex, brown to dark reddish in the theleoconch; pink coloured in the apex, theleoconch reddish to brown, or with a colour pattern of brown-reddish flecks.

Table 1 Ranges of shell parameter for morphotypes A and B. Nr=number of measured shells; Avg=mean values; Std=standard deviation; Min=minimum values; Max=maximum values; 5%, 25%, 50% (medians), 75%, 95%=percentiles of measured values. Linear measures are given in microns, angular measures in degrees.

| Nr | Morphotype A | | | | | | Morphotype B | | | | | |
|-----|--------------|-------|------|------|-----|----------|--------------|-------|------|------|-----|----------|
| | H | W | apH | apW | L A | α | H | W | apH | apW | L A | α |
| | 181 | 181 | 42 | 42 | 181 | 181 | 163 | 163 | 86 | 86 | 163 | 163 |
| Avg | 5599 | 6074 | 2796 | 3473 | 65 | 57.8 | 7321 | 7438 | 4637 | 5419 | 100 | 54.5 |
| Std | 1748 | 1474 | 1211 | 1420 | 36 | 3.8 | 1796 | 1411 | 549 | 594 | 40 | 3.9 |
| Min | 3066 | 3424 | 1601 | 2030 | 19 | 47.8 | 3737 | 4321 | 2225 | 2381 | 29 | 44.7 |
| Max | 10200 | 10000 | 5400 | 6100 | 177 | 68.6 | 11100 | 10200 | 5379 | 6561 | 190 | 63.7 |
| 5% | 3505 | 4184 | 1712 | 2093 | 27 | 51.0 | 4412 | 4911 | 3915 | 5000 | 39 | 48.9 |
| 25% | 4339 | 4956 | 1854 | 2246 | 39 | 55.7 | 5902 | 6485 | 4400 | 5200 | 70 | 51.7 |
| 50% | 5194 | 5886 | 2315 | 3020 | 55 | 58.6 | 7152 | 7385 | 4813 | 5600 | 95 | 54.0 |
| 75% | 6283 | 6986 | 3373 | 4838 | 78 | 60.5 | 8900 | 8650 | 4993 | 5700 | 133 | 57.8 |
| 95% | 9100 | 8900 | 5000 | 5700 | 140 | 62.7 | 10000 | 9290 | 5154 | 5997 | 160 | 61.1 |

Taphonomic remarks

Most shells, particularly those of morphotype B, are encrusted by a spirorbid species (Fig. 4). Besides, almost all shells of the morphotype A are bored by predatory drills (Fig. 4B), whereas specimens of the morphotype B are less frequently drilled and show damage scars along last whorls (Fig. 4K, O).

Morphometric analysis

Intraspecific variability was proved by statistical processing of morphometric parameters. The frequency curves, and particularly those relative to H, W, apH and apW, are clearly bimodal, pointing to a first peak with small-sized shells, and a second peak consisting of larger specimens (Fig. 5, Table 1). In histograms for H and LA, the first shell group is slightly more numerous and the flex of the curve is not too low. Conversely, curves representing the aperture values show two comparably numerous groups, separated by a very low flex (apH) or even by a gap (apW).

Interestingly, shells of the first peak of all curves mainly belong to the morphotype A, having widths almost equal to heights, and a relatively wide apical angle. On the other hand, the morphotype B is dominant in shells from the second peak (Fig. 5).

Box plots for standard deviation (Fig. 5) indicate that the two morphotypes show ranges partially overlapping for H and not overlapping for apH. This confirms that the aperture values have higher ranges in morphotype B than in morphotype A. The statistical analysis (t-student test)

shows that the distributions of H and apH are significantly different since confidence interval of delta distribution does not contain zero. The principal component analysis for all shell morphometric parameters (Table 1), further confirms variability in shell morphology, clearly segregating two clusters in the multivariate morphospace (Fig. 6). Specimens clustering in quadrants I and IV, are smaller-sized and relatively squat. Here, morphotype A is dominant both considering shells and apertures; seemingly, morphotype B, characterised by larger sizes and higher shells, is dominant in the cluster occupying quadrants II and III.

In the logistic regression statistics (Fig. 7) reporting relationships between shell heights and widths for both morphotypes, H and W are highly significant and positively related ($P < 0.0001$). Values of R^2 in morphotype A and B are respectively 0.953 and 0.928, the interpolated equation being $Y = 0.82 X + 1465$ in type A and $Y = 0.75 X + 1895$ in type B.

DISCUSSION

The studied sample of *C. myriamae*, entirely consisting of empty shells, raises some preliminary considerations, first about the high density of dead specimens of such species that in other sites is known by single living individuals or even by only a few dead specimens (see Gofas, 2005). In particular, the *C. myriamae* examined shells do not show any sign of abrasion and their exceptional preservation state is emphasised by the

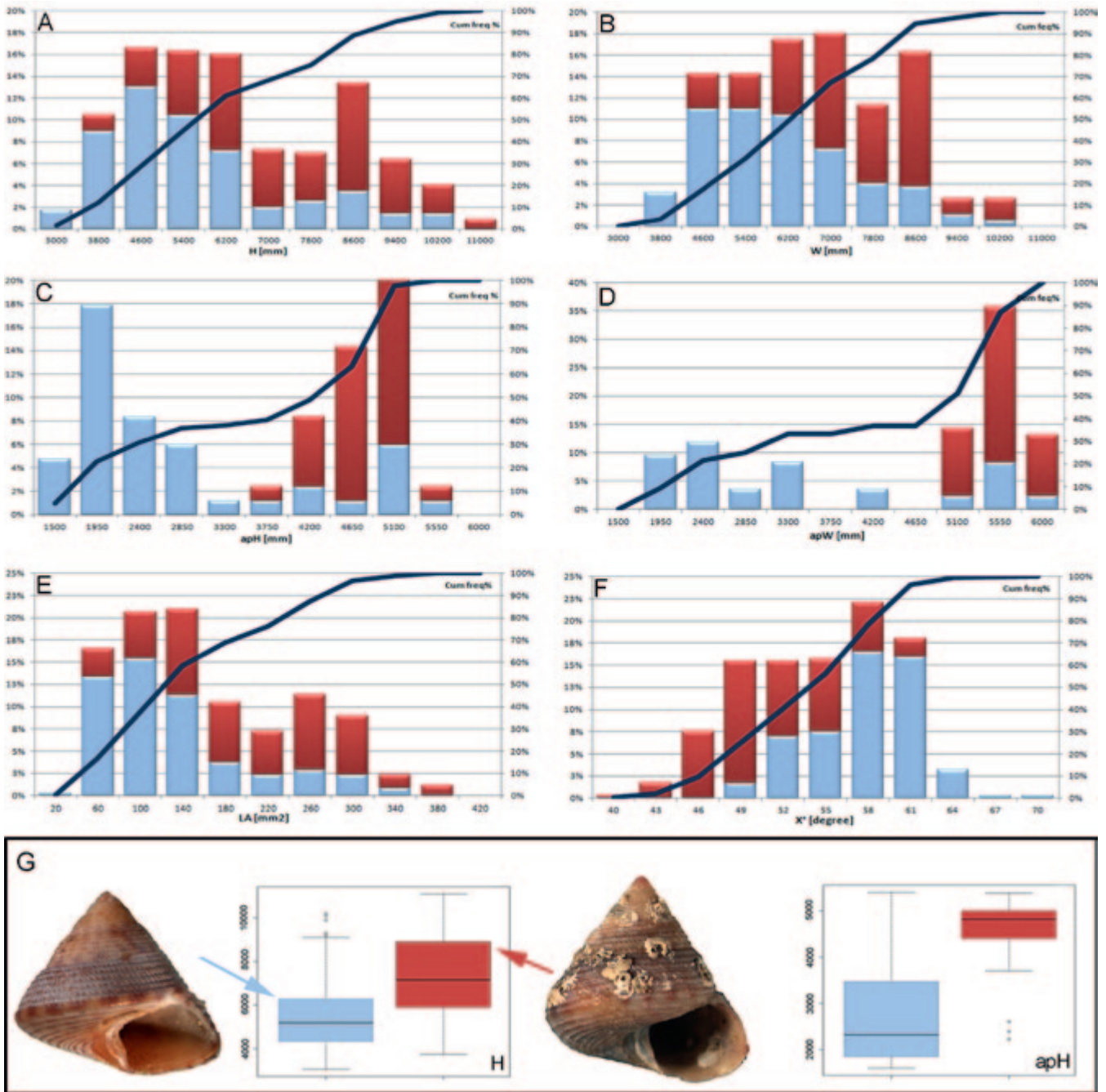


Figure 5 Frequency histograms showing the polymorphism of *C. myriamae* shells based on main shape characters: **A.** shell height (H); **B.** shell width (W); **C.** apertural height (apH); **D.** apertural width (apW); **E.** lateral area (LA); **F.** apical angle (α). Blue/light grey bars are for morphotype A, red/dark grey bars for morphotype B. Frequencies (ordinate) are reported as percentages of specimen numbers. The box plots below display the median value, the interquartile range containing middle 50% of values, extreme values and outliers of the inspected parameters H and apH, relative to both A (blue/light grey) and B (red/dark grey) morphotypes. The line inside the box is the sample median; box ends represent the 25th and 75th percentiles; whiskers indicate the 5th and 95th percentiles; dots represent outlier specimens.

bright colours (Fig. 4). The fresh-looking appearance is shared with that of other mollusc species, whose presence in the sampled site is consistent with their well-known distribution. A long time

accumulation from several generations is not supported by different conservation states; also concentration by passive transport should be excluded since banal trochid species with similar

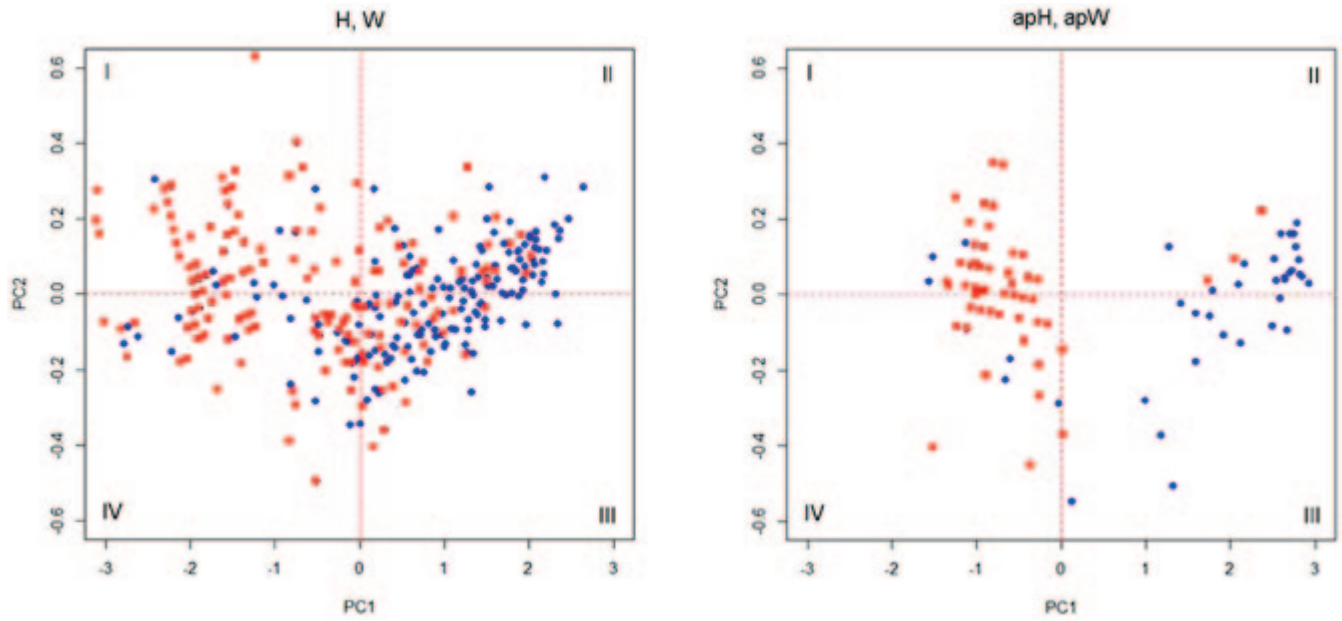


Figure 6 PCA scatterplots reflecting morphological differences in the shell parameters H and W (left), apH and apW (right) between morphotype A (squares) and morphotype B (circles).

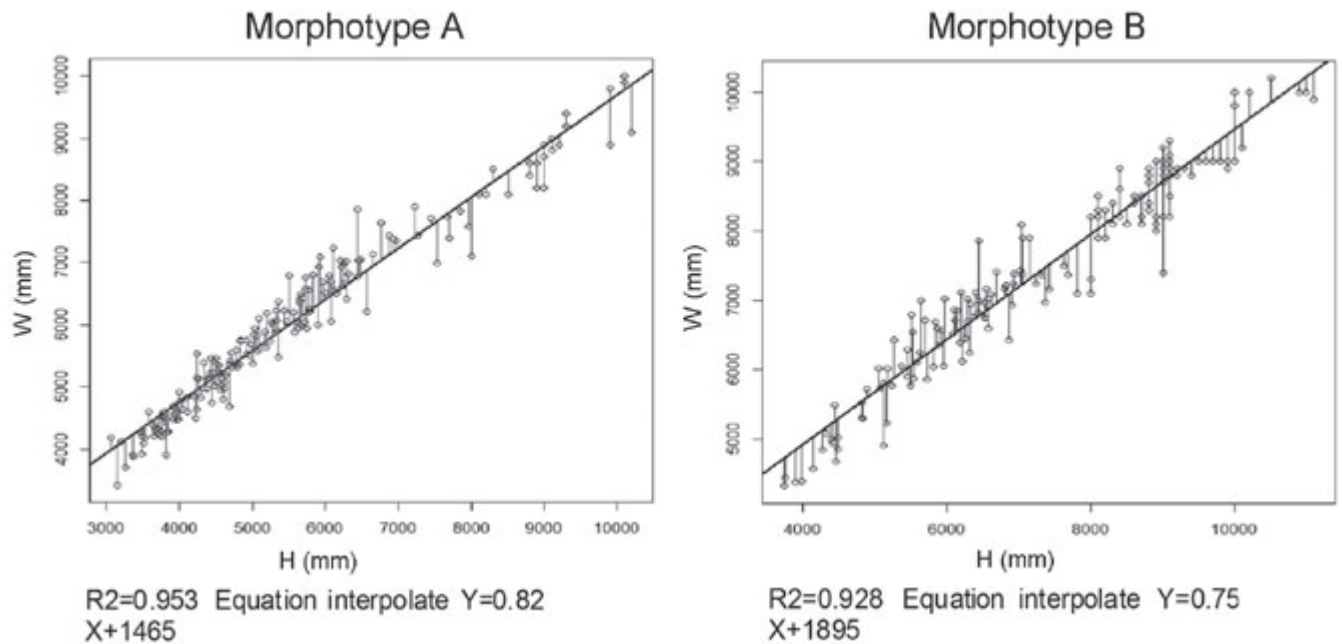


Figure 7 Regression analysis of the variables H and W with fitted regression line for morphotype A (on the left) and morphotype B (on the right). Centroid and y-residuals are displayed. A strong positive correlation is shown, data points being likely to fall along the straight line.

shapes and sizes (*Clelandella miliaris*, *Calliostoma* spp., *Jujubinus* spp.) are rare and dispersed in the same sediment sample. Furthermore, additional recent sporadic records (Vazzana, pers. comm.), if confirmed, will confirm the species actually lives in the Gioia Basin (Giacobbe & Di Bella, 2016). On the other hand, the observed low

density of living molluscs is in accordance with previous investigations in the area that delivered only dead assemblages (Di Geronimo *et al.*, 1995, 2001). In our opinion, such observations suggest that quite sparse populations of this species may give rise to localised demographic booms under favourable conditions.

The finding of live and dead specimens of *C. myriamae* in the Tyrrhenian Sea is relevant, as it extends the geographical, bathymetrical and ecological ranges of the species, contributing new information on its ecological requirements and further insights to trace back the history of its evolution. Until now *C. myriamae* was exclusively known from the Eastern Mediterranean where it was found deepest, in the lower bathyal (1693–2300m), on seamounts and mud volcanoes, as well as associated to cold seeps (Gofas, 2005; Gaudron *et al.*, 2010). The setting of the present collecting site is quite different because it concerns a relatively shallow bottom (almost 300m depth) neither in connection to seamounts neither to mud volcanoes or cold seeps, that are only known for major depths in neighbouring northern areas (Rovere *et al.*, 2013). Differently, the abundance of *Posidonia* rhizomes and fibres, possibly decanted and/or seasonally discarded together with other remains and organic debris from shallower depths (Cosentino & Giacobbe, 2008), could reasonably represent a possible source of food for *C. myriamae*. Decaying organic matter in the area agrees with the occurrence of thyasiriid bivalves (Di Geronimo *et al.*, 2001), which are known to obtain much of their carbon from bacteria (Dando & Southward, 1986). The presence of bacteria could also favour *C. myriamae*, a species recorded in experimental studies in association with organic substrata developed in the vicinity of chemosynthetic ecosystems by Gaudron *et al.* (2010). This hypothesis is in agreement with Gofas' (2005) opinion that small trochiids, like *C. myriamae*, unlikely harbouring bacterial symbionts within their tissues, probably feed on accumulations of decaying organic matter.

On describing the new species Gofas (2005) suggested that *C. myriamae* diversified in localities of the Eastern Mediterranean from the sympatric *C. miliaris*, evolving the ability to colonise deep environments with special conditions. Our SE Tyrrhenian record from depths and environmental conditions intermediate to those typical of *C. miliaris* and *C. myriamae* as previously known, question the hypothesis of Gofas (2005) regarding the area where the diversification occurred. Taking into account the short larval phase of trochiid gastropods, it is reasonable to assume that spreading towards major depths, as well as the migration throughout large areas of

the Mediterranean, occurred step-by-step and that the species will probably be discovered in intermediate (both bathymetrical and geographical) areas in the future.

The abundance of material, which allowed to implement the original description, also documented a wide morphological variability, ranging from small and thin shells (morphotype A) to large and thicker specimens (morphotype B). *A posteriori*, Gofas' mention of an "aberrant" form, corresponding to the extreme form shown by some specimens belonging to the morphotype B, foreshadowed the actual distinction of two morphotypes, even within the seven shells he studied.

Encrusters on shells belong to the species *Spirorbis cuneatus*, which live on shelf bottoms and become quite abundant (Knight-Jones & Knight-Jones, 1977) at a depth compatible with our sampling site. The presence of this spirorbid species on shells of morphotypes A and B indicates that both forms could co-occur in the same environment.

Shells of the morphotype A, heavily drilled, might be most susceptible to gastropod predation. Conversely, larger and thicker shells of the morphotype B were less frequently drilled, indicating they were not actively predated by gastropods. Furthermore, their external last whorls are severely scarred, as a consequence of crab and fish damages, but repaired, pointing to the capability of this morph to withstand predatory attacks (see Preston *et al.*, 1996). In this view, the energy investment in constructing a thicker shell and the achievement of large sizes of the morphotype B could be interpreted as a consequence of predatory pressure acting as disruptive selection, which eliminates average phenotypes and encourages the extremes, as shown by the bimodal distributions of shell parameters. Such a strategy agrees with an intertidal ecology paradigm in which gastropods from rocky-shore sites with different degrees of exposure to predators tend to differentiate two distinct phenotypes (see Boulding *et al.*, 1999, for a review). Defences against predators are attained by species developing thick shells (Reimchen, 1982; Vermeij, 1987) or growing fast to reach size refuge from predators (Reid, 1992). In considering this, we believe that the two different shell forms of *C. myriamae* may be interpreted according to such accepted phenotypical stereotype. Tied to

the defence strategies, a nacre layer in the wall structure of this species has been first described, following the Gofas (2005) macroscopic observations. Nacre-producing species are rare between gastropods, including *Clelandella*, *Gibbula* and *Trochus* within Trochidae. Nacre exhibits high fracture toughness, much greater than that of monolithic aragonite, because of its ingenious structure, also exhibiting energy absorption properties (Sun & Bhushan, 2012). Consequently, the presence of a nacreous shell in *C. myriamae* is possibly functional to withstand environmental stress, and particularly predation exposure.

Food availability, as another major factor affecting shell size variation, might be linked to the irregular supply of continental and shelf detritus. Detritus decay could allow the *C. myriamae* colonisation in accordance with the amount of available organic matter (Gofas, 2005, Gaudron *et al.* 2010). The scarcity and irregular availability of food could also account for the observed shell sizes and whorl numbers, that are slightly smaller than those reported by Gofas (2005).

ACKNOWLEDGEMENTS

The authors thank Serge Gofas, University of Malaga, for his constructive help with the manuscript. Prof. N. Spanò was responsible for the POR-CAL 2008 project. Paper financially supported by grants of the University of Catania and Messina. Catania Paleoecological Group contribution number 416.

REFERENCES

- ADAMS DC & COLLYER ML 2009 A general framework for the analysis of phenotypic trajectories in evolutionary studies *Evolution* **63**(5): 1143–1154.
- BOULDING EG, HOLST M & PILON V 1999 Changes in selection on gastropod shell size and thickness with wave exposure on Northern Pacific shores *Journal of Experimental Marine Biology and Ecology* **232**: 217–239.
- CHASE JM 1999 To grow or to reproduce? The role of life–history plasticity in food web dynamics *American Naturalist* **154**: 571–586.
- CHESSER D, DURFOUR AB & THIOULOUSE J 2004 The ade4 package—I– One–table methods *R News* **4**: 5–10.
- COSENTINO A & GIACOBBE S 2008 Distribution and functional response of sublittoral soft bottom assemblages to sedimentary constraints *Estuarine, Coastal and Shelf Science* **79**(2): 263–276.
- COTTON PA, RUNDLE SD & SMITH KE 2004 Trait compensation in marine gastropods: shell shape, avoidance behavior, and susceptibility to predation *Ecology* **85**: 1581–1584.
- CROTHERS JH 1970 The distribution of crabs on rocky shores around the Dale Peninsula *Field Studies* **3**: 263–274.
- CURREY JD & HUGHES RN 1982 Strength of the dogwhelk *Nucella lapillus* (Linnaeus) and the winkle *Littorina littorea* (Linnaeus) from different habitats *Journal of Animal Ecology* **51**: 47–56.
- DANDO PR & SOUTHWARD AJ 1986 Chemoautotrophy in bivalve molluscs of the genus *Thyasira*. *Journal of Marine Biology Association of the United Kingdom* **66**: 915–929.
- DI GERONIMO I, LA PERNA R, ROSSO A & SANFILIPPO R 1995 Primi dati sulle tanatocenosi bentoniche dei bacini di Cefalù e Gioia (Tirreno Sud-Orientale). In Faranda F.M. & Povero P. (eds) *Caratterizzazione ambientale marina del sistema Eolie e dei bacini limitrofi di Cefalù e Gioia (EOCUMM 94) Data Report* 289–302.
- DI GERONIMO I, ROSSO A, LA PERNA R & SANFILIPPO R 2001 Deep-sea (250–1,550m) benthic assemblages from Southern Tyrrhenian Sea. In Faranda F.M., Guglielmo L., Spezie G. (eds) *Mediterranean Ecosystems: Structures and Processes. Proc. First Nation. Congr. Marine Sc. "Diversità e Cambiamento", Ischia 11–14 Novembre 1998* **36**: 277–287 Springer Verlag, Berlin Heidelberg.
- GAMBERI F, ROVERE M & MARANI M 2011 Mass-transport complex evolution in a tectonically active margin (Gioia Basin, Southeastern Tyrrhenian Sea) *Marine Geology* **279**: 98–110.
- GAUDRON SM, PRADILLON F, PAILLERET M, DUPERRON S, LEBRIS N & GAILL F 2010 Colonization of organic substrates deployed in deep-sea reducing habitats by symbiotic species and associated fauna *Marine Environmental Research* **70**: 1–12.
- GIACOBBE S & DI BELLA A in press (2016) About the wide Mediterranean distribution of the "geographically localized" *Clelandella myriamae* (Gofas, 2005) (Gastropoda Trochidae). *Biodiversity Journal*, **2016**, 7 (2).
- GOFAS S 2005 Geographical differentiation in *Clelandella* (Gastropoda: Trochidae) in the northeastern Atlantic *Journal of Molluscan Studies* **71**: 133–144.
- IHAKA R & GENTLEMAN R 1996 R: A language for data analysis and graphics *Journal of Computational and Graphical Statistics* **5**: 299–314.
- KEMPT P & BERTNESS MD 1984 Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea* *Proceedings of the National Academy of Sciences of the USA* **81**: 811–813.
- KNIGHT-JONES P & KNIGHT-JONES EW 1977 Taxonomy and ecology of British Spirorbidae (Polychaeta). *Journal of the Marine Biological Association of the United Kingdom* **57**(2): 453–499.
- O'LOUGHLIN EFM & ALDRICH JC 1987 An analysis of shell shape variation in the painted top shell *Calliostoma zizyphinum* (Linnaeus) (Prosobranchia: Trochidae) *Journal of Molluscan Studies* **53**: 62–68.
- PRESTON SJ & ROBERTS D 2007 Variation in shell morphology of *Calliostoma zizyphinum* (Gastropoda: Trochidae) *Journal of Molluscan Studies* **73**: 101–104.

- PRESTON SJ, ROBERTS D & MONTGOMERY WI 1993 Shell scarring in *Calliostoma zizyphinum* (Linnaeus) (Prosobranchia: Trochidae) from Strangford Lough, Northern Ireland *Journal of Molluscan Studies* **59**: 211–222.
- PRESTON SJ, ROBERTS D & MONTGOMERY WI 1996 Crab predation as a selective agent on shelled gastropods: a case study of *Calliostoma zizyphinum* (Linnaeus) (Prosobranchia: Trochidae). In Taylor J.D. (ed) *Origin and evolutionary radiation of the mollusca*, 313–325, Oxford University Press, Oxford.
- REID DG 1992 Predation by crabs on *Littoraria* species (Littorinidae) in a Queensland mangrove forest. In Grahame J., Mill P.J. & Reid D.G. (eds) *Proceedings of the 3rd International Symposium on Littorinid Biology* 141–151 Malacological Society, London.
- REID DG 1996 Systematics and Evolution of *Littorina* The Ray Society, London.
- REIMCHEN TE 1982 Shell size divergence in *Littorina maria* (Sacchi & Rastelli) and *Littorina obtusata* (Linnaeus) and predation by crabs *Canadian Journal of Zoology* **60**: 687–695.
- ROBERTS D & KELL GV 1987 Shell colour in *Calliostoma zizyphinum* (Linnaeus) (Prosobranchia: Trochidae) in County Down, Northern Ireland *Journal of Molluscan Studies* **53**: 273–283.
- ROSSO A & CORSELLI C 1996 Evoluzione paleoecologica del sistema Eolie e Bacini limitrofi: rapporto sulla campagna Giugno-Luglio 1995. In Faranda F.M. & Povero P. (eds) *Caratterizzazione ambientale marina del sistema Eolie e dei bacini limitrofi di Cefalù e Gioia (EOCUMM 94) Data Report* 385–411.
- ROVERE M, GAMBERI F, MERCORELLA A, RASHED H, GALLERANI A, LEIDI E, MARANI M, FUNARI V & PINI GA 2014 Venting and seepage systems associated with mud volcanoes and mud diapirs in the southern Tyrrhenian Sea *Marine Geology* **347**: 153–171.
- SUN J & BHUSHAN B 2012 Hierarchical structure and mechanical properties of nacre: a review *RSC Advances* **2**: 7617–7632.
- TRUSSELL GC 2000 Phenotypic clines, plasticity, and morphological trade-offs in an intertidal snail *Evolution* **54**: 151–166.
- VERMEIJ GJ 1973 Morphological patterns in high intertidal gastropods: adaptive strategies and their limitations *Marine Biology* **30**: 319–346.
- VERMEIJ GJ 1980 Gastropod growth rate, allometry, and adult size: environmental implications. In D.C. Rhoads & R.A. Lutz (eds) *Skeletal growth in aquatic organisms* 379–394 Plenum Press, New York.
- VERMEIJ GJ 1987 *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton, New Jersey.
- VILVENS C, SWINNEN F & DENIZ GUERRA F 2011 A New species of *Clelandella* (Gastropoda: Trochoidea: Trochidae: Cantharidinae) from Western Sahara *Novapex* **12**(1–2): 49–55.
- YOURDKHANI M, PASINI D & BARTHELAT F 2011 Multiscale mechanics and optimization of gastropod shells *Journal of Bionic Engineering* **8**(4): 357–368.

