




# Predation governs the eulittoral distribution of a ubiquitous Mediterranean gastropod

Luka Seamus Wright 

Received: 6 July 2022 / Revised: 5 January 2023 / Accepted: 9 January 2023  
© Springer Nature Switzerland AG 2023

**Abstract** Topshell gastropods are among the most important intertidal biofilm grazers. Present throughout the Mediterranean, this sea's only exclusively eulittoral trochid, *Phorcus turbinatus*, is spatially separated from its infralittoral congeners, *P. articulatus*, *P. richardi* and *P. mutabilis*. Despite its ubiquity, data on its fundamental ecology are lacking. By a series of laboratory and field experiments, I show that predation fixes the lower boundary of the vertical range inhabited by *P. turbinatus* precisely at lowest astronomical tide (LAT). Predicted in situ predation risk rapidly increases from 30% d<sup>-1</sup> at the mean position of *P. turbinatus* (+0.31 m) to 84% d<sup>-1</sup> at 1 m below LAT. At least nine predators across all major phyla prey on *P. turbinatus*. Important in terms of abundance, zonation and frequency of predation events are the two muricids *Stramonita haemastoma* (+0.08 m) and *Hexaplex trunculus* (−1.73 m) on exposed and

sheltered coasts, respectively, along with *Thalassoma pavo* (−0.56 m) and *Hermodice carunculata* (−1.24 m). Physiological constraints seem to be of secondary importance since *P. turbinatus* survives up to 1 week fully immersed in situ. Therefore, predation risk likely is the ultimate driver of vertical distribution and thus physiological adaptation of littoral Mediterranean trochids.

**Keywords** Benthos · *Coscinasterias tenuispina* · *Episcomitra cornicula* · *Eriphia verrucosa* · *Pisania striata* · *Tarantinaea lignaria*

## Introduction

While the upper boundary of eulittoral animals is logically set by the physical constraints of the atmosphere (desiccation, variable salinity, temperature fluctuation, low fluid density), drivers of the lower limit are of ecological nature (competition, predation, food availability) and therefore less straightforward (Ricketts et al., 1985; Raffaelli & Hawkins, 1999). Of course, physical factors play a role in governing the lower limit of fauna whose physiology is adapted to the high shore (Tait, 1918; Bannister et al., 1966; Micallef & Bannister, 1967; Houlihan & Innes, 1982), but they are often unsurprising given the animal's distribution and cannot be seen as the ultimate cause of zonation. Initiation of physiological adaptation in the evolutionary past must thus be of ecological nature

Handling editor: Jonne Kotta

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10750-023-05143-4>.

L. S. Wright (✉)  
Qattus tal-Baħar Laboratory, Sqaq Wied tal-Qattus,  
Għammar GSR 1321, Għawdex, Malta  
e-mail: luka@wright.it; luka.wright@research.uwa.edu.au

L. S. Wright  
Oceans Institute, University of Western Australia, Perth,  
WA 6009, Australia

(Raffaelli & Hawkins, 1999). The lower limit of sessile organisms, such as mussels and barnacles in the Atlantic and Pacific, is principally set by interspecific interference competition and predation (Connell, 1961; Dayton, 1971; Paine, 1974). Less well studied than sessile organisms, the case of mobile fauna is backed by almost no evidence suggesting that interspecific competition or food availability controls vertical distribution (Underwood, 1979; Raffaelli & Hawkins, 1999). Predation therefore seems to be the main vertical structuring factor for gastropods, the dominant intertidal grazers (Underwood, 1979). Their lower boundary is governed by predators including starfishes (Phillips, 1976; Fawcett, 1984; Watanabe, 1984a), crabs (Fawcett, 1984; Yamada & Boulding, 1996; Perez et al., 2009) and molluscs (Garrity & Levings, 1981; McQuaid, 1982; Fawcett, 1984).

Optimal model systems to study biological constraints on the lower boundary of eulittoral gastropods are sets of morphologically similar congeners with different vertical distributions. Due to their close phylogenetic relationship, they provide evolutionary snapshots of an upward vertical migration and allow us to tease apart factors affecting their current distribution. Some of the best-studied sister species are to be found among the topshells (Trochidae), the key herbivores aside from limpets (Patellidae) and winkles (Littorinidae). The oldest known case is that of *Steromphala umbilicalis* (da Costa, 1778) and *S. cineraria* (Linnaeus, 1758) in the Northeast Atlantic, the former occurring between  $0.77 \pm 0.26$  and  $3.83 \pm 0.23$  m (mean  $\pm$  s.e.m.) above lowest astronomical tide (LAT), the latter below  $1.44 \pm 0.14$  m above LAT (Colman, 1933; Evans, 1947a, b; Smith, 1969; Underwood, 1973). Yet, although the distribution of these trochids has been mapped repeatedly, underlying mechanistic drivers remain unclear. Interspecific competition has been suggested on a correlative basis (Smith, 1969) but not proven experimentally (Underwood, 1979). The diets of these trochids are unfortunately insufficiently studied, but while only *S. cineraria* lives on kelp, both seem to consume it (Pessarrodona et al., 2019b; Gilson et al., 2021), so food availability may not be important. Even the case of predation is unclear since the taller shell of infralittoral *S. cineraria* is more vulnerable to crushing than that of eulittoral *S. umbilicalis* but this is behaviourally compensated with faster evasion (Cotton et al., 2004). In the Northeast Pacific, *Tegula funebris* (A.

Adams, 1855), *T. brunnea* (Philippi, 1849), *T. montereyi* (Kiener, 1850) and *T. pulligo* (Gmelin, 1791) occur in succession from lower eulittoral to mid infralittoral (Riedman et al., 1981; Watanabe, 1984a). The last three prefer the same kelp food (Watanabe, 1984b) and as there is no evidence in support of interspecific competition, predation seems to be the most important structuring agent (Watanabe, 1984a). However, even this factor remains obscure since *T. brunnea* and *T. pulligo*, expected to have the highest and lowest mortalities, respectively, both have inferior anti-predator defences to *T. montereyi* (Watanabe, 1983) and are consequently consumed more frequently (Watanabe, 1984a).

In contrast to these well-studied Atlantic and Pacific systems, there is no knowledge on the ecology of gastropods living in the microtidal Mediterranean eulittoral. The only trochid that exclusively lives in this zone, where it can reach densities of up to  $600 \text{ m}^{-2}$ , is *Phorcus turbinatus* (Born, 1778) (Bannister et al., 1966; Micallef & Bannister, 1967; Crothers, 2001; Schembri et al., 2005). *P. turbinatus* has three morphologically similar Mediterranean endemic congeners, *P. articulatus* (Lamarck, 1822), *P. richardi* (Payraudeau, 1826) and *P. mutabilis* (Philippi, 1851) (Sousa et al., 2018). Their geographical ranges overlap throughout the Mediterranean except for the coasts of southern Sardinia and north-western Africa (Donald et al., 2012). *P. turbinatus* is 8 [4, 13] Ma (posterior mode [95% highest posterior density interval]) old and its ancestor diverged from the ancestral line of the younger *P. articulatus*, *P. richardi* and *P. mutabilis* 14 [9, 19] Ma ago (Donald et al., 2012). In contrast to *P. turbinatus*, *P. articulatus* usually inhabits the upper infralittoral (Crothers, 2001; Cheour et al., 2014; Boulajfene et al., 2019) where it lives among and likely grazes on seagrass and macroalgae (Cheour et al., 2014; Zaabar et al., 2018). Sometimes it is found in the eulittoral (Houlihan & Innes, 1982; Crothers, 2001) but where it coexists with *P. turbinatus*, it lives lower on the shore (Crothers, 2001). *P. richardi* is also found in the upper infralittoral (Houlihan & Innes, 1982) and *P. mutabilis* is said to inhabit a similar zone (Gofas & Jabaud, 1997). Notwithstanding this vague knowledge on the zonation of these Mediterranean trochids, data on their vertical distribution in relation to LAT are entirely lacking. Besides physiology (Bannister et al., 1966; Micallef & Bannister, 1967; Houlihan & Innes, 1982), published

data are restricted to reproduction and anthropogenic impacts such as metal pollution and harvesting (Sousa et al., 2018). Therefore, severe knowledge gaps are present in our understanding of the fundamental ecology of Mediterranean littoral trochids, most notably the widespread *P. turbinatus*.

Here I aim to address these knowledge gaps by testing for mechanistic drivers limiting the distribution of *P. turbinatus* to the eulittoral. Due to the outlined evidence on other eulittoral gastropods, I hypothesised that the main driver is predation by an unknown number of unknown predators, which I sought to identify. Specifically, I conducted a field experiment to measure daily predation risk along a depth gradient. This experiment was designed to test if the probability of predation is affected by vertical position on the shore and therefore is important in fixing the lower boundary of the zone inhabited by *P. turbinatus*. This was followed up with a laboratory experiment on daily predation risk in confinement with confirmed predators where aquarium water level was varied to test if an increase in predator-free airspace affects predation probability. In a second field experiment, I measured the mortality of fully immersed *P. turbinatus* without predator access to account for mortality due to factors other than predation, such as oxygen and food limitation. To obtain knowledge of vertical and horizontal habitat preferences, I carried out field surveys alongside my experiments to determine the vertical distribution and density of *P. turbinatus* and various predators I had observed during the initial field experiment. The overarching goal of these experiments and observations was to achieve a better understanding of the fundamental ecology of *P. turbinatus* and propose a causal model for its evolution.

## Methods

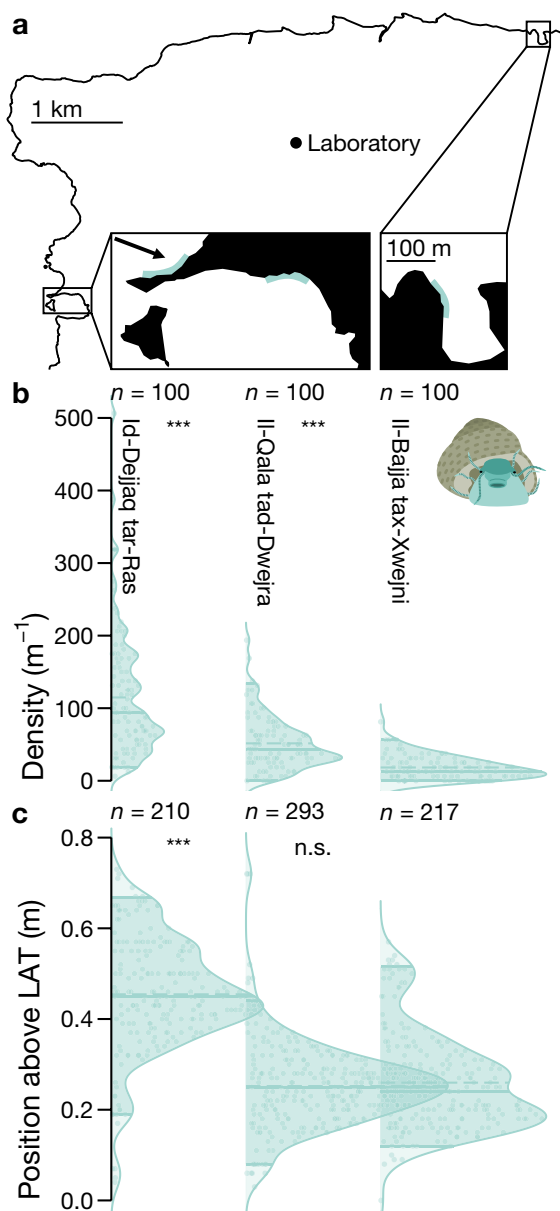
### Study site

The Maltese Islands are located almost exactly in the centre of the Mediterranean and are dominated by a rocky coastline due to their limestone karst nature (Pedley et al., 1976). Aside from *P. turbinatus* (Bannister et al., 1966; Micallef & Bannister, 1967; Crothers, 2001; Schembri et al., 2005; personal observation), the coastal waters of these islands are inhabited by other topshells including *P. articulatus* (Crothers,

2001; personal observation), *Steromphala divaricata* (Linnaeus, 1758) (Bannister et al., 1966) and the Maltese endemic *S. nivosa* (A. Adams, 1853) (Evans et al., 2011). There are no published observations on *P. richardi* or *P. mutabilis* living around the Maltese Islands and I have never encountered them on frequent dives. That being said, they may live less abundantly among the islands' seagrass meadows, consisting of *Posidonia oceanica* (Linnaeus) Delile and *Cymodocea nodosa* (Ucria) Asch., or shallow macroalgal forests, dominated by *Cystoseira compressa* (Esper) Gerloff et Nizamuddin and *C. amen-tacea* var. *stricta* Montagne (Cormaci et al., 1997), and I could easily have missed them. This study was conducted along the north-western coastline of Gozo (also Ġhawdex) (Fig. 1a) which is the second largest island of Malta and located in its north-west.

### Field surveys

Between 29th May and 30th June 2021, I carried out field surveys at three Gozitan rocky shore sites with contrasting exposure (Fig. 1a). The prevailing winds in Malta are north-westerlies and westerlies (Galdies, 2011). Consequently, I chose the sheltered side of Il-Bajja tax-Xwejni on the north coast (36.0795°N, 14.2475°E) as my most sheltered, inside Il-Qala tad-Dwejra on the west coast (36.0482°N, 14.1919°E) as my intermediate and the outside of Id-Dejjaq tar-Ras on the west coast (36.0483°N, 14.1893°E) as my most exposed site (Fig. 1a). Apart from these differences in wind and thus wave exposure, all sites likely experience similar irradiance and temperature due to their geographical proximity (max. 6.28 km distance, Fig. 1a). Il-Qala tad-Dwejra and Id-Dejjaq tar-Ras have a similar rock face slope (~45°) and are composed of lower coralline limestone (also Żonqor, 28.1–23.03 Ma) (Pedley et al., 1976). Il-Bajja tax-Xwejni is made of more shallowly sloping lower *Globigerina* d'Orbigny, 1826 limestone (also Franka, 23.03–20.43 Ma) (Pedley et al., 1976) and has an abundance of rock pools. The vertical section of limestone inhabited by *P. turbinatus* is devoid of macrophytes at all sites but borders onto *Cystoseira* C. Agardh forest below. It is possible that the sites differ in other minor factors that are difficult to observe but therefore likely have little effect. Within a 100-m rocky shore section at each site (Fig. 1a), I measured *P. turbinatus* density with 100 haphazardly placed



**Fig. 1** Effect of wind-driven wave exposure across three sites on the coast of north-western Gozo (**a**) on *Phorcus turbinatus* abundance (**b**) and vertical distribution in relation to lowest astronomical tide (LAT) (**c**). Maps are based on coordinate reference system WGS 84, rendered according to the equirectangular projection and oriented northward. Coloured coast-lines in **a** indicate the extent of sampling areas and their position relative to the prevailing north-westerly wind (arrow) and correspond to data vertically aligned below. Curves, solid and dashed lines in **b** and **c** are kernel density estimates, medians and means. Shaded regions are the central 95% of probability density. Annotations indicate statistical significance of pairwise contrasts at  $\alpha = 0.05$ : \*\*\* $P < 0.001$ , n.s. not significant

40×40-cm quadrats (cf. Underwood, 1973; Schembri et al., 2005; Perez et al., 2009) and vertical position in relation to seawater level with a folding rule ( $\pm 1$  cm). Position measurements were then standardised to lowest astronomical tide (LAT). Gastropod individuals were collected from their eulittoral zone at all sites for subsequent field and laboratory experimentation. In the case of in situ experiments, I always deployed individuals at their home site.

### Field experiments

Over the survey period, I performed two field experiments across all surveyed sites, one to assess survival with, the other without predator access. During the first, I tethered 100 *P. turbinatus* individuals across sites (36 at Il-Bajja tax-Xwejni, 33 at Il-Qala tad-Dwejra and 31 at Id-Dejjaq tar-Ras) to weights with thin cotton thread by drilling a 1-mm diameter hole in the last shell whorl (Fig. S1, cf. McQuaid, 1982; Watanabe, 1984a; Perez et al., 2009). After measuring shell length ( $\pm 0.01$  mm, digital callipers, ACCUD CO., LTD., Vienna, Austria) and total mass ( $\pm 0.01$  g, TGC 150–2, KERN & SOHN GmbH, Balingen, Germany), I randomly deployed each individual on the rocky shore. Position in relation to LAT, ranging from 0.84 m above LAT and 8.97 m below LAT, was measured with a folding rule as described above or with the depth sensors of a dive computer (Chromis, SCUBAPRO, Nürnberg, Germany) and underwater camera (Tough TG-5, Olympus SE & Co. KG, Hamburg, Germany). After 24 h, I recorded whether the snail had been eaten (1) or not (0) and by what predator, if present upon retrieval. Predation events were recorded with certainty since snails were either completely removed including the operculum, leaving behind an empty shell, or partially consumed in cases where predators were still present. Snails that succumb due to causes other than predation, such as suffocation or starvation, usually have intact opercula that they clamp shut. I therefore recorded 0 if the gastropod including operculum was present, regardless of dead or alive. I mapped the vertical distribution of the four most commonly observed predators using ruler, dive computer and camera as described above and measured the densities of the two most abundant predators with a 40×40-cm quadrat or 1×10-m belt transect (cf. Garrity & Levings, 1981; Fawcett, 1984; Rilov et al., 2001). Quadrats

were haphazardly placed and transects laid parallel to shore, all individuals within counted and the count divided by the area in square metres.

During the second experiment, I deployed a total of 200 *P. turbinatus* individuals across sites (80 at Il-Bajja tax-Xwejni, 40 at Il-Qala tad-Dwejra and 80 at Id-Dejjaq tar-Ras) below LAT under the exclusion of predators. To achieve this, groups of 10 or 20 gastropods were placed in one to four (total of 13) 20×20-cm mesh bags with 1-mm<sup>2</sup> mesh aperture across five experimental repeats (three at Il-Bajja tax-Xwejni and one each at the other sites). Each snail density was evenly represented across experiments ( $6 \times n = 10$  and  $7 \times n = 20$ ). As a weight, each bag contained a pebble of less than 10-cm diameter from the supralittoral of Il-Bajja tax-Xwejni and therefore free of biofilm. Bags were deployed between 0.5 and 4.37 m below LAT in the afternoon, retrieved precisely after 0.64–7 d (calculated to the minute) and survivals (1) and mortalities (0) recorded. Survivals were recorded with certainty by observing each gastropod for a few minutes by which time it usually started moving. In case it did not, I tapped against its closed operculum to look for a retraction response. I chose to vary the experimental duration to be able to model survival probability as a function of the explanatory variable immersion time. In addition, with the instrumentation described above I measured total mass, if the gastropod was still present in the shell, and shell length. For empty shells in cases of early mortality and progressed tissue decay, I derived total mass from shell length using the power equation  $y = 0.001x^{2.75}$  ( $t$  test of slope  $k$ ,  $t_{290} = 15.36$ ,  $P < 0.001$ ) which I obtained from 291 paired measurements by generalised nonlinear least squares (Fig. S2).

### Laboratory experiments

During laboratory experiments, I kept organisms in two 39×24×24-cm, 22.46-l glass aquaria (MARINA, HAGEN GmbH & Co. KG, Holm, Germany) filled with fresh seawater from Il-Bajja tax-Xwejni and aerated with an air pump equipped with air stones (air 275 R plus, sera GmbH, Heinsberg, Germany). Each aquarium was separated into two compartments of equal dimensions and covered with 1-mm mesh (*P. turbinatus* will readily crawl about the laboratory!). At the beginning of each 24-h experiment, I cleaned and refilled the tank with fresh

seawater and placed one confirmed muricid predator of known mass and shell length in each compartment with a single *P. turbinatus* for a total of 41 independent predator–prey pairs. Seawater temperature was monitored throughout the experiment using a digital thermometer ( $\pm 0.1$  °C, DigiScan, JBL GmbH & Co. KG, Neuhofen, Germany) and kept at  $0.71 \pm 1.92$  °C (mean  $\pm$  s.d.) above ambient sea surface temperature (Met Office, 2021). Thus, aquaria conditions were representative of the warmer and less stable eulittoral temperature and no specimens succumbed to in situ conditions. As with the first field experiment, I recorded whether the snail had been eaten (1) or not (0) after 24 h. Between experiments, water level was randomly varied at 4-cm intervals between 4 and 24 cm (3.74–22.46 l) to test its effect on predation risk. Each water level treatment was repeated four to eight times (mean = 5.67). In a single preliminary behavioural experiment, I compared the vertical movement response of five *P. turbinatus* individuals separated from one confirmed muricid predator by 1-mm mesh to five control individuals over a period of 15 min.

### Data analysis and visualisation

I analysed and visualised data in R v4.1.2 (R Core Team, 2022) within the integrated development environment RStudio v2021.09.2 (RStudio Team, 2022). My primary tool of statistical inference in this study are frequentist linear models and their generalised and multi-level derivatives. Model optimality was determined based on graphical scrutiny of residuals for homogeneity of variance and Gaussian distribution along with common information criteria (Zuur et al., 2009).

Due to their heterogeneity and right skew and the suboptimality of data transformation (Zuur et al., 2009), density data were analysed with a generalised linear model based on the gamma distribution and logarithmic link function. Vertical distribution data were also heterogenous but normal. I therefore weighted the residual variance by species with generalised least squares using nlme v3.1–153 (Pinheiro et al., 2021). The relationship between total gastropod mass and shell length is nonlinear, so I approximated it using a generalised nonlinear model with a power equation in nlme v3.1–153.



Due to their binomial nature (0, 1), in situ and in vitro predation risk along with survival data required modelling using generalised linear models based on the binomial distribution with cauchit, complementary log–log (cloglog) and probit link functions, respectively. In the case of survival data, groups of 10 or 20 gastropods were contained in the same mesh bag (see above) and are therefore not statistically independent, introducing additional uncertainty. This is a case of hierarchical design that requires hierarchical (multi-level) modelling. Therefore, I modelled these data using a generalised linear mixed effects model with a random intercept for each bag, allowing me to account for the additional uncertainty (variance of the random intercept). As different snail densities (10 or 20 per bag) could potentially affect the response of survival to immersion time, I tested for an interaction between time and density during model fitting. There was no interaction (likelihood ratio chi-square test,  $X^2=2.19$ ,  $P=0.14$ ), meaning the effect of time on survival probability is not different between densities, so the interaction term was removed in the optimal model. Since binomial data are not symmetrically distributed around the mean and normal approximation (Wald) is consequently suboptimal, asymmetric Wilson score s.e.m. were calculated with binom v1.1–1 (Dorai-Raj, 2015).

Data were visualised using the tidyverse v1.3.1 (Wickham et al., 2019) with cowplot v1.1.1 (Wilke, 2020). Maps were drawn in QGIS v3.28 (qgis.org). Data, maps and illustrations were juxtaposed in Affinity Designer v1.9.1 (Serif Ltd, Nottingham, United Kingdom). All analysis and visualisation steps can be scrutinised and replicated using the files provided at [github.com/lukaseamus/Phorcus](https://github.com/lukaseamus/Phorcus).

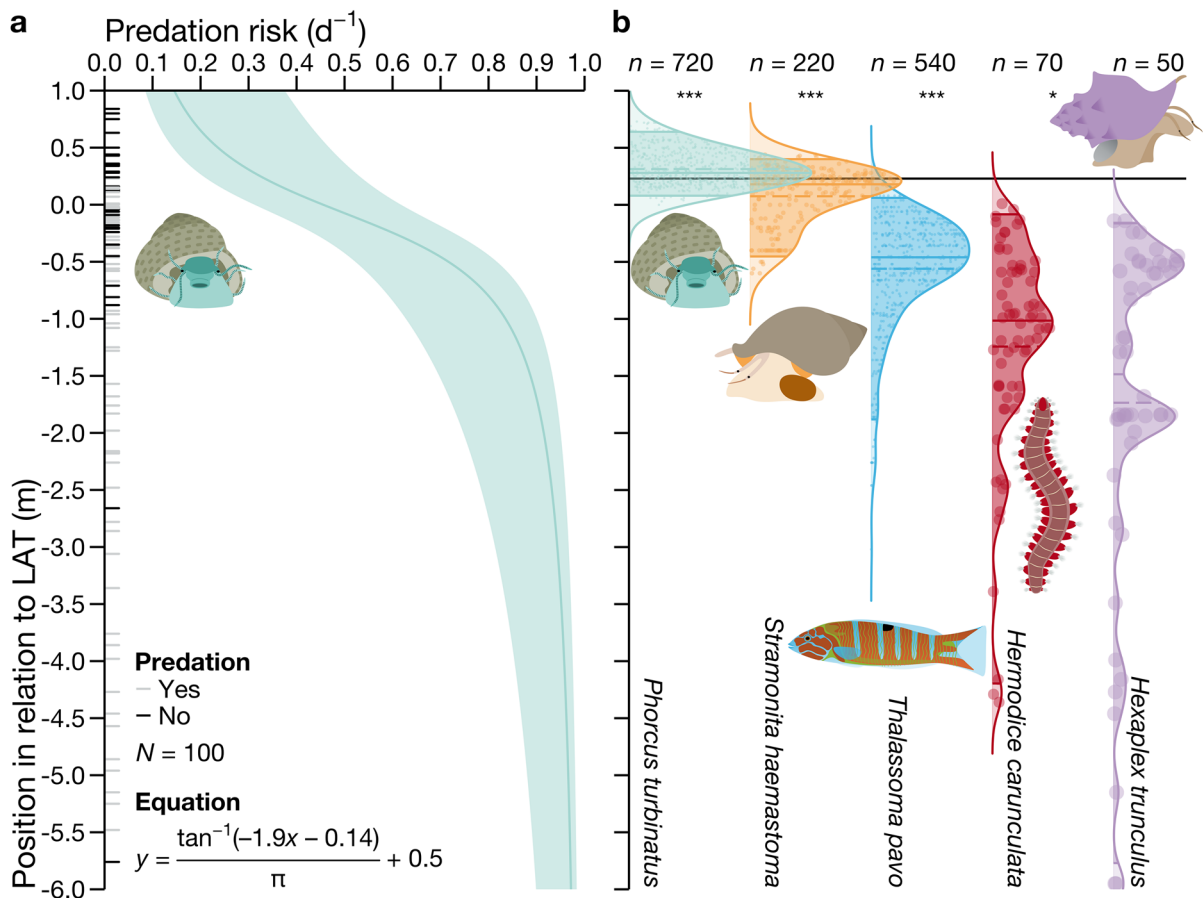
## Results

Around Gozo, *P. turbinatus* lives in a eulittoral band of 0.73 m width at average densities of  $62 \pm 4$  m<sup>-2</sup> (mean  $\pm$  s.e.m.,  $n=300$ ) but can reach up to 506 m<sup>-2</sup> (cf. 600 m<sup>-2</sup>, Schembri et al., 2005). It has an average mass and shell length of  $2.47 \pm 0.09$  g and  $15.9 \pm 0.23$  mm ( $n=291$ ) and the largest recorded individual had a mass and shell length of 8.41 g and 26.9 mm (Fig. S2, cf. 43 mm in Crothers, 2001). *P. turbinatus* clearly has an affinity for exposed coasts, where it is more abundant (Fig. 1b, likelihood ratio

chi-square test,  $X^2_{2,300}=258.38$ ,  $P<0.001$ ,  $n=300$ ) and positioned higher above LAT (Fig. 1c, F test,  $F_{2,717}=253.62$ ,  $P<0.001$ ,  $n=720$ , cf. Crothers, 2001; Schembri et al., 2005). At the most exposed site, *P. turbinatus* occurs at 5.27 times higher densities (pairwise  $t$  test,  $t_{198}=16.81$ ,  $P<0.001$ ,  $n=200$ ), is distributed  $0.19 \pm 0.01$  m further up the shore (pairwise  $t$  test,  $t_{425}=18.65$ ,  $P<0.001$ ,  $n=427$ ) and occupies 21% more vertical space than at the most sheltered site (Fig. 1b–c). Hence, wind-driven wave exposure seems to affect the abundance and vertical distribution of *P. turbinatus*.

Across sites, the vertical distribution of *P. turbinatus* is centred at  $0.31 \pm 0.01$  m above LAT ( $n=720$ ) with a lower boundary at exactly 0 m above LAT. Here, I propose that this pattern is ultimately caused by predation. The relationship between vertical position on the shore ( $v$ ) and the probability of predation ( $p$ ) is best described by the equation  $p = \frac{\tan^{-1}(-1.9 \times v - 0.14)}{\pi} + 0.5$  (Fig. 2a, likelihood ratio chi-square test,  $X^2_{1,100}=28.37$ ,  $P<0.001$ ,  $n=100$ ). The risk for *P. turbinatus* of being eaten within any given 24-h period increases 2.8-fold from 29.81 [18.59, 51.32] % (binomial model fit [95% confidence interval]) at its mean position above LAT to 83.53 [62.79, 90.04] % at 1 m below LAT. At 8.97 m below LAT, the maximum depth I tested, predicted predation risk is 98.12 [93.13, 98.91] % d<sup>-1</sup>. Thus, vertical position is a good predictor of predation risk. No predation events were recorded above 0.23 m above LAT (black line in Fig. 2b), where *P. turbinatus* is encountered with highest probability. Interestingly, daily predation risk does not change with gastropod mass (likelihood ratio chi-square test,  $X^2_{1,100}=2.16$ ,  $P=0.14$ ,  $n=100$ ), which was  $2.53 \pm 0.12$  g on average for tethered individuals.

I identified four key *P. turbinatus* predators with vertical distributions suggesting their importance in driving the trochid's eulittoral position (Fig. 2b). The red-mouthed rock shell *Stramonita haemastoma* (Linnaeus, 1767) has its vertical range centre at  $0.08 \pm 0.02$  m above LAT ( $n=220$ , Fig. S2, S3a), the ornate wrasse *Thalassoma pavo* (Linnaeus, 1758) at  $0.56 \pm 0.02$  m below LAT ( $n=540$ ), the bearded fireworm *Hermodice carunculata* (Pallas, 1766) at  $1.24 \pm 0.12$  m below LAT ( $n=70$ , Fig. S3b) and the banded dye murex *Hexaplex trunculus* (Linnaeus, 1758) at  $1.73 \pm 0.21$  m below LAT ( $n=50$ , Fig. S2, S3c–d). *S. haemastoma*, *T. pavo*, *H. carunculata* and



**Fig. 2** Effect of predation on the vertical distribution of *Phorcus turbinatus* above lowest astronomical tide (LAT). **a** Probability of predation on *P. turbinatus* in relation to vertical position across sites. The line and shaded regions are the caught binomial generalized linear model fit and 95% confidence interval. Note that two outlying datapoints at 6.57 m (1) and 8.97 m (0) below LAT are not plotted here but included in the model. **b** Vertical distribution of *P. turbinatus* and its most fre-

quent predators pooled across sites. Curves, solid and dashed lines are kernel density estimates, medians and means. Shaded regions are the central 95% of probability density. The black line indicates the position in relation to LAT above which no predation events were recorded. Datapoint size is inversely scaled to sample size. Asterisks indicate statistical significance of pairwise contrasts at  $\alpha=0.05$ : \* $P<0.05$ , \*\*\* $P<0.001$

*H. trunculus* are therefore distributed 0.24 m (pairwise  $t$  test,  $t_{938}=13.32$ ,  $P<0.001$ ,  $n=940$ ), 0.87 m (pairwise  $t$  test,  $t_{1258}=40.37$ ,  $P<0.001$ ,  $n=1260$ ), 1.56 m (pairwise  $t$  test,  $t_{788}=13.49$ ,  $P<0.001$ ,  $n=790$ ) and 2.05 m (pairwise  $t$  test,  $t_{768}=9.55$ ,  $P<0.001$ ,  $n=770$ ) lower on the shore, respectively, than *P. turbinatus*. This discrepancy in vertical distributions between predators and prey likely drives the observed vertical trend in predation risk and lends further support to the importance of predation in the zonation of *P. turbinatus*.

The muricids *S. haemastoma* and *H. trunculus* live on exposed and sheltered coasts, respectively,

but both coexist at Il-Qala tad-Dwejra, my site of intermediate exposure (Fig. 1). Mesh bags baited with live *P. turbinatus* readily attracted large groups of *S. haemastoma* (cf. Brown & Alexander Jr, 1994) and *H. trunculus* (cf. Peharda & Morton, 2006) at exposed and sheltered sites, respectively. While I was unable to clarify whether these muricids were attracted to chemical cues of live trochids or those that had succumbed inside the bags, this indicates they can actively hunt *P. turbinatus* via chemoreception and are not reliant on chance encounters. This is supported by laboratory observations of *H. trunculus* chasing and attacking *P. turbinatus* (Fig. S3c, d). *T.*

*pavo* and *H. carunculata* are ubiquitous although the latter only appears in summer. While the former is obviously an active hunter, I did not observe the latter aggregating as abundantly as the muricids so it may rely on chance encounters (cf. Simonini et al., 2017, 2018). I estimated the densities of the most abundant predators, *S. haemastoma* and *T. pavo*, to be  $8.63 \pm 0.77 \text{ m}^{-2}$  ( $n=100$ ) and  $0.8 \pm 0.06 \text{ m}^{-2}$  ( $n=40$ ), respectively. *H. trunculus* was generally rare except when occurring in feeding aggregations and *H. carunculata* only became more abundant as seawater temperature increased above 26 °C towards the end of my experimental period.

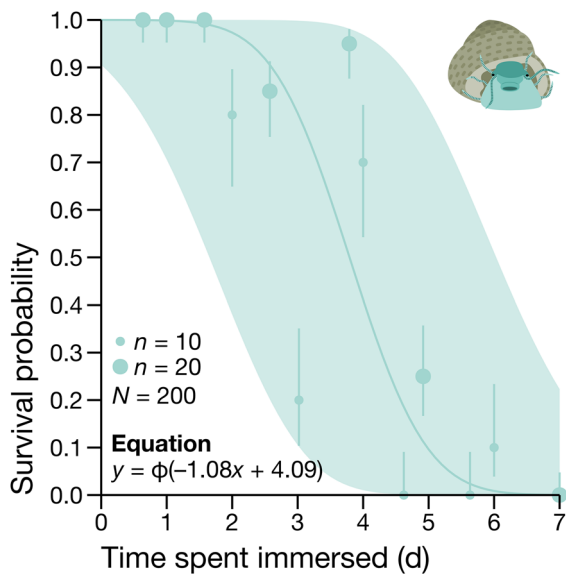
In subsequent in vitro experiments, I did not observe any of seven *S. haemastoma* eating *P. turbinatus* within a 24-h period but 35.29 [21.49, 52.09] % d<sup>-1</sup> ( $n=34$ ) succumbed to *H. trunculus*. Predation risk did not change with snail mass (likelihood ratio chi-square test,  $X^2_{1,34}=0.45$ ,  $P=0.5$ ,  $n=34$ ) or aquarium water level (likelihood ratio chi-square test,  $X^2_{1,34}=1.82$ ,  $P=0.18$ ,  $n=34$ ) but the visualised data suggest a slight decrease in risk with increasing water level (Fig. S4). This is contrary to my expectation that vertical air space helps *P. turbinatus* evade predation. Instead, *H. trunculus* may be a more successful hunter when the water volume is lower and the concentration of prey and its kairomones consequently higher. Conversely, *P. turbinatus* does not seem to respond to the mere presence of *H. trunculus*, since neither kairomone-treated nor control group individuals moved above water level. During attacks of *H. trunculus*, however, direct contact does not seem necessary to elicit chemically mediated avoidance behaviour either (Fig. S3c). This suggests that *P. turbinatus* may be unable to detect muricid kairomones from a distance and/or can only detect kairomones exuded during attack. Both results certainly need empirical validation considering their low sample size, statistical ambiguity and preliminary nature.

Aside from these primary predators in terms of abundance and frequency of predation events, I observed the starfish *Coscinasterias tenuispina* (Lamarck, 1816) preying on *P. turbinatus* (Fig. S3e) and groups of the small mitrid *Episcomitra cornicula* (Linnaeus, 1758) feeding inside the shells of dead individuals. The latter species is probably too small to kill *P. turbinatus* and may only be a scavenger. I could not determine their vertical range due to the former's rarity and the latter's crypsis. Over three months of

regular visits to the infralittoral, I only observed *C. tenuispina* twice. Interestingly, despite the presence of the shell-crushing crab *Eriphia verrucosa* (Forskål, 1775), not a single tethered *P. turbinatus* shell was broken after 24 h in situ. Nevertheless, I did observe *E. verrucosa* capturing dislodged and immersed *P. turbinatus*. This apparent paradox may be explained by my observation that *E. verrucosa* carries its prey into hiding to consume it, which is not possible with tethered snails. Tethering may underestimate predation risk in this regard which may in turn compensate potential overestimation due to restrained movement. Besides not being crushed, none of the tethered *P. turbinatus* shells displayed drill holes. While this at first seemed to rule out other molluscan predators such as *Octopus vulgaris* Cuvier, 1797, the drilling muricids *H. trunculus* and *S. haemastoma* surprisingly never drill *P. turbinatus* but instead force open its weaker operculum, so other molluscs could be acting similarly. The shells that were emptied (65%) were in fact in such good condition that 6% of them were occupied by the hermit crabs *Clibanarius erythropus* (Latreille, 1818) and *Pagurus anachoretus* Risso, 1827 (Fig. S3f).

Immersed *P. turbinatus* usually seek to position themselves at the air–water interface (cf. Underwood, 1979; Thain et al., 1985) but these snails nonetheless survive up to 7 d completely immersed in the infralittoral when predators are excluded. When submerged, the decline in survival probability ( $p$ ) with time ( $t$ ) is best described by the equation  $p = \phi(-1.08 \times t + 4.09)$  (Fig. 3, chi-square test,  $X^2_{1,200}=17.32$ ,  $P<0.001$ ,  $n=200$ ). Therefore *P. turbinatus* has an immersed half-life ( $t_{1/2}$ ) of 3.79 d or 91 h. Interestingly, submerged survival does not change with gastropod mass (chi-square test,  $X^2_{1,200}=0.34$ ,  $P=0.56$ ,  $n=200$ ), which was  $2.12 \pm 0.09$  g on average for bagged individuals, indicating that body mass may not influence the ability to incur oxygen debt. Survival of immersed *P. turbinatus* may also have been influenced by factors unrelated to physiology, which would cause the single week reported here (Fig. 3) to be an underestimate of maximal immersed survival. First, I observed muricids clinging to most retrieved bags, so some *P. turbinatus* may have been attacked and eaten through the mesh. Second, *P. turbinatus* may have starved since neither the mesh nor the pebble weight presumably had sufficient biofilm to sustain 10–20 individuals.

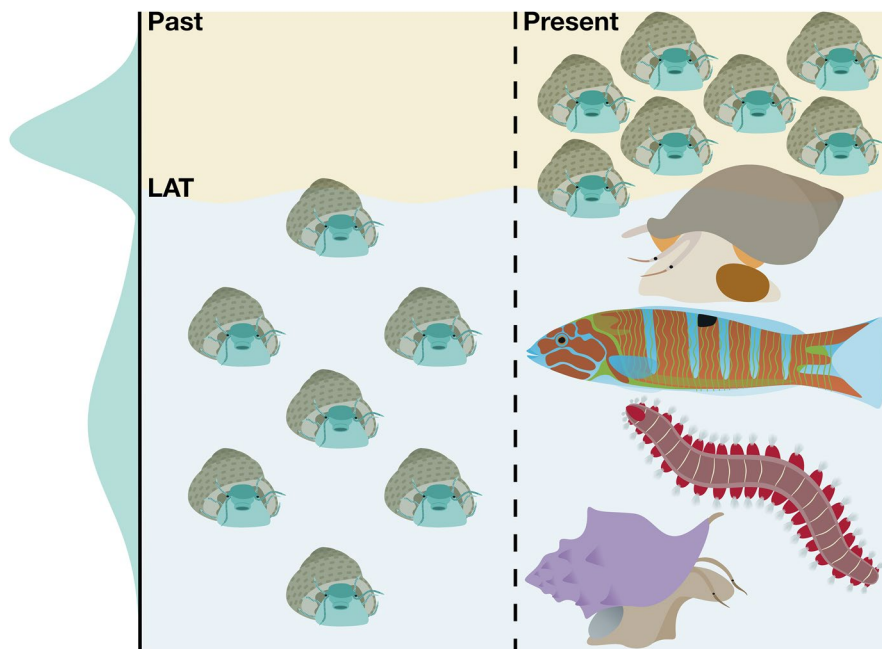




**Fig. 3** Effect of full immersion without predator access on the survival probability of *Phorcus turbinatus* across sites. The line and shaded region are the probit binomial generalised linear model fit and 95% confidence interval. Point-ranges are means  $\pm$  binomial standard errors. Note that the 95% confidence interval is adjusted to account for the intercept variance between mesh bags (points) as an additional source of uncertainty

## Discussion

Here, I present the first data on the fundamental ecology of *Phorcus turbinatus* and show unequivocally that predation is the primary mechanistic driver of its vertical zonation (Fig. 4). Predation risk for *P. turbinatus* predictably increases as it moves down the shore (Fig. 2a). This trend is further explained by the vertical ranges of confirmed predators (Fig. 2b). Interestingly, snail mass does not influence predation risk, suggesting that the probability of being eaten is so high for *P. turbinatus* in the infralittoral that it overrides any potential ontogenetic effect such as that described by Pessarrodona et al. (2019a) for the purple sea urchin *Paracentrotus lividus* (Lamarck, 1816). Nonetheless, factors unrelated to predation, such as oxygen and food limitation, could potentially be alternative causes of mortality among immersed gastropods. I rule out these confounders by showing that immersed gastropods without predator access survive far beyond the 24-h timescale in which they incur significant risk of predation (Fig. 3). While emersed *P. turbinatus* can apparently survive up to 2 d longer and has a 72% longer half-life ( $t_{1/2} = 6.5$  d, Houlihan &



**Fig. 4** Proposed causal model for *Phorcus turbinatus* zonation, which may explain the evolution of its current eulittoral distribution in relation to lowest astronomical tide (LAT) and concomitantly its required physiological adaptation. The “present” probability distribution is equivalent to the empirical kernel

density estimates shown in Fig. 2b while the “past” distribution is drawn according to the assumed zonation of the infralittoral ancestor of *P. turbinatus* which may have been similar to that of its contemporary Mediterranean congeners

Innes, 1982), likely due to the accumulation of a larger oxygen debt when immersed (Micallef & Bannister, 1967; Houlihan & Innes, 1982), its ability to respire in both fluids simply points towards perfect adaptation to the eulittoral (Micallef & Bannister, 1967; Houlihan & Innes, 1982). Therefore oxygen limitation cannot be regarded as the proximate determinant of the lower distributional limit of *P. turbinatus*. Regarding food limitation, the biofilm zone grazed by *P. turbinatus* is mostly free of predators (Fig. 2b), so the case is not as clear as with the trochid *Oxystele antoni* D. G. Herbert, 2015, where greatest food availability spatially coincides with highest predation risk (McQuaid, 1982). Nonetheless, there was unlikely enough food in the mesh bags so immersed mortality may have been due to starvation, indicating that this factor is also of secondary importance. A similar case in point is *Ligia oceanica* (Linnaeus, 1767) which, albeit inhabiting the more terrestrial supralittoral, can tolerate immersion for months without food (Tait, 1918) but is consumed by *Thalassoma pavo* within seconds of touching the sea surface (personal observation). The presented evidence clearly demonstrates that the immediate cause of the current zonation of *P. turbinatus* is predation, providing an ecological and evolutionary analogy to the previously introduced, well-known *Steromphala* spp. and *Tegula* spp. model systems in the Atlantic and Pacific and a causal model for eulittoral trochids more generally (Fig. 4).

In contrast to Atlantic and Pacific gastropod model systems, starfish and crab predation do not seem to be important in determining the distribution of Mediterranean eulittoral gastropods. While I observed that *P. turbinatus* is rarely eaten by the starfish *Coscinasterias tenuispina* or the crab *Eriphia verrucosa*, 89% of tethered *Littorina littorea* (Linnaeus, 1758) in the Northwest Atlantic (Perez et al., 2009) and 10% of *Tegula* spp. in the Northeast Pacific (Watanabe, 1984a) are consumed by shell-crushing predators and 90% of *Tegula* spp. are consumed by starfish (Watanabe, 1984a). Instead, predatory gastropods seem of primary importance in the Mediterranean. Notably, several lines of evidence suggest that besides the two confirmed muricid predators (Fig. 2b, Fig. S3a, c, d), the eulittoral pisaniid *Pisania striata* (Gmelin, 1791) (Taylor, 1987; Schembri et al., 2005) and the infralittoral fascioliid *Tarantinaea lignaria* (Linnaeus, 1758) (Taylor, 1987) also prey on *P. turbinatus*. First, when I placed these predatory snails in the ultimate

vicinity of *P. turbinatus*, they readily attack it, whereupon the trochid performs a defence response like that described by Hoffman (1980), Garrity & Levings (1981), and Watanabe (1983), featuring no retraction into the shell (Fig. S3c), violent shell rotation (Fig. S3d), escape and rapid ascent above the water surface. Second, trochid radula remains have been found in the digestive system of *P. striata* (Taylor, 1987). Third, *T. lignaria* preys on the cerithiid *Cerithium vulgatum* Bruguière, 1792 and the columbellid *Columbella rustica* (Linnaeus, 1758) (personal observation) and *P. striata* feeds on *C. vulgatum* (Taylor, 1987). Since *C. vulgatum* is often the main prey of *Hexaplex trunculus* (Taylor, 1987; personal observation) and this muricid also feeds on *P. turbinatus*, it seems likely that *T. lignaria* and *P. striata* with their similar diets would do so too. However, given the co-occurrence of *P. striata* and *P. turbinatus* in the lower eulittoral zone and the rarity of *T. lignaria* (Taylor, 1987; personal observation), it is unlikely that these predators have a strong additional influence on the vertical distribution of *P. turbinatus*. Taken together, there is ample evidence that predators across all major phyla (Annelida, Mollusca, Arthropoda, Echinodermata, Chordata) readily prey on *P. turbinatus*, but there are likely many more species which escaped my observation.

This is the first report of any of my confirmed predators (Fig. 2b) preying on *P. turbinatus*. While muricids (Hoffman, 1980; Garrity & Levings, 1981) and wrasse (Evans et al., 2011) are known to be involved in limiting trochid populations, annelid predators have to my knowledge never been reported to play a structuring role in a littoral community. Nevertheless, there is considerable knowledge on the diets of these predators. *Stramonita haemastoma* is also called the oyster drill and known to prey mostly on bivalves, but also barnacles, bryozoans (Brown & Alexander Jr, 1994) and vermetid gastropods (Rilov et al., 2001). *T. pavo* consumes a plethora of species including several trochids (Kabasakal, 2001; Sinopoli et al., 2017). *Hermodice carunculata* is a true generalist that feeds on the sea urchin *P. lividus* (Simonini et al., 2017; personal observation), starfish, corals, anemones, ascidians, sponges and chitons (Simonini et al., 2018). *H. trunculus* eats *P. lividus* (Pessarrodona et al., 2019a; personal observation), *C. vulgatum* (Taylor, 1987; personal observation) and the mussel

*Mytilus galloprovincialis* Lamarck, 1819 (Peharda & Morton, 2006). Although *H. trunculus* (Pessarrodona et al., 2019a) and other predatory snails (Hoffman, 1980; Garrity & Levings, 1981) are known to also have indirect, nonconsumptive effects on prey behaviour via chemical cues, I observed no evidence of this in the case of *P. turbinatus*. Only predation attempts involving direct contact or close proximity triggered the typical defensive response of shell spinning and simultaneous escape described above. While contact is expected to elicit a stronger response (Hoffman, 1980), this nevertheless indicates that *P. turbinatus* may be unable to detect passive-state and/or diluted muricid kairomones. A possible explanation is the rare immersion and consequently seldom encounter with predators underwater, potentially rendering early chemosensory detection inutile. However, a very similar experiment demonstrated that 67% of *Nerita scabricosta* Lamarck, 1822 escape after only 10 min in the same tide pool with their muricid predator *Plicopurpura columellaris* (Lamarck, 1816) (Garrity & Levings, 1981). Since many eulittoral gastropods readily respond to predator kairomones and defence elicitation depends on predator proximity and abundance (Underwood, 1979), additional experimentation is strictly necessary.

In summary, eulittoral *P. turbinatus* is preyed on by at least nine predators across all major phyla, causing over 98% mortality in the shallow Mediterranean infralittoral. When predators are excluded, *P. turbinatus* can survive in this zone for up to a week. Hence, the evidence presented here unequivocally points towards predation as the immediate and ultimate cause governing the lower distributional limit of this ubiquitous Mediterranean trochid. This study provides a first understanding of the fundamental ecology of *P. turbinatus* and hints at some evolutionary drivers that may have caused its ancestor to move up the rocky shore and diverge from the ancestor of its infralittoral congeners 14 million years ago (Fig. 4). Future studies should focus on comparing predation risk, defence mechanisms and dietary preferences between Mediterranean *Phorcus* spp. to further elucidate their ecology and finally reveal the interactions structuring a littoral that was already familiar to Aristotélēs.

**Acknowledgements** I would like to thank Sonja and Keith Wright for financing the acquisition, maintenance and repair of research vessel *Ruby* (red 1989 Vespa PK 50 cc). The help of Charlie Mintoff and Neville Magri was also instrumental in the repair of *RV Ruby*. Thank you to Teresa Nobre for showing me the best mesh bag sewing techniques, and Joseph A. Borg for helping me identify *Episcomitra cornicula* (Linnaeus, 1758).

**Funding** Open Access funding enabled and organized by CAUL and its Member Institutions. I received no funding for this work.

**Data availability** All data and code are available in the open-access repository at [github.com/lukaseamus/Phorcus](https://github.com/lukaseamus/Phorcus). I place no restrictions on data and code availability.

## Declarations

**Conflict of interest** I have no conflict of interest to disclose.

**Research involving animal rights** I followed Directive 2010/63/EU for the care and use of animals.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Bannister, W. H., J. V. Bannister & H. Micallef, 1966. A biochemical factor in the zonation of marine molluscs. *Nature* 211(5050): 747–747. <https://doi.org/10.1038/211747a0>.
- Boulajfene, W., E. Strogyloudi, M. Lasram, A. El Mlayah, C. Vassiliki-Angelique & S. Zouari-Tlig, 2019. Biological and biochemical assessment in *Phorcus articulatus* (Lamarck 1822): contamination and seasonal effect. *Environmental Monitoring and Assessment* 191(9): 555. <https://doi.org/10.1007/s10661-019-7726-3>.
- Brown, K. M. & J. E. Alexander Jr., 1994. Group foraging in a marine gastropod predator: benefits and costs to individuals. *Marine Ecology Progress Series* 112: 97–105. <https://doi.org/10.3354/meps112097>.
- Cheour, M. K., M. Cherif, R. B. Messaoud, N. Aloui-Bejaoui & A. Afli, 2014. Evaluation et cartographie du stock du

- gasteropode trochide *Phorcus articulatus* (Lamarck, 1822) le long du littoral des Iles Kerkennah (Golfe de Gabes, Tunisie). Bulletin de l'Institut National des Sciences et Technologies de la Mer de Salammbô 41: 37–49.
- Colman, J., 1933. The nature of the intertidal zonation of plants and animals. Journal of Marine Biological Association of the United Kingdom 18(2): 435. <https://doi.org/10.1017/S0025315400043794>.
- Connell, J. H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42(4): 710–723. <https://doi.org/10.2307/1933500>.
- Cormaci, M., E. Lanfranco, J. A. Borg, S. Buttigieg, G. Furnari, S. A. Micallef, C. Mifsud, F. Pizzuto, B. Scammacca, D. Seio, 1997. Contribution to the knowledge of benthic marine algae on rocky substrata of the Maltese Islands (Mediterranean Sea). Botanica Marina 40: 203–215. <https://doi.org/10.1515/botm.1997.40.1-6.203>.
- Cotton, P. A., S. D. Rundle & K. E. Smith, 2004. Trait compensation in marine gastropods: shell shape, avoidance behavior, and susceptibility to predation. Ecology 85(6): 1581–1584. <https://doi.org/10.1890/03-3104>.
- Crothers, J. H., 2001. Common topshells: an introduction to the biology of *Osilinus lineatus* with notes on other species in the genus. Field Studies 10(1): 115–160.
- Dayton, P. K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41(4): 351–389. <https://doi.org/10.2307/1948498>.
- Donald, K. M., J. Preston, S. T. Williams, D. G. Reid, D. Winter, R. Alvarez, B. Buge, S. J. Hawkins, J. Templado & H. G. Spencer, 2012. Phylogenetic relationships elucidate colonization patterns in the intertidal grazers *Osilinus* Philippi, 1847 and *Phorcus* Risso, 1826 (Gastropoda: Trochidae) in the northeastern Atlantic Ocean and Mediterranean Sea. Molecular Phylogenetics and Evolution 62(1): 35–45. <https://doi.org/10.1016/j.ympev.2011.09.002>.
- Dorai-Raj, S., 2015. binom: binomial confidence intervals for several parameterizations. R package v1.1–1. <https://CRAN.R-project.org/package=binom>
- Evans, J., J. A. Borg & P. J. Schembri, 2011. Distribution, habitat preferences and behaviour of the critically endangered Maltese top-shell *Gibbula nivos* (Gastropoda: Trochidae). Marine Biology 158(3): 603–611. <https://doi.org/10.1007/s00227-010-1584-4>.
- Evans, R. G., 1947a. The intertidal ecology of Cardigan Bay. Journal of Ecology 34(2): 273–309. <https://doi.org/10.2307/2256720>.
- Evans, R. G., 1947b. The intertidal ecology of selected localities in the Plymouth neighbourhood. Journal of Marine Biological Association of the United Kingdom 27(1): 173–218. <https://doi.org/10.1017/S0025315400014168>.
- Fawcett, M. H., 1984. Local and latitudinal variation in predation on an herbivorous marine snail. Ecology 65(4): 1214–1230. <https://doi.org/10.2307/1938329>.
- Galdies, C., 2011. The Climate of Malta: Statistics, Trends and Analysis. National Statistics Office, Valletta.
- Garritty, S. D. & S. C. Levings, 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. Ecological Monographs 51(3): 267–286. <https://doi.org/10.2307/2937274>.
- Gilson, A. R., D. A. Smale & N. O'Connor, 2021. Ocean warming and species range shifts affect rates of ecosystem functioning by altering consumer-resource interactions. Ecology 102(5): e03341. <https://doi.org/10.1002/ecy.3341>.
- Gofas, S. & A. Jabaud, 1997. The relationships of the Mediterranean trochid gastropods '*Monodonta*' *mutabilis* (Philippi, 1846) and '*Gibbula*' *richardi* (Payraudeau, 1826). Journal of Molluscan Studies 63(1): 57–64. <https://doi.org/10.1093/mollus/63.1.57>.
- Hoffman, D. L., 1980. Defensive responses of marine gastropods (Prosobranchia, Trochidae) to certain predatory sea-stars and the dire whelk, *Searlesia dira* (Reeve). Pacific Science 34(3): 233–243.
- Houlihan, D. F. & A. J. Innes, 1982. Respiration in air and water of four Mediterranean trochids. Journal of Experimental Marine Biology and Ecology 57(1): 35–54. [https://doi.org/10.1016/0022-0981\(82\)90143-5](https://doi.org/10.1016/0022-0981(82)90143-5).
- Kabasakal, H., 2001. Description of the feeding morphology and the food habits of four sympatric labrids (Perciformes, Labridae) from south-eastern Aegean Sea, Turkey. Netherlands Journal of Zoology 51(4): 439–455. <https://doi.org/10.1163/156854201X00206>.
- McQuaid, C. D., 1982. The influence of desiccation and predation on vertical size gradients in populations of the gastropod *Oxystele variegata* (Anton) on an exposed rocky shore. Oecologia 53(1): 123–127. <https://doi.org/10.1007/BF00377146>.
- Met Office, 2021. Sea surface temperature data for May and June 2021. Meteorological Office MIA plc., Luqa.
- Micallef, H. & W. H. Bannister, 1967. Aerial and aquatic oxygen consumption of *Monodonta turbinata* (Mollusca: Gastropoda). Journal of Zoology 151(1): 479–482. <https://doi.org/10.1111/j.1469-7998.1967.tb02890.x>.
- Paine, R. T., 1974. Intertidal community structure. Oecologia 15(2): 93–120. <https://doi.org/10.1007/BF00345739>.
- Pedley, H. M., M. R. House & B. Waugh, 1976. The geology of Malta and Gozo. Proceedings of the Geologists' Association 87(3): 325–341. [https://doi.org/10.1016/S0016-7878\(76\)80005-3](https://doi.org/10.1016/S0016-7878(76)80005-3).
- Peharda, M. & B. Morton, 2006. Experimental prey species preferences of *Hexaplex trunculus* (Gastropoda: Muricidae) and predator–prey interactions with the Black mussel *Mytilus galloprovincialis* (Bivalvia: Mytilidae). Marine Biology 148(5): 1011–1019. <https://doi.org/10.1007/s00227-005-0148-5>.
- Perez, K. O., R. L. Carlson, M. J. Shulman & J. C. Ellis, 2009. Why are intertidal snails rare in the subtidal? Predation, growth and the vertical distribution of *Littorina littorea* (L.) in the Gulf of Maine. Journal of Experimental Marine Biology and Ecology 369(2): 79–86. <https://doi.org/10.1016/j.jembe.2008.09.019>.
- Pessarrodona, A., J. Boada, J. F. Pagès, R. Arthur & T. Alcoverro, 2019a. Consumptive and non-consumptive effects of predators vary with the ontogeny of their prey. Ecology 100(5): e02649. <https://doi.org/10.1002/ecy.2649>.



- Pessarrodona, A., A. Foggo & D. A. Smale, 2019b. Can ecosystem functioning be maintained despite climate-driven shifts in species composition? Insights from novel marine forests. *Journal of Ecology* 107(1): 91–104. <https://doi.org/10.1111/1365-2745.13053>.
- Phillips, D. W., 1976. The effect of a species-specific avoidance response to predatory starfish on the intertidal distribution of two gastropods. *Oecologia* 23(2): 83–94. <https://doi.org/10.1007/BF00557847>.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, & R Core Team, 2021. nlme: linear and nonlinear mixed effects models. R package v3.1–153. <https://CRAN.R-project.org/package=nlme>
- R Core Team, 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Raffaelli, D. & S. J. Hawkins, 1999. Intertidal ecology, Kluwer Academic Publishers, Dordrecht.
- Ricketts, E. F., J. Calvin, J. W. Hedgpeth & D. W. Phillips, 1985. Between Pacific tides, Stanford University Press, Stanford.
- Riedman, M. L., A. H. Hines & J. S. Pearse, 1981. Spatial segregation of four species of turban snails (Gastropoda: *Tegula*) in central California. *Veliger* 24(2): 97–102.
- Rilov, G., Y. Benayahu & A. Gasith, 2001. Low abundance and skewed population structure of the whelk *Stramonita haemastoma* along the Israeli Mediterranean coast. *Marine Ecology Progress Series* 218: 189–202. <https://doi.org/10.3354/meps218189>.
- RStudio Team, 2022. RStudio: integrated development environment for R, RStudio Inc, Boston.
- Schembri, P. J., A. Deidun, A. Mallia & L. Mercieca, 2005. Rocky shore biotic assemblages of the Maltese Islands (Central Mediterranean): a conservation perspective. *Journal of Coastal Research* 21(1): 157–166. <https://doi.org/10.2112/03-0043R.1>.
- Simonini, R., S. Righi, I. Maletti, S. Fai & D. Prevedelli, 2017. Bearded versus thorny: the fireworm *Hermodice carunculata* preys on the sea urchin *Paracentrotus lividus*. *Ecology* 98(10): 2730–2732. <https://doi.org/10.1002/ecy.1919>.
- Simonini, R., I. Maletti, S. Righi, S. Fai & D. Prevedelli, 2018. Laboratory observations on predator–prey interactions between the bearded fireworm (*Hermodice carunculata*) and Mediterranean benthic invertebrates. *Marine and Freshwater Behaviour and Physiology* 51(3): 145–158. <https://doi.org/10.1080/10236244.2018.1502031>.
- Sinopoli, M., R. Chemello, A. Vaccaro & M. Milazzo, 2017. Food resource partitioning between two sympatric temperate wrasses. *Marine and Freshwater Research* 68(12): 2324. <https://doi.org/10.1071/mf16363>.
- Smith, D. A. S., 1969. *Some aspects of the biology of Gibbula cineraria (L.) with observations on Gibbula umbilicalis (Da Costa) and Gibbula pennanti (Phil.) (Mollusca: Prosobranchia)*. Durham University.
- Sousa, R., J. Delgado, J. A. González, M. Freitas & P. Henriques, 2018. Marine snails of the genus *Phorcus*: biology and ecology of sentinel species for human impacts on the rocky shores. In Ray, S. (ed), *Biological resources of water*, IntechOpen, London: 141–167. <https://doi.org/10.5772/intechopen.71614>.
- Tait, J., 1918. IV.—Experiments and observations on Crustacea: part I. Immersion experiments on *Ligia*. *Proceedings of the Royal Society of Edinburgh* 37: 50–58. <https://doi.org/10.1017/s037016460002349x>.
- Taylor, J. D., 1987. Feeding ecology of some common intertidal neogastropods at Djerba, Tunisia. *Vie et Milieu* 37(1): 13–20.
- Thain, V. M., J. F. Thain & J. A. Kitching, 1985. Return of the prosobranch *Gibbula umbilicalis* (Da Costa) to the littoral region after displacement to the shallow sublittoral. *Journal of Molluscan Studies* 51(2): 205–210. <https://doi.org/10.1093/oxfordjournals.mollus.a065902>.
- Underwood, A. J., 1973. Studies on zonation of intertidal prosobranch molluscs in the Plymouth region. *Journal of Animal Ecology* 42(2): 353–372. <https://doi.org/10.2307/3290>.
- Underwood, A. J., 1979. The ecology of intertidal gastropods. *Advances in Marine Biology* 16: 111–210. [https://doi.org/10.1016/S0065-2881\(08\)60293-X](https://doi.org/10.1016/S0065-2881(08)60293-X).
- Watanabe, J. M., 1983. Anti-predator defenses of three kelp forest gastropods: contrasting adaptations of closely-related prey species. *Journal of Experimental Marine Biology and Ecology* 71(3): 257–270. [https://doi.org/10.1016/0022-0981\(83\)90119-3](https://doi.org/10.1016/0022-0981(83)90119-3).
- Watanabe, J. M., 1984a. The influence of recruitment, competition, and benthic predation on spatial distributions of three species of kelp forest gastropods (Trochidae: *Tegula*). *Ecology* 65(3): 920–936. <https://doi.org/10.2307/1938065>.
- Watanabe, J. M., 1984b. Food preference, food quality and diets of three herbivorous gastropods (Trochidae: *Tegula*) in a temperate kelp forest habitat. *Oecologia* 62(1): 47–52. <https://doi.org/10.1007/BF00377371>.
- Wickham, H., M. Averick, J. Bryan, W. Chang, L. D. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry & J. Hester, 2019. Welcome to the Tidyverse. *The Journal of Open Source Software* 4(43): 1686. <https://doi.org/10.21105/joss.01686>.
- Wilke, C. O., 2020. cowplot: streamlined plot theme and plot annotations for ggplot2. R package v1.1.1. <https://CRAN.R-project.org/package=cowplot>
- Yamada, S. B. & E. G. Boulding, 1996. The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. *Journal of Experimental Marine Biology and Ecology* 204(1–2): 59–83. [https://doi.org/10.1016/0022-0981\(96\)02579-8](https://doi.org/10.1016/0022-0981(96)02579-8).
- Zaabar, W., R. Zakhama-Sraieb, F. Charfi-Cheikhrouha & M. S. Achouri, 2018. Composition of a molluscan assemblage associated with macrophytes in Menzel Jemil (Bizerte lagoon, SW Mediterranean Sea). *African Journal of Ecology* 56(3): 537–547. <https://doi.org/10.1111/aje.12490>.
- Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev & G. M. Smith, 2009. *Mixed effects models and extensions in ecology with R*, Springer, New York.