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No recovery: long-term monitoring reveals low and fluctuating populations of the endemic reef-building vermetid snail *Dendropoma anguliferum* on Levantine shores

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Abstract

Dendropoma anguliferum is an endemic reef-building vermetid gastropod of the southeastern Mediterranean that has historically been considered a key ecosystem engineer. In studies from the past decade and a half, this gastropod has been shown to have very low abundance compared to past anecdotal data. A recent study, based on a single survey at a single site, claims that there are signs of recovery of this species on the Israeli coast. Our study analyzed 16 years of seasonal monitoring data from four rocky shore sites to assess long-term population trends along this coast. Results show that *D. anguliferum* maintains a persistently low average cover (0–1.5%) at the seaward edge of the platform, with many temporal fluctuations, indicating no sustained recoveries. A comparative analysis with this recent short-term survey in a region similar to one of the monitoring sites yielded comparable abundance estimates, validating both methodologies for assessing the abundance of this sessile, aggregative, species. In contrast, the co-occurring vermetid, *Vermetus triquetrus,* exhibited much higher cover at some sites and strong fluctuations. This study emphasizes the value of persistent ecological monitoring over one-off snapshot surveys for evaluating species trajectories and developing conservation strategies. These findings also underscore the need for coordinated, continuous, Mediterranean-wide efforts using standardized protocols and advocates for the use of advanced technologies to assess the long-term status of vermetid reefs at the basin scale, especially in the face of increasing pressure due to climate change and other stressors.

Keywords: Vermetid reefs; Mediterranean; Climate change; Sampling.

Introduction

In an age of rapid human-driven ecological change, reliable knowledge of a species' past distribution and abundance is needed to determine its current ecological status. Continuous and consistent ecological monitoring is the most effective tool for determining the ecological status of a species, including its population dynamics and long-term trajectories, which may allow the attribution of possible causes of change (Gonzalez *et al.*, 2023). Only when monitoring data do not exist anecdotal historical records (quantitative, semi-quantitative, or descriptive) of a variety of types (e.g., local ecological knowledge) may be of use, but with much greater uncertainty regarding trends. One coastal region that is a major hotspot for shifts in species abundance and biodiversity, including the collapse of many native species and a rapid influx of invasive species, is the southeastern corner of the Mediterranean Levantine Basin (Rilov, 2016; Rilov *et al.*, 2018; Albano *et al.*, 2021). Unfortunately, many of the collapses of native species apparently occurred before continuous quantitative data were collected on this coast; thus, we have little knowledge of their dynamics (e.g., gradual or abrupt population decline) and can only speculate on their causes. For example, studies have suggested that the combination of ocean warming and competition for food with tropical invaders (mostly rabbitfish), which are abundant in this region, has contributed to the collapse of the purple sea urchin *Paracentrotus lividus* (Yeruham *et al.*, 2015; Yeruham *et al.*, 2020). However, this study was conducted at a time when the urchin populations were already very low; thus, direct attribution can only be speculative.

One of the most ecologically important species that have collapsed over the past several decades on the Levantine coast is the reef-building vermetid gastropod *Dendropoma anguliferum* (Galil, 2013; Rilov, 2016). Seven years of seasonal vermetid reef monitoring on the Israeli Levantine coast (Rilov, 2016; Rilov *et al.*, 2020) and surveys on the Lebanese shoreline (Badreddine *et al.*, 2019) have shown that *D. anguliferum* has very low abundance in the region, deeming it ecologically non-functional as an ecosystem engineer (see, Safriel, 1975). The Israeli monitoring data were compared to (1) the textual descriptions of the species presence from zonation surveys conducted in the 1960s, the data documented a live cover of approximately 3% at one site, Michmoret (Lipkin & Safriel, 1971), (2) descriptions of vermetid reef "microatoll" formation on the Shikmona coast (one of the current monitoring sites) where live *Dendropoma* "are confined to patches cleared of seaweeds by grapsid crabs" (Safriel, 1974), (3) a single quantitative data point taken in the mid-1990s in another one of the current monitoring sites (Habonim, near 40% live cover), and (4) many qualitative observations in other locations that suggested that its cover was quite high in some coastal areas in the 1990s (Rilov, 2016).

A recent study (Barneah *et al.*, 2024) described results from a single site (Habonim) on the Israeli coast using a different method of sampling and claimed that there is evidence of the recovery of the species in recent years. Barneah *et al.* (2024) quantitatively assessed the presence of *D. anguliferum* in December 2020 and February 2021 in three separate surveys of the reef edge (rim), each covering a different section of the coast. In their surveys, Barneah *et al.* (2024) counted and measured the patch size (using photographs) of all live *D. anguliferum* patches along a total reef rim area length of 612,000 cm. Along this coastal stretch, they found 195 live clusters (patches), most of which ranged in size from 5 to 20 cm in diameter, with an average diameter of 8.34 cm, which translates to a cumulative cluster length of 1626.3 cm (~16 m) along the total 6120 m surveyed. They described several longer clusters that occupied stretches of 40–70 cm at the rim and documented a mega-cluster of *D. anguliferum,* which occupied a rectangular belt of 3,900 × 50 cm on the distal part (back reef) of the platform and not on the rim (Fig. 1b).

Importantly, in Rilov *et al.* (2020), 7 years of ecological monitoring results (2009–2016) of the entire vermetid reef community indicated that although the *D. anguliferum* population was very low, it did show fluctuations, with a small ephemeral "recovery" in one of our study sites, Achziv, during 2013, which lasted for almost 3 years (see Fig. 1a in that publication), followed by an almost complete disappearance over the next 2 years. Here, we used 16 years of rocky shore biodiversity monitoring at four sites (including Habonim) from north to south on the Israeli coast to examine the long-term population trends of *D. anguliferum* and another vermetid, *Vermetus triquetrus,* on the Israeli coast. We used these data also to compare with the data from Barneah *et al.* (2024) to demonstrate that this species has not recovered and maintains low reef cover with considerable population fluctuations between zero and little average reef cover over almost two decades.

Methods

Using the dataset collected during the biodiversity surveys on Israeli vermetid reefs (methods described in detail in Rilov *et al.*, 2020) as part of the National Med-

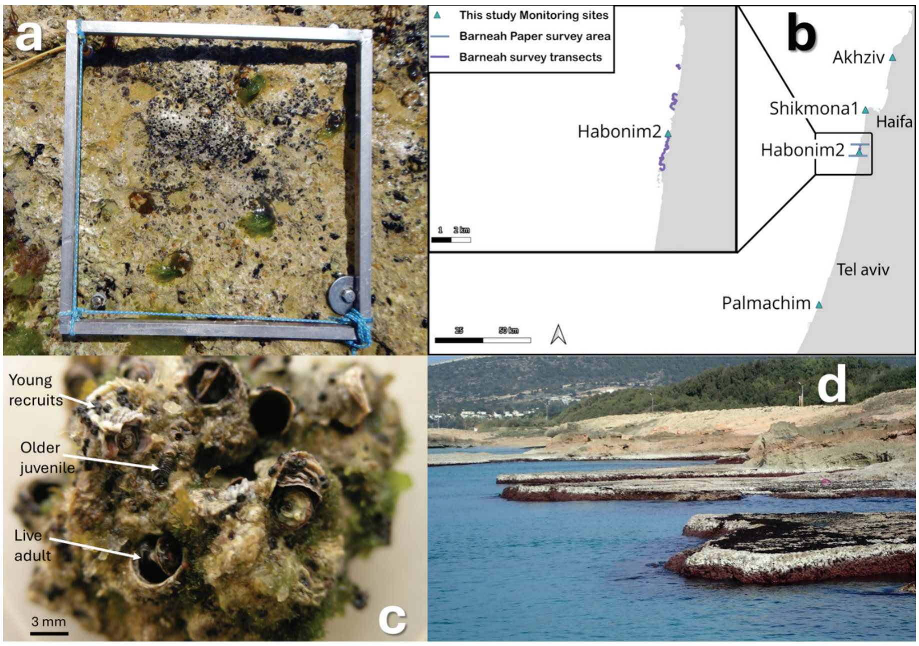

Fig. 1: Study sites, study species patchiness and recruitment, and an example of an extreme event. (a) Thin patch of live *Dendropoma* located near the edge of the monitored platforms in Achziv inside a fixed 25 × 25 cm quadrat. Such patches appeared first in 2013, were marked, and then followed for 3 years, until they disappeared in 2017; photo taken in June 2016. (b) Map showing the National monitoring study sites with an inset of the Habonim region, where Barneah *et al.* (2024) conducted their survey in 2020–2021. Our sites are indicated by green triangles; Barneah's survey stretches are indicated by purple lines. (c) Aggregate of live *Dendropoma* snails collected in 2013 for documentation and examination. Visible are a few adults with their opercula open, dark shells of recruits on the shells of adults, and older juveniles with visible growth rings. (d) Massive bleaching caused by prolonged desiccation event in Achziv in 2023. These events can cause mass mortality on reefs and may be responsible for fluctuations in vermetid populations. Photo credit: Rilov lab.

iterranean Monitoring Program run by the Israel Oceanographic and Limnological Research (IOLR) Institute at four study sites along the coast (Fig. 1b), we calculated the average percentage cover of the two main vermetid snails from the reef surface area on this coast across seasons and years in two zones: the platform edge where the *D. anguliferum* rim is present (Safriel, 1975) and the more sunken platform center, or cuvette (see, Chemello & Silenzi, 2011). Briefly, the surveys used 15 random 50 × 50 cm quadrats along a fixed, marked 50 m transect in each zone to estimate the average cover (algae and sessile invertebrates) or count (mobile invertebrates) of reef organisms. The transect-quadrat (or photoquadrat) method for estimating the count of slow mobile species and the cover of sessile species (mostly invertebrates and macroalgae) is widely used in rocky shore surveys and monitoring (e.g., Lubchenco & Menge, 1978; Schoch *et al.*, 2006; Livore *et al.*, 2021) and should thus apply well to aggregative vermetids.

To address the claim of *D. anguliferum* recovery, as suggested by Barneah *et al.* (2024), we compared our monitoring data with their findings for the same site and period. We compared the estimated percentage cover from their data at the reef edge to our data collected during regular monitoring surveys using the aforementioned method at the platform edge during springs of the same period (2020–2021) and at the same site, Habonim. Although Barneah *et al.* (2024) did not report the percentage cover of vermetids in the clusters, we performed a back-of-the-envelope calculation of the percentage cover of *D. anguliferum* along the entire surveyed coast by dividing the total length of the detected live clusters (1626.3 cm, deduced from the average patch diameter) by the total surveyed reef length (612,000 cm). *We also* calculated their average coverage using the average cluster area (converting the average reported diameter to average area, which comes to 54.6 cm^2 average cluster size), which translates to a 10,652 cm^2 total area of their clusters, and dividing it by a 0.5 m wide belt transect (similar to the width of our monitoring quadrat) with the length of their survey reef edge. The overall area of the belt transect was 30,600,000 cm^2 (612,000 × 50 cm).

Results and Discussion

The 16 years of National Monitoring data that include seasonal sampling in four coastal sites (Achziv, Shikmona, Habonim, and Palmachim; Fig. 1b) across two zones of the platform (edge and center) demonstrate that fluctuations in *D. anguliferum* population size are a consistent and recurring feature, with overall minimal coverage ranging between 0 and 1.5% of the rock surface on average (Fig. 2). The results showed that at the two sites, Shi-

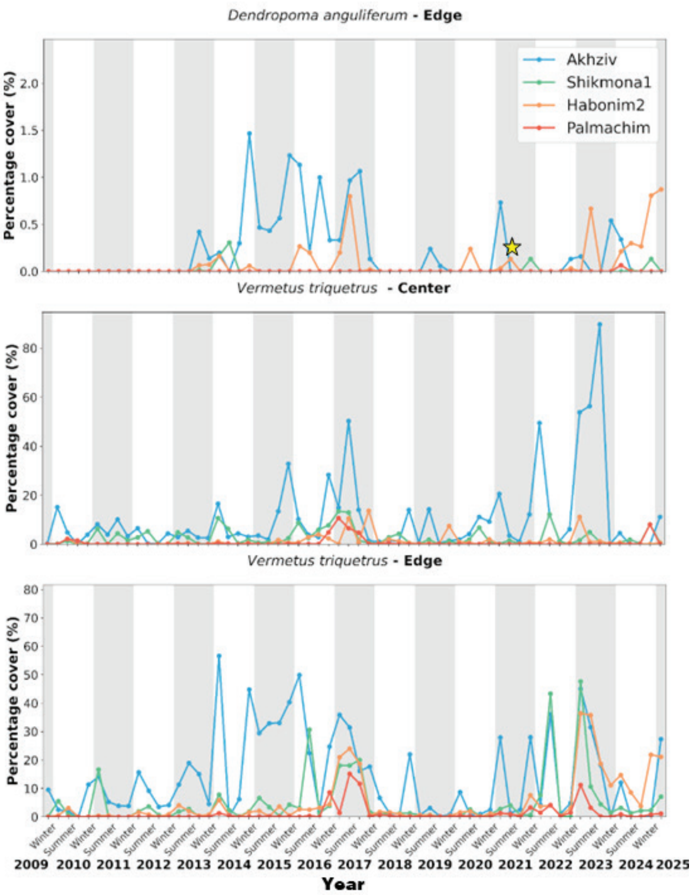

Fig. 2: Seasonal and multiyear average percentage cover of the two vermetid snails at the four monitoring sites along the Israeli coast. *Vermetus* is shown for the platform edge and center transects, whereas *Dendropoma* is shown only for the edge zone, as its presence was null to negligible in the center. The yellow star on the *D. anguliferum* graph indicates the calculated cover value based on the data from Barneah *et al.* (2024); see text.

kmona and Palmachim, the vermetid had no to negligible populations throughout the entire period, and at the other two sites, Achziv and Habonim, there was relatively low cover (never above 1.5% on average) but strong fluctuations, at times occurring simultaneously at both sites. In contrast, the other common reef vermetid, *V. triquetrus*, showed high cover levels (up to 80%) at both the reef edge and center, and strong fluctuations.

At this point, we cannot directly attribute fluctuations in the populations of either species to any specific driver or stressor. To the best of our knowledge, similar long-term monitoring of vermetids has not been conducted (or published) anywhere else in the Mediterranean (or elsewhere) to allow comparison among regions across the basin and to examine whether this dynamic is natural and common or unique to the southeast Levantine region. Some of the minor fluctuations may be the result of a true limitation of the random quadrat sampling method in capturing small patches of a rare species (i.e., if there is one patch along the 50 m marked transect, there is a reasonable chance that it will not be included in one of the 15 sampled quadrats along the transect). Rilov *et al.* (2020) suggested that the general low cover and fluctuations (at least the larger ones) of *D. anguliferum* may be related to increasing stress in environmental conditions, mainly ocean warming, and potentially an increase in the frequency and intensity of prolonged desiccation events (PDEs; Fig. 1d) on this coast, driven by shifts in synoptic systems that cause strong algal bleaching and mass mortality of invertebrates (Zamir *et al.*, 2018). Such shifts in synoptic systems (mostly the Red Sea Trough), and thus the intensification of PDEs, are projected to continue in the region, along with changes in seasonality (Hochman *et al.*, 2018a; 2018b). *D. anguliferum* creates live aggregations (clusters) mostly in elevated areas of rock at the platform edge (with occasional back reef presence, which we documented as well), where the rock is cleared from the macroalgae (Fig. 1a). These rock barrens were likely driven by grazing limpets and crabs (Lipkin & Safriel, 1971; Safriel 1975; Rilov's personal observations). These bare areas are exposed to direct sunlight and can thus experience high temperatures and desiccation levels during PDEs, which may cause high vermetid mortality. A strong desiccation event caused mass mortality of the sibling species *D. cristatum* on the Sicilian coast in the western Mediterranean during the summer of 2022 (Bisanti *et al.*, 2022), suggesting that PDEs may not be a local phenomenon occurring only in the Levant.

The drivers of larger population fluctuations (those that probably do not represent bias driven by sampling of a rare species) are intriguing, especially because the source population for the recruitment of new settlers to form new clusters remains unclear. The genus *Dendropoma* has crawl-away and not planktonic larvae, which means that hatchling juveniles crawl out of egg capsules found in adult tubes, move a very short distance, and permanently cement to the rock or shells of the adults to settle (Calvo *et al.*, 1998, Fig. 1c). Therefore, the source of new patches after a drop to zero cover on the entire platform should be nearby, perhaps from shallow subtidal populations (small live clusters have been observed in the past on the platforms' sublittoral walls at depths of ~0.5–1 m; Fig. 3, Rilov, personal observations in the 1990s). In contrast, *V. triquetrus,* a larger, less aggregative vermetid (which does not have a functional operculum to protect it from desiccation), is often found in dense, bushy macroalgal mats, typically of *Laurencia* and *Acanthophora* species, which can offer moisture and thus possibly protect it from heat and desiccation during PDEs. Studies on vermetid reefs in Sicily have indicated that macroalgal canopies facilitate the recruitment of *D. cristatum*, possibly by ameliorating extreme temperatures during low tides (La Marca *et al.*, 2024). However, the presence of dense macroalgae that cover many *V. triquetrus* aggregations may also explain some of the sharp drops in the coverage of this vermetid documented mainly on the reef's edge (Fig. 2) in the middle of high *Vermetus* coverage periods (for example, the drops to zero in spring 2013 and spring 2020; spring is the season with the highest macroalgal growth on this coast, Rilov *et al.*, 2020). This may possibly be because high macroalgal cover may lead to reduced detection capability of the presence of the species, and thus may represent an underestimation of true Vermetus cover and not sharp decreases in the population.

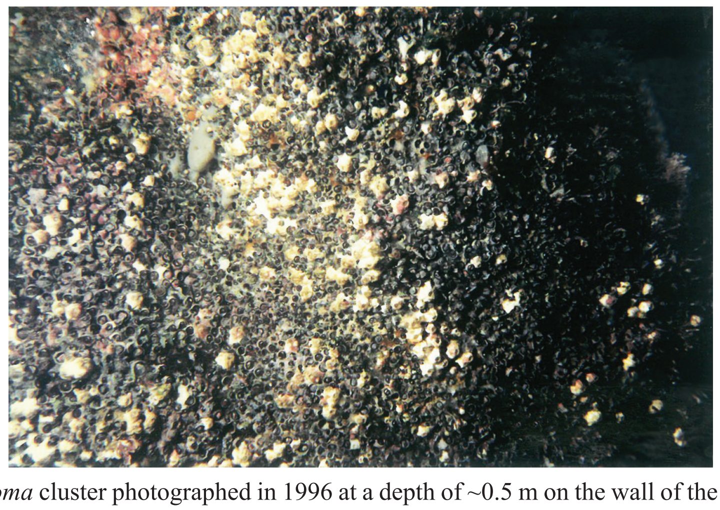

Fig. 3: Dense, live *Dendropoma* cluster photographed in 1996 at a depth of ~0.5 m on the wall of the Habonim platform below the site where our monitoring is conducted today. Photo credit: Gil Rilov.

The calculated percentage cover of live *D. anguliferum* along the entire reef edge in the Barneah *et al.* (2024) survey area, based on the patch diameter and total survey length, was ~0.27% ([{195×8.34}/612,000] × 100), as shown in the monitoring data in Fig. 2. The calculation based on patch area and a survey belt of 0.5 m in width of the edge (to compare with our quadrat size) resulted in a value an order of magnitude lower: 0.03% ([{195 × 54.6}/30,600,000] × 100). In our monitoring surveys for the same period (Spring 2020 to Spring 2021) at the same site, the live cover of vermetids at the platform edge (where the rim is) varied between 0 and 0.24% (Fig. 2). Considering only our winter 2021 data (surveyed on February 28), we observed a *D. anguliferum* cover of 0.033%, which was similar to the cover calculated from the Barneah et al (2024) survey (conducted only in the winter) data based on the cluster area. Overall, this comparison demonstrated remarkably similar and low values, indicating that both methods are valid for assessing vermetid abundance on reefs.

Nonetheless, the method used by Barneah *et al.* (2024) focuses only on *D. anguliferum,* whereas our method, which uses systematic sampling with quadrats (the stratified random method that is widely used on rocky shores, see, Murray *et al.*, 2006), samples the entire community, which provides broader insights into rocky shore biodiversity and more inferences on processes and patterns at the community level. We calculated that in 11% of our surveys over the past 16 years in Habonim, a cover of *D. anguliferum* within the range of 0.2–0.3% was observed, which is similar to that observed using both methods in 2021. In contrast, a cover of 0–0.1% was observed in 80% of the observations. Barneah *et al.* (2024) stated that routine comprehensive surveys aimed at the continuous monitoring of *D. anguliferum* have not been conducted in Israel in recent years. This is a puzzling statement. The vermetid coverage dynamics in the four study sites shown here have been reported for more than a decade as part of the ongoing biodiversity monitoring of vermetid reefs in the Mediterranean National Monitoring Report annually published by the IOLR (see, for example, the latest report, Rahav *et al.*, 2023), which should be known to the authors. We do see scientific value in conducting patch counts and sizing surveys, such as those conducted by Barneah *et al.* (2024). This is because cluster presence (count per reef length) and average cluster size, two important metrics for patchy, aggregative, organisms such as vermetids, can be monitored using this method, which is interesting and will be considered in our future monitoring studies.

Our monitoring data (Fig. 2) indicate that the coverage of *D. anguliferum* on the Habonim reef edge has gradually increased in recent years and approached 0.9% in the spring of 2025; unfortunately, at this point in time, we cannot suggest that this is a sign of long-term recovery for this species. This is because we observed in past years even higher cover values (between 1 and 1.5%) in Achziv between 2015 and 2018, which were followed by a sharp drop and then null or low cover in the following years. In addition, many other shores that we have surveyed for many years showed no *D. anguliferum* cover at all, another indicator suggesting that this species is not on a recovery trajectory. Continuous monitoring using persistence methods rather than snapshot surveys at a single site is the preferred tool for determining the status of a species and its population trajectory. Regarding survey or monitoring method, clearly, each rocky shore method (e.g., single contact points on a grid, line transects, quadrats, or photoquadrats) has its benefits and limitations (Miller & Ambrose, 2000; Murray *et al.*, 2006; Livore *et al.*, 2021) and should be fit for the purpose.

In conclusion, the future of *D. anguliferum* on the Levantine coast and that of other reef-building vermetids of the same genus (Calvo *et al.*, 2009) on Mediterranean coasts where vermetid reefs exist (Chemello & Silenzi, 2011) is uncertain. Their ecological status at local and basin scales may be difficult to determine in the future because the study of unique and endangered vermetid reef habitats has been neglected in most regions (Picone *et al.*, 2022). Therefore, we urge for the formation of a collaborative network of vermetid reef scientists to conduct synchronized monitoring using harmonized methods across institutions. Beyond conventional ecological monitoring methods, monitoring should leverage modern, rapidly developing technologies. For example, high-resolution laser mapping, either terrestrial (Rilov *et al.*, 2021) or airborne LiDAR, or 3D drone mapping of rocky shore habitats (Barbosa *et al.*, 2022; Barbosa *et al.*, 2025) for both topography and species cover, including hyperspectral cameras (Diruit *et al.*, 2024), can be used to monitor habitat integrity and species distribution and the impacts of extreme events on a biogeographical scale (e.g., the extent of bleaching during PDEs). This should be accompanied by continuous measurements of physicochemical conditions (temperature, humidity, water quality, etc.) at the local scale to allow for improved environmental attribution of observed ecological changes. The importance of such measurements is underlined by the fact that satellite-driven remote-sensing data often underestimate absolute values in coastal regions, especially at the extremes (which may be critical for the survival of a species), as previously demonstrated on the Israeli as well as other coasts (Rilov, 2016; Meneghesso *et al.*, 2020; Knobler *et al.*, 2025).

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