



# Bad neighbors? Niche overlap and asymmetric competition between native and Lessepsian limpets in the Eastern Mediterranean rocky intertidal

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## ARTICLE INFO

### Keywords:

Asymmetric competition  
Lessepsian invasion  
Intertidal hard substrates  
*Patella caerulea*  
*Cellana rota*  
Eastern Mediterranean Sea

## ABSTRACT

The Eastern Mediterranean Sea hosts more non-indigenous species than any other marine region, yet their impacts on the native biota remain poorly understood. Focusing on mollusks from the Israeli rocky intertidal, we explored the hypothesis that this abiotically harsh habitat supports a limited trait diversity, and thus may promote niche overlap and competition between native and non-indigenous species. Indeed, native and non-indigenous assemblage components often had a highly similar trait composition, caused by functionally similar native (*Patella caerulea*) and non-indigenous (*Cellana rota*) limpets. Body size of *P. caerulea* decreased with increasing *C. rota* prevalence, but not vice versa, indicating potential asymmetric competition. Although both species have coexisted in Israel for >15 years, a rapid ‘replacement’ of native limpets by *C. rota* has been reported for a thermally polluted site, suggesting that competition and regionally rapid climate-related seawater warming might interact to progressively erode native limpet performance along the Israeli coast.

## 1. Introduction

Biological invasions are considered one of the most serious threats to native biodiversity (e.g. Molnar et al., 2008; IPBES, 2019). Although human-mediated species translocations, both intentionally and inadvertently, have occurred for centuries to millennia (Ojaveer et al., 2018), the rate of introductions has drastically increased in recent decades due to the globalization of anthropic activities (Seebens et al., 2017), leaving hardly – if any – biogeographic region unaffected (McCarthy et al., 2019).

Among marine regions, the Mediterranean Sea hosts more non-indigenous species (NIS) than any other sea owing to its direct connection to the Red Sea via the Suez Canal (Rilov and Galil, 2009; Rilov et al., 2019). Since the opening of this canal in 1869, hundreds of Indo-Pacific species have successfully established populations in the warm Eastern Mediterranean (Galil, 2008), a process termed the ‘Lessepsian invasion’. In recent years, both the diversity and dominance of Lessepsian NIS have massively increased in local shallow-water habitats (e.g. Rilov and Galil, 2009; Edelist et al., 2012; Rilov et al., 2018; Galil et al., 2020). However, the ecological consequences of the invasion remain little understood, despite mounting evidence that they are significant (e.g. Rilov et al., 2019; Peleg et al., 2020; Yeruham et al., 2020).

Well-known examples of high-impact Lessepsian NIS are the rabbit fishes *Siganus luridus* (Rüppell, 1829) and *S. rivulatus* Forsskål & Niebuhr, 1775, which are notorious for overgrazing macroalgae on shallow-water hard substrates, leaving structurally and taxonomically impoverished turf barrens behind (Sala et al., 2011; Vergés et al., 2014); or the invasive Indo-Pacific mussel *Brachidontes pharaonis* (P. Fischer, 1870), which has colonized large areas of intertidal platforms that used to be devoid of mussel beds (Rilov et al., 2004) and is known to affect benthic community composition and its spatial variability (Bonnici et al., 2012).

Whereas the direct impacts of such non-indigenous ecosystem engineers are often obvious (e.g. Fishelson, 2000; Sala et al., 2011; Bonnici et al., 2012), competitive interactions between Lessepsian and native species remain less discernible, although they have been suspected to be a major driver of the massive declines of many formerly common native shallow-water species in the region (e.g. Mienis, 2003; Galil, 2007a; Edelist et al., 2012). Indeed, negative effects of Lessepsian NIS on the fitness of native species have been demonstrated for intertidal mussels (Safriel and Sasson-Frostig, 1988) and macroalgal herbivores (Lessepsian rabbit fishes and native sea urchins; Yeruham et al., 2020). However, recent trait-based studies considering many species suggested that in the subtidal realm, Lessepsian NIS tend to occupy niches distinct from native species, concluding that, overall, there is limited potential for

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<https://doi.org/10.1016/j.marpolbul.2021.112703>

Received 2 March 2021; Received in revised form 29 June 2021; Accepted 3 July 2021

Available online 27 July 2021

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strong resource competition (Azzurro et al., 2014; Givan et al., 2017; Buba and Belmaker, 2019). These findings are in line with a large body of ecological theory suggesting that niche complementarity and the exploitation of ‘resource opportunities’ by NIS with suitable traits are key determinants of invasion success (Darwin, 1859; MacArthur and Levins, 1967; Shea and Chesson, 2002).

A different situation, however, may occur if NIS establish in habitats where harsh abiotic conditions select for a limited set of trait combinations (Menge and Sutherland, 1987; Valdivia et al., 2017), such as intertidal hard substrates with simple surface reliefs, including those associated with coastal infrastructure (Firth et al., 2016; Aguilera et al., 2019a; Epstein et al., 2019). Such habitats are typically characterized by assemblages with a lower taxonomic and functional richness than those from structurally more complex intertidal substrates, or abiotically more benign subtidal environments (Sanders, 1968; Safriel and Lipkin, 1975; Saier, 2002; Bulleri and Chapman, 2004; Firth et al., 2016; Valdivia et al., 2017), and therefore might host a greater potential for niche overlap even among dominant species (e.g. Mason et al., 2008). So far, however, the degree of trait similarity between native and Lessepsian components of intertidal assemblages has received little attention, despite its value for providing insights into patterns of resource use and the potential for competition in this ecologically important transitional habitat, apart from work on a few selected species (reviewed by Safriel, 2014).

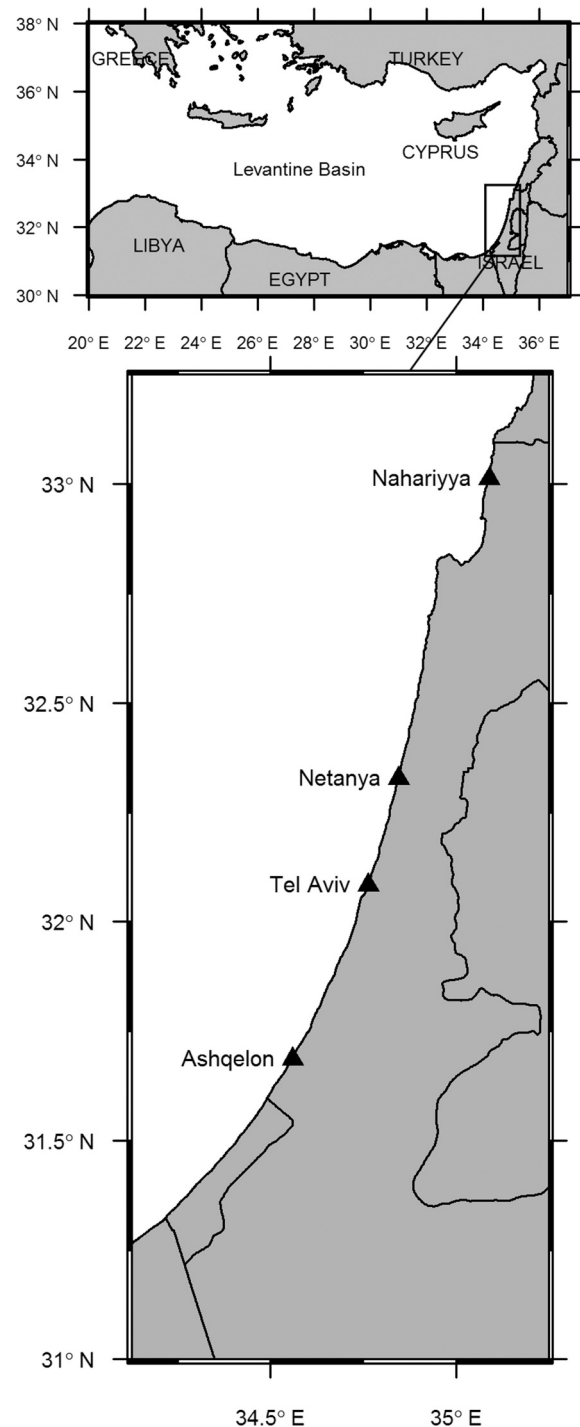
As on many rocky shores around the world, limpets constitute an ecologically important component of the intertidal fauna on the coast of Israel, most notably the abundant and widespread Mediterranean limpet *Patella caerulea* Linnaeus, 1758 (Lipkin and Safriel, 1971; Barash and Danin, 1992; Fishelson, 2000). In 1961, the Indo-Pacific nacellid limpet *Cellana rota* (Gmelin, 1791) was first recorded in the Israeli Mediterranean (Christiaens, 1967), and by the early 2000s had successfully become established on hard substrates along the country's entire coastline (Fishelson, 2000; Mienis, 2000; Fishelson et al., 2002; Mienis, 2002, 2003; Mienis and Ben-David-Zaslow, 2004; Atad, 2005). Because of its ecological similarity and sympatric occurrence, *C. rota* may constitute a major competitor of *P. caerulea*, raising concerns that it could eventually displace native limpets (Mienis, 2003; Atad, 2005). However, almost two decades later, information on the current status of *P. caerulea* and the impacts that *C. rota* might have on its populations is still lacking.

In this study, we assess the potential for competitive interactions between native and Lessepsian rocky intertidal mollusks on the Israeli Mediterranean coast. Using a complementary approach, we consider two distinct levels of biological organization: first, focusing on assemblage-level attributes and utilizing methods from biological traits analysis, we test the hypothesis that native and non-indigenous assemblage components from low-complexity habitats share similar trait distributions, indicating overlap in niches and resource use. Second, we seek empirical evidence for competitive interactions among a co-dominant native and non-indigenous species ‘pair’ with similar traits: the patelloidean limpets *P. caerulea* and *C. rota*. Focusing on body size distributions, we investigate the hypothesis that native limpet size is negatively related to the prevalence of *C. rota* in local assemblages, a response commonly observed in competing limpets (e.g. Branch, 1975, 1976, 1981; Dunmore and Schiel, 2003).

## 2. Materials and methods

### 2.1. Study area

The Israeli Mediterranean coastline forms a gently curved arc extending approximately 200 km in SW-NE direction (Fig. 1). Its southern part is characterized by sandy beaches, with coastal infrastructure – such as marinas, groins, or detached breakwaters made from limestone or dolomite boulders – often constituting the only intertidal hard substrates (Emery and Neev, 1960; Nir and Elimelech, 1990).



**Fig. 1.** Sampling locations along the Israeli Mediterranean coast, Eastern Mediterranean Sea. At the three southernmost locations, we scraped boulders of breakwaters, whereas at Nahariyya, flat beachrock was sampled within the local marina.

Towards the north, rocky shores become increasingly widespread and are a dominant feature in the northernmost part of the country (Almagor and Hall, 1984; Rilov et al., 2018).

### 2.2. Field sampling and sample treatment

Hard-substrate intertidal molluscan assemblages were sampled in spring and autumn 2018 at four locations covering the entire length of Israeli Mediterranean coastline (Fig. 1, Table S1 in Supplement 1). At

Ashqelon, Tel Aviv and Netanya, we sampled on the coastward (sheltered) side of detached breakwaters made of boulders with rather simple surfaces (Fig. 2a). At the northernmost site, Nahariyya, we collected on slabs of beachrock within the small local marina; like the quarried breakwater boulders, these slabs had flat and smooth surfaces, and were sheltered from heavy surf by the marina wall extending to approximately 50 m offshore (Fig. 2b). The decision to focus on assemblages from low-complexity substrates followed several scientific and practical considerations: (i) man-made boulders are the only available intertidal rocks in most of southern Israel; (ii) substrates with simple surface reliefs can be effectively sampled by scraping, reducing the chance of systematically overlooking small and/or cryptic species; (iii) low-complexity habitats generally host fewer species than topographically more complex structures (e.g. Firth et al., 2016); therefore, any effects of competition by NIS on native species may be more easily discernible than in taxonomically more diverse assemblages.

During the spring and autumn campaigns, at each site, three randomly selected 1-m<sup>2</sup> quadrats were carefully scraped with a spatula and samples preserved in 96% ethanol. Due to logistic constraints, Nahariyya was sampled only in autumn 2018. In the lab, all molluscan individuals were picked from the collected material, identified to species level, and counted. This study was based on the resulting 2169 specimens representing five native and three non-indigenous species (Table 1 and Supplement 2).

## 2.3. Datasets

### 2.3.1. Trait dataset

Trait-based approaches are a powerful means to describe species' ecological niches and the functioning of entire assemblages (Bremner et al., 2006; McGill et al., 2006). In this study, we used a set of six biological traits to characterize molluscan taxa: maximum adult body size (SI), feeding habit (FH), environmental position (EP), substrate affinity (SA), host-association (HO), and attachment mode (AT). These traits capture several important aspects of molluscan ecology and are related to strategies of resource use and competitive performance; furthermore, reliable information is available for the species covered in this study. Modalities (i.e., the different categories of a trait) were defined to fully cover the functional diversity of the more than 360 species of intertidal and shallow-water benthic mollusks recorded in our

2016–2018 field surveys in Israel (see Albano et al., 2021); thus, any systematic absence of trait modalities among intertidal mollusks may be indicative of environmental constraints potentially limiting trait diversity in low-complexity intertidal vs. higher-complexity and/or more benign subtidal environments. Details on the ecological relevance of the selected traits and modality definitions are provided in Table S2. Trait information was compiled from the published literature (see Supplement 3 for a reference list), augmented by observations on our specimens. As species may show affinities to more than one modality per trait (and often to a different degree), we used fuzzy-coding (Chevenet et al., 1994) to assemble the species × traits matrix. Species' affinity to modalities was described by the widely used scoring system taking values from 0 to 3, where '0' corresponds to 'no affinity', '1' to 'low affinity', '2' to 'high affinity' and '3' to 'exclusive affinity' (Bremner et al., 2003; Degen et al., 2018). If two or more modalities are expressed to a similar degree, each was scored with '2' by convention. After completion of the trait matrix, the raw modality scores within each trait were standardized to proportions totaling one (cf. Darr et al., 2014; Supplement 4).

### 2.3.2. Limpet size dataset

Competition among limpets often results in reduced growth and body size (e.g. Lewis and Bowman, 1975; Branch, 1976; Lasiak and White, 1993; Knox, 2001; Dunmore and Schiel, 2003); therefore, we focused on systematic patterns in size distributions of *Cellana rota* and *Patella caerulea*, considering both inter- and intraspecific effects (see Section 2.4.2). Limpet shell length (anterior-posterior dimension) and width (lateral shell dimension) were measured using a digital caliper (accuracy: 0.02 mm), and body size subsequently calculated as the geometric mean of these two dimensions. The geometric mean is commonly used in molluscan studies as it encapsulates more information on individuals than any single dimension, and because it correlates well with biomass (Roy et al., 2000; Kosnik et al., 2006). Individuals with damaged shell edges (due to scraping) could not be reliably measured and were therefore excluded from the size dataset; details on absolute sample sizes and numbers of measured individuals are provided in Table 2.



Fig. 2. Examples of sampled intertidal rocky substrates. Breakwater at Ashqelon, southern Israel, consisting of quarried boulders with a rather simple surface morphology (a). Slabs of beachrock at Nahariyya, northern Israel (b). The inset shows a close-up view of native limpets (*Patella caerulea*) in situ.

**Table 1**

Native and non-indigenous molluscan species sampled on intertidal hard substrates at four locations along the Israeli Mediterranean coast. The presence of a species at the different locations is indicated by a '+'. Detailed data on assemblage composition are provided in Supplement 2.

Class	Family	Species	Native?	Ashqelon	Tel Aviv	Netanya	Nahariyya
Gastropoda	Patellidae	<i>Patella caerulea</i> Linnaeus, 1758	Yes	+	+	+	+
Gastropoda	Nacellidae	<i>Cellana rota</i> (Gmelin, 1791)	No	+	+	+	
Gastropoda	Trochidae	<i>Phorcus turbinatus</i> (Born, 1778)	Yes				+
Gastropoda	Littorinidae	<i>Echinolittorina punctata</i> (Gmelin, 1791)	Yes	+	+	+	
Gastropoda	Littorinidae	<i>Melarhaphe neritoides</i> (Linnaeus, 1758)	Yes	+		+	+
Gastropoda	Siphonariidae	<i>Siphonaria crenata</i> Blainville, 1827	No		+	+	+
Bivalvia	Mytilidae	<i>Brachidontes pharaonis</i> (P. Fischer, 1870)	No	+	+	+	
Bivalvia	Mytilidae	<i>Musculus costulatus</i> (Risso, 1826)	Yes		+	+	

**Table 2**

Densities of native (*Patella caerulea*) and non-indigenous (*Cellana rota*) limpets on intertidal hard substrates on the Israeli Mediterranean coast, and proportional abundances of *C. rota* in the limpet assemblages (i.e., relative to the total abundance of the two limpet species). Numbers in parentheses correspond to the number of individuals with intact shells for which body size could be measured. N/A: not available.

Location	Season	Replicate	<i>Patella caerulea</i> [individuals m <sup>-2</sup> ] (measured)	<i>Cellana rota</i> [individuals m <sup>-2</sup> ] (measured)	Proportion of <i>Cellana rota</i>		
					Replicate-level	Season average	Annual average
Ashqelon	Spring	1	38 (38)	55 (54)	0.59	0.69	0.72
		2	29 (28)	76 (72)	0.72		
		3	24 (18)	70 (66)	0.74		
	Autumn	1	51 (37)	72 (69)	0.59	0.76	
		2	0 (0)	10 (10)	1		
		3	46 (41)	99 (95)	0.68		
Tel Aviv	Spring	1	29 (25)	1 (1)	0.03	0.06	0.03
		2	27 (21)	3 (3)	0.10		
		3	34 (25)	2 (2)	0.06		
	Autumn	1	24 (23)	0 (0)	0	0	
		2	19 (13)	0 (0)	0		
		3	45 (40)	0 (0)	0		
Netanya	Spring	1	24 (18)	26 (20)	0.52	0.50	0.26
		2	29 (24)	58 (58)	0.67		
		3	19 (10)	9 (6)	0.32		
	Autumn	1	81 (72)	3 (3)	0.04	0.02	
		2	56 (48)	2 (2)	0.03		
		3	56 (42)	0 (0)	0.00		
Nahariyya	Autumn	1	151 (149)	0 (0)	0	0	N/A
		2	317 (304)	0 (0)	0		
		3	84 (84)	0 (0)	0		
Total			1183 (1060)	486 (461)			

## 2.4. Data analysis

### 2.4.1. Trait composition of native vs. non-indigenous assemblage components

Multivariate trait profiles of native and non-indigenous assemblage components were ordinated by fuzzy correspondence analysis (FCA; Chevenet et al., 1994). To upscale species-specific trait information to the level of assemblage components (i.e., creating a modalities × assemblage component table), we weighted species' standardized modality scores (modalities × species table) by their relative abundances (species relative abundance × assemblage component table) using matrix multiplication (Oug et al., 2012). To take into account the fact that resource consumption and competition are density-dependent processes, we used untransformed relative abundances for this weighting step. Assemblage component samples consisting of less than five individuals (applied to five non-indigenous samples) were excluded from the analysis (Table S3). We further excluded trait modalities not represented in intertidal assemblages, as well as 'non-distinguishing' traits (Table S3). The latter are traits characterized by the exclusive affinity of all assemblage components to a single modality; therefore, while being important for the ecological characterization of assemblage components and indicative of potential environmentally driven trait selection, these traits do not contribute information relevant for the arrangement of

samples in ordination space.

Correlation ratios were used to assess the relevance of the different traits for the FCA axes (Chevenet et al., 1994), and thus identify those traits contributing most to the separation of native and non-indigenous components. To formally test whether native and non-indigenous assemblage components differ in trait composition, we conducted PERMANOVA (Anderson, 2001) on their scores for the first three FCA axes, using Euclidean distances and 9999 permutations. Prior to PERMANOVA, homogeneity of multivariate dispersions was checked and confirmed using PERMDISP (Anderson, 2006; 9999 permutations,  $F = 2.96$ ,  $df = 1$ ,  $p = 0.09$ ). Finally, we assessed the contribution of limpets to the overall trait (dis)similarity between native vs. non-indigenous assemblage components: considering all unique pairwise combinations of native and non-indigenous trait profiles, we modelled the relationship between their Euclidean distance in 3D-FCA space and the average proportion of *C. rota* and *P. caerulea* in the sample pairs by means of quantile regression (see Section 2.4.2). All statistical analyses were performed in the R programming language (v. 3.5.2; R Core Team, 2018). The 'ade4' (v. 1.7-13; Dray and Dufour, 2007) and 'vegan' (v. 2.5-4; Oksanen et al., 2019) packages were used to conduct FCA and PERMDISP/PERMANOVA, respectively.

#### 2.4.2. Limpet size analysis

To explore whether *C. rota* may adversely affect *P. caerulea* under field conditions, we tested for negative relationships between its body size and the prevalence of *C. rota* in limpet assemblages (i.e., considering only *P. caerulea* and *C. rota*). As competition-related effects on size distributions might become most evident near their upper boundaries, and because *P. caerulea* is a species with a multi-annual lifespan (Marra et al., 2018), we jointly considered spring and autumn datasets in statistical analyses. This approach not only increases sample size, but also reduces potential biases related to short-term demographic events. To judge whether the single-season dataset from Nahariyya is comparable to the other locations, we first assessed whether Israeli populations of *P. caerulea* – the only limpet species found at Nahariyya – exhibit seasonal differences in median body size. As (multimodal) size distributions tend to violate assumptions of traditional statistical tests, this was done by bootstrapping: after pooling seasonal datasets, we randomly sampled, with replacement, the same number of individuals as in the initial datasets and calculated the difference in median size; by repeating this procedure 10,000 times, we generated a resampling distribution of seasonal size differences. Finally, we judged the statistical significance of the empirically observed value by calculating two-tailed p-values as the proportion of simulations that yielded as large or greater absolute differences in median size. We found no significant seasonal differences at two out of three sites (Tel Aviv:  $p = 0.56$ ; Netanya:  $p = 0.54$ ), with the absolute difference at the only significant site (Ashqelon;  $|\Delta_{\text{median size}}| = 3.3 \text{ mm}$ ,  $p = 0.02$ ) being much smaller than the effect size (i.e., the size differences observed among locations differing in *C. rota* prevalence). Therefore, it was deemed appropriate to jointly consider the Nahariyya dataset with the other locations.

Size data were analyzed using two complementary approaches. First, focusing on seasonally pooled data, we used bootstrapping (as described above) to assess whether median and 95th percentile body size of native limpets significantly differed among locations with varying proportions of *C. rota*. While the median is a robust measure of central tendency, the 95th percentile is a useful proxy for maximum size but much less sample size-dependent (Fuksi et al., 2018). Proportions, rather than densities, of *C. rota* were used as predictor because (i) they reflect limpet assemblage composition and hence relative patterns of resource occupation by *P. caerulea* and *C. rota*; and (ii) because the mean total densities of these two limpets at our sampling locations (range: 30.7–184.0 individuals  $\text{m}^{-2}$ , mean across sites: 79.5 individuals  $\text{m}^{-2}$ ) were high enough to reasonably assume overlap of feeding ranges (for *Patella rustica* Linnaeus, 1758, another Mediterranean limpet of similar size as *P. caerulea* and *C. rota*, average activity area size was determined to be 399  $\text{cm}^2$ , i.e. c. 1/25  $\text{m}^2$ , by Della Santina (1994)). Second, we used quantile regression (Koenker and Bassett, 1978; Koenker and Machado, 1999) to model the relationship between *P. caerulea* body size (median and 95th percentile) and the proportion of *C. rota* in limpet assemblages based on replicate-level data; the same analysis was performed considering *C. rota* size as a function of native limpet proportions to assess any reciprocal effects. Quantile regression is a powerful analytical tool that allows exploring any part of a response variable's distribution, and detecting biologically relevant relationships even in datasets where other influencing factors have not been measured or explicitly accounted for, a common issue in ecology (Cade and Noon, 2003). Finally, to get a more complete picture of potential competition effects, we also tested for intraspecific interactions in *P. caerulea* and *C. rota*, using an analogous approach as for the study of interspecific effects. Instead of considering species' proportions in limpet assemblages, however, we used densities (individuals  $\text{m}^{-2}$ ) as predictor to model the conditional quantiles of body size in intraspecific models, thus directly considering the number of conspecific individuals competing for the available resources. Quantile regression and associated significance tests were performed using the 'quantreg' R-package (v. 5.38; Koenker, 2018).

### 3. Results

#### 3.1. Trait composition of native vs. non-indigenous assemblage components

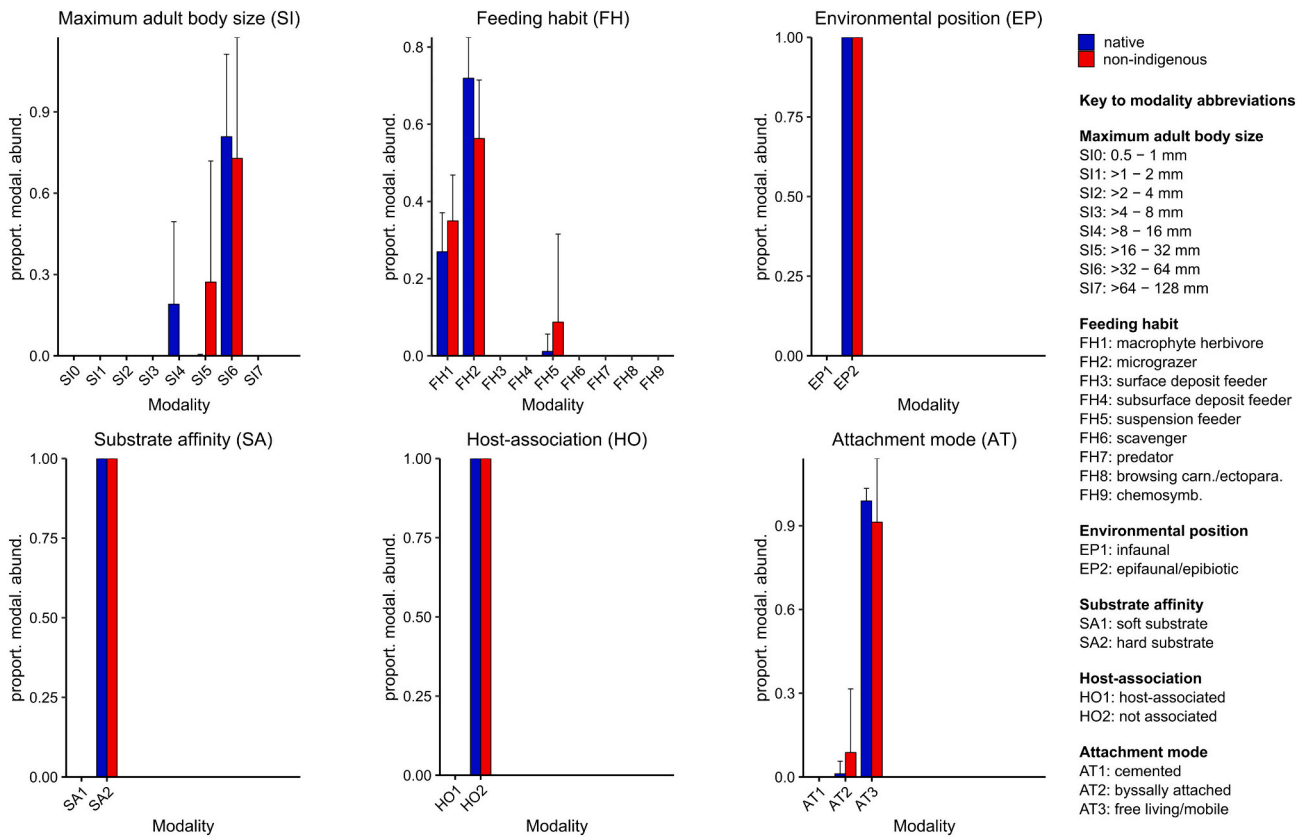
Trait diversity was limited in our intertidal samples, and only 11 out of 26 modalities in our scoring system for Israeli mollusks (42%) were actually represented in the studied assemblages: all eight species in our samples (Table 1) were exclusively epifaunal hard substrate dwellers without host association and, consequently, only differed with respect to 'maximum adult body size' (SI), 'feeding habit' (FH) and 'attachment mode' (AT) (Fig. 3, Supplement 4).

Abundance-weighted trait profiles of native and non-indigenous assemblage components partially separated along FCA axis 2 (explaining 34.1% of variance; Fig. 4) and, overall, occupied significantly different positions in ordination space (PERMANOVA, pseudo-F = 4.47,  $df = 1$ ,  $p < 0.001$ ,  $R^2 = 0.12$ ). 'Body size' had the highest correlation ratio for axis 2 (0.72), and thus was most relevant for this separation (Table 3). Indeed, two modalities of this trait – size classes SI4 (8–16 mm) and SI5 (16–32 mm) – were (almost) exclusively represented by native and non-indigenous assemblage components, respectively, whereas all other modalities, of all traits, were represented within both types of assemblage components (Fig. 3).

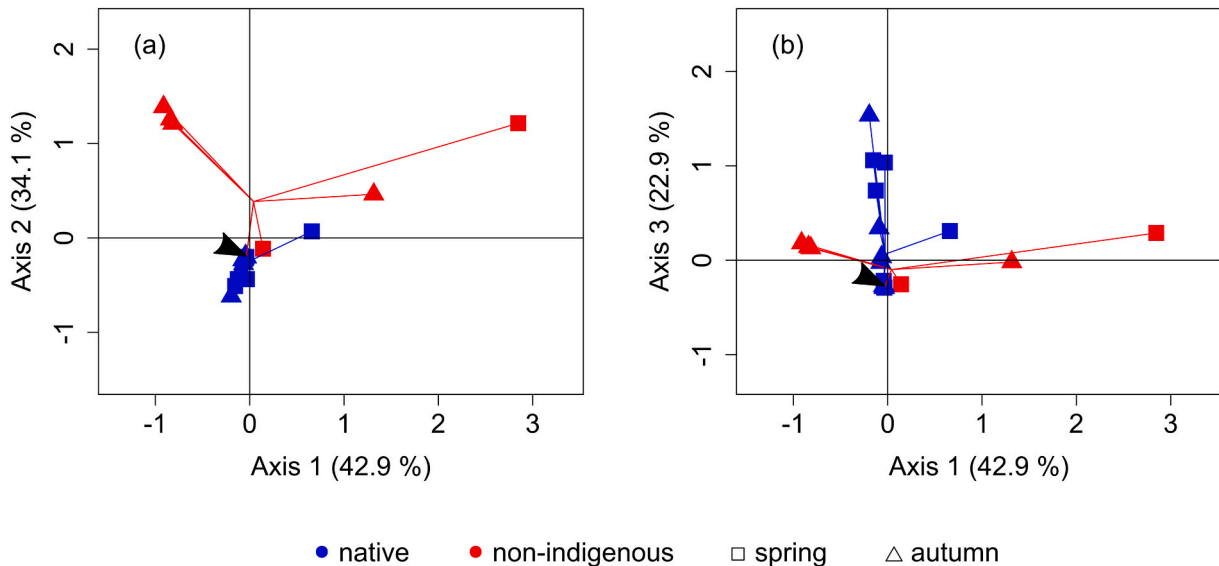
However, only 12% of the total variance in the PERMANOVA analysis was explained by the factor 'native – non-indigenous'. Native and non-indigenous trait profiles strongly overlapped along axis 1 (explaining 42.9% of variance, with traits 'feeding habit' and 'attachment mode' being most relevant, see Table 3), and to a lesser degree also along axis 3 (22.9% of variance, mostly related to 'body size'). Notably, 17 – seven non-indigenous and ten native trait profiles – out of 35 samples (i.e., 49%) had identical FCA scores in the global analysis (Fig. 4, black arrowheads). Within individual localities, native – non-indigenous overlap occurred at Ashqelon and Netanya, concerning 11 (four native, seven non-indigenous) trait profiles; five of these (two native, three non-indigenous ones, all from Ashqelon) also overlapped in season (spring), and four (two native, two non-indigenous ones) even represented corresponding native and non-indigenous assemblage components collected within individual 1- $\text{m}^2$  sample quadrats (Table S4). In all cases, native vs. non-indigenous trait overlap concerned assemblage components exclusively consisting of either the native *Patella caerulea* or the non-indigenous *Cellana rota*, two species with identical trait scores (Supplement 4). Patelloidean limpets were numerically dominant at all sampling locations: together, *P. caerulea* and *C. rota* contributed 68.7–94.2% of the total number of individuals in the assemblages (Fig. 5); accordingly, Euclidean distances between pairs of native and non-indigenous samples in 3D-FCA space were significantly negatively related to the average proportions of limpets (i.e., of *P. caerulea* and *C. rota*; quantile regression for the median:  $y = -3.75x + 3.75$ ,  $p < 0.001$ ,  $R^1 = 0.73$ , Fig. 6), highlighting their role as major determinants of trait similarity between native and non-indigenous assemblage components. In line with this finding, all except one of the well-separated non-indigenous profiles (i.e., those with positive scores on FCA axis 2) had low proportions of *C. rota* (0–20%; mean  $\pm$  SD:  $7.9 \pm 8.4\%$ ) and consisted predominantly of either the small pulmonate false limpet *Siphonaria crenata* Blainville, 1827 or the mussel *Brachidontes pharaonis* (P. Fischer, 1870).

#### 3.2. Limpet body size patterns

We measured 1060 and 461 individuals of *P. caerulea* and *C. rota*, respectively; their size distributions, by location and season, are shown in Figs. S1–S2. Median sizes of *P. caerulea* (Table 4) from Ashqelon and Netanya, the locations with the greatest proportion of *C. rota* in limpet assemblages (Table 2), were significantly smaller than those from Tel Aviv and Nahariyya (Tables 4–5; all  $p < 0.001$ ) where *C. rota* was rare or entirely absent. In contrast, no significant differences were found for



**Fig. 3.** Proportional abundances of trait modalities (proport. modal. abund., mean and SD) in native (n = 21) and non-indigenous (n = 14) components of intertidal molluscan assemblages from the Israeli Mediterranean coast, calculated as matrix products of standardized modality scores (modalities × species table) and species relative abundances (species relative abundance × assemblage component table); assemblage components consisting of less than five individuals have been excluded. Note that for the traits ‘environmental position’, ‘substrate affinity’ and ‘host-association’, all native and non-indigenous assemblage components showed exclusive affinity to a single modality each. browsing carn./ectopara.: browsing carnivore/ectoparasite; chemosymb.: chemosymbiont-bearing species.



**Fig. 4.** Fuzzy correspondence analysis of trait profiles of native (n = 21) and non-indigenous (n = 14) components of rocky intertidal molluscan assemblages from the Israeli Mediterranean coast – representations of axis 1 vs. 2 (a) and axis 1 vs. 3 (b). Lines connect trait profiles to their group centroid. Note that although PERMANOVA (pseudo-F = 4.47, df = 1, R<sup>2</sup> = 0.12, p < 0.001) indicated a significant separation of native and non-indigenous trait profiles in FCA space, 17 out of 35 samples (49%) had identical coordinates and are superimposed in the plots (marked by black arrowheads).

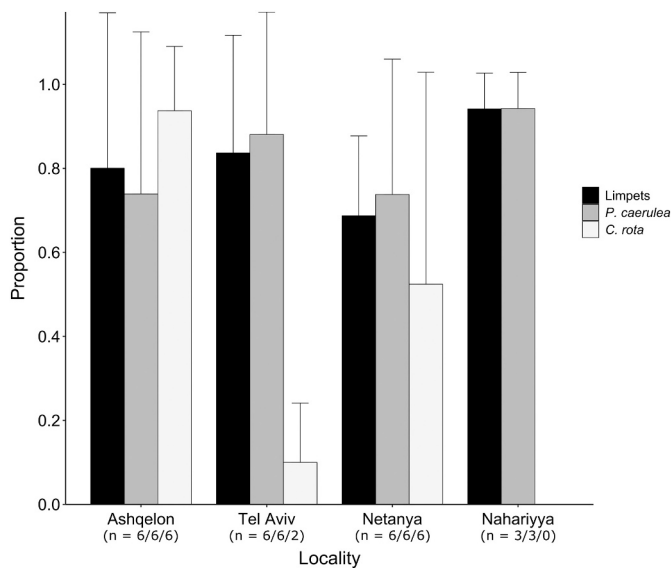
the comparisons Ashqelon vs. Netanya (p = 0.51) and Tel Aviv vs. Nahariyya (p = 0.58; Table 5), suggesting that the presence of *C. rota* may be a major driver of *Patella* median size. Similar to median size, the

95th percentile body size of *P. caerulea* was largest at Tel Aviv (35.0 mm) and Nahariyya (35.2 mm), with no significant difference between these locations (p = 0.81; Table 5). All other pairwise comparisons revealed

**Table 3**

Correlation ratios for the traits ‘maximum adult body size’ (SI), ‘feeding habit’ (FH) and ‘attachment mode’ (AT) for fuzzy correspondence analysis axes 1–3. These ratios represent, for each axis, the proportion of total variance explained by the separation of each trait’s modalities (Chevenet et al., 1994). The highest value for each axis is highlighted in bold font (due to their almost identical values, two ratios are highlighted for axis 1).

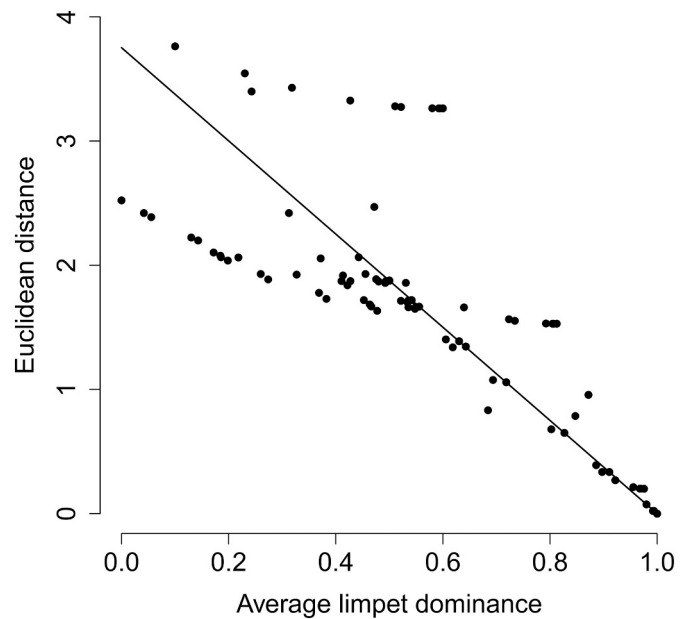
	Axis 1	Axis 2	Axis 3
SI	0.252	<b>0.718</b>	<b>0.574</b>
FH	<b>0.452</b>	0.112	0.032
AT	<b>0.450</b>	0.087	0.010



**Fig. 5.** Proportional abundances (mean and SD) of limpets within rocky intertidal molluscan assemblages from the Israeli Mediterranean coast. Black bars represent the proportion of limpets (i.e., *Patella caerulea* and *Cellana rota*) in molluscan assemblages from replicate 1-m<sup>2</sup> quadrats; dark and light grey bars show the proportions of *P. caerulea* and *C. rota* within the native and non-indigenous molluscan assemblage components, respectively. Assemblage components consisting of less than five individuals have been excluded. n: number of replicates for black, dark grey and light grey bars, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significant differences (all  $p < 0.01$ ). The smallest value for the 95th percentile size was observed at Netanya (24.3 mm, Table 4; proportion of *C. rota*: 0.26), followed by Ashqelon which, however, had a significantly greater value (30.6 mm,  $p < 0.001$ , Tables 4–5), despite a greater proportion of *C. rota* (0.72).

Median and 95th percentile body sizes of *P. caerulea* were significantly negatively related to the proportion of *C. rota* in replicate 1-m<sup>2</sup> quadrats (quantile regression, both  $p < 0.001$ ; Fig. 7a, Table 6). In contrast, there was no significant relationship between the size of *C. rota* and the proportion of *P. caerulea* (Fig. 7b, Table 6;  $p = 0.69$  and  $0.26$  for median and 95th percentile size, respectively). Considering intraspecific interactions, the shape of the relationship between *P. caerulea* size and density remained unclear due to the almost complete lack of quadrats with densities between 80 and 300 individuals m<sup>-2</sup> (Fig. 7c). Quadratic (unimodal) relationships with a peak of limpet size at intermediate densities, however, provided considerably better fits than straight lines ( $R^1 = 0.11$  vs.  $0.01$  and  $0.09$  vs.  $0.03$  for the median and 95th percentile, respectively). Although the fitted curves must be interpreted with caution, they suggest a positive relationship between *P. caerulea* size and density (i.e., a lack of negative intraspecific effects), at least up to a density of 150 individuals m<sup>-2</sup>, which covers most of the samples. In



**Fig. 6.** Euclidean distances between native and non-indigenous trait profiles in 3D-FCA space (see Fig. 4) vs. average limpet dominances. For any unique pairwise combination of native and non-indigenous trait profiles, average limpet dominance was calculated as the mean proportion of *Patella caerulea* and *Cellana rota* in the native and non-indigenous assemblage component, respectively. The strong negative relationship indicated by quantile regression ( $\tau = 0.5$ ,  $y = -3.75x + 3.75$ ,  $p < 0.001$ ,  $R^1 = 0.73$ ) highlights that *P. caerulea* and *C. rota* are major drivers of trait similarity. Accordingly, the marked deviations from the straight-line relationship at low limpet dominance reflect the influence of the traits of other molluscan species on Euclidean distances between native and non-indigenous trait profiles.

**Table 4**

Median and 95th percentile body size, and their bootstrapped 95% confidence intervals (CI; in parentheses), for *Patella caerulea* from the four sampling locations along the Israeli Mediterranean coast. Information on the average proportion of *Cellana rota* in limpet assemblages at these locations is provided in Table 2.

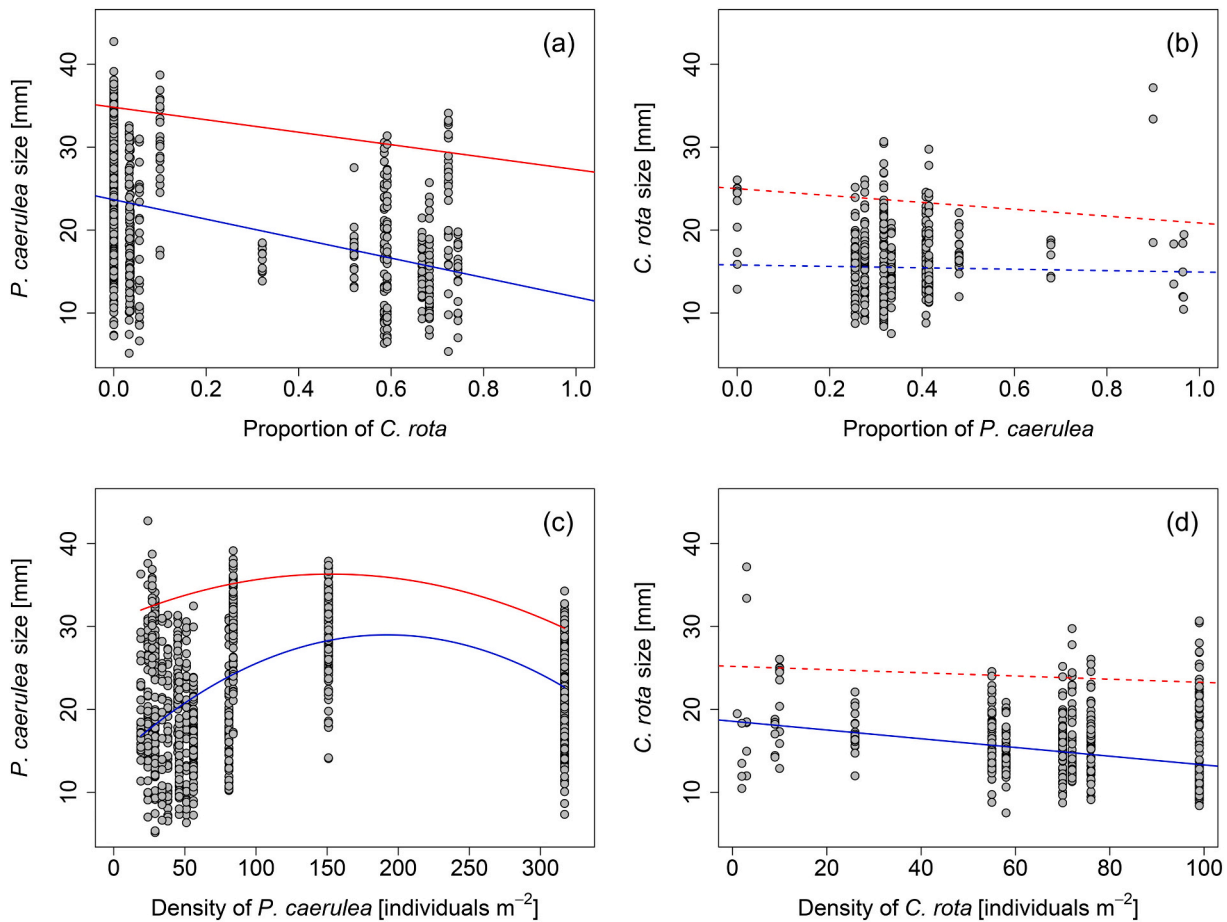
	Median (CI) [mm]	95th percentile (CI) [mm]
Ashqelon	16.6 (15.4–17.9)	30.6 (27.6–31.5)
Tel Aviv	25.5 (24.4–26.6)	35.0 (31.8–36.7)
Netanya	16.9 (16.2–17.6)	24.3 (22.8–29.0)
Nahariyya	25.2 (24.6–25.7)	35.2 (34.4–36.0)

**Table 5**

Absolute differences in median (values above the diagonal) and 95th percentile (values below the diagonal) size of *Patella caerulea* among sampling locations. Two-tailed p-values were obtained by bootstrapping, with significant pairwise comparisons ( $\alpha = 0.05$ ) highlighted in bold font.

Location	Ashqelon	Tel Aviv	Netanya	Nahariyya
Ashqelon	–	<b>9.0 mm</b> ( $p < 0.001$ )	0.4 mm ( $p = 0.505$ )	<b>8.6 mm</b> ( $p < 0.001$ )
Tel Aviv	<b>4.4 mm</b> ( $p = 0.005$ )	–	<b>8.6 mm</b> ( $p < 0.001$ )	0.3 mm ( $p = 0.576$ )
Netanya	<b>6.3 mm</b> ( $p < 0.001$ )	<b>10.7 mm</b> ( $p < 0.001$ )	–	<b>8.3 mm</b> ( $p < 0.001$ )
Nahariyya	<b>4.6 mm</b> ( $p < 0.001$ )	0.2 mm ( $p = 0.807$ )	<b>10.9 mm</b> ( $p < 0.001$ )	–

*C. rota*, median size declined with intraspecific density ( $p < 0.001$ ), whereas the relationship with the 95th percentile was not significant (Fig. 7d).



**Fig. 7.** Upper row: relationships between *Patella caerulea* (a; n = 1060 individuals) and *Cellana rota* (b; n = 461 individuals) body size vs. the other species' proportional abundance in limpet assemblages from replicate 1-m<sup>2</sup> quadrats. Lower row: intraspecific relationships between limpet body size and density for *P. caerulea* (c) and *C. rota* (d). Blue and red lines represent linear quantile regression fits for medians and 95th percentiles, while solid and dashed lines represent statistically significant ( $\alpha = 0.05$ ) and non-significant relationships, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 6**

Summary of quantile regression parameters for relationships ( $y = \beta_0 + \beta_1x + \epsilon$  or  $y = \beta_0 + \beta_1x + \beta_2x^2 + \epsilon$ ) between limpet (*Patella caerulea* and *Cellana rota*) size and predictors (proportion of the other limpet species and limpet density for inter- and intraspecific relationships, respectively) as shown in Fig. 7. Bold font marks relationships with significant ( $\alpha = 0.05$ ) slopes. Prop.: proportion in the limpet assemblage (i.e., relative to the total density of *P. caerulea* and *C. rota*); Dens.: density [individuals m<sup>-2</sup>]; SE: standard error.

Response variable	Predictor	Fig. 7	$\tau$	Intercept (SE)	Slope (SE)	t (slope)	p (slope)	R <sup>1</sup>
Size <i>P. caerulea</i>	Prop. <i>C. rota</i>	(a)	<b>0.50</b>	<b>23.66 (0.30)</b>	<b>-11.73 (0.93)</b>	<b>-12.66</b>	<b>&lt;0.001</b>	<b>0.091</b>
			<b>0.95</b>	<b>34.81 (0.43)</b>	<b>-7.51 (1.75)</b>	<b>-4.29</b>	<b>&lt;0.001</b>	<b>0.032</b>
Size <i>C. rota</i>	Prop. <i>P. caerulea</i>	(b)	0.50	15.80 (0.80)	-0.85 (2.17)	-0.39	0.694	0.001
			0.95	25.00 (0.73)	-4.14 (3.69)	-1.12	0.262	0.005
Size <i>P. caerulea</i>	Dens. <i>P. caerulea</i>	(c)	<b>0.50</b>	<b>13.97 (0.86)</b>	<b><math>\beta_1</math>: 0.16 (0.02)</b>	<b><math>\beta_1</math>: 10.04</b>	<b><math>\beta_1</math>: &lt;0.001</b>	<b>0.105</b>
					<b><math>\beta_2</math>: -0.00 (0.00)<sup>a</sup></b>	<b><math>\beta_2</math>: -9.68</b>	<b><math>\beta_2</math>: &lt;0.001</b>	
			<b>0.95</b>	<b>30.65 (1.15)</b>	<b><math>\beta_1</math>: 0.07 (0.01)</b>	<b><math>\beta_1</math>: 5.55</b>	<b><math>\beta_1</math>: &lt;0.001</b>	<b>0.091</b>
					<b><math>\beta_2</math>: -0.00 (0.00)<sup>b</sup></b>	<b><math>\beta_2</math>: -7.22</b>	<b><math>\beta_2</math>: &lt;0.001</b>	
Size <i>C. rota</i>	Dens. <i>C. rota</i>	(d)	<b>0.50</b>	<b>18.57 (0.33)</b>	<b>-0.05 (0.01)</b>	<b>-7.81</b>	<b>&lt;0.001</b>	<b>0.030</b>
			0.95	25.19 (1.13)	-0.02 (0.02)	-1.04	0.297	0.009

<sup>a</sup> Non-rounded value for  $\beta_2$  (SE): -0.00041 (0.00004).

<sup>b</sup> Non-rounded value for  $\beta_2$  (SE): -0.00024 (0.00003).

#### 4. Discussion

##### 4.1. Trait patterns of native vs. non-indigenous assemblage components

Our trait analysis suggests that both niche complementarity and overlap occur among native and non-indigenous components of the species-poor molluscan assemblages inhabiting low-complexity

intertidal hard substrates along the Israeli Mediterranean coast. Native and Lessepsian trait profiles were partially separated along FCA axes 2 and 3, mainly reflecting differences in the relative abundance of body size classes. Non-indigenous components with distinct trait profiles were characterized by a high proportion of either the mussel *Brachidontes pharaonis* or the pulmonate false limpet *Siphonaria crenata*, two species with traits different from any native species in our samples: *B. pharaonis*



is considerably larger than the confamilial native bivalve *Musculus costulatus* (Risso, 1826). *S. crenata*, in contrast, is smaller than the native patelloidean limpet *Patella caerulea*; furthermore, due to their smaller, non-mineralized radular teeth, siphonariid limpets rely to a greater degree on soft and foliose macroalgae than patelloideans whose strong radulae can excavate the microalgae-rich surface layer of intertidal rocks (e.g. Creese and Underwood, 1982; Lasiak and White, 1993; Ocaña and Fa, 2003). The preponderance of NIS with unique trait combinations in some of the assemblage components fits findings for Lessepsian fishes which tend to become established in 'vacant' or marginal regions of the recipient trait space, thus showing little niche overlap with native species (Azzurro et al., 2014; Givan et al., 2017). Indeed, the availability of 'resource opportunities' (sensu Shea and Chesson, 2002) has been considered an important factor underlying the great invasibility of the Eastern Mediterranean Sea (Taviani, 2002; Oliverio and Taviani, 2003) which, owing to its recent geological history and particular oceanographic properties, hosts a naturally lower species diversity than the western sector of the basin (Coll et al., 2010; Sabelli and Taviani, 2014; but see Albano et al., 2020).

However, in stark contrast with this hypothesis and the apparent importance of niche opportunities for subtidal NIS (Azzurro et al., 2014; Givan et al., 2017), we frequently observed highly similar – and in 49% even overlapping – trait profiles in native and non-indigenous components of the studied intertidal assemblages. Trait overlap occurred at all spatial scales considered, from the Israeli coast to assemblage components sampled within individual 1-m<sup>2</sup> quadrats. This pattern was driven by two species of limpets, the Mediterranean *P. caerulea* and the Lessepsian *Cellana rota*, which have identical species-specific trait score profiles. Limpets are important components of Israeli rocky intertidal assemblages (e.g. Barash and Danin, 1992; Zamir et al., 2018), and at our sampling locations, *C. rota* and *P. caerulea* together accounted for 69–94% of the molluscan individuals (averages across replicates). Within native assemblage components, *P. caerulea* constituted, on average, 74–94% of the individuals, while within non-indigenous components, *C. rota* dominance ranged from 0 to 94%. Seventeen out of 35 assemblage component samples even exclusively consisted of either *P. caerulea* or *C. rota*. The presence of co-dominant species with highly similar niches is expected by community ecology theory for systems under strong influence of environmental filtering (e.g. Keddy, 1992; Mason et al., 2008; Gallien et al., 2014): harsh and variable abiotic conditions, typical of rocky intertidal environments (Underwood and Chapman, 2013), are considered to limit the diversity of successful life strategies and, hence, the range of traits represented within biological assemblages (Menge and Sutherland, 1987). Such negative relationships between environmental stress levels and the functional richness of benthic assemblages have recently been demonstrated empirically across different sea surface temperature and primary productivity conditions for the Chilean rocky intertidal (Valdivia et al., 2017). Similarly, low-intertidal amphipod assemblages from India had a greater functional group richness than those inhabiting abiotically harsher and structurally less complex upper intertidal habitats (Srinivas et al., 2020).

In our study system, the limited topographic complexity of the sampled substrates also might have contributed to promote a co-dominance of native and non-indigenous species with highly overlapping niches. Low-complexity habitats provide fewer microhabitats than more complex environments and therefore often host functionally and taxonomically less diverse assemblages (e.g. Kostylev et al., 2005; Willis et al., 2005; Aguilar-Medrano and Arias-González, 2018). Indeed, although our field campaign covered multiple localities and two seasons, we only recorded eight species of intertidal mollusks representing six unique trait combinations, much fewer than, for example, the 16 molluscan species found at upper to mid-intertidal height in topographically more complex natural rocky shores at Mikhmoret, central Israel (Lipkin and Safriel, 1971). Furthermore, several trait modalities in our scoring system for Israeli mollusks were not represented among

intertidal species; for three out of six traits, all species exhibited just a single modality each: they were epifaunal hard substrate dwellers without host association. In line with theoretical expectations (e.g. Mason et al., 2008), our findings indicate that native – non-indigenous niche overlap, and hence the potential for resource competition, could indeed be more prevalent in abiotically harsh, low-complexity intertidal habitats than in the subtidal realm.

#### 4.2. Competition among limpets

We found evidence for potential asymmetric competition between the functionally highly similar limpets *P. caerulea* and *C. rota*: median and 95th percentile body size of *P. caerulea* were significantly larger for populations from Tel Aviv and Nahariyya, where *C. rota* was rare or entirely absent, than at Ashqelon and Netanya, where *C. rota* constituted 72% and 26% of the individuals in limpet assemblages, respectively. Likewise, considering samples from all locations, quantile regression revealed a significant negative relationship between the size of *P. caerulea* (both median and 95th percentile) and the prevalence of *C. rota*, but not vice versa. A reduction of (maximum) body size is a typical outcome of competitive interactions between limpets, both intra- and interspecifically, and has been documented in various intertidal settings worldwide (e.g. Branch, 1975, 1976, 1981; Boaventura et al., 2002). Food, in particular, has been considered a limiting resource for mobile intertidal grazers (e.g. Creese and Underwood, 1982; Underwood, 1984; Lasiak and White, 1993), suggesting that any adverse effects of *C. rota* on *P. caerulea* could be related to its consumption of microalgal biomass. Indeed, trophic competition may be particularly intense among patelloidean limpets compared to other herbivorous gastropods like trochids, littorinids and siphonariids, because only the former are capable of almost completely removing algae and spores from grazed surfaces (Hawkins et al., 1989; Lasiak and White, 1993; see also previous section); as a result, patelloidean grazing not only leads to a stronger depletion of food resources, but likely also slower rates of renewal, which mainly depends on algal recruitment, rather than the regeneration of cropped thalli (Lasiak and White, 1993).

We acknowledge that processes other than competition may result in body size patterns similar to those observed on the Israeli shore. First, *P. caerulea* and *C. rota* might subtly differ in their microhabitat preferences; if so, dominance and body size patterns may mainly reflect the degree of species-specific habitat suitability within individual sampling quadrats. As local conditions approach the optimum for one species, they may become less suitable for the other, resulting in reduced densities and dominance, as well as smaller body size of the latter (cf. Sonin et al., 2007; VanDerWal et al., 2009). This scenario, however, predicts a symmetric negative relationship between limpet size and the other species' dominance, which contrasts with our observations: the size of *C. rota* was unrelated to *P. caerulea* dominance. Furthermore, densities of limpet species were not significantly negatively correlated (Spearman's rho = -0.29, p = 0.21) as would be expected if their microhabitat preferences differed appreciably (e.g. Branch, 1976). Second, anthropogenic exploitation can lead to a reduction in density and body size of targeted limpet species (e.g. Guerra-García et al., 2004; Martins et al., 2010). Although intertidal mollusks are not commercially exploited in Israel, recreational fishermen may collect them as bait (Ariel and Oren, 2014). The impact of this activity on local limpet populations is unknown, but it is highly unlikely that only *P. caerulea* but not *C. rota* would be affected since both species are, due to shell erosion, often difficult to distinguish in the field (Shefer et al., 2015; Zamir et al., 2018, own observations). Therefore, although experimental approaches are ultimately required to demonstrate causality, we consider competition, a widespread aspect of the life history of intertidal limpets (e.g. Branch, 1981; Creese and Underwood, 1982; Underwood, 1984), the most likely explanation for the empirically observed body size patterns.

*Patella caerulea* is the most abundant – and in many places the only – native limpet species inhabiting the Israeli Mediterranean shore (Barash

and Danin, 1992; Mienis, 2003). While this species does not seem to be affected by intraspecific competition except at very high densities (see also Espinosa et al., 2006), our findings suggest that *C. rota* may have the potential to negatively influence its fitness and population dynamics, considering that gonad weight and fecundity in limpets are strongly positively related to body size (Branch, 1974, 1975; Kido and Murray, 2003).

#### 4.3. The future of native limpets in Israel

Due to the scarcity of baseline information on native limpet densities along the Israeli shore, population trends in *P. caerulea* are difficult to detect. Data in the grey literature (Atad, 2005) and observational evidence (Mienis, 2002, 2003, 2004), however, suggest population declines in recent years at several locations in Israel. These declines were attributed to competitive displacement by *C. rota*, raising concerns that it may eventually outcompete *P. caerulea* along the Israeli shore (Mienis, 2003, 2004; Galil, 2007b). While our results indeed suggest that *C. rota* may negatively affect native limpet fitness, we did not observe an almost complete loss of *P. caerulea* as previously documented by Mienis (2002): in 2001, limpet assemblages near Ashdod, southern Israel, almost entirely consisted of *C. rota*, whereas a few years earlier, only *P. caerulea* had been present at the very same location. The rapidity of this decline suggests that, most likely, it cannot solely be attributed to interspecific competition, considering that by the time of our sampling *C. rota* had been established for at least 15 years all along the Israeli coast (Mienis and Ben-David-Zaslow, 2004; Atad, 2005) and no such 'replacements' had occurred at any of our study locations. Furthermore, it has been experimentally demonstrated that even in systems with markedly asymmetric competition between limpets, intraspecific interactions prevent the superior competitor from reaching densities sufficient to fully exclude the less competitive species (Creese and Underwood, 1982); indeed, such interactions may be indicated by the negative relationship of median size and intraspecific density in *C. rota*, and are also known from congeneric species (Underwood, 1978; Lasiak and White, 1993).

There is mounting evidence that rapid seawater warming in the Eastern Mediterranean Sea (e.g. Ozer et al., 2017), naturally one of the hottest parts of the basin, has driven an unprecedented collapse of native species' populations in shallow subtidal habitats (Rilov, 2016; Givan et al., 2018; Albano et al., 2021). While until now, intertidal mollusks have been less affected – likely due to their greater physiological tolerance of extreme and fluctuating temperatures (Albano et al., 2021) – point-source thermal pollution can have detrimental effects on populations of *P. caerulea* (Manelis and Fishelson, 1989). Indeed, Mienis (2002) sampled limpets just downstream of a cooling water outlet of the Ashdod power plant, where local seawater temperatures likely were artificially elevated above background levels. Though speculative at this point, thermal pollution may have amplified the effects of the ongoing seawater warming and, together with interspecific competition with *C. rota*, locally eroded the physiological performance of native limpets; in contrast, *C. rota* may still have been able to survive due to its greater heat tolerance (see Rilov et al., 2019). This interpretation is supported by that fact that Israeli *P. caerulea* constitute a trailing 'warm' edge population (Rilov et al., 2019). Such populations are often particularly vulnerable to abiotic and biotic stressors as individuals may have a lower physiological fitness than conspecifics from core distribution areas where environmental conditions are more optimal (Rilov, 2016; Aguilera et al., 2019b). Furthermore, Atad (2005) reported the presence of *P. caerulea* at Ashdod and the local power plant in spring 2002 and 2004, suggesting that the loss of native limpets observed by Mienis (2002) either had occurred in a very limited area or was confounded by reimmigration of individuals during the cooler winter months (see Manelis and Fishelson, 1989).

Indeed, the importance of considering the interaction of multiple stressors in the study of native population declines has recently been

highlighted by Yeruham et al. (2020), who experimentally demonstrated that seawater warming, in conjunction with competition with non-indigenous grazers, can explain the almost complete loss of the formerly abundant native sea urchin *Paracentrotus lividus* (Lamarck, 1816) along the Israeli coast. Like *P. lividus* in the subtidal, intertidal limpets are keystone grazers and important structuring agents of hard substrate assemblages (Branch, 1981; Safriel et al., 1994; Bulleri et al., 2000); in the light of the results presented herein, dedicated manipulative studies combining field (e.g. Creese and Underwood, 1982; Boaventura et al., 2002) and temperature-controlled laboratory/mesocosm experiments (cf. Yeruham et al., 2020) thus constitute an important next step to gain further insights into the nature and relative importance of competitive interactions between and within populations of native and non-indigenous intertidal species, and how their outcome may be affected by temperature regimes and species-specific physiological tolerances.

## 5. Conclusions

The Israeli intertidal is a rapidly changing ecosystem, simultaneously affected by warming, an increasing frequency of prolonged desiccation events, and biological invasions (Zamir et al., 2018; Rilov et al., 2019). The presence of dominant NIS whose niches overlap with key native species, likely favored by environmental filtering and – in our specific case – low habitat complexity, may put further pressure on native populations through increased interspecific competition (cf. Epstein et al., 2019). This is exemplified by native vs. non-indigenous limpets: while for the past two decades, *P. caerulea* and *C. rota* have coexisted, it is likely that with ongoing warming, the relative fitness of *P. caerulea* and *C. rota* will further shift to the benefit of the latter, potentially heralding the eventual collapse of native limpet populations (Rilov et al., 2019). Such a turnover might have already occurred at a thermally polluted site near Ashdod, southern Israel (Mienis, 2002), highlighting the urgent need to regularly monitor intertidal assemblages along the heavily impacted Israeli Mediterranean shore, and to gain experimental insights into the joint effects of NIS and abiotic stressors on their taxonomic and functional composition.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2021.112703>.

### Data statement

Data and R-codes are available online from the figshare repository: <https://doi.org/10.6084/m9.figshare.c.5484774> (Steger et al., 2021).

### CRediT authorship contribution statement

**Jan Steger:** Conceptualization, Methodology, Software, Formal analysis, Visualization, Data curation, Writing – original draft, Writing – review & editing. **Beata Dunne:** Investigation, Formal analysis, Visualization, Writing – review & editing. **Martin Zuschin:** Validation, Resources, Writing – review & editing. **Paolo G. Albano:** Conceptualization, Methodology, Investigation, Resources, Writing – review & editing, Project administration, Funding acquisition.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgements

This work was conducted in the framework of the project 'Historical ecology of Lessepsian migration' funded by the Austrian Science Fund (FWF; grant number P28983-B29, PI: Paolo G. Albano). Beata Dunne

was supported by an ERASMUS+ Traineeship. Jonathan Belmaker provided invaluable help in planning field activities and obtaining sampling permits. Angelina Ivkić, Martina Stockinger, Karolina Czechowska and Justina Givens contributed to sampling. We thank Adam Tomašových, Johann Hohenegger, Rafał Nawrot and Diego García-Ramos for fruitful discussions, and Bella S. Galil, Winston F. Ponder, John K. Hall and Daniel Golani for providing copies of relevant literature. Eduard Fadeev helped with translations from Hebrew, and three anonymous reviewers provided constructive feedback. The Israel Nature and Parks Authority kindly granted permit 41928 for field sampling.

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