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Shape matters: relevance of carapace for brachyuran crab invaders

Marc Farré · Antoni Lombarte · Víctor M. Tuset · Pere Abelló

Abstract The increasing trend of biological invasions is one of the most concerning threats for ecosystems functioning. The identification of optimal characters determining the invasive potential of non-native species has always been a challenge in conservation studies. Morphological features can be used as a good proxy to address the invasive success in fish species, assuming that anatomical differences in comparison to native species can provide to newcomers ecological opportunities increasing their probability to become successful. Considering this, the present study constitutes the first applicative attempt of a model based on geometric morphometrics to demonstrate the importance of the carapace shape in the invasive ability in marine decapod crustaceans. The study was performed on the native brachyuran community of Alfacs Bay, in the Ebro Delta, the largest estuarine zone along the north-western Mediterranean, in which two recently established non-native crab species coexist: *Dyspanopeus sayi* and *Callinectes sapidus*. Results suggested that invaders with extreme carapace traits located peripherally in the community morphospace, such as *C. sapidus*, usually possess ecological advantages contributing to understand their success. Conversely, intermediate morphologies within the morphospace, such as *D. sayi*, imply ecological overlapping with native species reducing their community relevance. Besides, we also assessed the effect on the community morphospace of a hypothetical future invasive event from another crab species (*Portunus segnis*) with high probabilities to also colonize the community. Our outcomes confirm that the morphometric approach could be an alternative tool for assessing the potential ability of invasive crab species. However, further studies at different spatial and temporal scales, including additional traits and quantitative data from invasions, would be necessary to confirm the efficacy and usefulness of the methodology.

Keywords Invasive crabs · Carapace shape · Geometric morphometric analysis · Morphospace · Ecological competition · Estuarine community

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Introduction

Within the current broadly accepted context of global change, multiple human-associated phenomena altering marine ecosystems at different levels of

organization have already been identified (Harley et al. 2006; Halpern et al. 2008; Hoegh-Guldberg and Bruno 2010). Direct (e.g., fishing overexploitation, pollution or habitat loss) and indirect (e.g., global warming, ocean acidification or transport of ballast water) anthropogenic activities are intensively affecting the dynamics of biological communities, causing shifts in geographical distribution range and abundance of species (Parmesan and Yohe 2003; Perry et al. 2005; González et al. 2017) and changes in population dynamics of species affecting their recruitment, dispersion and performance at different life stages (Cury et al. 2008; Pörtner and Farrell 2008; Hidalgo et al. 2011) or in the biodiversity and structure of communities (Hughes et al. 2003; Philippart et al. 2011; Wernberg et al. 2013). However, one of the most concerning events, both for the scientific community and society, is the occurrence and establishment of alien invasive species in native communities, due to its impact on the ecosystem functioning and by their potential economic and ecological costs on ecosystem services (Harris and Tyrrell 2001; Stachowicz et al. 2002; Karatayev et al. 2009; Katsanevakis et al. 2014). Most studies related with the effects of biological invasions have been focused on the assessment of their ecological consequences on native communities (Grosholz 2002; Simberloff et al. 2013) or in the understanding of causes, vectors, pathways and mechanisms of invasive processes (including introduction, colonization, establishment and spread, see Walther et al. 2009) in order to, at larger extent, identify the optimal and common traits of successful invaders and attempt to predict their invasive potential (Kolar and Lodge 2001; Ficetola et al. 2007).

In the Mediterranean Sea, there are up to 45 different known species of allocthonous brachyuran crabs (Galil et al. 2002; Galil 2011), most of them inhabiting the benthic or demersal domain from sublittoral, littoral and estuarine zones, areas especially susceptible to biological invasions due to their high productivity and strong physicochemical fluctuations (Grosholz 2002; Lejeusne et al. 2014). Among them, some of the most common and better established in the western Mediterranean are native from western Atlantic waters, as the case of the American blue crab *Callinectes sapidus* (Rathbun, 1896) (with first reports detected in 2012 in the Ebro Castejón and Guerao 2013), and the Say mud crab *Dyspanopeus sayi* (Smith, 1869) (first record in 2005 in the Ebro Delta,

Schubart et al. 2012). Both are euryhaline and eurythermal species native from the western Atlantic Ocean inhabiting shallow estuaries and coastal lagoons (Williams 1984; Nizinski 2003; Nehring 2011). They expanded eastwards probably through human-induced actions and they are currently widely expanded along the eastern Atlantic and most of the Mediterranean Sea (Froglia and Speranza 1993; Micu et al. 2010; Nehring 2011). Especially worrisome is the case of *C. sapidus*, since its wide environmental tolerance and adaptation, aggressive competition for resources, large size, high fecundity rates and large dispersal capacity (Hill et al. 1989; Nehring 2011; Mancinelli et al. 2013) turn him a successful invader representing a serious threat for native ecosystems. In fact, presently it is already considered one of the 100 'Worst Invasive Alien species in the Mediterranean' (Streftaris and Zenetos 2006). However, most of the invader species in the Mediterranean are native from tropical areas of the Indo-Pacific Ocean and Red Sea, which have entered through the Suez Canal. The most highlighting case is the blue swimming crab *Portunus segnis* (Forskål, 1775), another portunoid crab with similar invasive behavior than *C. sapidus* that recently showed a dramatic increase in abundance in the southern central Mediterranean (Gulf of Gabes, Tunisia, Crocetta et al. 2015). It inhabits sandy-muddy and seagrass bottoms of coastal and intertidal areas and is native from the western Indian Ocean, Persian Gulf and Red Sea (Lai et al. 2010; Rabaoui et al. 2015). It is considered one of the earliest alien crabs identified in the Mediterranean (Galil 2011) and its current distribution comprises the southern shores of the eastern and central Mediterranean. *P. segnis* is an opportunistic benthic carnivore species with high competitive ability and a great invasive potential given its efficient and fast reproductive and growth ability (Pazooki et al. 2012; Safaie et al. 2013; Rabaoui et al. 2015) that would probably produce important impacts in the structure of local communities. Considering the state of biodiversity change that the Mediterranean Sea is experiencing in the last decades (Galil 2007; Katsanevakis et al. 2014), it could be expected that this species would show a large process of geographical expansion.

In brachyuran crabs, the presence of specific morphological features (e.g., spines, stronger carapaces, efficient claws or adapted appendages) are common in many invasive species since they influence

positively their successful performance within native communities (Hartnoll 1971; Lee 1995; Weis 2010; Daly et al. 2020). According to this, the main goal of the present study is to determine the degree of morphological variability of the carapace shape of brachyuran crab invaders in relation to native species from the local littoral community of Alfacs Bay, in the Ebro Delta (NW Mediterranean). We selected this brachyuran community because it is well-known for decades (Fusté 1988) and because is affected by two invader currently well-established species (*C. sapidus* and *D. sayi*). Our initial hypothesis is that brachyuran invaders with uncommon carapace shapes may possess certain ecological advantages in some essential life-history habits (such as physiological adaptations to environment, reproduction efficiency, habitat use or predator avoidance) as occurs in fishes with body shape (Azzurro et al. 2014; Smith et al. 2016; Rojas-Vélez et al. 2019). Additionally, a hypothetical future scenario of entrance of a not yet detected new invasive species in the study area, but already abundant in relatively nearby areas (*P. segnis*) was also analyzed. Thus, the present study represents the first attempt to apply a morphological methodology to explore the potential invasive ability in marine decapod crustaceans.

Materials and methods

Study area and native crab community

The selected community of study was the brachyuran community inhabiting between 0 and 1 m in the Alfacs Bay, a semi-enclosed estuary of 3 m mean depth at the south side of the Ebro Delta region (NW Mediterranean), which is isolated from the open sea by a sandbar of 5 km long and 300 m wide (Fig. 1). This bay is mainly formed by sandy, muddy bottoms and seagrass meadows and receives freshwater from early spring to autumn through discharge channels that flow out from its northern extreme (Camp and Delgado 1987; Solé et al. 2009). Given its estuarine and brackish conditions, this area has been the object of several crab invasions during the last decades (Schubart et al. 2012; Castejón and Guerao 2013), this being the main reason why this location and faunistc assemblage were selected for the present study.

The specific composition of the native crab community was extracted from Fusté (1988), who studied monthly the decapod fauna from the bay during two years (march 1984–1986) using two different gears, traditionally used by the local artisanal fleet (trammel nets and 'rastell' bottom-towed dredges, Fusté 1988) over sandy and muddy bottoms of about 0–1 m depth. A total of 19 crab species belonging to 13 superfamilies were identified and considered as the native or base-line community (Table 1). Unfortunately, since then no additional similar samplings have been performed to determine the composition of the crab assemblage of this area. However, personal communications with local fisheries administration and fishermen suggest that changes on composition do not seem to be noticeable, and therefore it was considered the assemblage defined by Fusté (1988) as representative of the current crab assemblage.

Carapace shape characterization and morphospace construction

The morphological description was performed using landmark-based geometric morphomterics. The specimens used for the present study were obtained from the Biological Reference Collections (CBR, http://cbr.icm.csic.es) of the Institute of Marine Sciences of Barcelona (ICM). Due to the noticeable sexual and ontogenetic dimorphism that crabs present in their general body shape (Rufino et al. 2004; Alencar et al. 2014), as well as for the higher availability of male specimens for most of species, only adult males were analyzed in the present study in order to avoid bias during the comparative shape analysis (Table 1). The initial intention was to include the measurement of both carapace and other appendages (claws and pleopods) shape. However, given the fragility of appenadages and the state of conservation of the specimens, in many cases they were incomplete and lacked of the claws, pleopods or both. Thus, in order to avoid bias along the comparative morphometric process, we decided to discard both type of appendages from the study and only describe the carapace shape. Firstly, each specimen was photographed in dorsal view in standardized and scaled positions. The scheme of landmarks (fixed homologous points) and semilandmarks (sliding or mobile non-homologous points), consisting in 10 different points defining the general dorsal carapace shape (Fig. 2), was selected
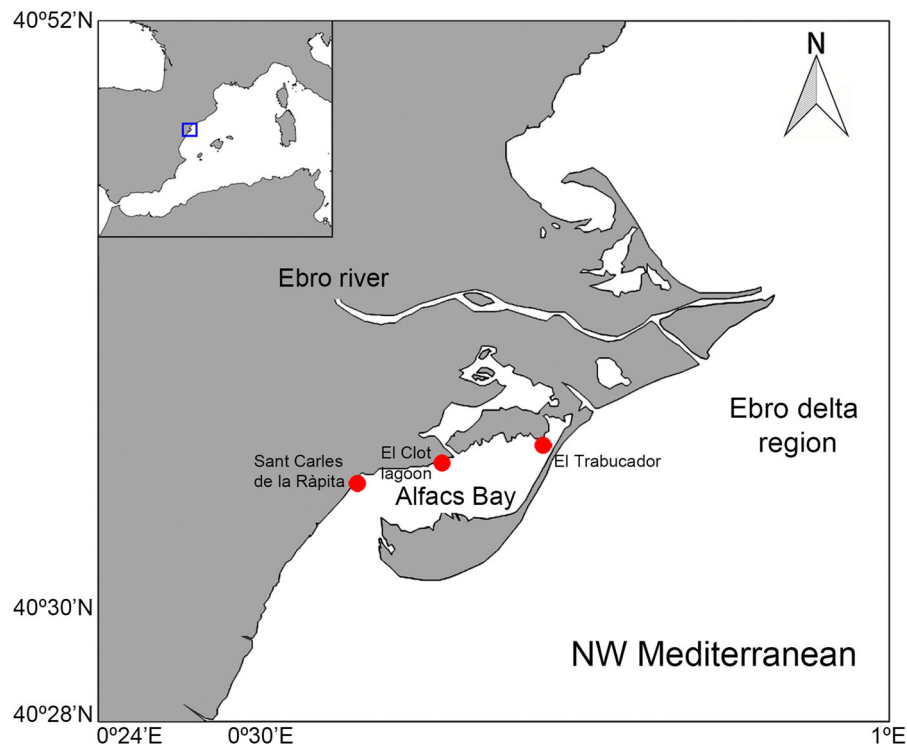
Fig. 1 Map of the study area (Alfacs bay, Ebro Delta region, NW Mediterranean) and specific areas where non-native species were collected. Adapted from Schubart et al. (2012)

based on commonly used configurations in previous morphometric studies with the aim of capturing the maximum of body shape information (a detailed description of the meaning of landmarks and semi-landmarks and the used bibliography is provided in Supplementary material, Table S1). In order to avoid duplication of equivalent landmarks in symmetrical structures (as is the case of the crabs carapaces) that causes computation distortions during the analytical process, only one side of the carapace was considered in the definition of landmarks (Rohlf and Slice 1990; Rufino et al. 2004, 2006).

The digitalization of landmarks and semilandmarks in all male specimens of each species was performed using tpsDig v. 2.30 (Rohlf 2017a). Then, assuming that intraspecific variability is lower than interspecific morphological variability, we obtained a consensus configuration for each species that were used as the mean shape of each species in the remaining analyses. In order to remove scale, orientation and size distortions not related with shape, a generalized Procrustes analysis (GPA) was applied using tpsRelw v. 1.69 (Rohlf 2017b), which translates all configurations to a common centroid position in the coordinate system, scales them to unit centroid size and rotates them to minimise the distances between corresponding landmarks (Adams et al. 2004; Zelditch et al. 2012). Initially, GPA coordinates are not expressed within an Euclidean space shape. To project these Procrustes coordinates in a tangent space and test whether shape variation is small enough to consider this new space a good image of the Euclidean space (Rohlf 1999), we computed the correlation between the tangent and Procrustes distances using tpsSmall v. 1.34 (Rohlf 2017c). The results of correlation (uncentered correlation = 0.999933, root mean square error = 0.000501) confirmed that both spaces were nearly identical for our data.

GPA also generates the uniform components of the shape variation for each analyzed object (relative warps, RWs) by applying the thin-plate spline procedure, which creates a consensus configuration by averaging the coordinates of all the landmarks. Each relative warp represents a specific set of morphological characteristics, allowing to visualize the changes in shape between species (Zelditch et al. 2012; Farré

Table 1 Specific composition of the crab assemblage inhabiting the Alfacs Bay (Ebro Delta, NWMediterranean), including native and alien species, for the three assessed temporal moments: native crab community (NCC), current crab community (CCC) and future crab community (FCC)

Origin	Superfamily	Species	ID	N	Native crab community (NCC)			Current crab community (CCC)			Future crab community (FCC)		
					NND (ID)	VOR	MD	NND (ID)	VOR	MD	NND (ID)	VOR	MD
Native	Calappoidea	*Calappa granulata*	3	8	0.099 (17)	5883.0	0.0002	0.099 (17)	**9637.0**	0.0002	0.099 (17)	9637.0	0.0002
	Cancroidea	*Atelecyclus rotundatus*	1	19	0.077 (10)	12,375.0	0.0009	0.077 (10)	12,375.0	0.0009	0.077 (10)	12,375.0	0.0009
	Corystoidea	*Corystes cassivelaunus*	6	6	0.068 (10)	9230.0	0.0004	0.068 (10)	9230.0	0.0004	0.068 (10)	9230.0	0.0004
	Dorippoidea	*Medorippe lanata*	17	14	0.057 (16)	13,853.0	0.0013	0.057 (16)	**15,262.0**	0.0013	0.057 (16)	15,262.0	0.0013
	Dromioidea	*Dromia personata*	7	9	0.084 (17)	18,862.5	0.0005	0.084 (17)	**18,659.0**	0.0005	0.084 (17)	18,659.0	0.0005
	Goneplacoidea	*Goneplax rhomboides*	9	9	0.150 (18)	3681.1	0.0009	0.150 (18)	**8575.5**	0.0009	0.150 (18)	**8559.5**	0.0009
	Grapsoidea	*Brachynotus sexdentatus*	2	5	0.010 (5)	4986.6	0.0011	0.010 (5)	4986.6	0.0011	0.010 (5)	4986.6	0.0011
	Leucosioidea	*Ilia nucleus*	10	6	0.067 (6)	11,609.5	0.0013	0.067 (6)	11,609.5	0.0013	0.067 (6)	11,609.5	0.0013
	Majoidea	*Macropodia linaresi*	14	7	0.006 (15)	1.2	0.0042	0.006 (15)	1.2	0.0042	0.006 (15)	1.2	0.0042
	Majoidea	*Macropodia rostrata*	15	16	0.006 (14)	14,097.5	0.0018	0.006 (14)	14,097.5	0.0018	0.006 (14)	14,097.5	0.0018
	Majoidea	*Maja crispata*	16	7	0.039 (19)	8682.0	0.0027	0.039 (19)	8682.0	0.0027	0.039 (19)	8682.0	0.0027
	Parthenopoidea	*Parthenopoides massena*	19	6	0.039 (16)	30,054.5	0.0009	0.039 (16)	30,054.5	0.0009	0.039 (16)	30,054.5	0.0009
	Pilumnoidea	*Pilumnus spinifer*	20	15	0.028 (18)	6521.5	0.0017	0.028 (18)	**16,642.0**	0.0017	0.028 (18)	**15,056.8**	0.0017
	Portunoidea	*Carcinus aestuarii*	5	7	0.011 (2)	3182.3	0.0008	0.011 (2)	3182.3	0.0008	0.011 (2)	3182.3	0.0008
	Portunoidea	*Liocarcinus navigator*	12	7	0.016 (5)	2361.2	0.0007	0.016 (5)	2361.2	0.0007	0.016 (5)	2361.2	0.0007
	Portunoidea	*Liocarcinus depurator*	11	10	0.018 (18)	2913.7	0.0024	0.018 (18)	2913.7	0.0024	0.018 (18)	2913.7	0.0024
	Portunoidea	*Liocarcinus vernalis*	13	7	0.023 (12)	7412.0	0.0003	0.023 (12)	**2887.1**	0.0003	0.023 (12)	2887.1	0.0003
	Portunoidea	*Necora puber*	18	6	0.018 (11)	7850.8	0.0004	0.018 (11)	**8015.3**	0.0004	0.018 (11)	8015.3	0.0004
	Xanthoidea	*Xantho poressa*	22	6	0.098 (13)	7671.5	0.0018	**0.067 (8)**	33,399.5	0.0018	0.067 (8)	**27,427.0**	0.0018
Non-native	Portunoidea	*Callinectes sapidus*	4	5	–	–	–	0.1579 (22)	12,332.5	0.0012	**0.0486 (4)**	**830.4**	0.0012
	Xanthoidea	*Dyspanopeus sayi*	8	5	–	–	–	0.0322 (13)	7808.0	0.0002	0.0322 (13)	7808.0	0.0002
	Portunoidea	*Portunus segnis*	21	9	–	–	–	–	–	–	**0.0486 (4)**	18,746.5	0.0004

ID, identification code; N, number of adult males individuals used for the morphological analysis; NND, the nearest-neighbor distance; VOR, Voronoi polygon area; MD, morphological disparity. Species changing its NND or VOR by invasion of new crabs are marked in bold. The taxonomical classification (superfamily) of each species is provided
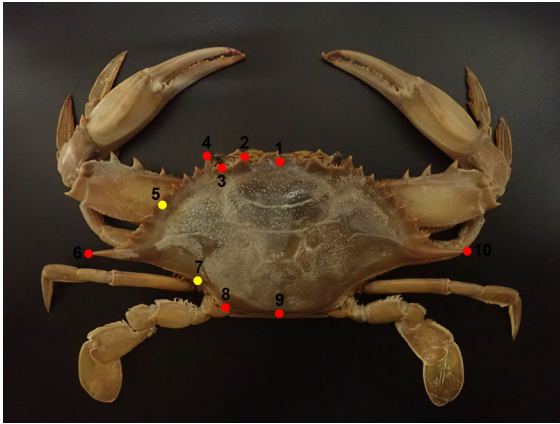
Fig. 2 Scheme of the landmarks (N = 8, red points) and semilandmarks (N = 2, yellow points) used for description of the dorsal carapace shape of crabs. The definition of the meaning of landmarks and semilandmarks is detailed in Supplementary material, Table S1. The specimen of the image is an individual of *Callinectes sapidus* from the Biological Reference Collections (CBR) of the Marine Science Institute (ICM-CSIC) of Barcelona

et al. 2016). The scores of the first two warps, which reached more than 85% of the total morphological variation, were used to plot the morphological position of each species in a two-dimensional graphic (morphospace) using PAST software v. 3.16 (Hammer et al. 2001).

Morphological variability analysis

The morphological dissimilarity within the morphospace of the community was computed from methods based on the position of all species in the native morphospace and the distances between them. Specifically, four variables were estimated: (a) the convex hull, which was used to measure the total dimension and shape of the assemblage morphospace and for further analyses. It is defined as the smallest space enclosing all the individuals of a group (e.g., species of a community or specimens of a species, Cornwell et al. 2006) and was computed in two different ways: at specific level, in order to group by species and determine the intraspecific morphological variability for each species within the morphospace, and at community level (obtained using the consensus configuration of each species, see morphospace construction section) for the later computation of Voronoi polygons. In both cases, it was built using Delone

software v. 1.0.1.19; (b) the nearest-neighbour Euclidean distances (NND) between all the species within the morphospace, which identify their 'closest' neighbours (Smith et al. 2016) and measure the distances between them, and that were obtained using the package *spatstat* v. 1.59 (Baddeley et al. 2015) in R (R Development Core Team 2017); (c) the configuration and area of Voronoi polygons (VOR), a tessellation method determined by distances among species in the space that creates polygons enclosing the area belonging to each species (Du et al. 2012), which were estimated using Image-Pro Plus, v. 5.0.0.39 software (Media Cybernetics, Inc.). Voronoi polygons were created from the convex hull of the overall community morphospace obtained from the consensus configuration of each species. The position within the community morphospace and the size of the Voronoi cells can be explanatory of the available 'niche opportunities' for species within a community (Azzurro et al. 2014; Smith et al. 2016); and finally (d) the morphological disparity (MD), which measured the intraspecific morphological variation among species (Zelditch et al. 2012) and that was obtained with the package *geomorph* (Adams et al. 2020) in R (R Development Core Team 2017).

In order to characterize and assess the temporal evolution of the crab community morphospace until present time, as well as consider possible future scenarios of hypothetical new invasions, the morphospace representation and the estimation of all variables (convex hull, VOR, NND and MD) were computed at three different temporal moments: (1) considering the native crab community (NCC) described by Fusté (1988); (2) including the non-native but currently established species *D. sayi* and *C. sapidus* to the native community (current crab community, CCC); and (3) considering the hypothetical future entrance of *P. segnis* to the current crab community, thus imagining a potential future crab community (FCC). Assuming that the three scenarios are temporally consecutive, changes in the morphospace structures and dissimilarity measures were only compared (as shifts in magnitude) with respect to the previous time period.

Results

Morphospace configurations evidenced morphological variability along the crab communities (Fig. 3a–c). Species segregated along the *x* axis (RW1, 70.3% of total variance) based on the general carapace shape (total width and antero-posterior elongation). In the positive extreme were found species with antero-posteriorly elongated and laterally compressed carapaces, with shorter postero-lateral margins (*Macropodia* spp., *Parthenopoides massena*, *Corystes cassivelaunus*), whereas in the negative extreme were located species with wider and antero-posteriorly shorter carapaces as well as longer postero-lateral margins (*Goneplax rhomboides*, *C. sapidus*, *P. segnis*). In contrast, throughout the *y* axis (RW2, 15.8% of total variation) species spread according to the relation between the size of the anterior and posterior regions of the carapace. The negative side was occupied by species with anterior and posterior regions of similar sizes (*C. cassivelaunus*, *Atelecyclus rotundatus*, *Ilia nucleus*), while in the positive side were placed species with anterior regions more developed than posterior regions (*C. sapidus*, *P. segnis*, *Calappa granulata*, *Medorippe lanata*).

The morphospace and convex hull of the native community (NCC, Fig. 3a) was markedly modified by the extremely outside location, oversteping the native limits, of *C. sapidus* (CCC, Fig. 3b). Its particular carapace shape led the species to occupy a relatively large morphospace portion away from the closest species, *Xantho poressa* (Table 1). Nevertheless, it located relatively near from the core of hexagonal shapes, being one of the species that showed higher intraspecific phenotypic variation (Table 1). By contrast, *D. sayi* showed a similar morphology to some portunoid, grapsoid and xanthoid native species (*Liocarcinus* spp., *Necora puber*, *Carcinus aestuarii, Brachynotus sexdentatus, X. poressa)* and thus located close to these native species more centrally inside the convex hull of the morphospace, taking up less space and supplying little morphological disparity in relation to closer species (Fig. 3b; Table 1).

Finally, in the future hypothetical scenario of new invasion in the current community (FCC), the potential invader *P. segnis* presented a strong carapace shape similarity with *C. sapidus* although not so extreme, locating inside the limits of the convex hull (Fig. 3c). The shape resemblance with the currently established invader caused that presented low morphological disparity (Table 1). However, its specific location allowed him to acquire a high VOR value (Fig. 3c; Table 1), noticeably affecting to the occupied space by their surrounding species (*G. rhomboides*, *Pilumnus spinifer*, *X. poressa* and especially *C. sapidus*).

Discussion

The present study analyzed the carapace morphological variability of a local brachyuran crab assemblage of the Ebro delta, one of the largest estuarine zones of the Mediterranean Sea (Camp and Delgado 1987; Guillén and Palanques 1997), affected by the invasion of several non-native species. Our findings revealed a large interspecific diversity of carapace shapes for the native species, including pyriform (*Macropodia* spp.), triangular (*P. massena*), circular (*I. nucleus*, *A. rotundatus*), longitudinally ovate (*C. cassivelaunus*, *Maja crispata*), transversely ovate (*X. poressa*), subovate (*C. granulata*), pentagonal (*M. lanata*), squarish (*G. rhomboides*) and a majority of hexagonal (*Liocarcinus* spp., *B. sexdentatus*, *C. aestuarii*, *N. puber*) shapes (following the terminology described by Ng 1998). Instead, the non-native species *D. sayi* possesses a carapace with an intermediate shape between transversely ovate and common hexagonal, whereas the invader *C. sapidus* presents an exclusive transversely hexagonal shape characterized by extremely lengthened lateral spines. These phenotypes allowed them positioning in different zones of the native morphospace: while *D. sayi* was noted within the morphospace close to other native species, *C. sapidus* expanded the original limits of the morphospace and was located in the periphery, distant from the nearest native species, occupying an 'empty' zone. This dissimilarity in carapace shape showed by the newcomers coincides with ecological theories supporting that successful invaders usually possess noticeable differences in many life-history (including morphological) traits when compared with native species that allow them to reduce, avoid or overcome competition with residents (Shea and Chesson 2002; Catford et al. 2009; Weis 2010; Parravicini et al. 2015). Carapace shape is recognized as an important trait in defining ecological and biological habits of crab species related with reproductive, physiological, habitat or behavioral
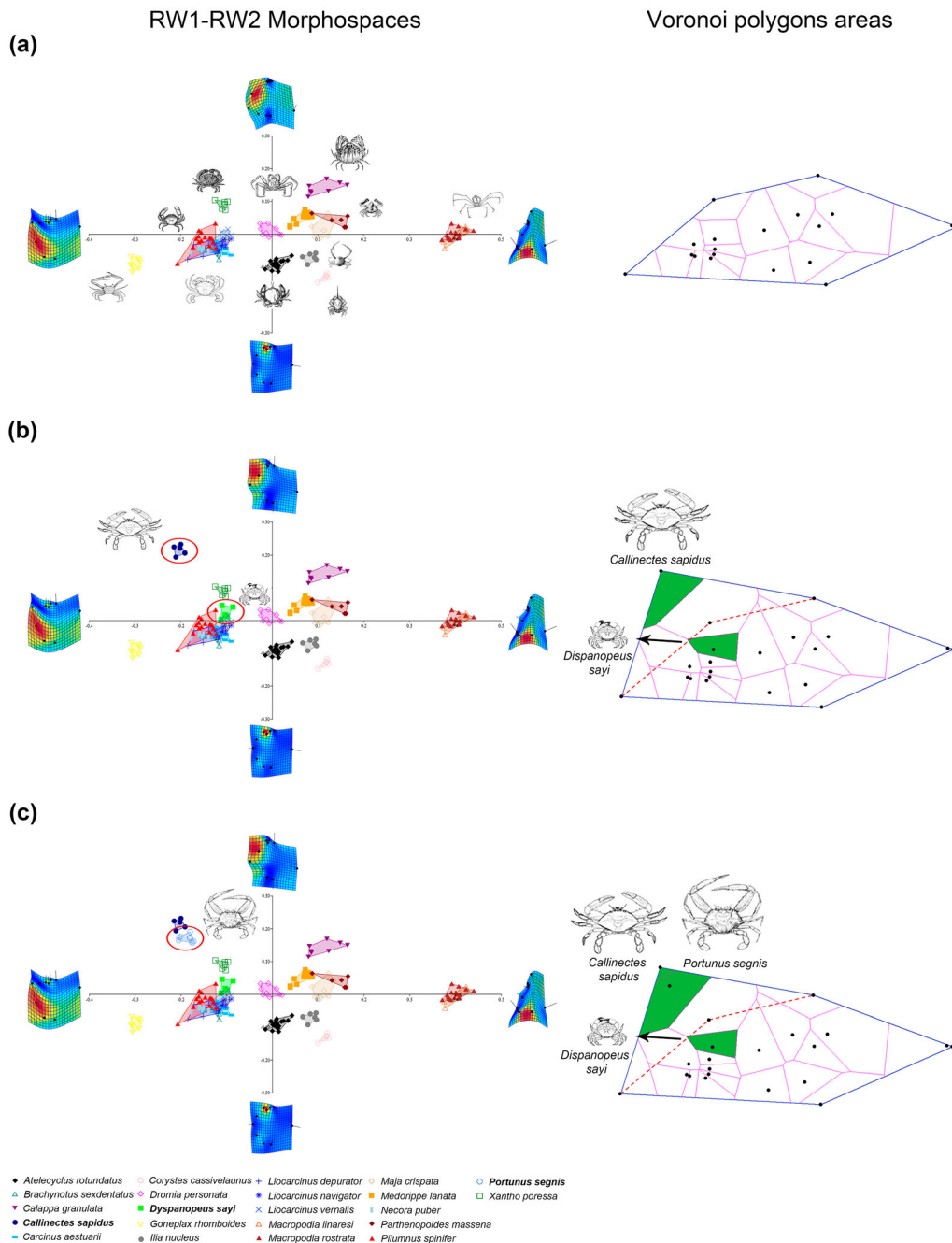
Fig. 3 Two-dimensional (RW1-RW2) morphospace representations and Voronoi polygons representation of the **a** native (NCC), **b** current (CCC) and **c** future crab community (FCC) of Alfacs Bay (Ebro Delta, NW Mediterranean). In the morphospaces, the different convex hulls enclose all specimens of each species, and the color range of symbols is related with the taxonomical similarity (superfamily) of species. Deformation grids indicating the shape variation along the axes and a draw of most representative species are also provided. The position of the non-native species (in bold in legend) in CCC and FCC is highlighted by a red circle. In the Voronoi polygons representation, the position and occupied area by the non-native species is colored in green. The red dashed line represents the original outline of the native morphospace, underlying the increase of the morphological space produced by the non-native species

strategies (Rufino et al. 2004; Silva et al. 2009; Olesen 2013). For instance, its variability can be illustrative of strategies of sheltering and predator avoidance, determining refuge preferences on rocky shores and salt marsh habitats (Idaszkin et al. 2013) or the burrowing and burying ability of crabs in soft bottoms, since excavating mechanics, depth of concealment and associated physiological adaptations are usually related with the carapace shape (Taylor and Atkinson 1991; Bellwood 2002; Veas et al. 2014). Also the presence of spination over and around the carapace margins is identified as an anti-predator adaptation (Davie et al. 2015; Daly et al. 2020).

The real magnitude of success of crab invasive processes importantly depends on many other factors beyond the carapace morphology of species related with, among others, the ecological, biological and behavioural adaptability of non-native species (e.g., body size, agressivennes, competition degree, larval lifespan and dispersion, physiological tolerance) and with the abiotic and biotic environmental conditions (e.g., presence of predators, pathogens, interactions and resistance with native species) of the receiving ecosystem (Catford et al. 2009; Weis 2010; Ricciardi et al. 2013). Nevertheless, diverse studies suggest that non-native species locating in peripheral positions within morphospaces, such as *C. sapidus*, tend to be highly successful or top invaders (Azzurro et al. 2014; Smith et al. 2016; Rojas-Vélez et al. 2019; Tuset et al. 2020). Considering the high invasive potential of *C. sapidus*, which has led the species to colonize practically the entire Mediterranean basin (Galil et al. 2002; Streftaris and Zenetos 2006), including the study area (López and Rodon 2018), it is reasonable to assume that its particular carapace shape (completely disimilar to the remainig species) could also partially contribute, among many other factors, to its successful performance for several reasons: (a) the over-development of the anterior part of the carapace (noted by the considerable expansion in *y* axis) entails a widening of the branchial region and antero-lateral margin. This would allow an enlargement of the gill chambers and surface, improving thus its respiratory efficiency (Millikin and Williams 1984; DeFur et al. 1988) and the capability to avoid desiccation by assuring more water conservation (Hopkins and Thurman 2010; Hampton et al. 2014); (b) its large-sized stout, thick and flattened carapace characterized by strong spines along the antero-lateral margin

finishing with especially lengthened lateral spines (Pyle and Cronin 1950; Millikin and Williams 1984) would act as a defensive adaptation against predators, even providing advantages over native competitors (Davis et al. 2004; Young et al. 2008); or (c) this wider-shaped carapace would also contribute to the reproductive efficiency, providing females with a larger surface and volume for carrying and brooding fertilized eggs and favoring high fecundity rates (Van Engel 1958; Prager et al. 1990; Jivoff et al. 2007; Darnell et al. 2009). Instead, the intermediate positioning of *D. sayi* within the morphospace may indicate a higher ecological overlap, and thus direct competition, with the morphologically close native residents. Its carapace shape, between hexagonal and transversely ovate, can be considered a strategical advantage for occupying tridimensional complex habitats (Williams 1984; Micu et al. 2010; Cabiddu et al. 2020). In fact, the species is able to coexist with species typically from sandy and muddy bottoms (*Liocarcinus* spp., *B. sexdentatus*, *C. aestuarii*, Froglia and Speranza 1993; Mistri 2004) as well as with species over boulders and cobbles in fragmented rocky shores (*X. poressa*, Reuschel and Schubart 2007; Spivak et al. 2010). This high habitat adaptability of the species can help to understand its colonization along almost the whole Mediterranean Sea (Froglia and Speranza 1993; Mizzan 1995; Micu et al. 2010; Schubart et al. 2012; Thessalou-Legaki et al. 2012; Ulman et al. 2017). However, when habitat complexity is more reduced, given its small size and that it rarely buries, this species can be preyed by larger-sized species such as *C. aestuarii* (Gehrels et al. 2016). This higher vulnerability to predation, together with the interspecific competition that would have to confront with morphologically-close species, would support that the species, despite its expansive and establishment ability, show a lower invasive potential than *C. sapidus*. Following the same premises, results suggest that *P. segnis* might also be a top invader since its morphological similarity in carapace shape with *C. sapidus* provides it with a similar ecological and biological performance (Safaie et al. 2013; Crocetta et al. 2015; Rabaoui et al. 2015). Here the interest would lie in assessing the result of its probable direct competition with the closer residents especially with *C. sapidus*, since it would probably exercise resistance limiting the entrance of the newcomer, as occurred in experiments between *C. sapidus* and *Carcinus maenas*

(DeRivera et al. 2005). In any case, given that the direct competence would affect all species, it would be plausible that *P. segnis* could stand competence and coexist with the previously established species (MacDonald et al. 2007), and therefore become a invader with a high probability to establish within the community (Katsanevakis et al. 2014).

Brachyuran crabs are the most numerous and diverse group of decapods occupying a wide spectrum of ecological niches and lifestyles (Davie et al. 2015) and their particular crab-shape and high phenotypic variability have always been considered as fundamental to explain their great diversity and evolutionary success (Števčić 1971; Förster 1985; Scholtz 2014). The local crab community analyzed in the present study represents a good illustrative example of this morphological diversification, showing a broad range of different carapace shapes and some redundancy of hexagonal shapes characteristic from portunoid (*Liocarcinus* spp., *C. aestuarii*, *N. puber*), grapsoid (*B. sexdentatus*) or pilumnoid (*P. spinifer*) species. Considering that under particular environmental conditions the selection towards certain specialized phenotypes that maximize the ecological efficiency of species is common (environmental filtering hypothesis, Zobel 1997), this carapace shape (similar to that of invader species) could be interpreted as an optimal trait for the specific studied area. Therefore, the entrance of newcomers (including the future hypothetical case) would probably entail negative effects, at greater or lesser extent, to these native species with similar morphologies by increasing competence and reducing their ecological niche. On the other hand, native species with higher phenotypic variability (e.g., *Liocarcinus depurator* or *X. poressa*) could exhibit a higher resilience to the perturbations caused by the invasive processes (Allen and Holling 2010; Berthon 2015). In any case, the occurrence of invader species will produce certain degree of alteration in the structure and functioning of the native assemblage. However, it is difficult to identify and quantify the real specific impacts that invaders would cause to native residents considering only the carapace shape as niche trait and with no abundance data from the community. A more complete definition of the ecological niche of the community would be necessary to unravel the real effects of invaders on the residents, which would require considering other morphological features (e.g., body size, size and shape of claws or presence of

transformed appendages such as flattened paddle-like swimming pleopods and pereiopods) essential by habits such as with foraging, locomotion, defensive, aggressiveness, competitive and mating strategies of crabs (Hartnoll 1971; Vermeij 1977; Hines 1982; Lee 1995; Sneddon et al. 1997; Mariappan et al. 2000). Unfortunately, the measuring of some of these structures (claws and pleopods) could not be included in the present study due to methodological difficulties, entailing evident limitations for the ecological interpretations of the study, and thus are effusively encouraged to be included in further studies.

In conclusion, the present study represents a first attempt to evaluate the potential effects of the entrance of marine crustacean alien species (brachyuran decapods) within native assemblages using a methodological approach based on the analysis of external morphology of species, currently only applied in fishes both for body shape (Azzurro et al. 2014; Smith et al. 2016; Rojas-Vélez et al. 2019) or for sensory structures such as otoliths (Tuset et al. 2020). The study was performed in a local specific community, including a relatively small sampling size and from a very enclosed environment in terms of spatial and temporal coverage, which entails evident limitations. Further studies at larger spatial and temporal scales, including larger sets of species that encompass higher ecological and functional variability, should be performed in order to more robustly contrast the efficacy of this model in decapod crustaceans. Besides, a more complete morphological description including other anatomical structures of ecological interest such as claws and other appendages (Hartnoll 1971; Vermeij 1977; Lee 1995; Davie et al. 2015), would be necessary for a more deeply assessment of the ecological conclusions from the morphospace results. However, results based on carapace shape, a morphological trait also strongly related with the ecological performance of species, suggest that invaders that present differential morphological traits can possess ecological advantages that would increase their likelihood to establish themselves since they avoid competition with similar residents. The study demonstrates that this straightforward morphometric protocol can be employed as an alternative effective tool to preliminary assess the effects of invasive processes of species from different taxa and phyla as well as when ecological data of invader species is scarce. Notwithstanding, it should be complemented by studies

incorporating accurate quantitative ecological information of the invasive events to extract more robust conclusions about the evolution of invasive species within native communities.

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