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Research Article

First record of the invasive swimming crab *Charybdis hellerii* (A. Milne Edwards, 1867) (Crustacea, Portunidae) off Martinique, French Lesser Antilles

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Abstract

Charybdis hellerii (A. Milne Edwards, 1867), a crab native to the Indo-West Pacific, was introduced in the western Atlantic in the late 1980s, likely through transport of larvae in ballast water of ships. It has since been reported from North Carolina, southeastern coast of United States, to southern Brazil. This report from Martinique is the first from the Lesser Antilles. Specimens were collected during scuba-diving surveys conducted during March/April 2016 to study the population size, distribution, and habitat-use of this invader. Two hundred and thirteen transects, each 60 m^2, were searched, in 2–15 m depths, in five coves of the southwestern peninsula of the island. We observed 150 individuals, of which 135 were collected. Most (89 %) specimens were mature with a male:female sex ratio of 2.4:1. Carapace widths ranged between 17.3 and 58.1 mm, with males significantly larger than females. Most crabs (93%) were found in dense seagrass beds of *Halophila stipulacea*, although a few (7%) were found on bare substrate with rocks and artificial mooring blocks. *C. hellerii* was absent from sand, coral with rocks and sponges, and mixed beds of algae and seagrass, possibly due to the presence of predators. The maximum observed density in the dense seagrass beds was 0.37 crab m^{-2}. Predatory behavior of *C. hellerii* on other crabs was observed, suggesting this alien crab could alter existing community structure and functioning.

Key words: Brachyura, invasive alien marine species, exotic species, seagrass beds, *Halophila stipulacea*, SCUBA survey, line transect survey

Introduction

The swimming crab (Crustacea, Portunidae) *Charybdis hellerii* (A. Milne-Edwards, 1867) was described from New Caledonia and later was reported in the Indo-West Pacific from South Africa/Madagascar to Japan/Hawaii (Edmonson 1954; Crosnier 1962; Stephenson 1972; Kensley 1981; Wee and Ng 1995). It was first detected in the Mediterranean Sea in 1929, presumably invading through the Suez Canal (Steinitz 1929; Galil 1992; Yokes et al. 2007). In the 1980s, this species was detected in the western Atlantic, probably transferred by ocean-going vessels. *C. hellerii* has since been collected in North Carolina (Fofonoff et al. 2016), Florida (Lemaitre 1995), Cuba (Gómez and Martínez-Iglesias 1990), Belize (Felder et al. 2010), Colombia (Campos and Türkay 1989), Venezuela (Bolaños et al. 2012), French Guyana (Tavares and Amouroux 2003), and Brazil (Tavares and Mendonça 1996; Mantelatto and Dias 1999; Boos et al. 2010; Sant'Anna et al. 2012). Fofonoff et al. (2016) provide a detailed invasion history of *C. hellerii* in the western Atlantic as does The Global Invasive Species Database (GISD 2009). While this invasive species is now widely spread in Mediterranean Sea and western Atlantic Ocean, it has yet to be recorded from the eastern Atlantic Ocean (Udekem d'Acoz 1999).

In the Lesser Antilles islands of the Caribbean (Virgin Islands to Grenada), *C. hellerii* was unknown until this study. The first visual observation of this species was made on 4 January 2013 in Martinique in a cove named "*Grande Anse d'Arlet*" (14.50098;

−61.086327) at a depth of 3–8 m (Ferry 2013) where it appeared to be abundant in beds of the seagrass *Halophila stipulacea* (Forsskål, 1775). A specimen was collected in March 2013 confirmed to be *C. hellerii* (Figure 1). As a follow-up, scuba-dive surveys were conducted at night in 2016 at five selected coves on the southwestern part of Martinique. In this study, we report selected aspects of the biology of *C. helleri*; including: sex ratio, description of habitats occupied, abundance, size, and behavior. A few additional records of *C. hellerii*, made recently in other Islands of the French Lesser Antilles (Guadeloupe, Saint Martin and Saint Barthélemy), are also documented.

Figure 1. The swimming crab *Charybdis hellerii* photographed off Martinique: top) dorsal view of a male, scale bar 10 mm; bottom) the crab in a seagrass beds of *Halophila stipulacea* at site c.4 "*Grande Anse d'Arlet*". Photographs by R.Ferry.

Material and methods

Survey sites

This study was conducted in Martinique during March and April 2016. We surveyed five coves situated on the southwestern peninsula of the island (Figure 2). Geographic coordinates of the study sites are as follows: c.1) "*Anse Mitan*" (14º33′05.04″N; 61º03′16.06″W); c.2) "*Anse Noire*" (14º31′39.27″N; 61º05′14.23″W); c.3) "*Anse Dufour*" (14º31′32.95″N; 61º05′22.53″W); c.4) "*Grande Anse d'Arlet*" (14º30′10.82″N; 61º05′08.40″W); and c.5) "*Anse d'Arlet*" (14º29′20.97″N; 61º04′51.63″W).

In each cove, transect surveys were conducted by scuba divers in water 2–15 m depth deep. Sampling was conducted at night (between 20:00 and 23:00h) because crabs could be observed and captured more easily by using dip-net and thick gloves. A mesh bag was used to retain the crabs collected at each transect. All crabs were taken to the laboratory for detailed biological analysis. The location was determined by means of a Garmin® GPS (Model eTrex® 20; Garmin LTD, Schaffhausen, Switzerland). For each station the various habitat types (sand, rock, seagrass, coral, etc.) were also mapped. Transects and habitats were then reported as layers on a background map by using QGIS software (2.12.3-Lyon).

We surveyed 213 transects (30 m length by 2 m wide), surface area of 60 m^2, most of which were parallel to the shore (Figure 3, supplementary Table S1). The transects were searched by two scuba divers swimming side by side. Transects were laid out in parallel were at least 10 m apart. Positions of the transect were selected to ensure the various types of habitat were searched. Transects where *C. hellerii* was not observed at night were also checked during the day to confirm the crabs were absent.

The "*Grande Anse d'Arlet*" (c.4; N = 77) and "*Anse d'Arlet*" (c.5; N = 46) had the greatest number of transects, and there were 23 to 35 transects in the other three sites (Table 1). The seven distinct habitats identified during the dives were: 1) sand; 2) rocks with corals and sponges; 3) bare rocks and mooring blocks; 4) sparse seagrass beds of *H. stipulacea*; 5) dense seagrass beds of *H. stipulacea*; 6) mixed seagrass beds of *H. stipulacea*, *Thalassia testudinum* K.D.Koenig, 1805 and/or *Syringodium filiforme* Kützing, 1860; and 7) mixed sparse algae and seagrass. The outlines of these habitats were mapped (Figure 3, supplementary Table S1). Most of the transects were made on habitats n°4 (T = 69), n°2 (T = 46), n°1 (T = 44), n°6 (T = 34) and n°5 (T = 16) (Table 1). The two others habitats, n°3 (T = 2) and n°7 (T = 4) were of more limited size and less often sampled.

Identification and preservation

All specimens collected were taken to the laboratory. Species identification was based on recognition characters in Lemaitre (1995) and identification keys in Crosnier (1962), Stephenson (1972) and Tavares and Mendonça (1996). Several morphological characters

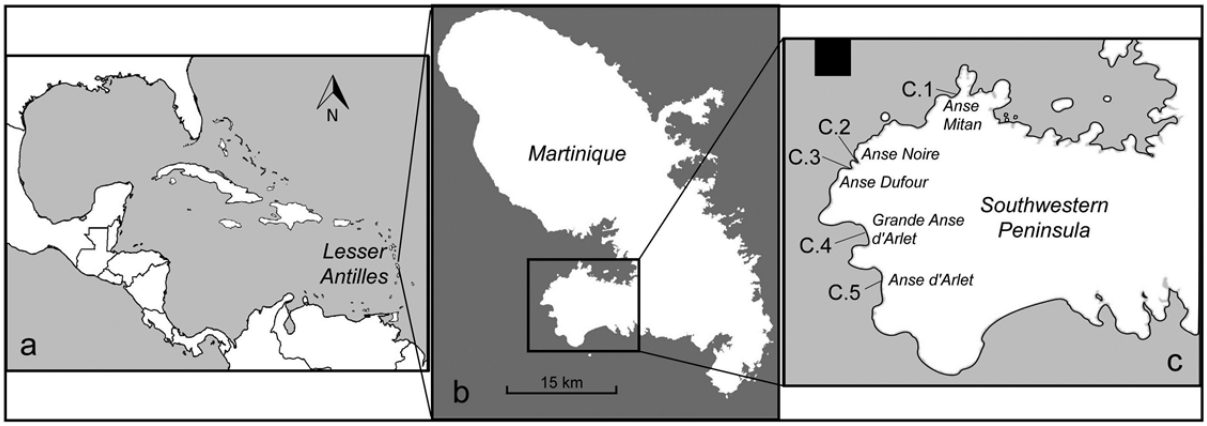

Figure 2. Location of Martinique in the Lesser Antilles and sites of observation in the Island: a) Gulf of Mexico and the Caribbean Sea; b) Martinique; c) Southwestern Peninsula with sites of observation; c.1) "*Anse Mitan*"; c.2) "*Anse Noire*"; c.3) "*Anse Dufour*"; c.4) "*Grande Anse d'Arlet*"; c.5) "*Anse d'Arlet*". Black square indicates anchorage area for ship containers.

Table 1. Repartition of the crab *Charybdis hellerii* by habitat for each station: T, numbers of transects; N, number of crab collected. * specimen caught under a buoy mooring block within a sparse seagrass beds transect. *H.s.*, *Halophila stipulacea*; *T.t., Thalassia testudinum*; *S.f.*, *Syringodium filiforme*.

Habitat \ Site of observation	*Anse Mitan* (c.1)		*Anse Noire* (c.2)		*Anse Dufour* (c.3)		*Grande Anse d'Arlet* (c.4)		*Anse d'Arlet* (c.5)		Total	
	T	N	T	N	T	N	T	N	T	N	∑T	∑N
1) Sand	10		4		4		14		12		44	0
2) Rocks with corals and sponges	7		10		10		10		9		46	0
3) Bare rocks and mooring blocks			2	10							2	10
4) Sparse seagrass beds of *H. stipulacea*	5		19		9		23	1*	11		69	1
5) Dense seagrass beds *H. stipulacea*	4	10					12	114			16	124
6) Mixed seagrass beds of *H.s., T.t., S.f.*	6						14		14		34	0
7) Mixed sparse algae and seagrass							4				4	0
∑T | ∑N	32	10	35	10	23	0	77	115	46	0	213	135

indicated in Felder et al. (2010: 184) were also verified on the smallest specimens because they can be confused with *Cronius ruber* (Lamarck, 1818) and, to a lesser extent, with *Achelous* spp. The sex was determined by inspection of abdominal morphology with crabs classified as males (M), non ovigerous females (NOF) or ovigerous females (OF). All samples were preserved in 90% alcohol and deposited in BIOSPHERES laboratory collection at "*Université des Antilles*", Martinique.

Laboratory analyses

Crabs were sorted by sex and carapace width (CW) was measured (±0.01 mm) using digital calipers.

Statistical tests to compare two (two-tailed t test) or multiple means (one way ANOVA) were performed using the Excel© spreadsheet analysis ToolPak. A two-tailed Chi-square test was used to detect departure from the expected sex ratio of 1:1.

Results

We captured 135 of the 150 crabs observed during the dives. Of the 213 transects searched, crabs were only detected in 16 transects (Figure 3, supplementary Table S1). No crabs were observed on sites c.3 (23 transects) and c.5 (46 transects). The majority of crabs (N = 115; 13 of 77 transects) were collected from site c.4 with relatively few specimens collected sites c.1 (10 crabs from 2 of 32 transects) and c.2 (10 crabs in 1 of 35 transects). Nearly all crabs were captured in dense seagrass beds but a few captured near or under mooring blocks (Table 1).

The density of crabs, on transects where crabs were detected, ranged between 0.02 and 0.37 individuals/m^2 (Table 2). The sex ratio (male:female) of the animals taken to the laboratory was 2.4:1, which was significantly different (χ^2 = 11.7, df = 1, p = 0.0006) from 1:1. The vast majority of captures

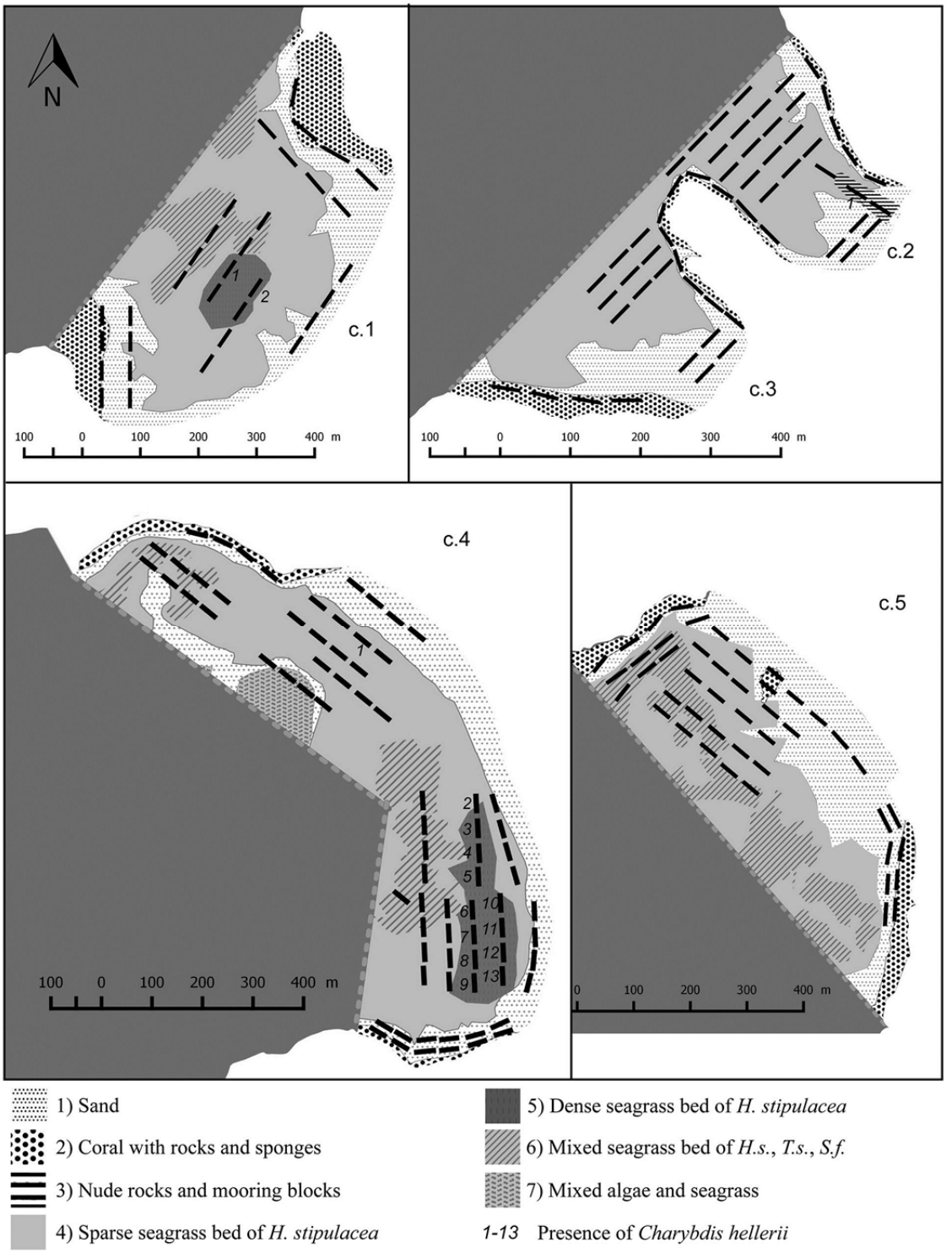

Figure 3. Location of the 213 sampling transects (bold lines) conducted for each site of observation (c.1 to c.5, open sea in dark grey, separated from coves by a dashed line; land side is in white) with distinction of seven habitats (1–7). Transects with presence of *Charybdis hellerii* are identified with a number (1–13). *H.s.*, *Halophila stipulacea*; *T.t., Thalassia testudinum*; *S.f.*, *Syringodium filiforme* (for details see supplementary Table S1).

Table 2. Abundance of *Charybdis hellerii* for the 16 transects where it was present. Abbreviations are: T, transect; M, male; NOF, non ovigerous female, OF, ovigerous female. Surface of each transect, used to calculate the density, is 60 m^2. Transects with more than 10 crabs are in bold.

	Transect	M	NOF	OF	Collected	Observed	Total	Density(/m^2)	Mating	Sex ratio
Anse Mitan	T1	5	2		7		7	0.12		1:0.25
(c.1)	T2	3			3		3	0.05		
Anse Noire (c.2)	T1	7	3		10		10	0.17		1:0.43
	T1	1			1		1	0.02		
	T2	4			4		4	0.07		
	T3	2	1		3		3	0.05		
	T4	5	1		6		6	0.10	1	
	T5	3	2	1	6		6	0.10	1	
Grande Anse	T6	7		2	9		9	0.15		1:0.44
d'Arlet	T7	6	1	1	8		8	0.13		
(c.4)	T8	5	3	1	9		9	0.15	2	
	T9	**10**	**1**	**4**	**15**	**3**	**18**	**0.30**		
	T10	**8**	**2**		**10**	**3**	**13**	**0.22**		
	T11	**13**	**2**	**3**	**18**	**4**	**22**	**0.37**	1	
	T12	**9**	**2**	**3**	**14**	**3**	**17**	**0.28**	1	
	T13	**7**	**1**	**4**	**12**	**2**	**14**	**0.23**		
∑	16	95	21	19	135	15	150	0.16	6	1:0.42

Table 3. Descriptive statistics for CW by site of observation and sex; calculated for 135 crabs *Charybdis hellerii* collected off Martinique. M, males; NOF, non ovigerous female; OF, ovigerous females, CW, carapace width; N, number of individuals; Min, minimum; Max, maximum; SD standard deviation.

		M		NOF		OF	
		N	CW	N	CW	N	CW
Anse Mitan c.1	Min	8	28.28	2	36.33	0	
	Max		58.12		47.49		
	Mean		**43.38**		**41.91**		
	±SD		±9.10		±7.89		
Anse Noire c.2	Min	7	40.54	3	29.28	0	
	Max		57.89		33.08		
	Mean		**48.25**		**31.04**		
	±SD		±6.55		±1.91		
Anse Dufour c.3	-	0		0		0	
Grande Anse d'Arlet c.4	Min	80	28.32	16	17.30	19	27.03
	Max		56.07		46.45		46.13
	Mean		**43.76**		**36.47**		**38.23**
	±SD		±6.12		±7.64		±4.88
Anse d'Arlet c.5	-	0		0		0	
Total	Min	95	28.28	21	17.30	19	27.03
	Max		58.12		47.49		46.13
	Mean		**44.06**		**36.21**		**38.23**
	±SD		±6.47		±7.39		±4.88

Table 4. Additional observations of *Charybdis hellerii* (A. Milne Edwards, 1867) in the French Lesser Antilles in 2012, at Guadeloupe, specimens deposited in Paris MNHN collection (MNHN 2017) and Saint Martin, specimens deposited in Gainesville UF collection (Maréchal and Paulay 2013). Color photographs available in the Internet database of Legall and Poupin (2016).

	Saint Martin	Guadeloupe			
Date	20/04/2012	02/05/2012	28/05/2012	28/05/2012	12/05/2012
Collection	UF32327	MNHN-IU-2013-6824	MNHN-IU-2013-6823	MNHN-IU-2013-4917	MNHN-IU-2013-5230
Station	Baie Embouchure	GM01	GM37	GM37	GD19
Latitude	18º04'22.3"N	16º13.41′N	16º14.62′N	16º14.62′N	16º12.69′N
Longitude	63º00'52.0"W	61º31.83′W	61º19.39′W	61º19.39′W	61º47.13′W
Depth	–	1 m	2 m	2 m	8 m
Method	Scuba dive	Hand, low tide	Hand, low tide	Hand, low tide	Dredge 8 m
Habitat	Unspecified	Unspecified	Unspecified	Unspecified	Seagrass beds

were from a single seagrass bed in site c.4 (Figure 3). Five transects within this bed accounted for more than half the crabs captured.

Overall, the CW ranged between 17.30–58.12 mm with males attaining larger maximum size (Figure 4). The mean CW for males was 44.1 mm, which was significantly larger (t = 5.69, df = 133, P < 0.01) than the mean CW of 37.2 mm for all females (Table 3). The mean CW for ovigerous females was 38.2 mm compared to 36.2 for non-ovigerous females, which did not differ significantly (P > 0.05).

On three occasions, we observed *C. hellerii* preying on other crabs, either the Portunid species *Cronius ruber* (Lamarck, 1818) or the Mithracid species *Mithraculus sculptus* (Lamarck, 1818). On six occasions at site c.4 we observed mating behaviour of*C. hellerii*. Lastly, we observed about a dozen specimens of the Portunid *Callinectes ornatus* Ordway, 1863 at site c.2 in sparse seagrass habitat (n°4) from which *Charybdis hellerii* was absent.

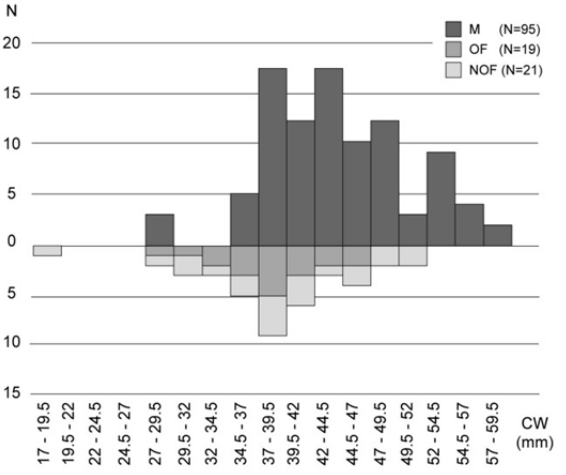

Figure 4. Carapace widths (CW mm) of male, M (N = 95), non ovigerous female, NOF (N = 21) and ovigerous female, OF (N = 19) *Charybdis hellerii* collected from Martinique in the Lesser Antilles during March and April 2016.

Discussion

Several sampling techniques have been used previously to study *C. hellerii* such as: hand collection in the intertidal zone and/or snorkeling in the shallow (> 2 m) subtidal zone (Dineen et al. 2001; Sant'Anna et al. 2012); traps of different kinds (Boos et al. 2010; Dineen et al. 2001; Morán and Atencio 2006; Sant'Anna et al. 2012), and several kinds of trawls towed along transects in shallow (~3–10 m) waters (Dineen et al. 2001; Mantelatto and Garcia 2001; Sant'Anna et al. 2012). We used scuba diving at night to collect *C. hellerii* because: a) it was a non-destructive technique that can explore and distinguish a wide variety of habitats close to each other between the surface to 20 m depths; b) it allowed complementary observations during the dives, such as mating or predatory behaviors that are of primary importance for studying the ecology of the crab; c) the exact position of the crabs in each habitat could be observed; d) the surface sampled could be estimated confidently with two divers operating side by side, hence the density of the crab population could be estimated. There are, however, limitations. It is difficult to detect and capture very small crabs in dense seagrass and large specimens may detect, and avoid (unseen) the divers. Also, there was a learning period for the divers using a dipnet to capture crabs. Some that escaped were, however, accounted for as visual observations. By the end of the survey, the skill of the divers has improved and almost all crabs seen were captured.

According to Dineen et al. (2001) and Tavares and Amouroux (2003), *C. hellerii* has several characteristics that help this species disperse and invade new areas. These are: 1) relatively long larval life (44 days) that facilitates dispersion; 2) rapid growth and maturation which contributes to a short renewal time; 3) ability to store sperm and to produce multiple broods; 4) carnivorous diet; and 5) ability to use a variety of habitats.

In the western Atlantic, initially documented beginning in 1987, *C. hellerii* quickly spread and now occurs from Cape Hatteras, North Carolina (USA, 35°15′N) to Brazil (Lemaitre 1995; Boos et al. 2010; Fofonoff et al. 2016), although records are scarce for some parts (especially islands) of the Caribbean Sea and Gulf of Mexico. In the Lesser Antilles, *C. hellerii* was reported previously from Tortuga (Lira 2004), the Islands of Margarita, Venezuela (Morán and Atencio 2006; Bolaños et al. 2012), and then in Saint Martin and Guadeloupe Islands during field studies conducted in these Islands (Table 4, supplementary Table S2) with Internet based images posted by Legall and Poupin (2016). While this contribution was in press the crab was also reported from Saint Barthélemy (Questel 2017).

The mode of colonization of the Lesser Antilles by *C. hellerii* is unknown. With a long larval period, the larvae may have been transported from the Greater Antilles (e.g. Cuba) or, based the main oceanic currents (Gyory et al. 2017), from the South American coastline (e.g. from Venezuela and/or Brazil). It is possible that *C. hellerii* has colonized most of islands of the Caribbean arc; however, it has yet to

be reported from most of them. Another potential vector would be in ballast water from the Mediterranean Region, or any other region of the western Atlantic where the crab has already settled, to the main harbors of the Lesser Antilles, such as Fort-de-France in Martinique or Pointe-à-Pitre in Guadeloupe. In support of this latter hypothesis, all the sites sampled during the present study are situated near the harbor of Fort de France, with an anchorage of container ships nearby (black square in Figure 2c, ~14º33′46.6″N; 61º5′25.3″W / 14.562944, −61.090361). Finally, the presence of many recreational boats in the various coves in the study area raises the hypothesis of transport via these boats. Indeed, *C. hellerii* was strongly associated with dense beds of the seagrass *H stipulacea*—itself an invasive species thought to have been spread on anchors of recreational boats (Willette et al. 2014).

In this study males were significantly larger than females, which Sant'Anna et al. (2012) suggests is due to differences in energy allocation between males and females. Females would seem to direct more energy into gonad development (Hartnoll 1985). In addition, the difference in size could facilitate the copulation (Santos et al. 1995) during which males holding females in amplexus need to fend off other males and predators (Abelló et al. 1990).

The maximum carapace width (CW) observed in this study for males was 58.1 mm for males and 47.5 mm for females. These values are low. Much larger specimens are reported in the Western Atlantic (males–females, respectively): 83.2–65.6 mm (Venezuela; Morán and Atencio 2006); 79.0–77.0 mm (Florida, USA; Dineen et al. 2001); 75.0–63.1 mm (Brazil; Tavares and Mendonça 1996; Mantelatto and Dias 1999; Mantelatto and Garcia 2001; Sant'Anna et al. 2012); and 75.0–55.6 mm (Colombia; Campos and Türkay 1989). These differences in size may indicate that the population of *C. hellerii* has recently colonized around Martinique or it could be a sampling artefact with larger individuals able to escape our divers undetected. A few traps could be set in the future to test this hypothesis.

The smallest specimen collected in the present study was 17.3 mm CW while specimens < 10 mm CW were collected elsewhere by hand in the intertidal zone or by trawl in shallow waters (Mantelatto and Garcia 2001). It should not be surprising that very small specimens (CW < 10 mm) were not detected by our divers, especially in dense seagrass beds where small crabs can easily hide.

The male:female sex ratio seems to vary widely between reports. In this study, the male: female sex ratio (2.4:1) was strongly male-biased. Similar male-biased sex ratios have been observed in Venezuela (1.45:1; Morán and Atencio 2006) and Brazil (3.13:1, Sant'Anna et al. 2012). In Florida, the sex ratio was near unity (1.06:1, Dineen et al. 2001) and even reversed in a different part of Brazil (0.83:1, Mantelatto and Garcia 2001). Moreover, the sex ratio may vary seasonally as monthly inversions of the sex ratio were seen by Mantelatto and Garcia (2001). How much of this variation is real and how much a sampling artefact is unknown. A cryptic behavior of mature females has been sometimes invoked for crabs to explain skewed sex-ratio (Davanso et al. 2013).

Only 48% of the female *C. hellerii* captured were ovigerous and all were collected from within a dense seagrass bed. The smallest ovigerous female was 27.03 mm CW, which is smaller than the size at maturity of 35–40 mm CW reported by Fofonoff et al. (2016). If the size at maturity threshold is set at 27 mm CW, then we only collected two juveniles. Small individuals likely were present but the sampling method was not designed to capture them.

Our sampling was conducted in March/April; therefore, we cannot make any conclusions on seasonal aspects of reproduction. We did, however, note six instances of mating behavior, which indicates that March/April is part of the mating season. Work conducted in Florida (Dineen et al. 2001) suggests female *C. hellerii* produce broods year round—there may be no seasonal peaks of spawning activity. While Sant'Anna et al. (2012) have observed that ovigerous females occurred unevenly during the year at their site in Brazil, they also suggest a continuous reproductive pattern.

Previous studies show *C. hellerii* prefers soft bottom habitats but that it can be observed in a wide variety of habitats between intertidal to ~50 m depths, in riprap jetties, coralline ledges, mangrove roots, gravel, rocks, and dense algae (GISD 2016; Fofonoff et al. 2016). In contrast, our results indicate a marked preference of *C. hellerii* for dense beds of the seagrass *H. stipulacea* with almost all the crabs being caught there. The explanation for this discrepancy is unknown.

In our study, *Charybdis hellerii* was much less abundant in habitat consisting of bare rocks and mooring blocks and was absent from the other habitats sampled. Moreover, we confirmed the absence during dives made during daytime in these habitats. In at least one area (rocks with corals and sponges), we observed a few individuals of *Octopus vulgaris* Cuvier, 1797. This octopus has been identified by Sampaio and Rosa (2006) as a potential predator of *C. hellerii,* and this could explain the absence of the crab from the rocky habitat. The absence of *C. hellerii* from sparse seagrass beds may have been due to the presence of large specimens of the Portunidae *Callinectes ornatus*, another known

predator on *C. hellerii* (Mantelatto and Garcia 2001). Thus the concentration of *C. hellerii* in dense seagrass beds may be due to the need for a refuge at least early in the colonization process.

Charybdis hellerii is not fished commercially in Martinique. The only limit to its expansion around the island seems to be the availability of the favorable dense seagrass habitat. Colonization of rocky areas by *C. hellerii* would, however, be possible in the zones where *O. vulgaris* is subject to intensive fishing. Thus *C. hellerii* is vulnerable to native predators and may be habitat limited by these predators. Conversely, we observed *C. hellerii* eating other crab species, which suggests the non-native crab could have a significant impact on the local food web. In a few studies, *C. hellerii* may have displaced several species of crabs and even spiny lobster *Panulirus* sp. from shallow-water habitats in Belize and Brazil (Felder et al. 2010; Sant'Anna et al. 2012); however, the results were not conclusive and additional work is needed to evaluate the consequences of *C. hellerii* becoming established in west-Atlantic coastal areas. The colonization process seems to be in its early stages and further monitoring, targeting more diverse habitats such as intertidal, estuaries, and mangroves, is necessary to verify the presence and spread of this invasive crab around Martinique and to assess the consequences of the increasing population on the existing species assemblages.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Geo-referenced information on transects where *Charybdis hellerii* was found in Martinique.

Table S2. Additional observations of *Charybdis hellerii* in the French Lesser Antilles.

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