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The complete disappearance of a long standing sacoglossan sea slug population following Hurricane Irma, despite recovery of the local algal community

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Abstract
Hurricanes often have large impacts on shallow marine ecosystems and the organisms living within. Here we document the impact of hurricane Irma to a long-standing population of sacoglossan sea slugs in the Florida Keys, USA. For many decades, researchers have been studying a population of *clarki* ecotype *Elysia crispata* at a borrow pit (limestone excavation) on Crawl Key, FL. This sea slug has been of interest due to an unusual relationship with its food algae termed kleptoplasty, where the slug sequesters chloroplasts taken from the food algae inside of its own cells and uses them for photosynthesis. Following Hurricane Irma, multiple intensive searches failed to find any *E. crispata.* This population, which at one point numbered in the thousands, has now been completely eliminated from this habitat for over two years following the hurricane. However, the algal population which previously sustained these slugs has fully recovered. Although this habitat now appears to be ideal for these slugs in terms of food availability, they have failed to recolonize. The reasons for this are unclear, but are likely due to the very short dispersal larval stage in this species. The loss of this population is unfortunate as it was the one best studied populations of photosynthetic sea slugs.

Keywords Hurricane Irma · Florida Keys · Sacolossa · *Elysia crispata* · *Clarki* · Population loss

1 Introduction

The impacts and recovery of nearshore marine habitats from large scale disturbances caused by hurricane passage have been described in varying detail depending on the habitat and the severity of the storm (Woodley et al. 1981; Rogers et al. 1991; Rogers 1993; Connel 1997; Bythell et al. 2000; Gardner et al. 2005; Rogers and Miller 2006; van Tussenbroek and Barba-Santos 2011). Most studies have focused on hurricane impacts on corals, sponges, and fishes (Woodley et al. 1981; Fenner 1991; Wulff 1995) but the effect of the storms on the free-living invertebrates is less well known and, in particular, almost nothing is known on those species living in off reef, nearshore habitats (but see for example, Kobluk and Lysenko 1993; Knowlton et al. 1990). Serendipitously, we have had occasion to observe the effects of two hurricanes (Wilma, in October 2005 and Irma, in September 2017) on a population of sacoglossan sea slugs residing in a borrow pit (limestone quarry) in the Florida Keys. Wilma, on a SW to NE track, passed offshore just to the north of the chain of Keys as a Category 3 storm before making landfall on the west Florida coast (Pasch et al. 2006). Although the eye moved 48 km or so north of the islands, there was a storm surge of 1.5–2.4 m from the south as the storm was arriving and a reverse surge of 1.5–2.4 m from the north the next day after the storm passed (Pasch et al. 2006). In many places along the island chain US Highway 1 was completely inundated. Irma was on a S to N track and the eye crossed Cudjoe Key as a Category 4 storm causing catastrophic destruction, especially along the east side of the storm (Cangialosi et al. 2018). Our study site (see cover image and below) was about 32 km to the east of the eyewall of Irma and was impacted by both storms.

The lettuce slug *Elysia crispata* (Mörch, 1863), the largest sacoglossan species in the Caribbean, is one of the better studied sea slugs (Clark 1994; Pierce and Curtis 2012; Pierce et al. 2015). Unlike most sacoglossans, *E. crispata* does not use

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kleptoplastic chloroplasts from a single algal species, but instead is able to acquire chloroplasts from a variety of siphonaceous green algal species (Curtis et al. 2006, 2015; Christa et al. 2014; Middlebrooks et al. 2014, 2019). After suctorially feeding on the algal filaments, the slug intracellularly sequesters chloroplasts in cells lining the digestive tubules. The chloroplasts can then perform photosynthesis for 3–4 months post feeding providing nutrition to the slug a process called kleptoplasty (Middlebrooks et al. 2011, 2012). Additionally, the slug shows reduced feeding activity for several months after chloroplasts are sequestered (Middlebrooks et al. 2011) and is able to synthesize chlorophyll, necessary in maintaining functional chloroplasts (Middlebrooks et al. 2012). *Elysia crispata* lives in shallow, coral reef habitats, commonly on algae-overgrown coral rocks or rubble. In mangrove swamps, mooring canals and borrow pits in the Florida Keys occurs a group of lettuce slugs that differ morphologically, developmentally, and molecularly from the *E. crispata* reef dwelling populations (Nuttall 1987; Pierce et al. 2006). In addition, while there is some dietary overlap between slugs from both habitats, each group feeds on unique algae (Middlebrooks et al. 2014, 2019). Based on differences in allelic frequencies determined by starch gel electrophoresis, the reef and mangrove dwelling slugs were initially described as different subspecies (Nuttall 1987). Subsequently Pierce et al. (2006) named the mangrove dwelling populations from the Florida Keys *E. clarki* based on careful morphological, developmental, and molecular analyses. However, *E. clarki* was recently synonymized with *E. crispata* using statistical similarities in the sequences mitochondrial CO1 and nuclear H3 gene sequences (Krug et al. 2016). Nevertheless, because of the striking, non-overlapping suite of biological and habitat differences between the two groups, *clarki* was retained as a distinct ecotype (Krug et al. 2016; Middlebrooks et al. 2019). For the purposes of this paper, we will use "*clarki*" for the slugs we studied in the Keys as we have no information on the offshore reef populations, which in the Florida Keys always display the typical *crispata* ecotype and never the *clarki* ecotype.

Within the Florida keys the *clarki* ecotype has been found from Lake Surprise in Key Largo to the east to Key West in local habitats such as mangrove swamps, mooring canals, and borrow pits (Pierce et al. 2006; Middlebrooks et al. 2014), although slugs displaying the *clarki* ecotype have also been reported in the Bahamas (Krug 2016). Borrow pits, as referred to in this study, are limestone quarries used during construction of the road beds and causeways of the Overseas Highway (US1) and the Key West Extension of the Florida East Coast (F.E.C.) Railway (sometimes incorrectly called the Overseas Railway). The latter was destroyed by the Category 5 hurricane in 1935. The pits are now full of seawater and have exposed vertical limestone walls, low water flow, and no wave action (Clark and DeFreese 1987). The limestone walls support a diverse assemblage of macroalgae and invertebrates varying amongst the pits, and sometimes include *clarki*. A particular borrow pit located on Crawl Key Florida (the Pit hereafter, Fig. 1) has been the population source of slugs for a great variety of studies (e.g. Marcus and Marcus 1962; Clark and DeFreese 1987; Clark 1994; Pierce et al. 2006; Curtis et al. 2006; Middlebrooks et al. 2011, 2014; Curtis et al. 2015 [These publications all mistakenly list the location of the pit on Grassy Key, likely due to incorrectly placed local road signage]). The Pit is located on the Florida Bay side of Crawl Key, to the Northwest of US 1 (24°44′58.4"N 80°58′ 44.2"W) between mile markers 56 and 57.

The age and original purpose of this particular borrow pit is unclear. Barham (1991) states that it was dug in the early 1900s without any supporting reference. However, the Pit is not noted in F.E.C. Railway right of way and track blueprints of the area created in 1916 and later modified in 1927 (Bramson Archive 2019). Furthermore, a comparison of maps of the Key Vaca and Crawl Keys shorelines in 1937 versus 2000 also suggests that the pit was not yet present in 1937 (Gallagher 2004). More likely, the Pit was used to supply limestone fill for the Overseas Highway (or some other construction project) after 1937. Archival aerial photography indicates that by 1955 the Pit was present (Fig. 1a), but apparently abandoned, so it has been there for at least 70 and perhaps over 80 years.

The Pit is roughly square, approximately 180 m along the edge parallel to US 1, and 165 m on the edge extending towards Florida Bay. It has a flat bottom mostly 3 m deep, with occasional patches up to 10 m in depth, and several shallow (< 1 m depth) points which may be exposed at low tide (Barham 1991 and our own measurements). It was full of water in the 1955 photo, open to the sea through a space in the mangrove swamp on the Northside, with the rest of its margin surrounded by moderate mangrove vegetation and solid limestone walls (Fig. 1a). In July 1961, the bay side of Crawl Key, likely referring to the Pit, was noted to contain "numerous specimens" of *E. crispata* some of which were collected and deposited at the museum at the University of Miami Marine Lab (now RSMAS Marine Invertebrate Museum) by C. R. Robins and Reeve M. Bailey (UMML 30. 2713) (Marcus and Marcus 1962). Clark (1994) reported that populations of *E. crispata* in the Pit numbered over 1000 in the 1970s with densities over 1 slug m^{-2} but cautioned that the overcollection of slugs for the commercial aquarium trade and for research had reduced that population to under 100 individuals. No studies since have focused on conservation of these species, and besides the Pit little is known about population sizes for other locations. However, so called "lettuce slug" populations, which are likely a combination of *crispata* and *clarki*, in the Florida Keys have survived despite continuous commercial fishing which peaked at over 16,000 slugs collected in 2009 (Table 1, FWCC 2019).

Six weeks after Hurricane Wilma passed to the north of the Pit in 2005, we found no slugs in either the Pit or the adjoining mangrove swamp to the north and the Pit was full of floating

Fig. 1 Aerial photographs of the Crawl Key Borrow Pit from **a** 1955 (Monroe County Library Collection (2019a), Photo courtesy of Edwin O Swift III); **b** 1987 (Monroe County Library Collection (2019b)); and **c** 2018 (2018 Google), scale for (C) = 100 m. All photos have the Atlantic Ocean (south) at the top and the mangrove swamp which opens into Florida Bay is at the bottom. The road running vertically across the upper part of the images is US 1 which follows the original railroad right of way, while the trail paralleling US 1 just above the Pit is the original simple road bed completed in 1930 which extended from Grassy Key to Knights Key and is now a bicycle path. Since 1955 there has been a gradual increase in the surrounding mangrove forest area and density to the extent now that the Pit is almost completely walled off from the sea by mangroves

dead seagrass leaves washed in from the shallow adjacent seagrass flats in Florida Bay. We were not able to do any regular collecting or surveys during the following months but after about 18 months, the dead sea grass had disappeared and the *clarki* had returned. Surveys conducted by us at the Pit, post Wilma, in 2008 and 2009 found that the *clarki* population had recovered a peak density of ~3 slugs m^{-2} (Middlebrooks et al. 2014). Also, in 2008–2009 surveys, the site had algal communities similar, although not identical, to those described by Clark and DeFreese (1987), Middlebrooks et al. (2014). Following a very cold winter in 2010 where nearby air temperatures reached a record low of 4 °C (National Weather Service 2010), the population of *clarki* was reduced to ~1 slug m^{-2} (Middlebrooks et al. 2014), but recovered subsequently to a similar density as seen in previous years. We were able to continue field and lab research on slugs collected from the Pit up through the summer of 2017.

On September 10, 2017 Hurricane Irma made landfall in the Florida Keys as a Category 4 storm about 40 km west of the Pit with winds over 180 km/h and a greater than 3 m storm surge (Cangialosi et al. 2018). In the present study, we document the complete disappearance of the *clarki* ecotype population from the Pit following Hurricane Irma, and the changes in the present algal community from surveys on several pre-Irma dates.

2 Methods

Following Hurricane Irma, exhaustive searches for *clarki* using 4 or 5 trained collectors were made during the day at the Pit and adjoining mangrove swamp on April 6, 2018; November 10, 2018; March 16, 2019; April 26, 2019; and November 8, 2019 for ~3 h during each search period. An additional search was conducted on June 11, 2019 in

Table 1 The number of landings of Lettuce Sea Slugs (*Elysia crispata*, with no designation for ecotype or specific collection site) collected by commercial fishermen as reported to the Florida Fish and Wildlife Conservation Commission

Year	*Elysia crispata* commercial landings
2009	16,361
2010	12,415
2011	7485
2012	10,743
2013	14,104
2014	9717
2015	6083
2016	6034
2017	5006
2018	3430
2019[a]	2838
Grand Total	94,216

[a] 2019 data are preliminary (FWCC 2019)

conjunction with detailed surveys of the algal community using similar survey protocols and in the same areas surveyed and described by Middlebrooks et al. (2014). A total of 93 $1m^2$ non-overlapping quadrats were examined along the limestone wall of the Pit which previously contained hundreds of slugs (Clark 1994; Middlebrooks et al. 2014). Slugs and algae can utilize both horizontal and vertical substrate, therefore quadrats were adjusted to include vertical surfaces as necessary. In each quadrat the presence of all green macroalgae was recorded to the lowest taxonomic level possible and percent cover was estimated for each quadrat. In addition, each quadrat was carefully examined for *clarki*, as well as any egg masses which might belong to the slugs. Detailed care was taken to adequately search for slugs that might be in hidden locations such as the base of algae or in crevices in the limestone.

The average total cover for each algal species was calculated across the entire survey area by dividing the cumulative sum of algal cover by the number of total quadrats sampled. In order to compare how the algal diversity has changed over time species richness (total number of green macroalgal species present) and the Shannon Diversity Index (H′) were calculated for the current study and 2008, 2009, and 2010 surveys from Middlebrooks et al. (2014) using the following equation (Shannon 1948):

$$H' = -\sum p_i \ln p_i$$

where $p_i = n_i/N$, where n_i is the number of individuals in species i and N is the total number of individuals in each sample year. Higher H' values indicate a more diverse habitat. Because determining the number of individuals of a given alga is complicated due to variation in morphology and vegetative growth, and because Middlebrooks et al. (2014) only recorded presence/absence data for each quadrat the number of individuals for each algal species was determined as the number of quadrats containing a given algal species for the purposes of calculating H'. Only green macroalgae were included in those calculations.

3 Results

The first examination of the Pit following Hurricane Irma in April 2018 indicated catastrophic biological damage. Both the surface and floor of the Pit were completely covered with a thick layer of rotting turtle grass (*Thallasia testudinum*) leaves that had washed in from Florida Bay to the north. The visibility in the water in the Pit was greatly reduced. Although this first inspection of the Pit was cursory, no individuals of *clarki* were found. Furthermore, no slugs have been found during the subsequent, organized surveys of the Pit and they are still absent from this location as we write. Once the dedicated surveys began in June 2019, a few quadrats were found to contain egg masses that might have been sacoglossan, but the coloration and egg mass morphology did not match those described for either *E. crispata* ecotype (Pierce et al. 2006; Krug et al. 2016). During the search of the Pit on April 6, 2018, a large number of *Elysia subornata* were found on *Caulerpa* spp. During subsequent surveys the *E. subornata* were not present, but bright orange egg masses were found on June 11, 2019 that matched the description of *E. subornata* egg masses (Clark and Goetzfriend 1978; Krug 2009). However, species source of egg masses cannot be conclusively determined solely by visual examination in the field.

The most common alga during the 2019 surveys was a microalgal mat consisting of multiple species of unidentified microalgae, which covered ~30% of the surveyed surface of the habitat. However, many species of green macroalgae were also present, the most common of which was *Caulerpa mexicana* (~12% cover). Other common algal species included *Acetabularia* spp. (~6% cover), *C. cupressoides*(~5% cover), *C. verticillata*(~4% cover), *Halimeda incrassata*(~3% cover), and *Penicillus capitatus*(~3% cover). Less common species (less than 2% cover) included *Avrainvillea* spp., *Batophora* spp., *Bryopsis* spp., *C. ashmeadii*, *C. sertularoides, C. prolifera*, *P. lamourouxii*, *P. dumetosis, Udotea* spp. as well as the seagrass *Syringodium filiforme*.

The green macroalgal composition of the Pit was more diverse in 2019, almost 3 years post-hurricane, compared to 2008, 2009, and 2010 (Middlebrooks et al. 2014) and included seven species of algae not previously recorded in that habitat (Table 2). In 2019 the Pit had a green macroalgal species richness of 15 and a Shannon Diversity Index (H′) of 2.21 compared to 2008 where species richness was 6 and H′ =

Table 2 Comparison of the number of quadrats (*) that contained a given algae species by year at the Pit (*n* = 80 quadrats in 2008, 2009, 2010; *n* = 93 quadrats in 2019)

Year	AC	AV	BT	BR	C Ash	C cup	C mex	C pro	C ser	C ver	H mon	H inc	P cap	P dum	P lam	UD
2008	57*	0	14	0	0	0	50	0	0	35	1	0	0	0	0	6
2009	77	0	3	0	0	0	65	0	0	50	0	0	0	0	0	9
2010	25	0	1	5	0	0	71	0	0	4	0	16	2	0	16	4
2019	78	2	32	1	1	10	80	1	11	46	0	54	55	9	8	47

AC, *Acetabularia* spp.; AV, *Avrainvillea* spp.; BT, *Batophora* spp.; C ash, *Caulerpa ashmeadii*; C cup, *C. cupressoides*; C mex, *C. mexicana*; C pro, *C. prolifera*; C ser, *C. sertularoides*; C ver, *C. verticillata*; H mon, *Halimeda monile*; H inc, *H. incrassata*; P cap, *Penicillus capitatus*; P lam, *P. lamourouxii*; UD, *Udotea* spp.

1.46; 2009 where species richness was 6 and H′ = 1.26; and 2010 where species richness was 9 and H′ = 1.55.

4 Discussion

Following Hurricane Irma, the population of *clarki*, present in the Pit for at least 5 decades, had disappeared. Although Clark (1994) warned that the Pit population might be at risk from overharvesting and Hurricane Wilma transiently lowered the *clarki* numbers for about 18 months, our survey in 2008 found that the slug population had greatly increased (Middlebrooks et al. 2014). However, in the more than 2 years since Irma, we have not found a single individual in the Pit. Coinciding with the demise of the Pit *clarki*, the number of lettuce slugs (both *crispata* and *clarki* ecotypes) caught for the commercial aquarium trade has declined sharply throughout the Keys since the hurricane, based on the data reported by the Florida Fish and Wildlife Conservation Commission (FWCC). However, many slugs reported to the FWCC were collected elsewhere in the Keys and other factors such as decline in demand for the species in the aquarium trade could impact commercial landings. In addition, the local fishermen may have been occupied rebuilding their homes and businesses post hurricane instead of catching slugs. Regardless, there is a sharp decline in lettuce slug landings in the years following Hurricane Irma.

Although the *clarki* failed to repopulate the Pit following Hurricane Irma, the algae in that habitat have recovered and are now more diverse than previously recorded (Clark and DeFreese 1987; Middlebrooks et al. 2014). The algae now present include not only many species used as chloroplast sources for *clarki*, such as *Penicillus* spp. and *Halimeda* spp. but also *Bryopsis* sp. which is one of the only algal species on which juvenile *clarki* feed immediately post-metamorphosis (Curtis et al. 2007). Additionally, the Pit now contains algal species like *Udotea* and *Avrainvillea* which provide a flat vertical substrate that the slugs preferentially use to oviposit (Krug et al. 2016). Nevertheless, despite the recovery of algae and habitat conditions, the *clarki* ecotype has not recolonized following Irma.

The *clarki* ecotype may eventually reestablish in the Pit. We have found them elsewhere along the Keys, although in much smaller numbers in habitats on Key Largo, Summerland Key, and Key West (unpublished data), so the *clarki* ecotype is not extinct. The exact cause of the Pit population's demise is not known, however there at least two likely possibilities. First, it is possible that debris and potentially hazardous materials were washed into the pit from other areas of the Keys and negatively affected the local population. Initially, the large mass of rotting sea grass blades present immediately after the storm not only blocked sunlight, but likely greatly reduced oxygen and increased the bacterial and perhaps anaerobic protist populations in the water for months, until the dead plant material finally rotted away. However, other photosynthetic organisms like green macroalgae, the Symbiodiniaceae containing sea anemone, *Exaiptasia pallida* and two species of the upside-down jelly fish, *Cassiopea frondosa* and *C. andromeda* have all either survived or recolonized the area. In addition, during the November 2018 search, a motorcycle and a washing machine were in the Pit, and have since either been removed, or slid to the deeper parts of the pit. We previously found a submerged pickup truck and building debris scattered in and around the Pit without noticeable effects on the slugs, so the mass of dead seagrass may well have been the lethal agent. Second, and perhaps in addition, the storm surge produced by the powerful hurricane may have washed the *clarki* out into the adjacent swamp or further into Florida Bay. The *clarki* ecotype is only found in very low wave energy environments (Pierce et al. 2006; Krug et al. 2016) and its less well developed foot, compared to the more muscular, well developed foot of the reef dwelling *crispata* ecotype, may have been unable to maintain attachment to the substrate during the storm surge of the hurricane.

The reasons for the failure to repopulate the Pit are not clear. Although many sacoglossan species have fairly long lived veliger larvae providing a capacity for long distance colonization (Krug 2009), both ecotypes of *E. crispata* have either encapsulated metamorphosis or lecithotrophic larvae with a very short 24–48 h planktonic stage before metamorphosis (Clark and Jensen 1981; DeFreese and Clark 1983; Pierce et al. 2006; Curtis et al. 2007; Krug et al. 2016). A short or absent planktonic period combined with the preference for low wave energy habitat would reduce the chances for dispersal. In addition, the aerial photos (Fig. 1) show that since the 1950s, the mangroves fringing the Pit have slowly increased in density (Fig. 1a–c) to the point that the only opening to the sea on the northern side of the Pit is now almost completely closed off, with only a small shallow mangrove tunnel allowing tidal waters to flow directly into the pit. Thus, larval access to the Pit from outside sources is limited and may eventually be cut off completely. Indeed, over the years we have searched many borrow pits and other similar habitats which appear suitable for large slug populations in terms of wave energy and available algae that nonetheless contained no slugs. Successful establishments of *clarki* into unoccupied locations may be a relatively rare event and even if a few individuals populate an area the lack of genetic connectivity might reduce the chances of a successful population establishing.

Algal populations in the Pit completely recovered by the June 2019 surveys. Similarly, algal communities in Puerto Rico, including many of the same species found in the Pit, recovered within 1 year of hurricane disturbance (Ballentine 1984). However, mixed seagrass and rhizophytic algal beds took longer to recover after a hurricane (Fourqurean and Rutten 2004). In fact, the diversity of green macroalgae in the Pit at the end of our survey period was greater than that previously observed prior to Hurricane Irma. The elimination of the large slug population in the Pit was potentially an important factor in the algal recovery. Similarly, there was also an increase in algal diversity in the Pit in 2010 when the population of *clarki* declined following a very cold winter (Middlebrooks et al. 2014), although temperature effects might have also been involved. Other photosynthetic sacoglossans have significant impacts on algal production in their local habitats. For example, *E. velutinus* suppresses growth of *Halimeda* by up to 50% (Rasher et al. 2015).

The complete elimination of *E. clarki* population at the Pit following Hurricane Irma represents a loss of a large, easily collected source of this ecotype, which has been one of the most extensively studied kleptoplastic species. Local slug habitats are known to have been affected by the passage of Hurricanes, particularly Hurricane Wilma as mentioned previously, and Hurricane Bob in 1991 that wiped out a population of *Elysia chlorotica* on Martha's Vineyard MA, that we have studied since the 1980s (e.g. Pierce et al. 1983, 2003, 2016). In the latter cases, the slugs reappeared in both habitats after about 18 months, essentially a generation later. In the Pit, they seem to be gone. Periodic monitoring of the habitat could provide valuable information about sacoglossan dispersal and colonization, if the slugs ever return.

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