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Safeguarding Florida's Coral Reefs: The Urgency of Assisted Gene Flow for Elkhorn Coral Conservation

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Abstract:

The devastating 2023 heatwave is the latest in a series of disasters that has decimated the Florida population of elkhorn coral (*Acropora palmata*) to a critically low level, pushing this species to a precarious tipping point. Precautionary management currently forbids outplanting of corals from outside Florida. This precaution is intended to prevent the introduction of novel genes that could cause outbreeding depression and to preserve local adaptive variation in the Florida population. However, the multi-decadal decline of Florida's elkhorn corals indicates a lack of adaptation to the shifting environmental conditions on Florida reefs. The potential risks of outbreeding depression associated with introducing new genetic variants from outside sources pale in comparison to the continuous demographic decline through successive heat waves, and the threat of inbreeding depression. Operational risks of Assisted Gene Flow (AGF) can be managed by introducing non-Florida alleles via outplanting of the existing lab-based juveniles rather than adults sourced from the wild. Further, the extent to which new genetic material is introduced should be proportional to Florida's founder population. NOAA's Florida Genetic Management Plan (F3P) can guide the introduction of non-Florida alleles versus the introduction of sexually produced offspring from the limited floridian parental stock. We conclude that assisted gene flow via lab-based crossing of Florida's elkhorn with elkhorn from elsewhere in the Caribbean is a strategy with manageable risks and mission-critical benefits. AGF should be implemented urgently to introduce new genetic variants, thereby increasing the elkhorn coral's genetic diversity, and enhancing the resilience of these populations to future stress. Without such intervention, coupled with the high probability of additional 2023-scale heatwaves, the grim prospect of completely losing all elkhorn corals from Florida's reefs within this decade becomes increasingly probable.

Introduction

The dire status of reef-building corals has prompted increasing consideration of interventions involving breeding and/or translocation of individuals beyond their natural dispersal range. Such "conservation translocation" or "assisted gene flow (AGF)" (depending on the details of implementation) has become a common tool for many non-coral species to increase genetic variation, facilitate natural adaptation, and offset extinction risk under rapidly changing environmental conditions (Karasov-Olson et al. 2021; IUCN/SSC 2013; Seddon et al. 2014; Berger-Tal et al. 2020). However, despite many successful introductions (e.g., wild dogs in South Africa, Davies-Mostert et al. 2009; Iberian lynx, Simón et al. 2012; wolves in Yellowstone National Park, Smith and Peterson 2021), these measures are inherently complex and carry a number of theoretical risks.

These risks must be evaluated against the cost of inaction. For many coral species and locations, risks of inaction include local extinction and further loss of the coral reef ecosystem functions and services upon which coastal communities depend (Costanza et al. 2014; Kleypas et al. 2021). The perceived risks of genetic mixing of historical coral populations must also be weighed against a backdrop of ongoing climate-induced species invasions and range shifts, which have already altered biotic interactions and will continue to do so into the future. Such changes justify altering earlier paradigms of what “local” means. For example, many species of coral are already undergoing range expansions (Precht and Aronson 2004; Kumagai et al. 2018) and climate change is likely also driving changes in patterns of association between corals and their microbial associates (e.g., increases in the dominance of invasive heat-tolerant *Durusdinium trenchii*).

Here, we summarize evidence showing that the guiding principles of coral conservation genetics (“local is best” and “gene flow beyond historically connected populations is not allowed”) are no longer precautionary in the rapidly changing oceans (Phelan et al. 2021). Overestimation of genetic risk has so far prevented AGF; meanwhile permanent loss of genotypic and allelic diversity from certain areas of Florida’s coral reef has been occurring, even prior to 2012 (Williams et al. 2014). Species now must adapt to survive conditions that are rapidly warming and more stochastic, and some populations have dwindled to the point that inbreeding risk is high. Strict adherence to banning outplanting of corals resulting from assisted gene flow is likely to lead to local extinctions. Instead, dynamic conservation measures are required to prevent inbreeding depression of locally decimated populations and enrich the pool of genetic variation to promote adaptation. Such measures can be implemented responsibly by better utilizing the coral stock already in hand, as well as by pursuing additional, Caribbean rangewide genetic diversity. We specifically advocate for the need to immediately implement assisted gene flow strategies to reduce the risk of bottlenecks, inbreeding depression, and local extirpation of corals.

Status and trends of *Acropora palmata* populations in the Florida Keys

The elkhorn coral, *Acropora palmata*, is an iconic Caribbean reef-building species, and the key constructor of protective reef crest and spur structure in the western Atlantic region. It features as the primary target species in NOAA’s “Mission: Iconic Reefs” restoration plan for the Florida Keys (NOAA, 2019) and was formally listed under the US Endangered Species Act in 2006. However, this species continues to display precipitous declines in Florida. The decline of *A. palmata* in the Florida Keys started in the 1980s when white band disease swept through the Caribbean (Aronson and Precht 2001). Continued episodic disturbances such as a 2010 cold-water mortality event (Lirman et al. 2011), heatwaves in 2014 and 2015 (Williams et al. 2017), and Hurricane Irma in 2017 (Williams et al. 2020), have resulted in a continual ratcheting down of the population with essentially no signs of recovery between events (Williams et al. 2008, 2014).

In the Upper Florida Keys, *A. palmata* stands have been intensively monitored since 2004, providing reliable data on genotypic abundance and a robust database for projecting the near-term prognosis. Each individual fragment within fixed permanent plots has been genotyped and tracked in this area over the last ~20 years (Williams et al. 2006, 2014). Over this 20-year period, **no new larval recruits have been observed in this population** (Williams et al. 2008, 2014, 2024). By 2022, a perilously small population of only 84 “wild” genets of *A. palmata* remained in the Upper Keys (50 km span from Turtle Rocks to Conch Reef), down from 158 in 2002 (Williams et al. 2024), prompting the formation of the Florida Palmata Population Program (F3P), which concluded that careful genetic management of this species was needed in restoration actions to prevent additional loss of genetic diversity via inbreeding and genetic drift (Rodriguez-Clark et al. 2023). Unfortunately, the 2023 heatwave (June-Oct) further reduced the population of wild genets in the Upper Keys to only 23 (Williams et al. 2024, Appendix B). Heroic efforts prior to the 2023 bleaching event ensured that tissue of all known 187 genets, sourced from throughout the Florida Reef Tract, survives in captivity. Yet, the loss of 61 of the 84 wild Upper Keyes genets (72%) in just over 20 years is dramatic. Worse still, many of the remaining *A. palmata* stands are monoclonal with no mating partner nearby and the genets persist only as remnant ‘scraps’ of tissue which are not capable of gametogenesis and spawning for the next 2-3 years. Our best understanding is that elkhorn corals in the middle and lower Keys fared even worse (Manzello et al. in prep). The last remaining wild genet of *A. palmata* in the Dry Tortugas and the five upper Keys genets that had been translocated there in 2018 (Kuffner et al. 2020) have been extirpated. The Mission: Iconic Reefs program has reported that <5% of >1,000 *A. palmata* fragments outplanted across the Florida Keys survived the 2023 heatwave (Lesneski et al., unpublished). Based on these data, it may be presumed that *A. palmata* has been functionally extinct (i.e. unable to recover through natural recruitment) for some time, and local extirpation of this population is projected within this decade. In summary, the outlook for elkhorn corals in Florida is dire, and the need to implement assisted gene flow, and other more aggressive strategies, is urgent.

Potential Intervention Risks:

Outbreeding Risks

Assisted gene flow is the movement of alleles via human intervention. Presumed genetic risks of AGF, such as the potential for outbreeding depression, are rooted in the assumption that geographically distant populations, at or near isolation, perform best at their ‘native’ reef site and that this performance advantage has a genetic basis. For example, *A. palmata* populations in Curacao may have increased frequency of alleles that increase their growth, survival, and/or reproduction when growing on Curacao reefs, but these same alleles might decrease survival or fecundity at other reef sites. As such, their prospective offspring would lose such adaptive phenotypes if grown on reefs outside Curacao, or interbred with coral from them. While outbreeding depression has been discussed as a theoretical risk, evidence for outbreeding depression as a result of conservation action is rare in animals (Frankham et al. 2011; Frankham 2015, 2016). In cases where outbreeding depression has been observed, Frankham et al. (2017) indicate that fitness is recovered in all cases. Modeling studies also provide support for the notion that hybrid populations are better able to adapt to novel environments than their parents (Kulmuni et al. 2024).

Risks of outbreeding depression depend on the life history of the species under consideration in addition to the unique evolutionary history of the specific population(s). Because corals can be easily fragmented, outplanting of a fragment to an unsuitable environment results in the loss of that fragment but not the loss of the genet provided the genet survives elsewhere. In addition, *A. palmata* colonies spawn many millions of gametes over their long lifespan, so a large number of local and foreign crosses can be attempted, both in nature and under human assistance, to test their survival potential. The small risk of producing potentially poorly adapted offspring due to outbreeding depression must be weighed against the potential benefit of producing novel phenotypes better suited to changing environmental conditions.

Causes for outbreeding depression most often include 1) chromosomal differences that prevent successful sexual reproduction in the F1 or later generations, 2) population bottlenecks and genetic drift, and 3) adaptive differences between populations (Frankham et al. 2011).

1) Chromosomal differences are unlikely to produce outbreeding depression in *A. palmata*. Only two extant Acropora species are found within the Caribbean: *A. palmata* and its sister species *A. cervicornis*. The species diverged around 3 mya with an estimated genome-wide sequence divergence of approximately 10% (33Mb), but have retained a remarkable degree of synteny across their genomes, each featuring 14 chromosomes (Locatelli et al. 2023). When comparing genomic data from *A. palmata* and *A. cervicornis* collected throughout the Caribbean, conservatively 1,692,739 single nucleotide polymorphisms and 149,036 short insertion/deletion sequences (≤ 20 bp) were variable between species (Vollmer and Palumbi 2002; Kitchen et al. 2019). Indeed, these two species occasionally interbreed to form F1 hybrids (aka *A. prolifera*) and rare backcrossing into both parent species is observed (Vollmer and Palumbi 2002; Kitchen et al. 2019). Given that chromosomal synteny is high between sister species, it is expected to be high among populations within the species.

2) Population bottlenecks and genetic drift affect small populations and populations that have experienced rapid demographic declines. *A. palmata* populations were historically large and genetic bottlenecks are not yet evident (Locatelli et al. 2023). *A. palmata* can be separated into the eastern and western Caribbean regions, based on neutral genetic markers with mendelian inheritance (Baums et al. 2005). Levels of absolute genetic differentiation are low, even between reefs in the eastern and western regions

(Devlin-Durante and Baums 2017). Higher resolution genetic markers (single nucleotide polymorphisms or SNPs) have since resolved additional populations within each region on the scale of islands and reef tracts (pairwise F_{st} values from <0.01 between Belize and Honduras to <0.15 between Belize and the US Virgin Islands, Locatelli et al. pers. comm). No population structure could be detected along the Florida Keys from Dry Tortugas to Key Largo based on genetic data for most of the known extant *A. palmata* genets in Florida. A. *palmata* populations spawn concurrently across the range and studies to date on crosses between *A. palmata* colonies from the eastern and western regions (Florida and Curacao) demonstrate gametes are fertilization-compatible and result in healthy coral juveniles (Hagedorn et al. 2021). Populations from across the range should therefore be regarded as potential sources of allelic diversity, regardless of their physical distance or genetic similarity to Florida *A. palmata.*

3) The extent of adaptive differences present in *A. palmata* populations in the Caribbean are not fully understood and not easy to predict. Florida represents the northern limit of the species distribution and its ocean temperatures are more strongly seasonal than anywhere else in the Caribbean. Summer temperatures are warmer and winter temperatures are colder, on average, than at sites further south. However, relative to their local mean monthly maximum temperature, populations outside of Florida, including Curacao have experienced more frequent heat stress. Other factors such as prevalence of infectious diseases, nutrient profile of the water, water clarity and others also differ across the range. Importantly, no performance deficits are evident in aquarium based experiments among offspring (Muller et al. in prep), either from between-region crosses (Florida and Curacao) or from within-region crosses (Curacao/Puerto Rico) (Hagedorn et al. 2021) .There is no guarantee that the AGF recruits will survive better than the native corals on Florida's reefs. Yet, these crosses carry novel allele combinations and could introduce much needed genetic variation into the genetically and genotypically depauperate Florida populations (Muller et al. in prep). Such introduction could fast track adaptation via natural selection to Florida's novel environmental conditions that will lie outside either parent population's environmental envelope (Kulmuni et al. 2024).

Transplantation studies of Florida acroporids both within and among Florida reef locations have found no evidence to date that 'foreign' transplants yield more negative restoration outcomes. In a transplant of *A. palmata* from the upper Florida Keys to the Dry Tortugas (DRTO), Kuffner et al. (Kuffner et al. 2020) and Chapron et al. (Chapron et al. 2023) identified a strong environmental component affecting coral performance (i.e., all transplants exhibited higher growth and lipid content at Lower Keys reefs and especially in the DRTO), but no "home advantage" was detected for the lone DRTO genet at DRTO reefs. Similarly, in a transplant experiment among several reefs in the upper Florida Keys, Drury et al. (Drury et al. 2017) identified both genetic and environmental effects on the growth of *A. cervicornis*, but 'foreign' transplants actually outgrew the 'native' genets. A similar pattern was found for *A. cervicornis* originating from the Lower Keys: native coral genets were not the top performers at their home reef (Million et al. 2022). Similarly, rapid heat stress assays of *A. cervicornis* exchanged among Florida nurseries found that native corals (maintained at their own nursery) were not the most thermally tolerant one year after the exchange, and that the nursery grow-out environment was a much more important driver of thermotolerance for these exchanged corals (Johnson-Sapp 2024).

Inbreeding risks

A. palmata population in Florida is currently at the state where risk of inbreeding depression is particularly high, because it is a historically large population experiencing a very strong and abrupt demographic bottleneck. Large populations tend to contain high numbers of recessive deleterious alleles, so-called inbreeding load (Kardos et al. 2021), which could lead to pronounced fitness decline in the offspring after sudden onset of inbreeding e.g., (Fraimout et al. 2023).

The dramatic demographic decline of *A. palmata* population along the Florida Keys has not yet been accompanied by an increase in homozygosity among their sexual offspring (Locatelli et al., in prep). This is largely because the founder *A. palmata* genets themselves are representatives of older, pre-bottleneck populations that have largely failed to produce sexual offspring over the past decades. This implies that the purging of the inbreeding load as a result of population reproducing while maintaining small size (Kardos et al. 2021) has not yet occurred. Assuming *A. palmata* extinction does not happen and sexual reproduction restarts, the risk of inbreeding depression past the first generation would be very high indeed. Founder genets can be maintained more or less indefinitely via fragmentation in captivity but breeding them now carries increasing risks of inbreeding depression without the addition of alleles from elsewhere in the Caribbean. The difficulties of breeding *A. palmata* are due to asynchronous spawning in the wild and in captivity as well as frequent incompatibility between local genets (Miller et al. 2018). These issues are compounded when there are few genets of reproductive size. Even batch crosses often result in sib and half-sib families that are on average more related to each other than any known wild population of *A. palmata* (Kitchen et al. 2020).

Operational Risks

Operational risks of translocation include the potential for unintended introduction of new pathogens, parasites, or predators. Kuffner et al. (Kuffner et al. 2020) demonstrated that, with appropriate protocols, it is possible to translocate small coral fragments across hundreds of kilometers from the upper Florida Keys to the Dry Tortugas without these negative consequences. Moreover, the existing Florida x Curacao *A. palmata* colonies have been continuously reared (from the larval stage) in biosecure land-based facilities in Florida that are also regularly used as sources of 'native' acroporid outplants to the Florida Reef Tract. With standard vet check protocols we conclude that the risk of unintended introduction is no greater than for 'native' acroporid outplants. Planned translocations are a common recovery strategy for Endangered Species Act-listed species, were instrumental in the recovery and delisting of 47 species (30%), and have "overwhelmingly led to beneficial intended consequences" (Novak et al. 2021). In short, these successful planned translocations provide multiple precedents and convincing evidence for the benefits of such a strategy for *A. palmata* and other endangered coral species.

Risks of Inaction

Based on the population trajectory over the past four decades, and particularly since July 2023, the risk of extirpation of *A. palmata* from Florida is extremely high, and is consistent with, if not exceeding, earlier predictions (Williams et al. 2020). As restoration efforts intensify to rebuild this population, inbreeding depression and/or drift are of increasing concern, but can be minimized with genetic management planning and introduction of additional genetic variation (Rodriguez-Clark et al. 2023). Although the risks of AGF are not zero, they pale compared to the risk of extirpation of *A. palmata* from Florida as a result of continued inaction. We need to act now and facilitate the implementation of assistent gene flow and translocation management strategies.

Recommended Actions:

To assess any potential risk associated with assisted gene flow, the existing Florida x Curacao colonies created in 2018 (Hagedorn et al. 2021) should be outplanted to Florida reef populations and monitored to inform F3P genetic management planning. Outplanting of these novel genets in an area of Florida's coral reef where local extinction of *A. palmata* has already been reported (e.g., the Dry Tortugas) provides a low risk setting for testing their survivorship, phenotypic performance and reproductive behavior (Frankham et al. 2011). In fact, outplanting and monitoring the AGF corals in Florida is a unique opportunity to investigate the risks and benefits AGF may provide. These corals are currently isolated in land-based facilities at Mote Marine Laboratory's gene bank facility in Sarasota, and represent the successful completion of the most difficult breeding steps in an assisted gene flow program and are consequently of considerable conservation value.

Additional AGF actions should also be pursued to incorporate more genetic diversity from across *A. palmata*'s range. Here, existing population genomic data can guide the creation of a balanced portfolio of AGF crosses to introduce novel genetic and phenotypic diversity from across the entire species range. Evidence shows a range in thermotolerance in *A. palmata* populations across the Caribbean (Gomez-Campo et al, unpublished). Given the high likelihood of additional severe bleaching events in Florida going forward, sourcing corals from an even wider range of environments, and indeed finding locations where *A. palmata* experience warm temperature maxima that are as high or higher than Florida's, may be essential. To maximize benefits and minimize risks, a balanced approach of introducing novel genetic and phenotypic diversity while maintaining the Florida founder genets guided by the F3P genetic management plan.

Other coral species will soon be in critical need of genetic rescue as well and it would be prudent to examine these strategies prior to conditions becoming so dire. Early detection and speed of response will be critical to meet future management and restoration goals. *Dendrogyra cylindrus* is already at this point and is also recommended for immediate genetic rescue and assisted gene flow. Other ESA listed species will come next. Given the long time it takes to get permits and international collaborations in place to secure donor parents and/or larvae, we must act swiftly.

Specific projects that are currently at standstill because of the permitting block.
- A permit to outplant any remaining Curacao x FL APAL (still needed) (Hagedorn, others)
- A permit to outplant FL x HONDURAS APAL (and/or PSTR, DLAB) and HONDURAS x HONDURAS APAL (and/or PSTR, DLAB) if generated this summer (Baker)
- A permit to outplant FL x CAYMAN APAL (and/or ACER, CNAT, PSTR, DCYL) and CAYMAN x CAYMAN APAL (and/or ACER, CNAT, PSTR, DCYL) if generated this summer (Baker)

A call to action, starting with least risky.

Only Actions 1 and 2 are discussed here in detail.

1. Continue to preserve FL genets in land- and ocean-based nurseries.
2. Outplant land-facility produced recruits to Florida reefs that have one non-Florida parent.
3. Outplant land-facility produced recruits to Florida reefs which have two non-Florida parents.
4. Outplant recruits to Florida reefs that have two non-Florida parents and were imported to Florida as larvae or settled recruits.
5. Outplant non-Florida parental colonies to Florida reefs.

Appendix A.

Common terms for understanding the genetic basis of traits

Adaptive Trait: A feature of an organism that enables or increases the probability of that individual surviving and reproducing in a particular environment.

Assisted gene flow: Assisted gene flow is the movement of alleles via human intervention.

Allele: The variant form of a gene or genetic marker.

Allelic diversity: A measure based on the number of different genetic variants (alleles) segregating in the population.

Crosses: Human assisted sexual reproduction via combining gametes. Can be done as batch crosses when gametes from several parent genets are combined into one cross.

Genetic variants: Alternative alleles for the same gene.

Genetic diversity: The collection of genetic variants across all genes within an individual, population, or species. Usually estimated as the average frequency of genetic variants (expected heterozygosity).

Genotype: “Is the genetic makeup of a sample for a given (set of) genetic marker(s). When enough markers are assayed, a sample can be assigned to a genet based on its genotype”

Genets: “Are formed by sexual reproduction. All colonies and tissue that can trace their ancestry back to the same fertilization event belong to the same genet”.

Genetic load: The sum of recessive deleterious mutations an individual or a population carries. It is unmasked by inbreeding, leading to inbreeding depression.

Inbreeding Depression: Reduction of a population's fitness as a result of breeding closely related individuals due to the increased probability that an offspring will inherit alleles that are identical by descent (i.e., nonrandom mating). Inbreeding depression may result from either partial dominance (the effect of exposing deleterious recessive alleles) or overdominance (decline in heterozygosity advantage). Therefore, inbreeding depression is an a priori concern for any population with a high probability that offspring will inherit alleles that are identical by descent.

Outbreeding Depression: Reduction of fitness in a population as a result of breeding individuals from a (genetically) distant population with local individuals. Can be due to incompatibility of foreign genetic variants with local ones, and/or because foreign variants are maladaptive in the local environment. Unlike inbreeding depression, the risk of outbreeding depression depends on both the life history of the organism and the unique evolutionary histories of the (near-) isolated populations. Consequently, the risk of outbreeding depression can only be assessed a posteriori based on prior knowledge of the unique history of the populations in question.

Outplants: Coral ramets that have been translocated between sites or from captivity to the wild.

Population: a population is a group of genets that breed mostly or solely amongst themselves, as a result of geographic proximity, albeit they could breed with other members of the species. Populations can be distinguished using population genetic statistical models that analyze allele frequency differences derived from neutral genetic markers.

Parental colonies: Colonies from which gametes have been collected

Stands: Aggregation of coral colonies on a reef, often the result of fragmentation.

Appendix B:

Genet inventory of extant 'wild' *A. palmata* genets in the upper Florida Keys (~ 50 km span of the reef tract between Turtle Rocks and Conch Reef). A) Total inventory of founder genets cumulated from samples collected from reefs across this region between 2002-2022 based on the STAGdb. B) Extant 'wild' genets on demographically monitored reefs before and after the 2023 heatwave, parsed by colony size which is indicative of reproductive potential (colonies termed 'reproductive' had at least one ramet > 40 cm in largest dimension which is deemed minimum reproductive size). Sixty-one out of 84 (73%) were lost and only one site retains more than one potentially reproductive genet. Our best current understanding is that the situation in the lower Keys was worse, with higher heat exposure and even less survivorship of *A. palmata*. Data from Williams et al. 2024[1]

A)

Reef	Founder Genets
Allans	1
Carysfort	10
Conch	4
Elbow	35
French	13
Grecian	4
Horseshoe	3
Key Largo Dry Rocks	8
Little Conch	2
Little Elbow	2
Little Grecian	3
Molasses	21
North Dry Rocks	4
North North Dry Rocks	6
Phils	1
Pickles	9
Sand Island	7
Snapper Ledge	1
South Carysfort	7
South Carysfort Patch	1
Triple A	3
Turtle Rocks	6
U91	1
Watsons	6
Grand Total	158

B)

	Early Summer 2023		Post- Bleaching Fall 2023		
Reef	**Repro-ductive**	**Remnant**	**Repro-ductive**	**Remnant**	**Summer Dead**
Allan's	1	0	0	0	1
Carysfort	3	2	0	1	4
Conch	2	1	0	0	3
Elbow	24	4	12	6	10
French	2	2	0	1	3
Grecian	2	2	0	0	4
Horseshoe	2	0	0	0	2
Little Conch	2	0	0	0	2
Little Elbow	2	0	1	1	0
Little Grecian	2	0	0	0	2
Molasses	4	0	0	0	4
North Dry Rocks	4	0	0	0	4
North North Dry Rocks	4	0	0	0	4
Phil's	1	0	0	0	1
Pickles	1	1	0	0	2
Sand Island	1	1	0	0	2
South Carysfort	3	1	0	0	4
South Carysfort Patch	1	0	0	0	1
Triple A	1	0	0	0	1
Turtle Rocks	1	0	0	0	1
U91	1	0	0	0	1
Watson's	6	0	0	1	5
Total	70	14	13	10	61

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[1] Williams DE, Nedimyer K, Bright AJ, Ladd MC (2024) Genotypic inventory and impact of the 2023 marine heatwave on *Acropora palmata* (elkhorn coral) populations in the Upper Florida Keys, USA: 2020-2023. NOAA Fisheries SEFSC, Miami, FL 30p

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