Population Connectivity of Shallow and Mesophotic Coral Ecosystems: Role of Population Genetics

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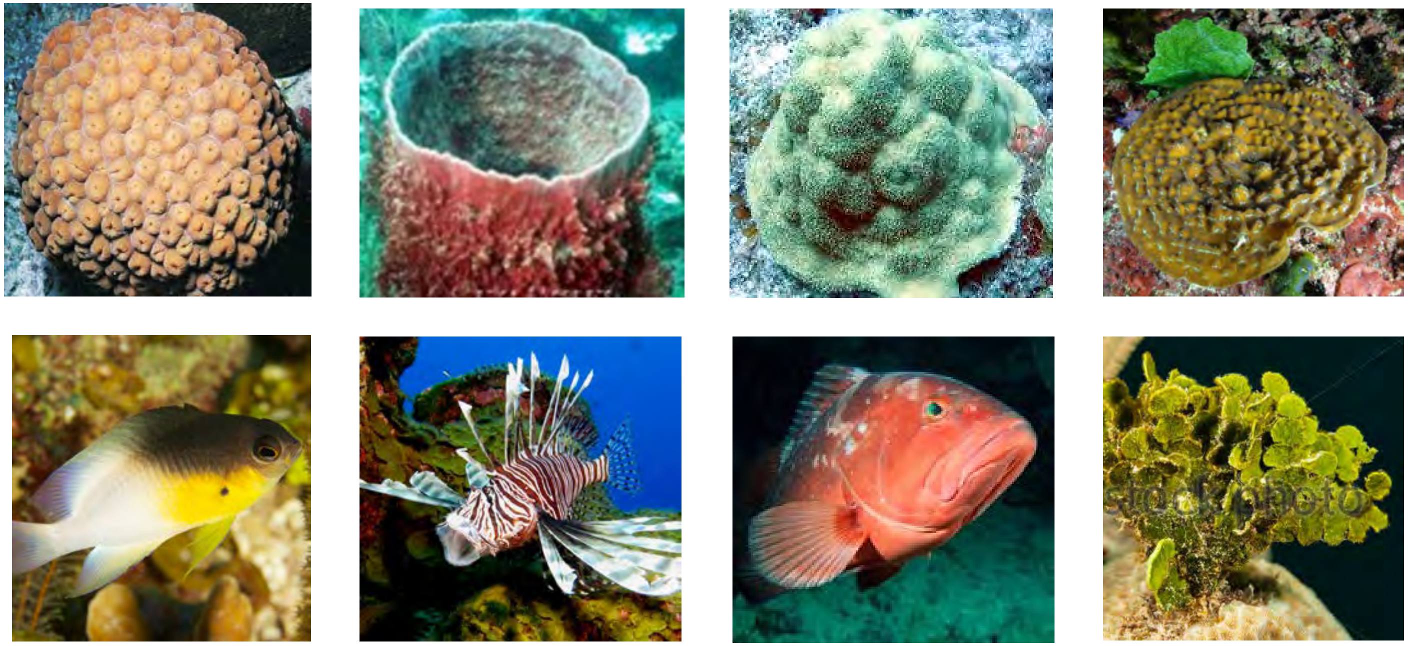

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Goal: To understand population genetic connectivity between Pulley Ridge and the Florida Keys

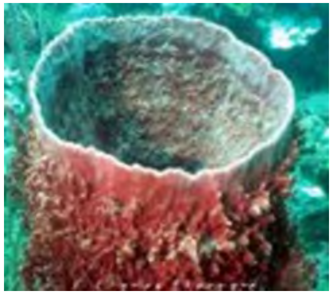
Objectives:

- Assess genetic connectivity for up to 8 model species in the region
- Quantify the magnitude and direction of connectivity between populations where possible
- Compare genetic data to biophysical model predictions of connectivity for selected species

Target species

Great star coral
Montastraea cavernosa

Giant barrel sponge
Xestospongia muta



Mustard hill coral
Porites astreoides

Lettuce corals
(Scleractinia; Agariciidae)

Bicolor damselfish
Stegastes partitus

Lionfish
Pterois volitans

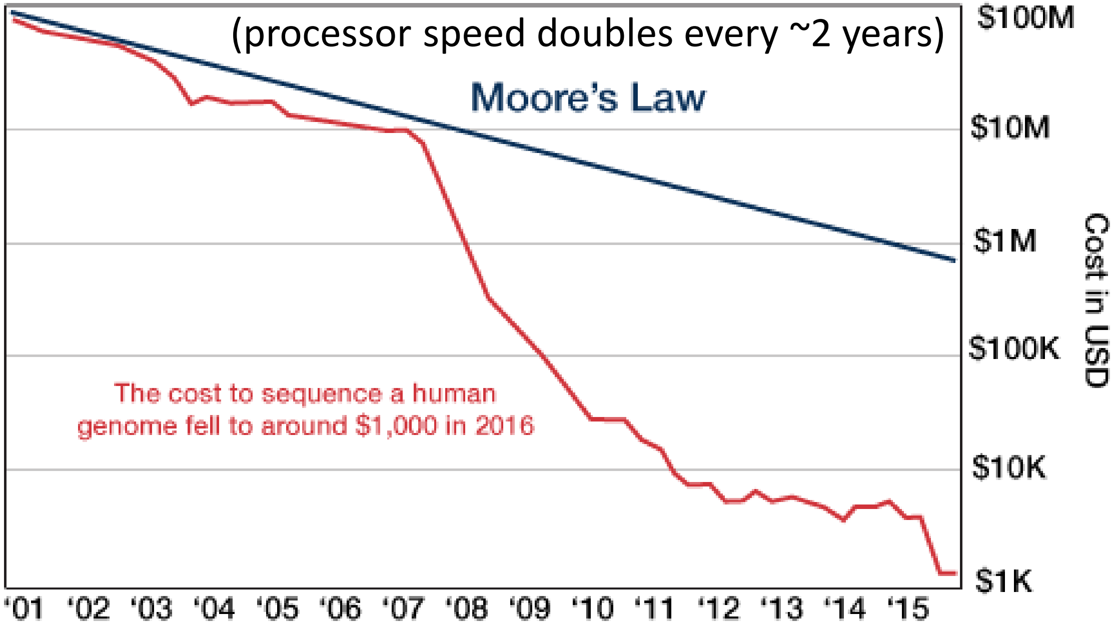
Red grouper
Epinephelus morio

Green cactus algae
Halimeda spp.

Multiple cryptic, deep-water species

Mixture of vertebrates and invertebrates with different life histories, including foundational, invasive, and commercially valuable species

The genomic era of discovery....



Cost of sequencing a human genome

2003: 2.7 billion (over a decade)
2001-08: Followed Moore's law
2008: 5X Moore's law
2016: $1,000
2020: <$100?

"$1,000 genome"
vs. "$1-million interpretation"

Implications for genetic study of marine species

Then: Microsatellites (msats)

Only assess a tiny fraction of the entire genome (typically 10-20 markers or "loci")

Reveal large-scale differences in population structure and can be used to check identity or clonality

Now: Single nucleotide polymorphisms (SNPs)

Organisms can be SNP-genotyped at 1000s or 10,000s of markers ("loci")

Much larger fraction of the genome is assessed, revealing fine-scale differences in population structure

Life history: Corals

Foundational habitat-building taxa on reefs

Great star coral

- Common and widespread
- Colonies are gonochoric (either male or female)
- Broadcast spawner
- Larval competency "several days to weeks" (Goodbody-Gringley 2009)

Mustard hill coral

- Common and widespread
- Broods internally-fertilized eggs
- Colonies are either hermaphroditic or female
- Pelagic larval duration (PLD) "unknown"

Great star coral

(*Montastraea cavernosa*)

Depths: 3-100m

Broadcast spawner

Potentially long larval duration

("several days to weeks")

⬇

↑ Dispersal?

↑ Connectivity?

Mustard hill coral

(*Porites astreoides*)

Depths: 1-70m

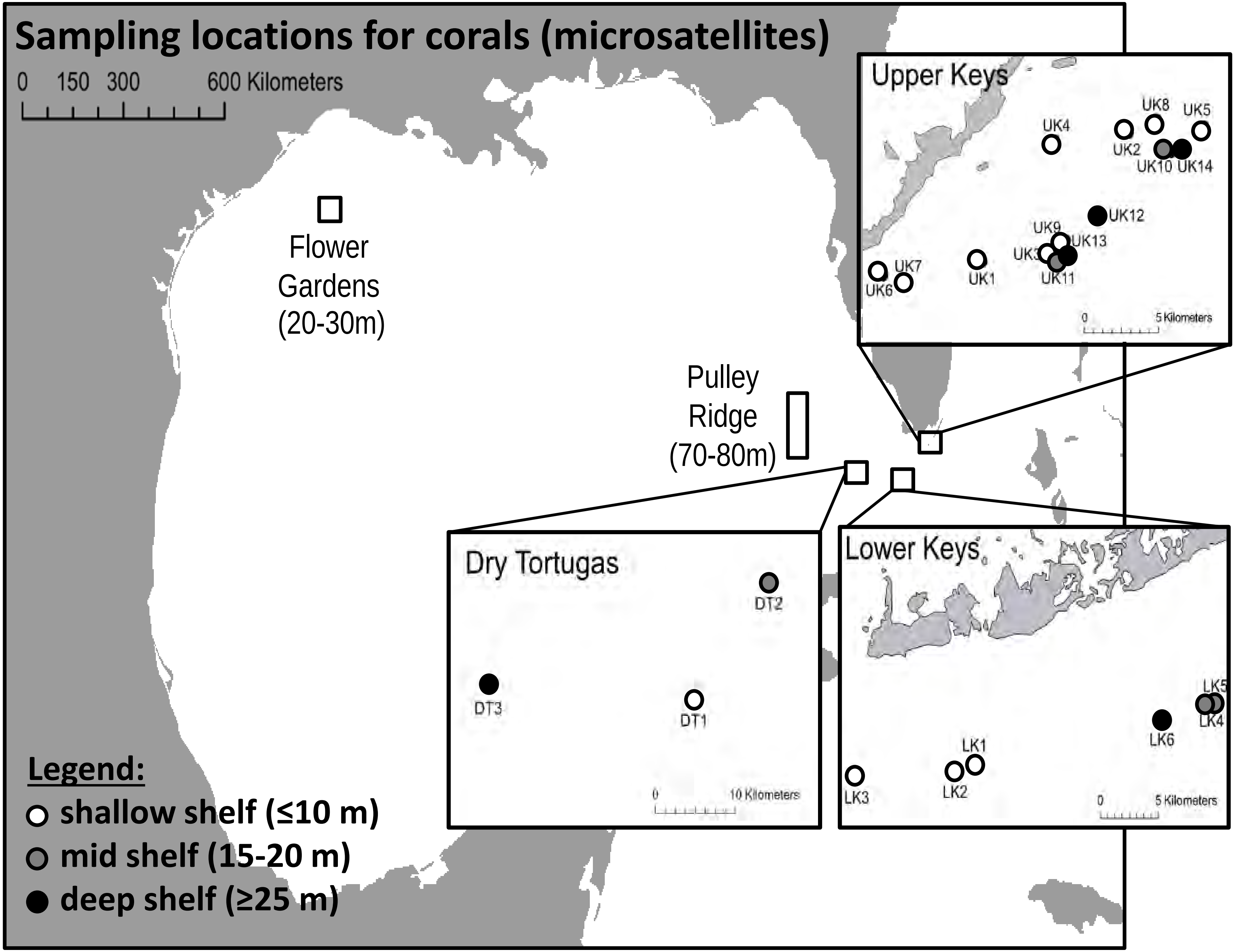
Brooder

Potentially short larval duration

⬇

↓ Dispersal?

↓ Connectivity?

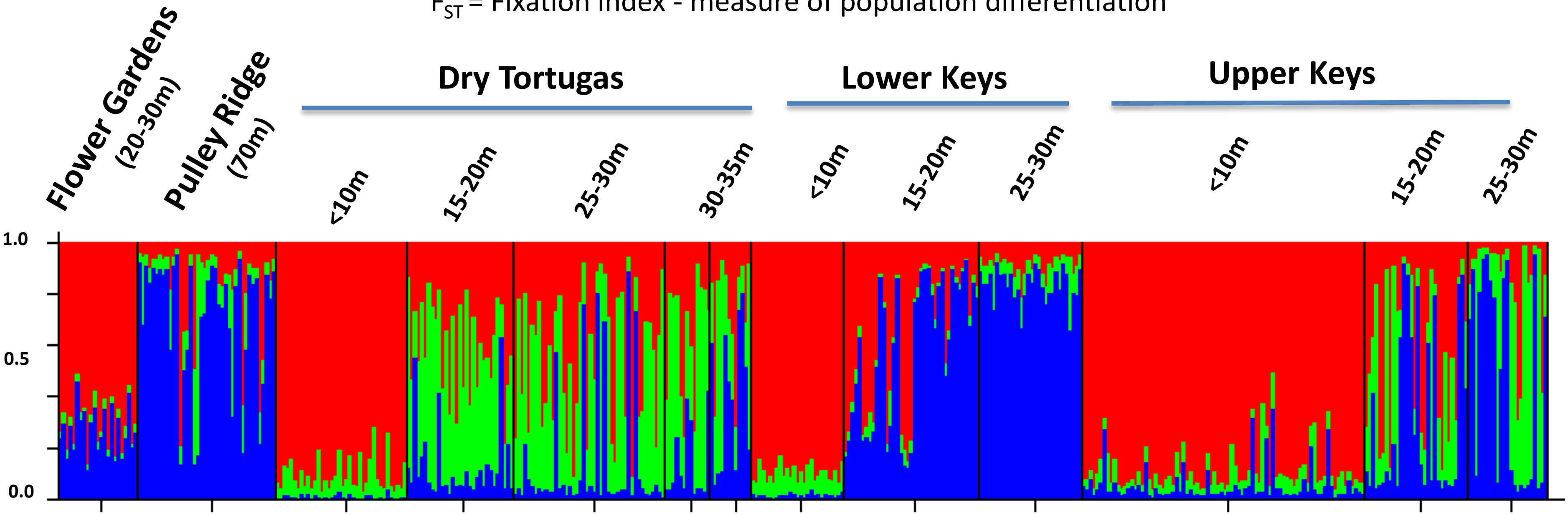

Sampling locations for corals (microsatellites)

Great star coral (*Montastraea cavernosa*) - Microsatellite results

Different populations at deep and shallow sites (N=432)

Pairwise F_{st} (shallow-deep) = 0.05-0.09

F_{ST} = Fixation index - measure of population differentiation



Pulley Ridge belongs to the same population as deeper sites in the Lower Florida Keys, but not the Dry Tortugas.

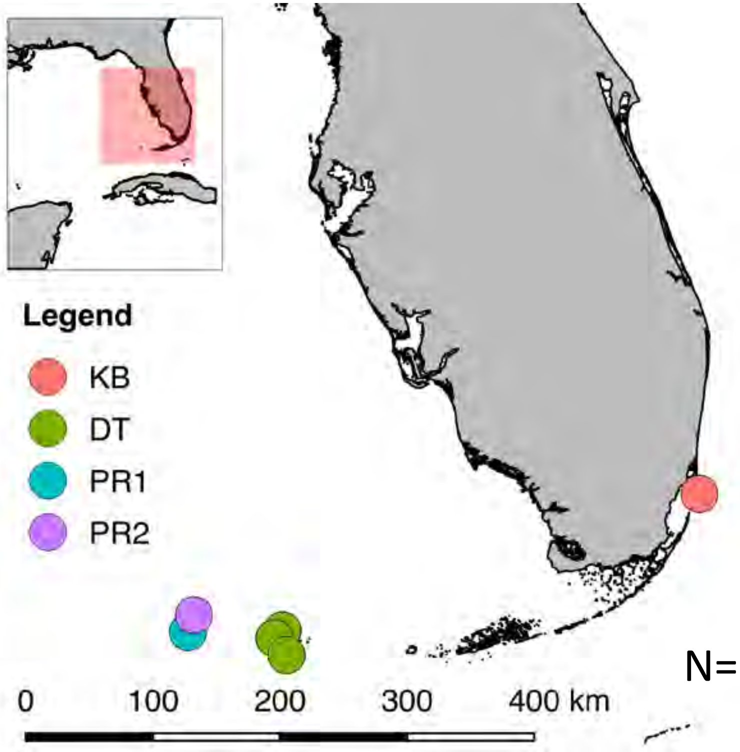
Flower Gardens belongs to the same population as shallow sites in the Florida Keys.

Dry Tortugas samples >10 m may be a third population, which may also be present in the Upper Keys at intermediate and deeper depths.

Serrano et al. (2014), Serrano et al. (in prep)

Great star coral (*Montastraea cavernosa*) - SNP genotyping results

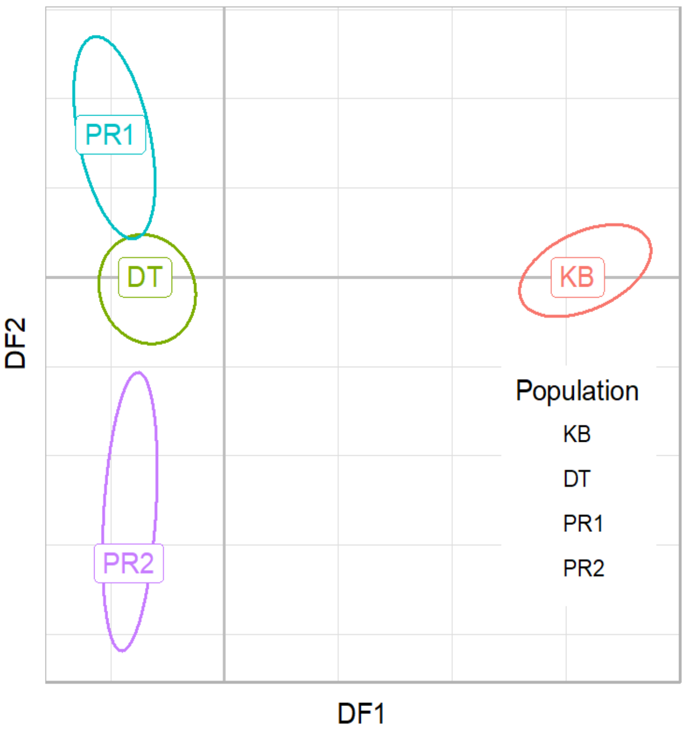
Pulley Ridge (72-73m), Dry Tortugas (28-36m), Key Biscayne (5m)
- 20,667 loci, but SNP genotyping requires **high quality DNA** (not alcohol-preserved)

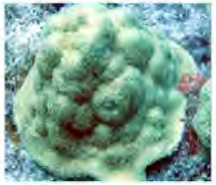


N=71

REGION	N SAMPLES	N SITES	DEPTH (M)
KEY BISCAYNE (KB)	14	1	5
DRY TORTUGAS (DT)	36	3	28-36
PULLEY RIDGE (PR)	21	2	72-73

Reveals additional differentiation among deep/mesophotic sites

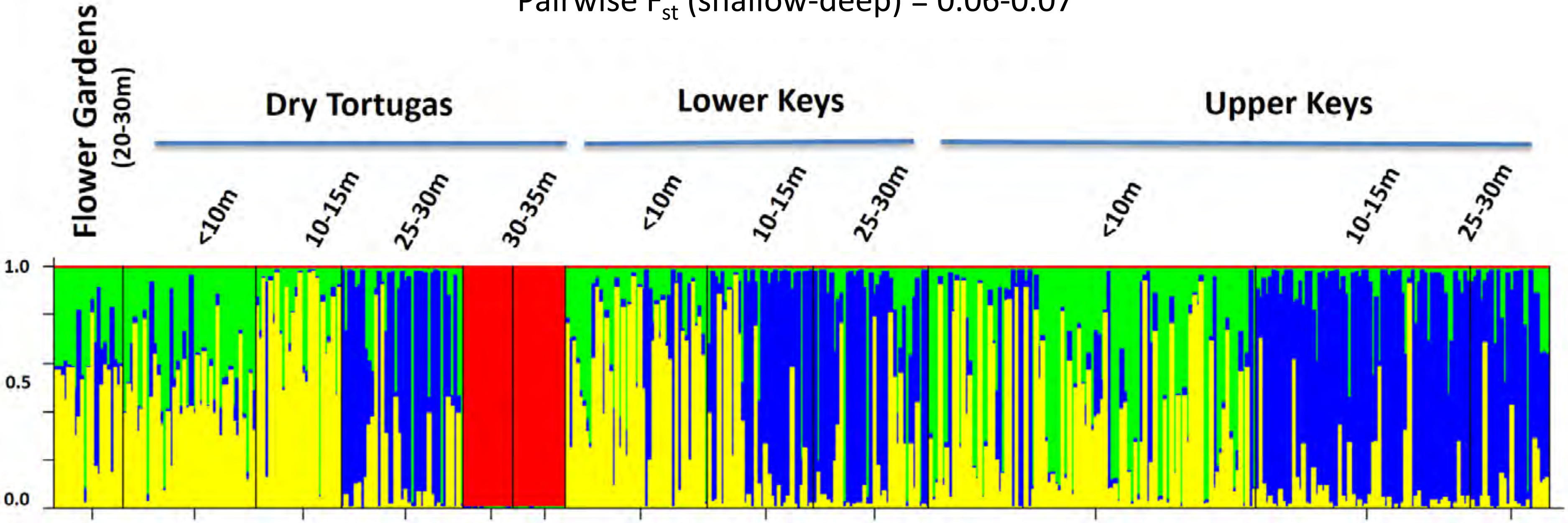




Mustard hill coral (*Porites astreoides*) - Microsatellite results

Also has different populations at deep and shallow sites (N=453)

Pairwise F_{st} (shallow-deep) = 0.06-0.07



Not observed at Pulley Ridge

Flower Gardens (20-30 m) belongs to the same population as shallow sites in the FL Keys.

Dry Tortugas samples >30 m appear to cluster as a completely separate population not present anywhere else in the FL Keys.

Serrano et al. (2016), Serrano et al. (in prep)

Corals: Conclusions and management implications

Pulley Ridge (70-80 m) appears to be an important larval source for deep (25-30 m) coral populations of *M. cavernosa* in FL. Connectivity with the FL reef tract via stepping-stone dispersal.

Dry Tortugas appears to be an area of local high retention, as evidenced by genetic and modeled connectivity.

Shallowest sites at the Flower Garden Banks (20-30 m) appear to be an important larval source for shallow (<10 m) coral populations in FL.

Sponges: Life history

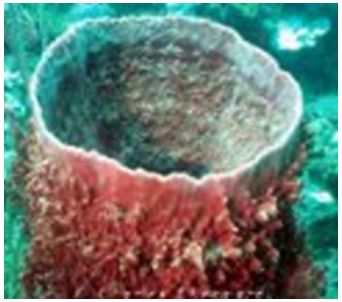
Sponges play key ecosystem role across coral reefs:

- Link benthic and pelagic processes (i.e., carbon and nutrient cycling)
- Serve as habitat for other organisms; house microbial communities

X. muta:

- Highly abundant in coral reef ecosystems
- Very large (>2m height, >1m diameter)
- Exceptionally long-lived: 2000 years (McMurray et al. 2008)
- At risk from cyclical bleaching events and fatal orange band disease

- Previous studies found high levels of population structure, with some subtle genetic differentiation across the Florida Reef Tract and evidence for cryptic speciation (Richards et al. 2016, Swierts et al. 2017)



Giant barrel sponge

(*Xestospongia muta*)

Broadcast spawner

Potentially short larval duration

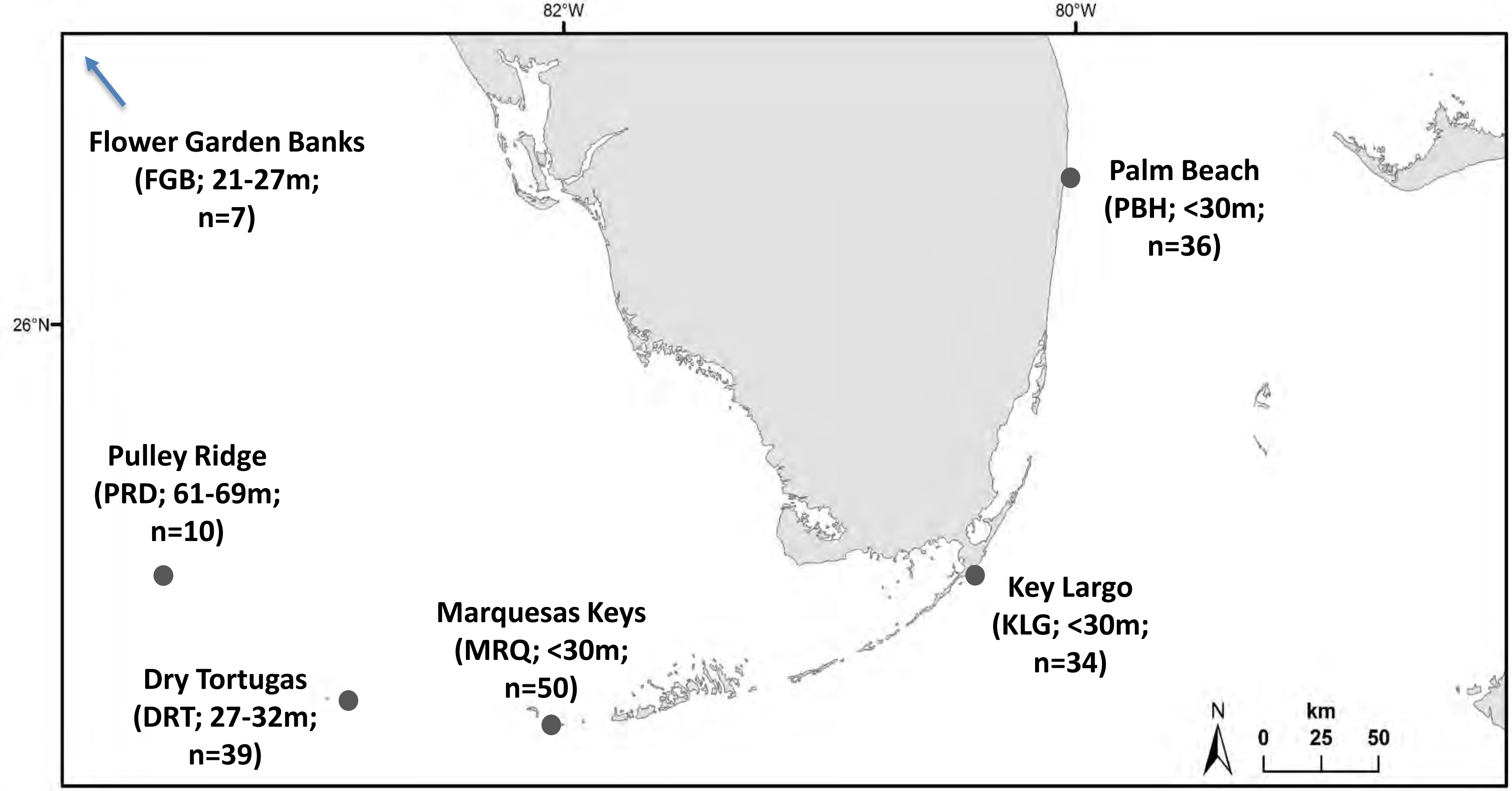
(3-4 days based on *X. bergquista*)

↓

↓ Dispersal?

↓ Connectivity?

Methods and Approach: sampling locations, sizes, and statistics



176 individuals genotyped at 8 microsatellite loci across six locations

Tested for pairwise population-level (F_{ST}; high statistical power) and individual-based (STRUCTURE; low statistical power) population genetic differentiation

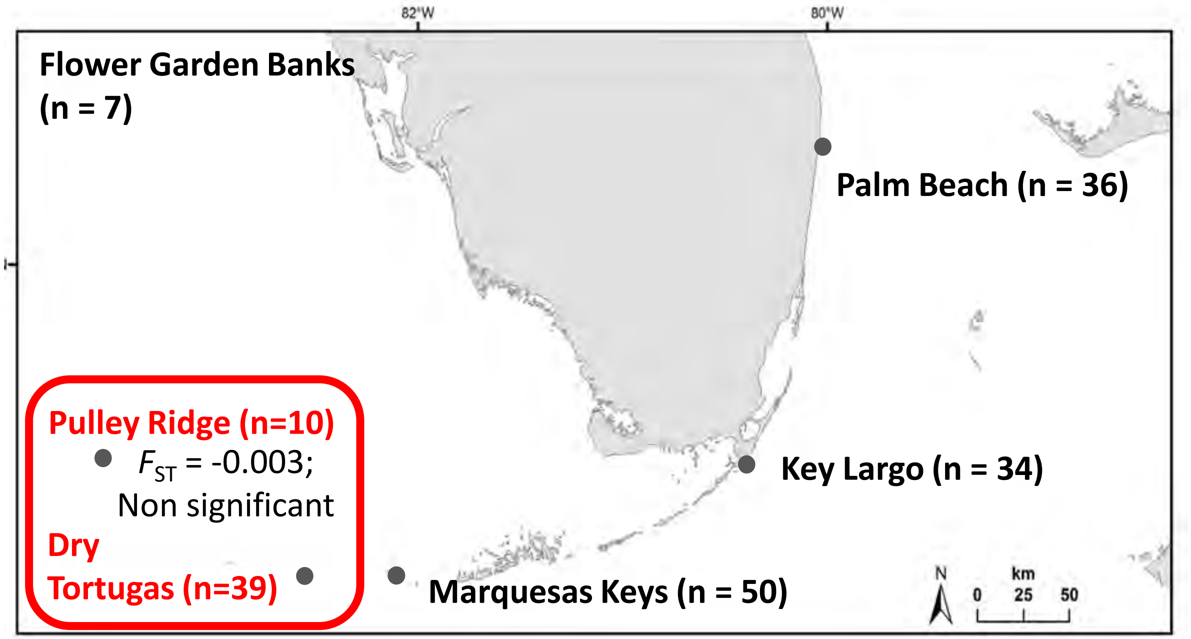
Individual-level analyses important to identify migrants and cryptic species

Principal Findings

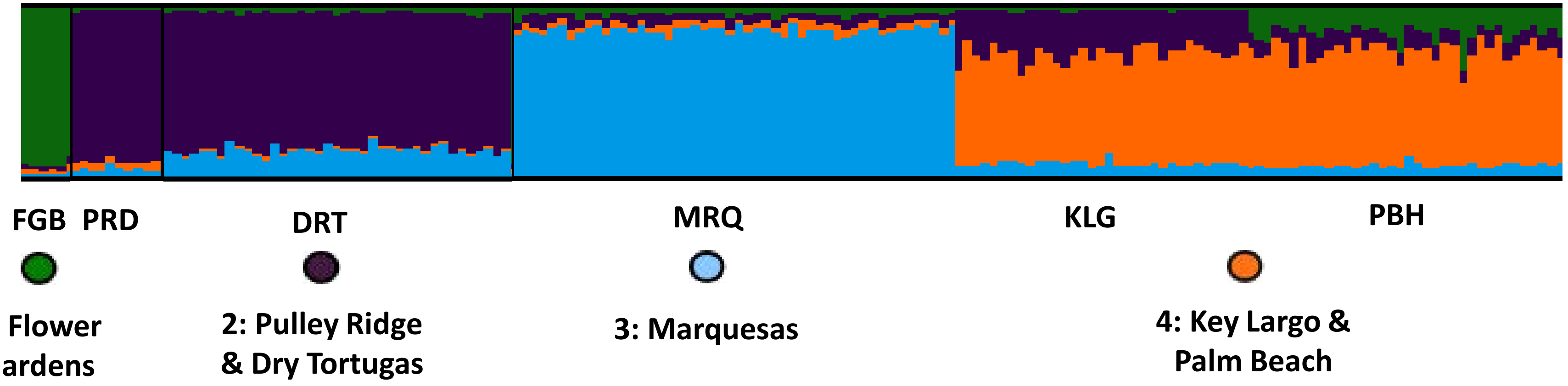
No significant genetic differences between individuals from Pulley Ridge and the Dry Tortugas

Significant population genetic structure found between *all other* sampling locations

Range: F_{ST} = 0.011-0.074, $P < 0.05$



Four clusters identified using STRUCTURE



Conclusions and management implications – Sponges

High levels of self-recruitment across most of the surveyed *X. muta* populations

However, analyses at the population level (high statistical power) and the individual level (low statistical power) suggest high connectivity between Pulley Ridge and the Dry Tortugas

So gene flow occurring, but across limited spatial scales (likely due to short larval settlement time)

Pulley Ridge may have limited capacity to influence the recovery of downstream highly impacted reef systems (FL Keys)

Red grouper: Life history

- Plays key ecosystem role as predators and ecosystem engineers across coral reefs and benthic communities.

- Excavated limestone solution holes provide habitat and refuge (e.g., settlement sites and habitat complexity) for other taxa (including many juvenile life-stages)

- Does not form spawning aggregations

- Important commercial species – especially on western Florida shelf (GOM) and the currently overexploited Campeche Bank (Mexico)

- Previous studies found high connectivity across US Gulf of Mexico and western Atlantic, but were of limited geographic scope and used few markers with low resolution (Richardson and Gold 1997, Zatcoff et al. 2004)

Red grouper

(*Epinephelus morio*)

Broadcast spawner

Potentially long larval duration

(34-46 days)

↓

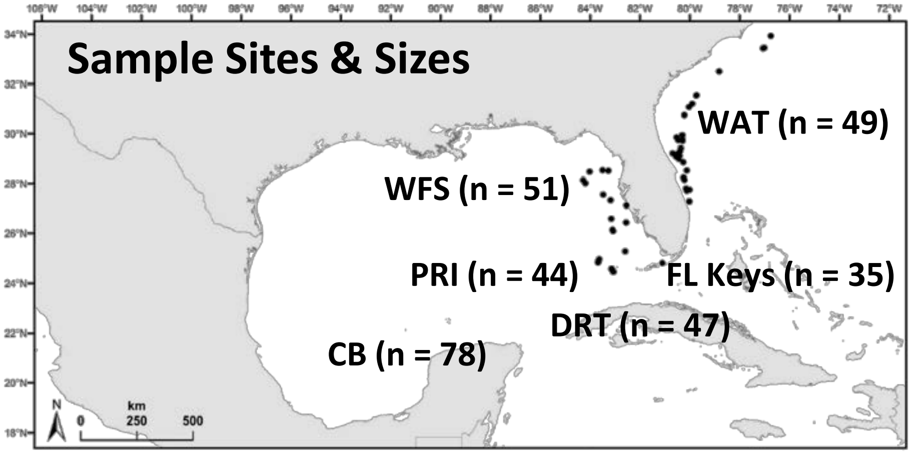
↑ **Dispersal?**

↑ **Connectivity?**

Methods and Approach

Sampling locations, markers

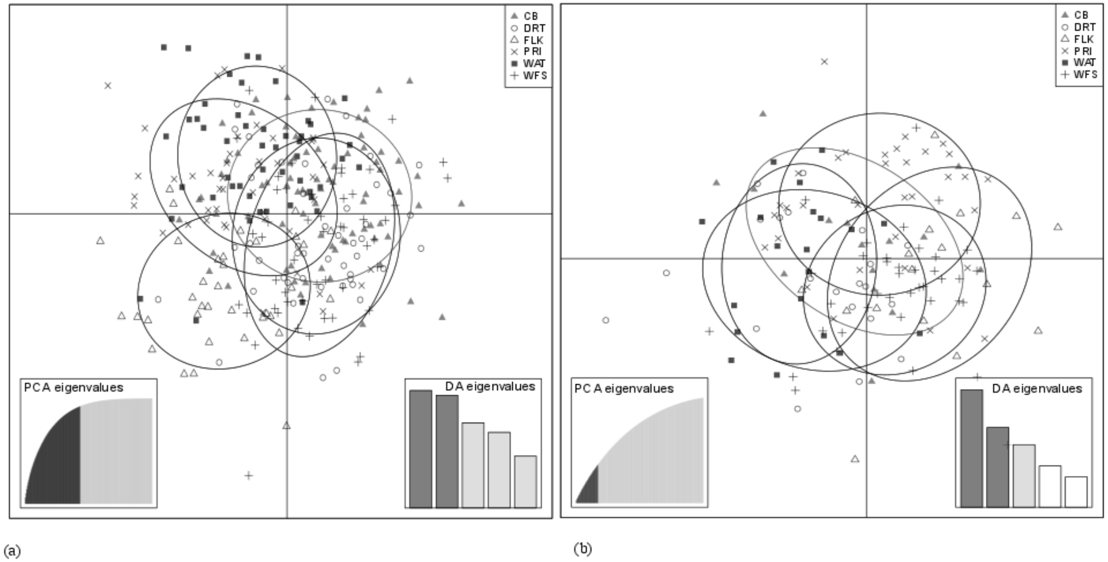
- 13 microsatellite markers (n=304)
- 468 SNPs (n=145)



Principal findings

No significant population structure across both marker types

(Msats: F_{ST} Range = -0.0040-0.0036, NS; SNPs: F_{ST} Range= 0.0001-0.0082; NS)



(a) **Microsatellite DNA**

(b) **Single nucleotide polymorphisms**

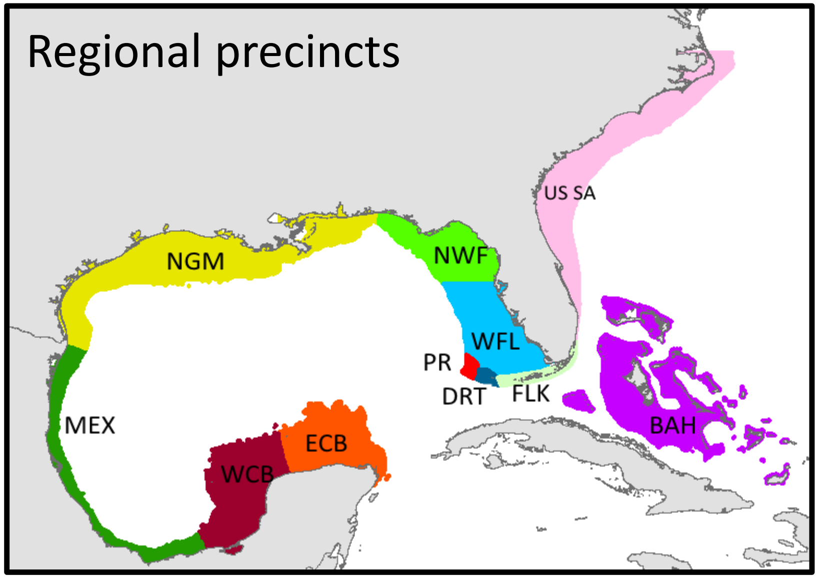
Discriminant Analysis of Principal Components (DAPC)

Overlapping clusters

Red grouper: Biophysical modeling

Model parameterization

- Habitat precincts defined through study area
- Identify source and sinks
- Founder populations = breeding adult females
- Model duration = 5 generations
- Pelagic Larval Duration = 37-50 days

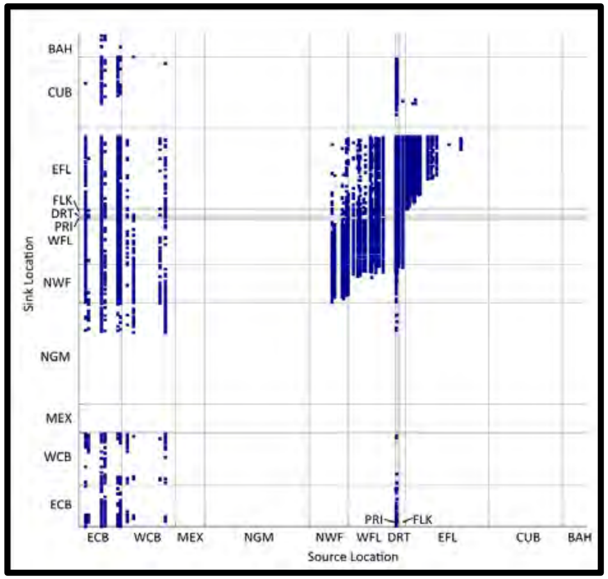


Regional precincts

Findings

- General SW to NE connectivity over generations
- Campeche Banks and Pulley Ridge recruited to all other sampled precincts
- All sampled precincts showed some level of self-recruitment, but larval retention highest in Western Florida Shelf and US Western Atlantic
- **High modeled connectivity** mirrors high genetic connectivity

Connectivity Matrix



Conclusions and management implications – Red grouper

1. High genetic and ecological connectivity likely due to long pelagic larval duration (37-50 days) of red grouper and strong Gulf of Mexico circulation patterns (loop current)

2. Genetic and ecological connectivity found across USA Management Areas (Gulf of Mexico & western Atlantic) and national jurisdictions (USA & Mexico)

3. High connectivity indicates that red grouper should be managed as a single population – **cooperation between management agencies and national governments is required**

4. High connectivity is significant because of red grouper's economic importance to USA fisheries and currently overexploitation across parts of its surveyed range (Campeche Bank) – i.e., decline in population size at Campeche Bank could have downstream consequences for population integrity at the western Florida shelf

5. Pulley Ridge (in addition to Campeche Banks) may be an important source site

Bicolor damselfish: Life history

- Widely used model coral reef fish species because it is abundant, widely distributed, and has a broad depth range. It also has a pelagic larval duration that is similar to many reef fish species.
- Lays benthic eggs with male nest guarding.
- Multiple life stages are easily studied: late-stage larvae can be collected in light traps, juveniles settle at large sizes (~10 mm), and adults maintain easily located territories for repeated observations (Goldstein, 2015).
- Previous studies show genetic connectivity at large geographic scales with subtle, but significant, genetic structure at smaller geographic scales, which may be due to stochastic effects on larval dispersal and microgeographic effects (Hepburn et al., 2009).

Bicolor damselfish

(*Stegastes partitus*)

Brooder

Potentially long larval duration

(22 to 36 days)

↓

↑ Dispersal?

↑ Connectivity?

Bicolor damselfish: Methods and Approach

Sampling: 314 samples from Upper Keys (UK), Lower Keys (LK), Dry Tortugas (DT), and Pulley Ridge (PR)

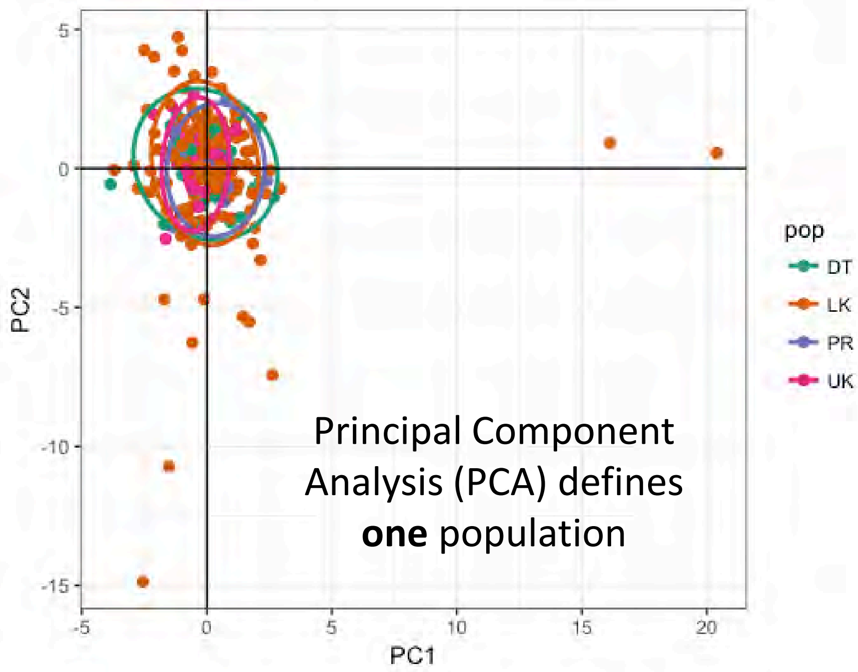
SNP genotyping: 9,355 markers (loci)

Findings

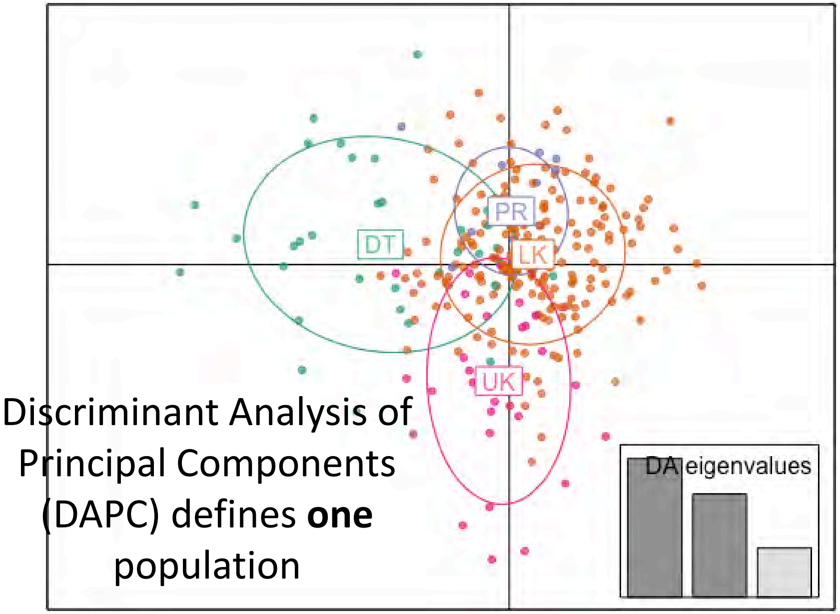
No significant population structure (F_{ST} values all < 0.01%).

Individuals at all sites are well connected, forming a single demographic population

STRUCTURE yields 1 population and AMOVA finds 1 population



Principal Component Analysis (PCA) defines **one** population



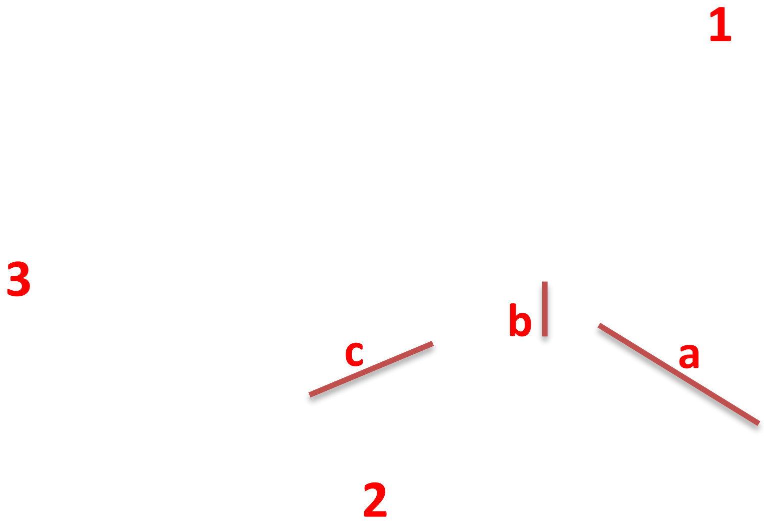
Discriminant Analysis of Principal Components (DAPC) defines **one** population

Lionfish: Life history

- Invasive introduced species from the Indo-Pacific, first reported in 1985 off Dania Beach, FL

- Early 2000s: east coast of US, Bermuda, Bahamas.
- 2009: FL Keys, Yucatan, Caribbean, south America.
- Now: into western GoM along southern US

- Previous study of *P. volitans* using mtDNA found major genetic discontinuities (a, b and c) and genetically isolated areas (according to the temporal invasion progression as 1, 2 and 3)



Lionfish

(*Pterois volitans*)

Broadcast spawner

Potentially long larval duration

(~30 days)

↓

↑ Dispersal?

↑ Connectivity?

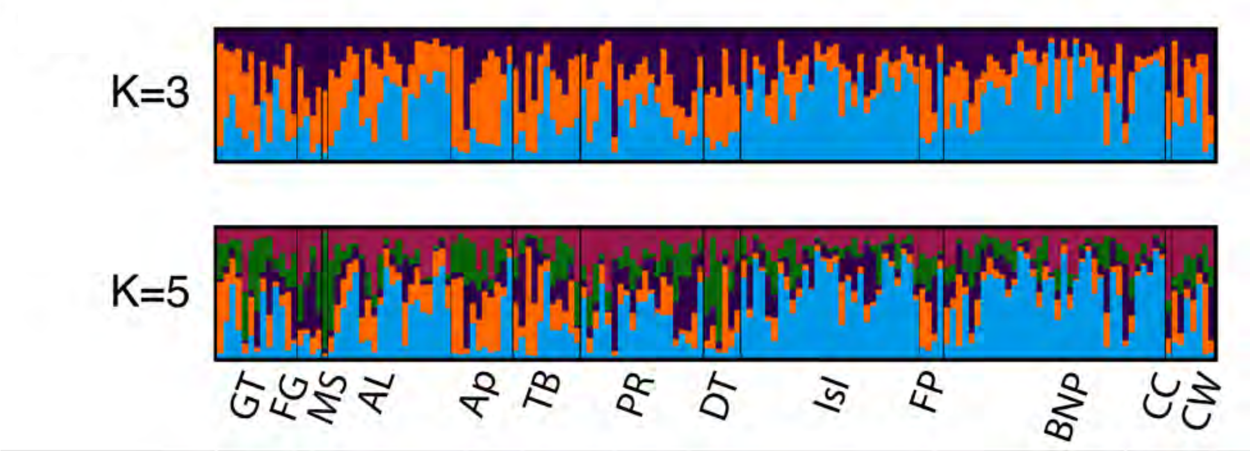
Lionfish: Methods and approach

Sampling (2013-15)
Sites included both the first and last area of the lionfish invasion in US waters, and several sites in the NW Atlantic (east coast of Florida) and the Gulf of Mexico.

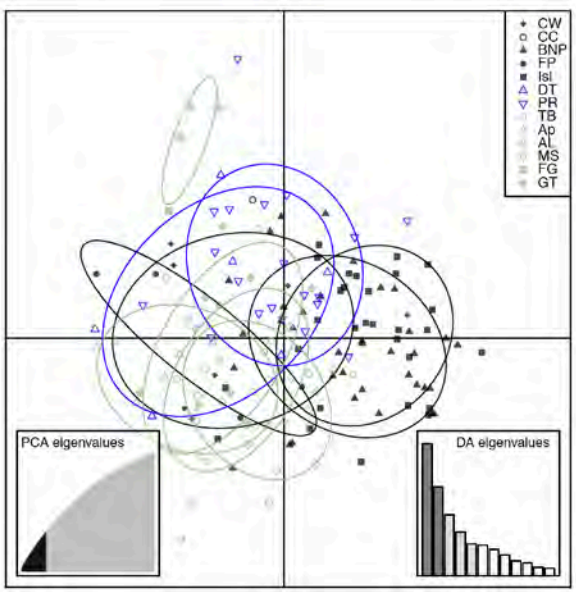
N=162 samples, 1,220 markers (SNP loci)

Findings

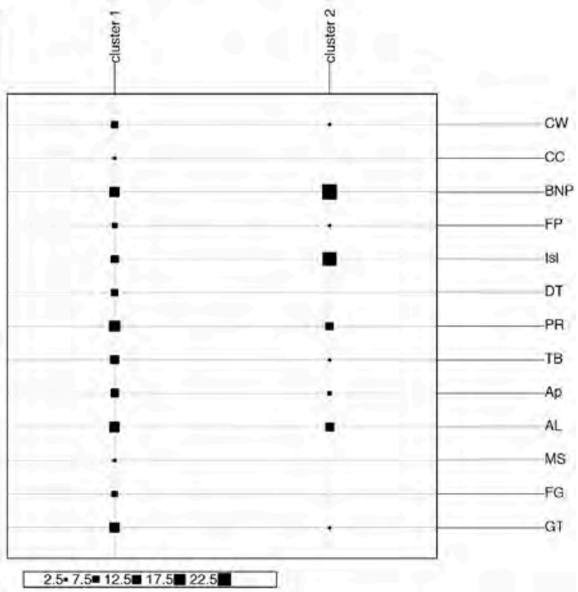
STRUCTURE found no evidence for population structure across sites



DAPC found two groups, but little spatial structure



Grey=NW Atlantic, blue=Dry Tortugas and Pulley Ridge, light green=Gulf of Mexico



Group membership

These findings reveal genetic **homogeneity**, with sufficient gene flow between the NW Atlantic and Gulf of Mexico to erase the previous signals of secondary spreading and bottlenecks that were observed in previous studies

These results indicate **fast genetic changes** in populations over space and time during the lionfish invasion, resulting in a **single population**, which has important implications for invasive species management

General Management Implications – all taxa

Mobile vertebrate species (fish):

- Long planktonic larval stages (3-7 weeks)
- Low population structure
- High connectivity among sites and depths
- Pulley Ridge can be managed as part of a regional management plan. However, it may also be **an important regional source for some commercially important species** (e.g., red grouper)

Sessile invertebrate species (corals, sponges):

- Shorter planktonic phases (days to a week or so)
- Higher population structure
- Lower connectivity
- Some coral species show strong population structure by depth, with **connectivity across some depths but not others**
- **Flower Gardens may be seeding shallow reefs in the Florida Keys** and Dry Tortugas, but **Pulley Ridge may be seeding deeper reefs in the Florida Keys**. However, **deeper reefs in the Dry Tortugas are seeded from elsewhere**
- **Dry Tortugas shows unusual population structure** suggesting novel inputs from elsewhere and high local retention
- Recognizing the existence of different populations and incorporating patterns of connectivity by depth could/should be incorporated into management