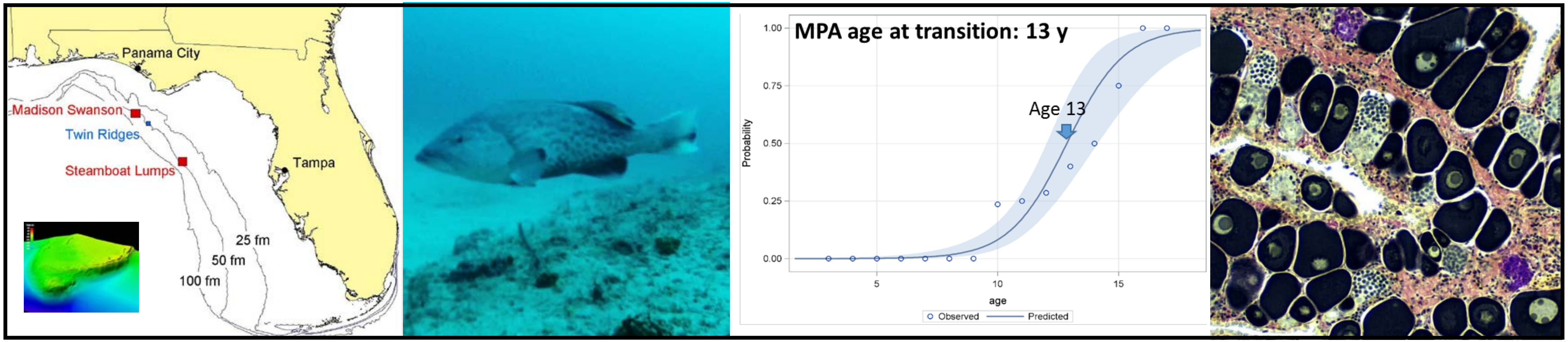
# Testing assumptions about sex change and spatial management in the protogynous gag grouper, *Mycteroperca microlepis*

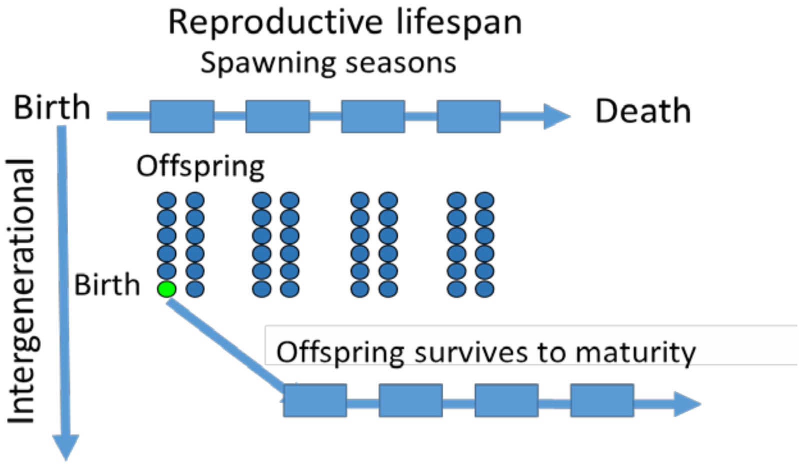



## What makes a male, how many are there & does it matter?

Susan K. Lowerre-Barbieri

UNIVERSITY of FLORIDA

# A little about me: Pop Dy background & current research




Reproductive success=producing offspring which survive to reproductive age

**Dissertation:** Life history and fisheries ecology of weakfish

| | Before 1950 | 1950-69 | 1970-93 |
|---|---|---|---|
| NY | Max. TL=865 mm | TL=760 mm | TL=950 mm |
| DE | | TL=392 mm | TL=960 mm |
| CB | Max. TL=720 mm | TL=445 mm | TL=875 mm |
| NC | Max. age=8 years | 6 years | 11 years |

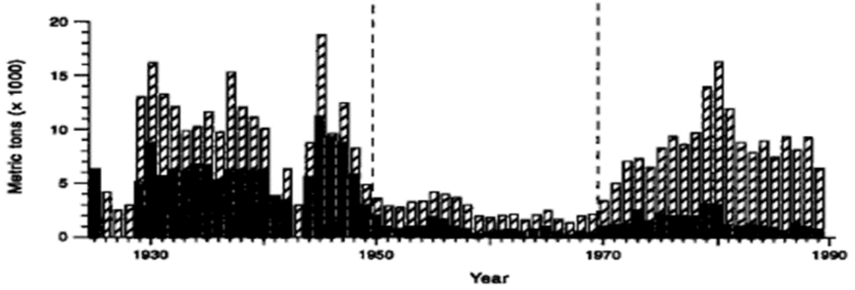
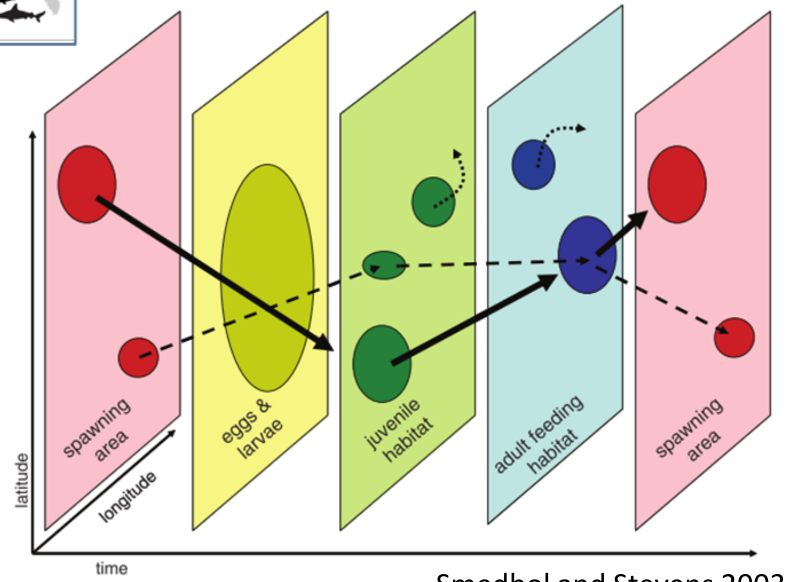



**Figure 11**

Commercial landings of weakfish, *Cynoscion regalis*, coastwide (hatched bars) and in Chesapeake Bay (black bars), 1925–89, with maximum reported sizes and ages (in years) for periods of high and low landings. Taken from: [a]Nesbit (1954), [b]Perlmutter et al. (1956), [c]Taylor (1916), [d]reported in Seagraves (1981), [e]Massmann (1963), [f]Merriner (1973), [g]Shepherd (1988), [h]Villoso (1989), [i]present study, [j]Hawkins (1988).

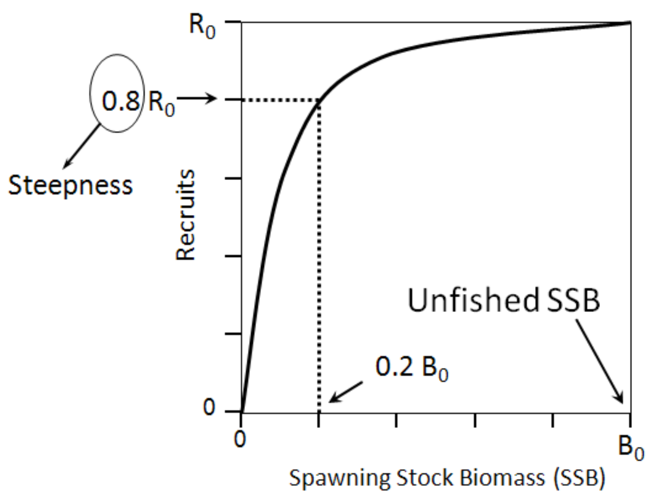
Spatial ecology and movement



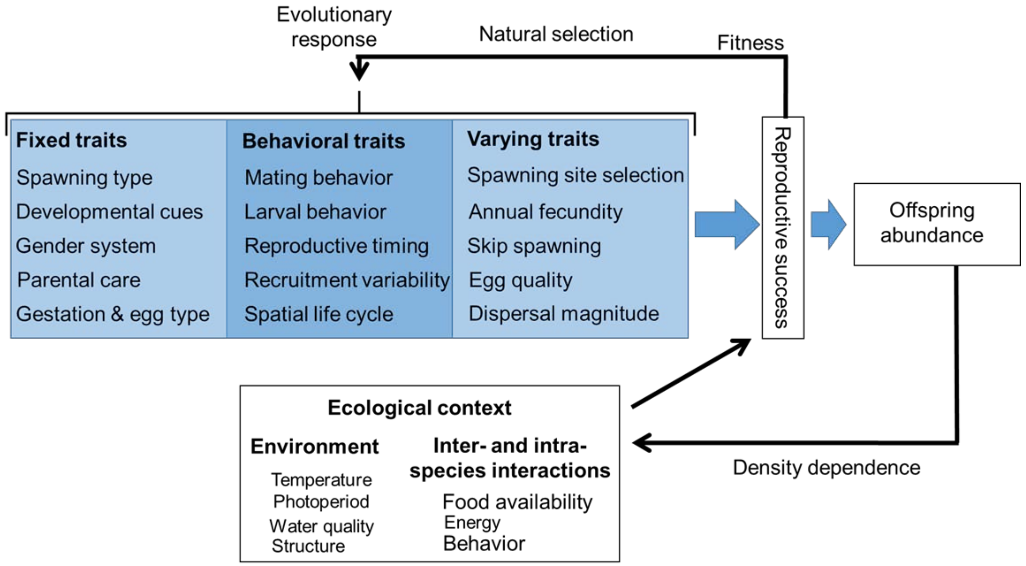

Smedbol and Stevens 2003

# Processes in spawner-recruit systems

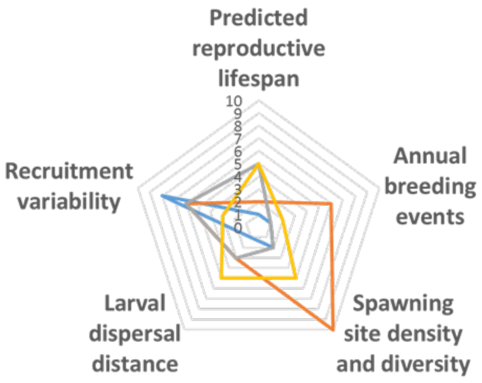
## Spawner-recruit theoretical relationship




## Spawner-recruit systems




## Spawner-recruit Trait space




Lowerre-Barbieri et al., 2017

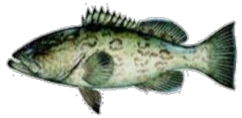
Recent studies suggest underlying S-R assumptions may be incorrect.

- <20% of stocks showed productivity consistently driven by adult abundance
  Vert-pre et al. 2013
- Only 39% showed a positive relationship between recruitment and spawning biomass Szuwalski et al., 2015

**Reproductive resilience:** the capacity of a population to maintain the reproductive success needed to result in long-term population stability despite disturbances such as climate change and fishing.

- Species fall along a continuum from low to high reproductive resilience due to species-specific spawner-recruit traits.

# Reproductive potential & spawner-recruit traits



Reproductive potential and spawner-recruit system traits

| | **Assumption** | **Decision criterion** |
|---|---|---|
| Gonochoristic | Traditional: Productivity driven by abundance & fecundity | Data availability |
| | Emerging: Spatial ecology & age distribution affects productivity | BOFFFs<br>Spatio-temporal reproductive behavior |
| Sequential hermaphrodite | Productivity in protogynous fishes may be sperm limited | Sperm limitation affected by: spawning unit size, distribution of spawning groups, & mode of transition |

Modified from: Lowerre-Barbieri et al., 2017; SEDAR best practices

Growing awareness of the need for spatial stock assessment models that match the spatiotemporal management and biological structure of marine fish
Kerr et al, 2016; Berger et al., 2017; Cadrin 2019; Goethel et al., 2019

Spatial structure will often be a consequence of movement processes, habitat, or spatial distribution of fishing effort, and may change over time…. Of particular concern are changes in spatial distribution over time due to movement of the stock, recruitment dynamics, and/or local depletion. CAPAM, 2019

# Outline

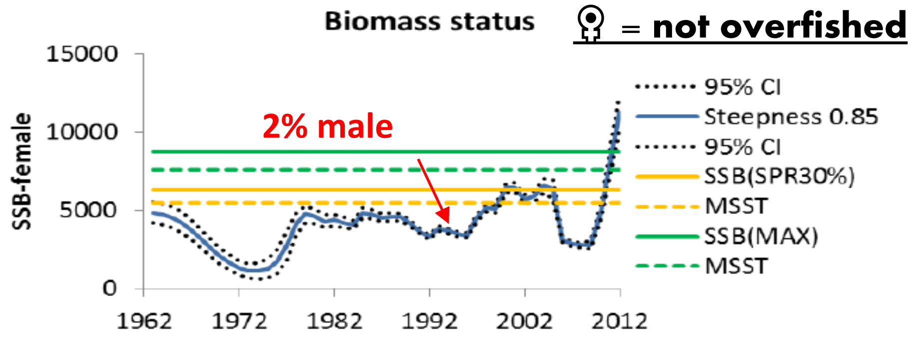
**(1) 2014 Gag assessment results and uncertainty**

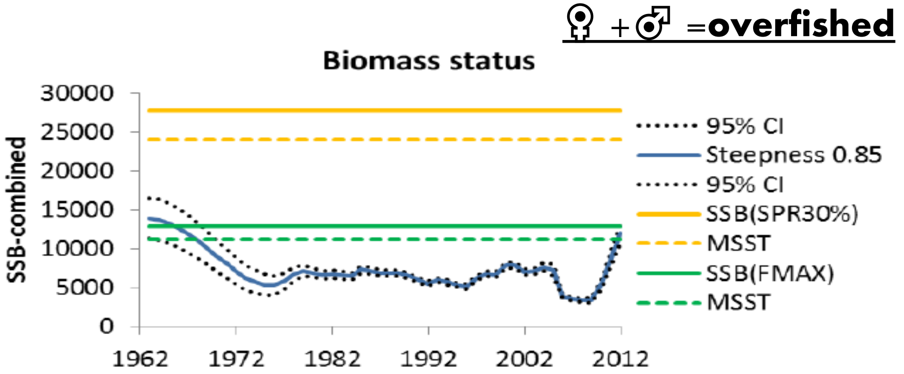
**(2) 2014: knowns & known unknowns**

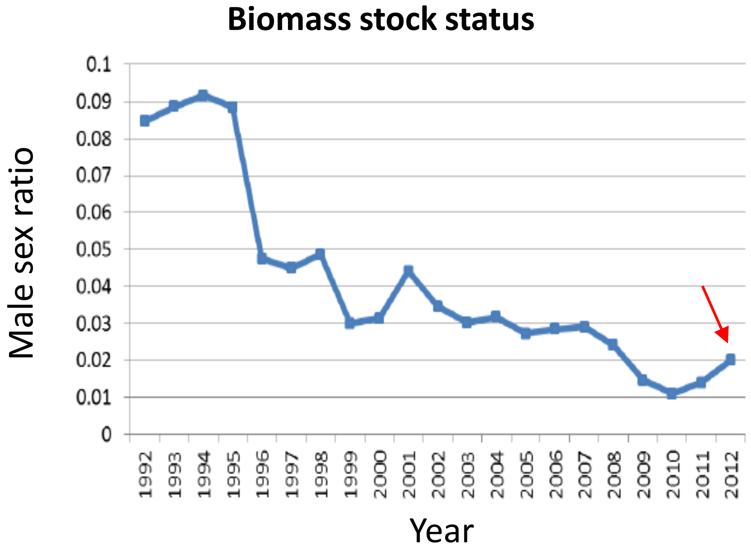
**(3) Testing assumptions about sex change and spatial management in the protogynous gag grouper**

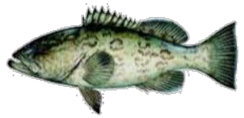
**(4) Where do we go from here?**

# Gag grouper stock assessment 2014 results



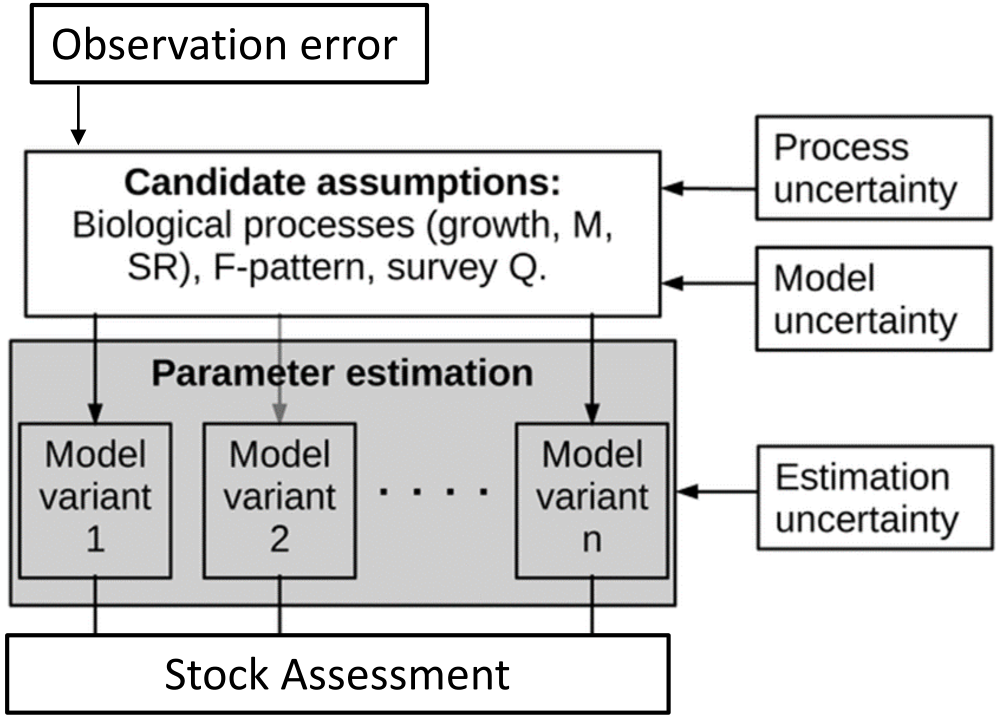



- Stock status differed depending on measure of reproductive potential;
- But combined sexes seemed unrealistic, suggesting the stock had been over-fished since the 1960's
- Low male sex ratio predicted from the model; but little empirical data to confirm this (2 studies with low sample sizes ~ n=200).
- This was thought to be incorrect due to model predictions indicating spawning site MPAs would increase male abundance

# Gag assessment 2014: identified uncertainties




(1) Rapid recent recovery and its dependence on the headboat index; apparently due to 2006 and 2007 being strong year-classes and these fish maturing in a lowered fishing mortality environment;

(2) Whether to base stock determination on Female SSB or combined sexes SSB;

(3) Video and catch-based indices did not agree;

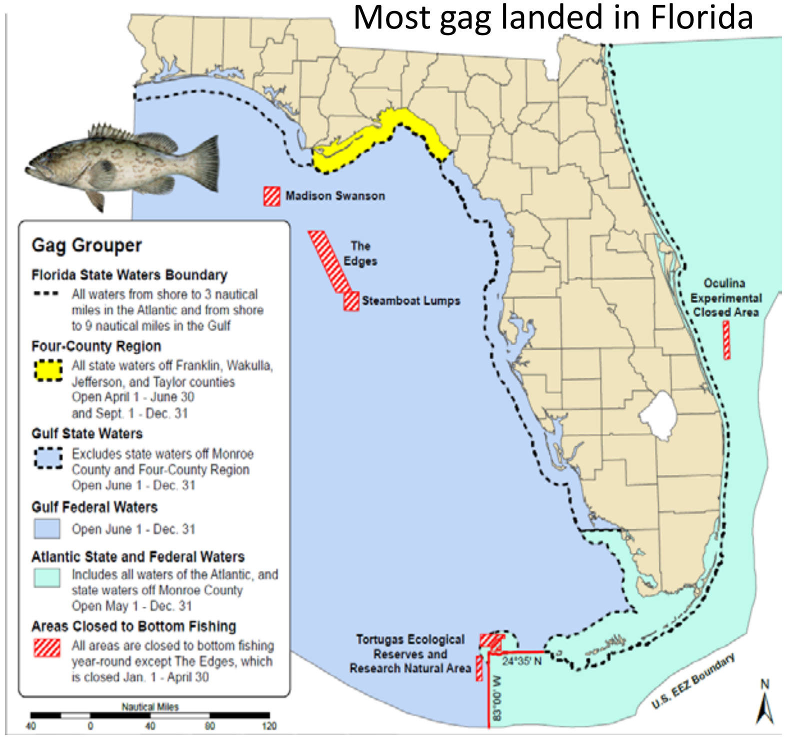
(4) Steepness for this stock is considered highly uncertain, as is the estimate of virgin biomass. It was fixed at 0.85.

# Accepted ecological knowns 2014

Not your average fish

**Accepted ecology:**

- Protogynous: all fish born female, with older fish transitioning into males (Koenig et al., 1996);
- Gag aggregate to spawn at the shelf edge (Koenig et al., 1996);
- Males remain in these deeper waters (~50 m or deeper) year-round; females use shallower water and undergo spawning migrations (Heppell et al., 2006);
- Spawning aggregations form from December to May, with peak spawning in February and March (Coleman et al., 1996);
- Long pelagic larval duration (35-45 d), travel 100s of Kilometres to estuarine nursery habitat (Fitzhugh et al., 2005);
- Sex change believed to occur on the spawning grounds, mediated by social interactions (male abundance or size of fish in the spawning aggregations) during the spawning season or just after it (Koenig et al., 1996; Ellis and Powers 2012).
- Transitionals believed to remain on the spawning grounds (Koenig et al., 1996)
- Spawning reserves will increase male sex ratios (Heppell et al., 2006; Ellis and Powers 2012)




**Highly Regulated:**

- IFQ for commercial fishermen can catch fish any time
- Minimum size limit=24” (610 mm TL)
- Area closures: typically Jan 1-May 31; rec bag limit (2/harvester)
- Spatial management (two MPAs at spawning sites developed in 2000, and a seasonally-closed spawning reserve established in 2009).

**Known unknowns:**

- Efficacy of the MPAs to increase male sex ratios;
- If male sex ratios have increased since ~2-3% in the 1990s;
- What cues sex change;
- Optimal male sex ratio.

# Objectives

**Testing assumptions about sex change and spatial management in the protogynous gag grouper *Mycteroperca microlepis***

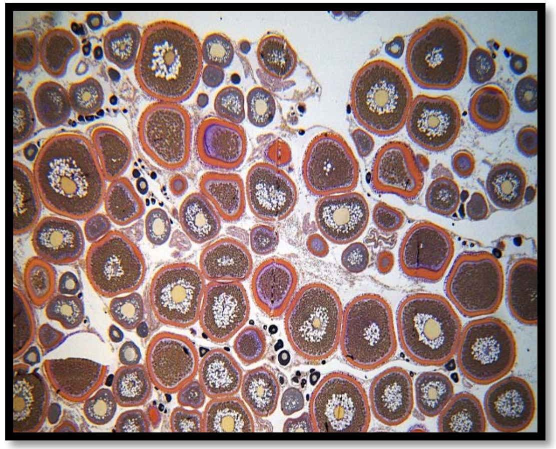
- Assess spatial ecology to determine if females form pre-spawning aggregations in fall/early winter, prior to females migrating to deep-water spawning sites, where males remain year-round;
- Estimate current male sex ratios and how they differ with spatial management;
- Assess where and when sex change occurs and its relationship to size and age;
- Compare male sex ratio results with those in prior studies and other species.


Targeted study

- Sampled with hook and line and video;
  - MPA (Madison Swanson), the Edges (closed seasonally: Jan-April), & open area NE of Madison Swanson;
- Monthly sampling December-May 2016-2018; opportunistic sampling in additional months;
- Effort: zones were created ~6nm, with the goal to fish each zone once a month ~4hours;
- Hook and Line (electric and bandit reels), recorded fishing time for effort, live and/or cut bait
- Video: $300^0$ view and deployed in each zone for 20 minutes prior to fishing.

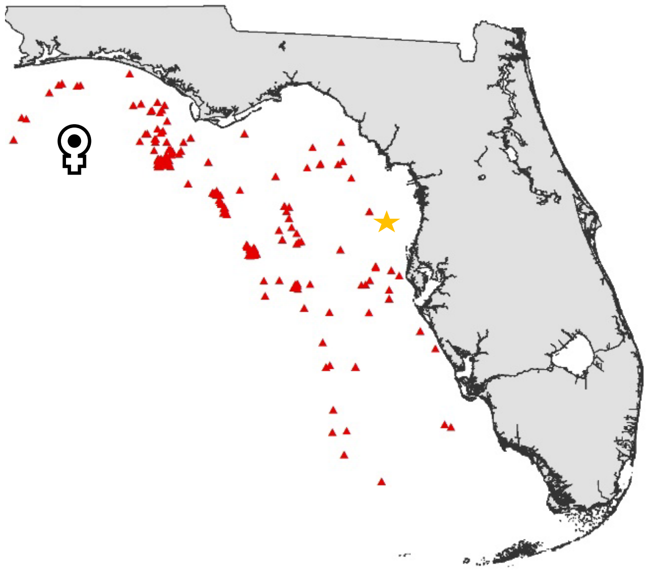
Integrated data from the targeted study (n=615; 2016-2018) with data from: FWC reef fish survey (n = 345; 2009-2018), FWC fishery dependent sampling (n=639; 2015-2019) & commercial hook-and-line fisherman (n = 58);

3) Biological data: Total length, total weight, gonad weight, external pigment, otoliths to assign age, gonadal tissue for histological processing and assignment of reproductive state, time and location of capture, blood for hormone analysis

$H_0$ : **Females form pre-spawning aggregations in December, January, and February**

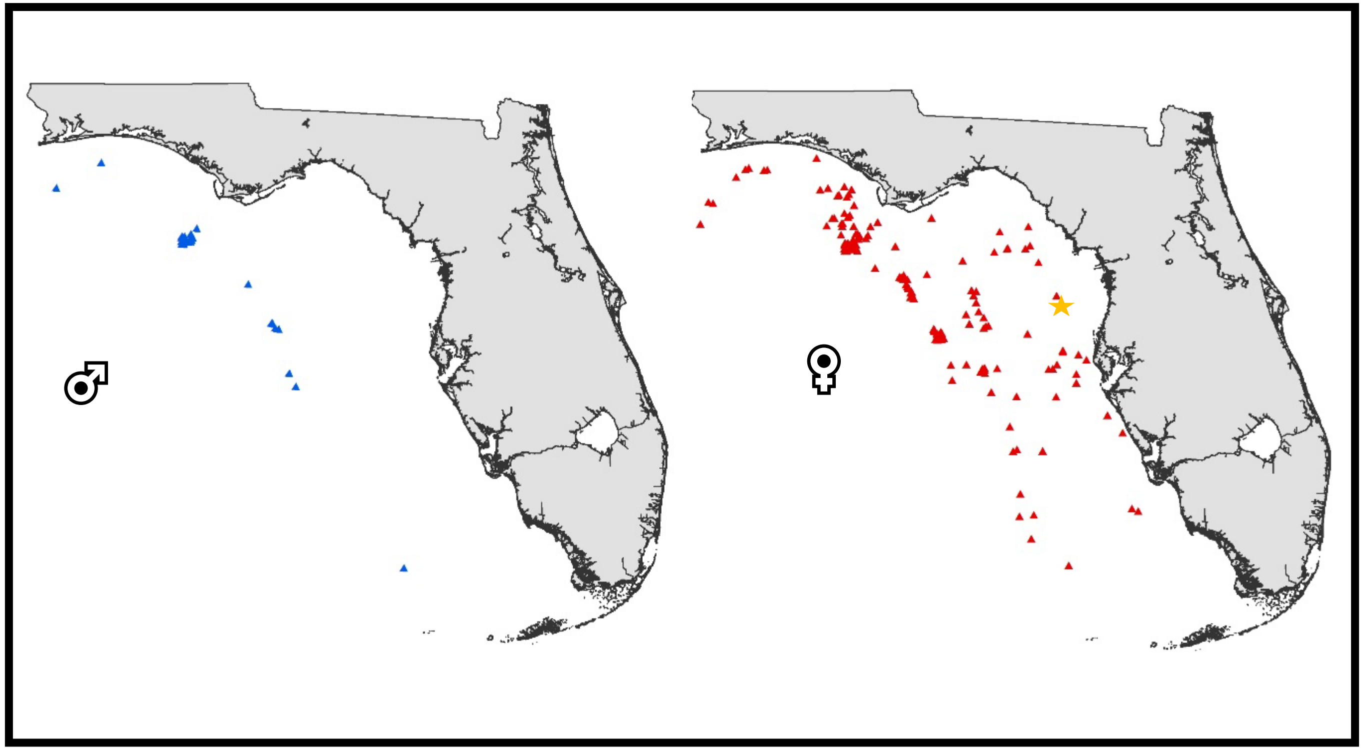
**Results**: pre-spawning aggregations occurred consistently in shallow waters, resulting in catch rates much higher than what we saw in the MPA during the spawning season



- ★ Prespawning aggregating behavior consistently occurred at the shallow sites(~15 m) that our collaborative fisher targeted; it was also observed at the deep-water Open area northeast of Madison Swanson in one yer.
- The commercial fisher captured fish as early as November and as late as mid-February. Maximum catch per day at his shallow sites peaked at ~100 fish on 22 January 2016 (maximum number caught in Madison Swanson=23).
- Of these 100 fish, 21 of the largest were sampled for biological data. Among the sampled fish, 100% were female and 50% had developing or spawning-capable ovaries.

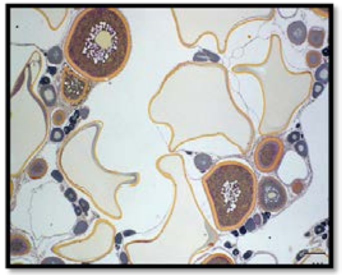
$H_0$ : **Gag use deep-water spawning aggregation sites, where males remain year-round**

**Results**: Gag exhibited sex-specific spatial ecology, with males occuring only at deep-water sites (> ~50 m); male and female depths and locations overlapped at active spawning sites (Madison Swanson and the Edges); spawning season 1 February to 18 April based on actively spawning females.



Mean depth at capture differed significantly with sex (T-test, n=1,017, $P < 0.0001$)
Minimum depth ♀ = 4.6 m; ♂ =49.1 m

Actively spawning females collected from 1 February to 18 August in depths of 65 to 99 m
Male depth range 49-128 m;
Males & actively spawning females both occurred in Madison Swanson and the Edges (spawning grounds)



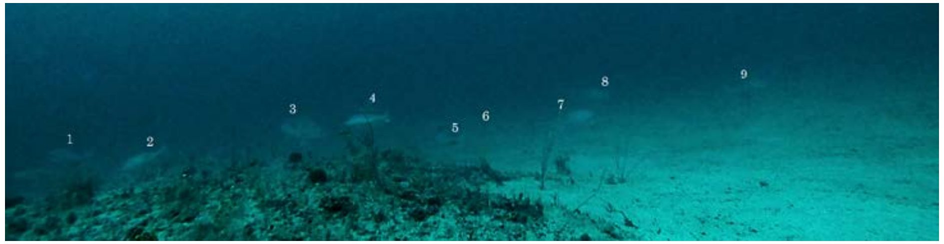
# Results: spawning aggregations

$H_0$ : **Gag form spawning aggregations**

**Results:** no evidence of large spawning aggregations

- Spawning aggregations defined as fish repeatedly concentrating for the purpose of spawning at a predictable space and time, with at least a 4-fold increase in density (Domeier 2012).

- Spawning season: 1 February through 18 April and consistent observations of spawning activity at Madison Swanson and the Edges



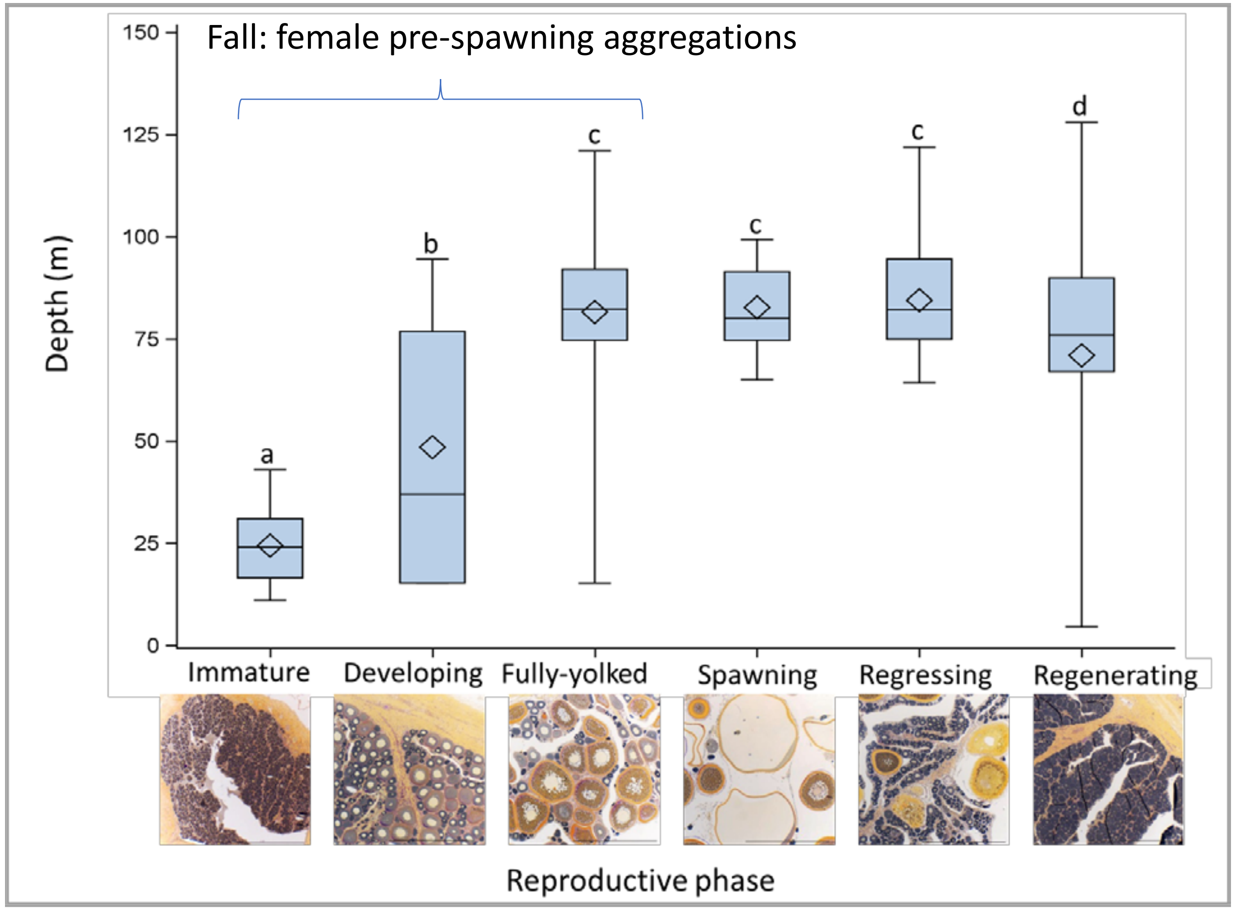
| Area | CPUE (fish $h^{-1}$) | | | | $MaxN_C$ (n fish) | | $MaxN_V$ (n fish) | |
|---|---|---|---|---|---|---|---|---|
| | Mean S | Mean NS | Max S | Max NS | S | NS | S | NS |
| Madison Swanson | 1.9 | 1.5 | 38 | 8 | 17 | 10 | 8 | 4 |
| Edges | 0.3 | 0.2 | 7.4 | 4 | 8 | 2 | 7 | 9[a] |
| Open | 0.2 | 0.2 | 3.5 | 5 | 1 | 1 | 2 | → 12 |

[a]These data are from 30 January 2016, i.e. 1 d before the spawning season. The maximum number observed in the remainder of the non-spawning season was 6 fish

$H_0$ : **Females make spawning migrations to deep-water spawning sites, remaining there only during the spawning season**

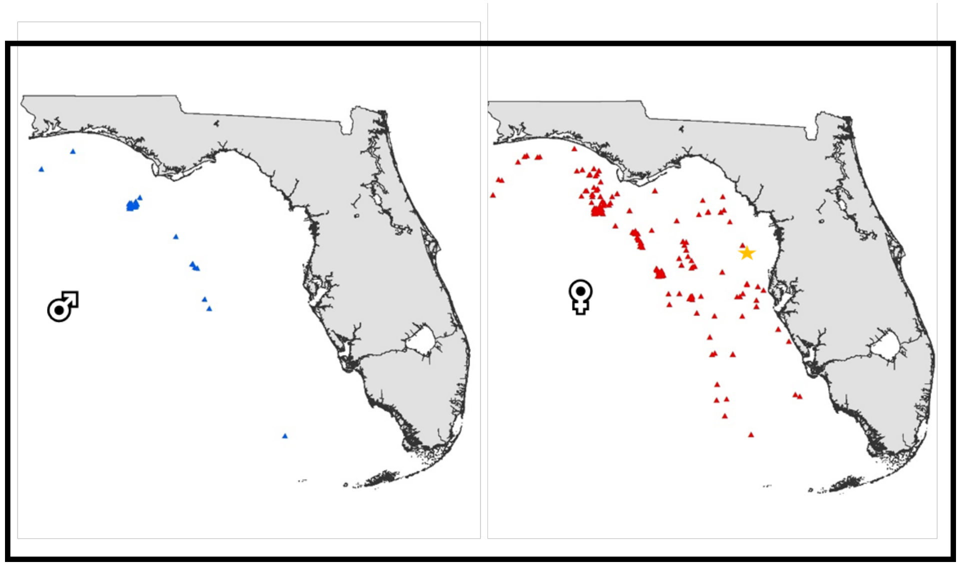
**Results**: evidence of female spawning migrations, but also adult females which may remain at Madison Swanson year-round

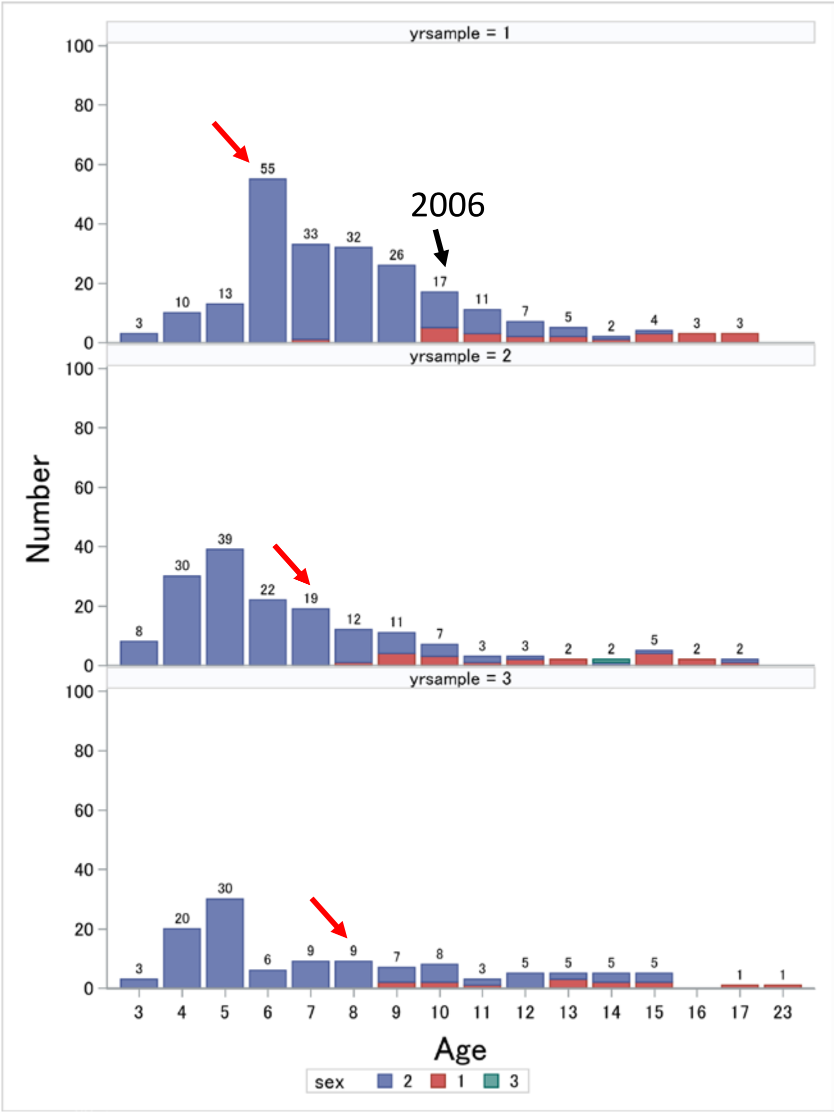
- Female depth at capture differed significantly with reproductive phase (ANOVA, $F=33.26$, $P < 0.0001$) whereas male depth at capture did not (ANOVA, $F=1.03$ $P=0.4036$);
- Only mature females sampled on the spawning grounds & female abundance increases during the spawning season;
- But females were 85% of the catch in June, July, & October in Madison Swanson, suggesting some females are year-round residents.



$H_0$ : **Most females do not remain on the spawning grounds**

**Results**: the decrease in numbers of the 2010 year-class over the three-year sampling in Madison Swanson supports this hypothesis





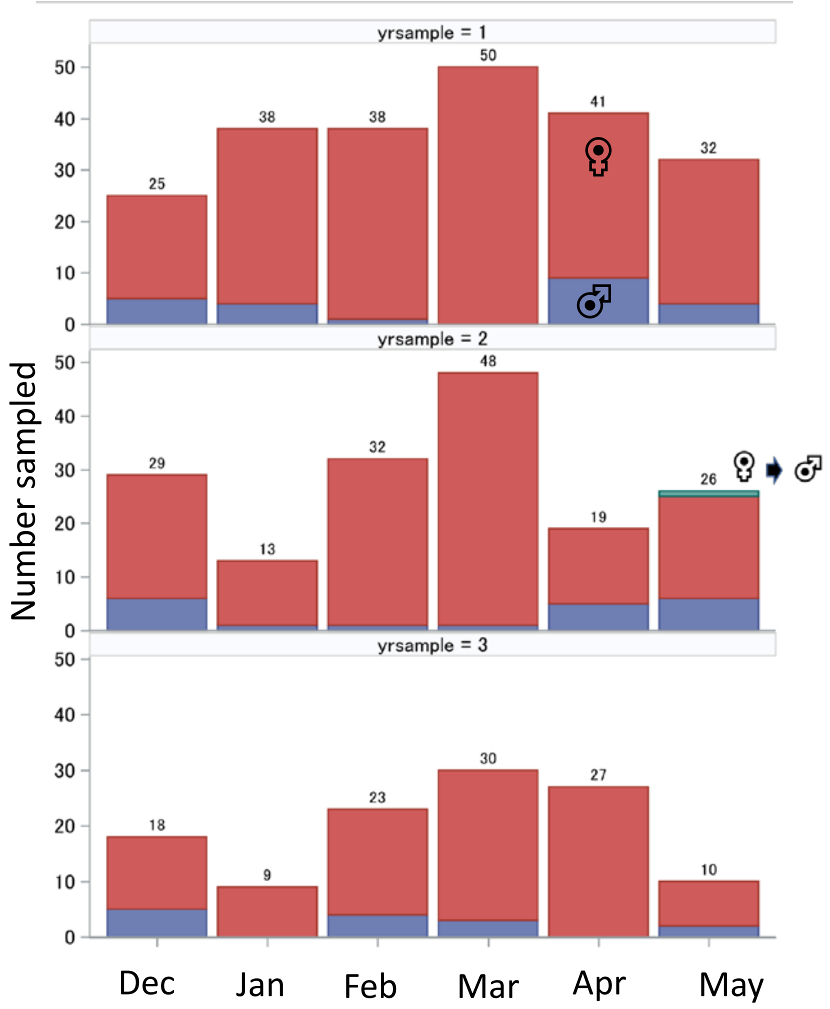

- Assuming all age classes in Madison Swanson have the same catchability, the decrease in the 2010 year-class over time can only occur if those fish leave the MPA and either don't return or are removed.
- There was no signal of greater than expected abundance from the 2006 and 2007 year classes

# Results: sex ratio Madison Swanson

$H_0$ : **% males will have increased in the MPA (15% predicted by Heppell et al. 2006 ~5% predicted by Ellis and Powers 2012)**

**Results**: Female migration to the spawning grounds affects monthly sex ratios; male sex ratio in Madison Swanson was 11% (Dec-May combined), but 5% in the spawning season, when both sexes are on the spawning grounds

- Madison Swanson sex ratios estimated for December-May were similar across years (10-12%); but monthly sex ratios ranged from 0% to 28%.
- Sex ratio is difficult to accurately estimate due to sex-specific spatial ecology and a poor understanding of female migration; without that knowledge the most representative measure of sex ratio is assumed to be that occurring during the spawning season and on the spawning grounds.

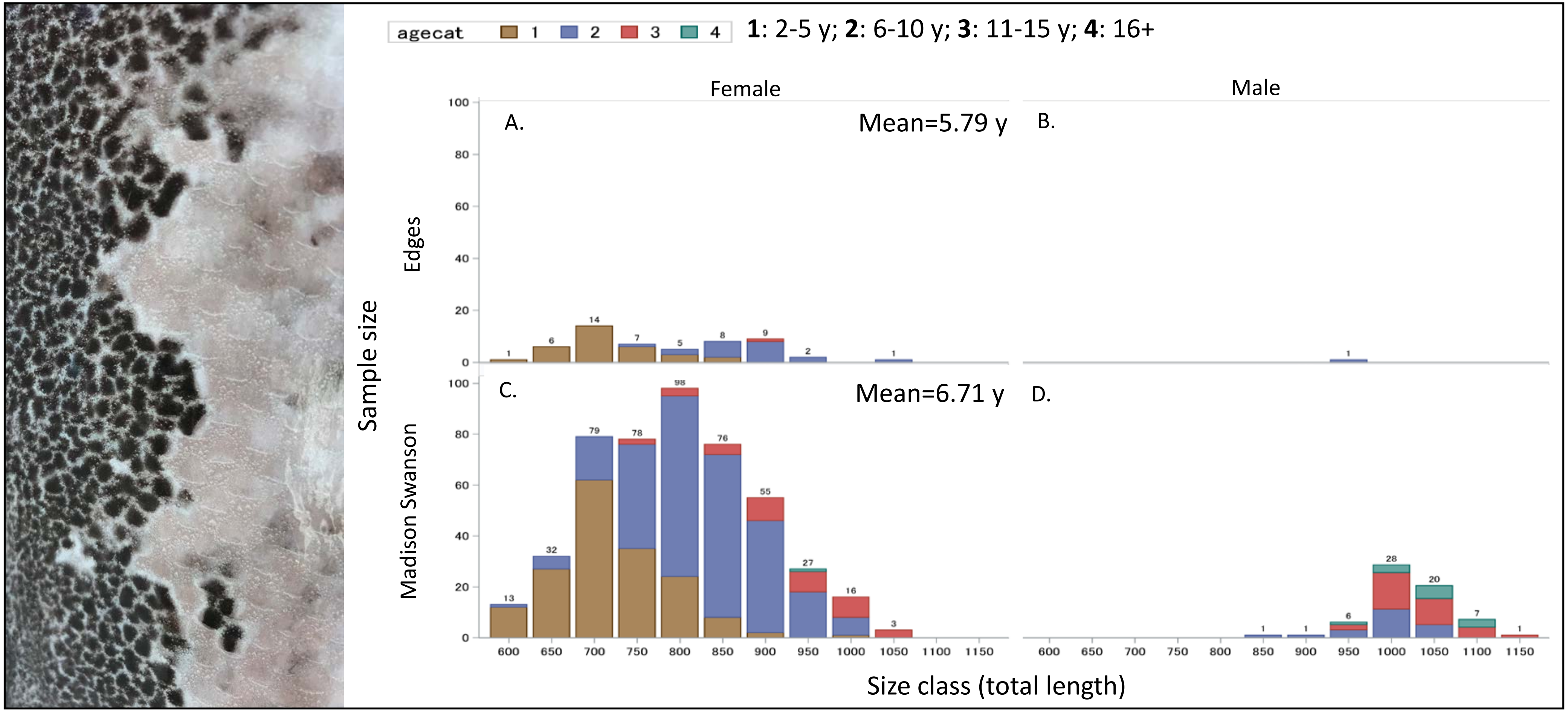


# Results: sex ratio outside the MPA

$H_0$ **: Sex ratios will be higher in the MPA than seasonally-closed and open area**

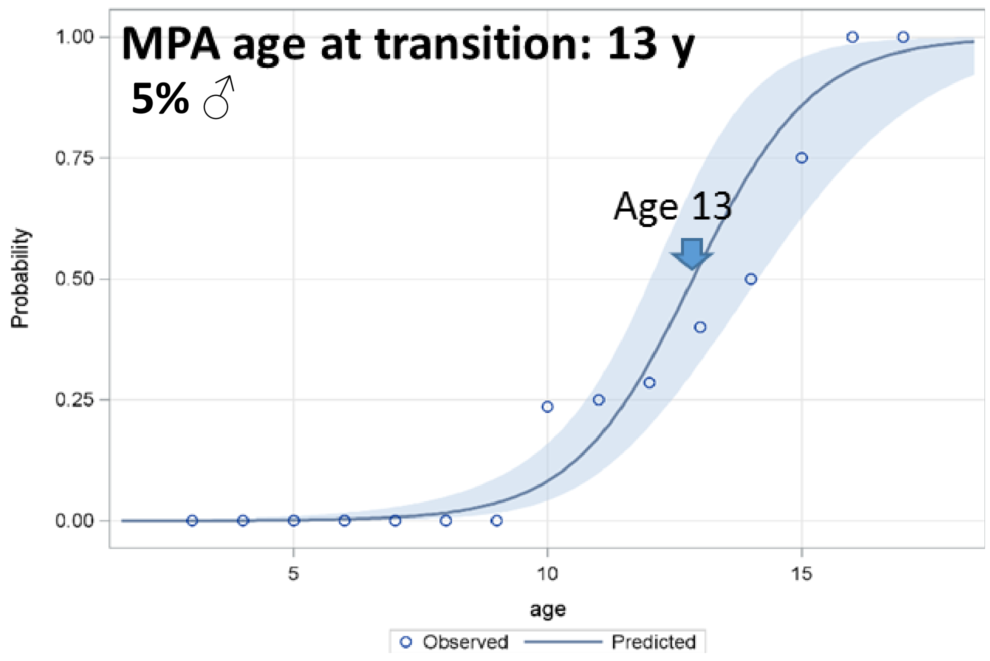
**Results:** Within the spawning season sex ratio=0% in Edges & Open Area; sex ratio of all fishery independent samples outside MPA (n=479) = 1%

Sample sizes: Open area n=9; Edges n=56; Madison Swanson n=568.

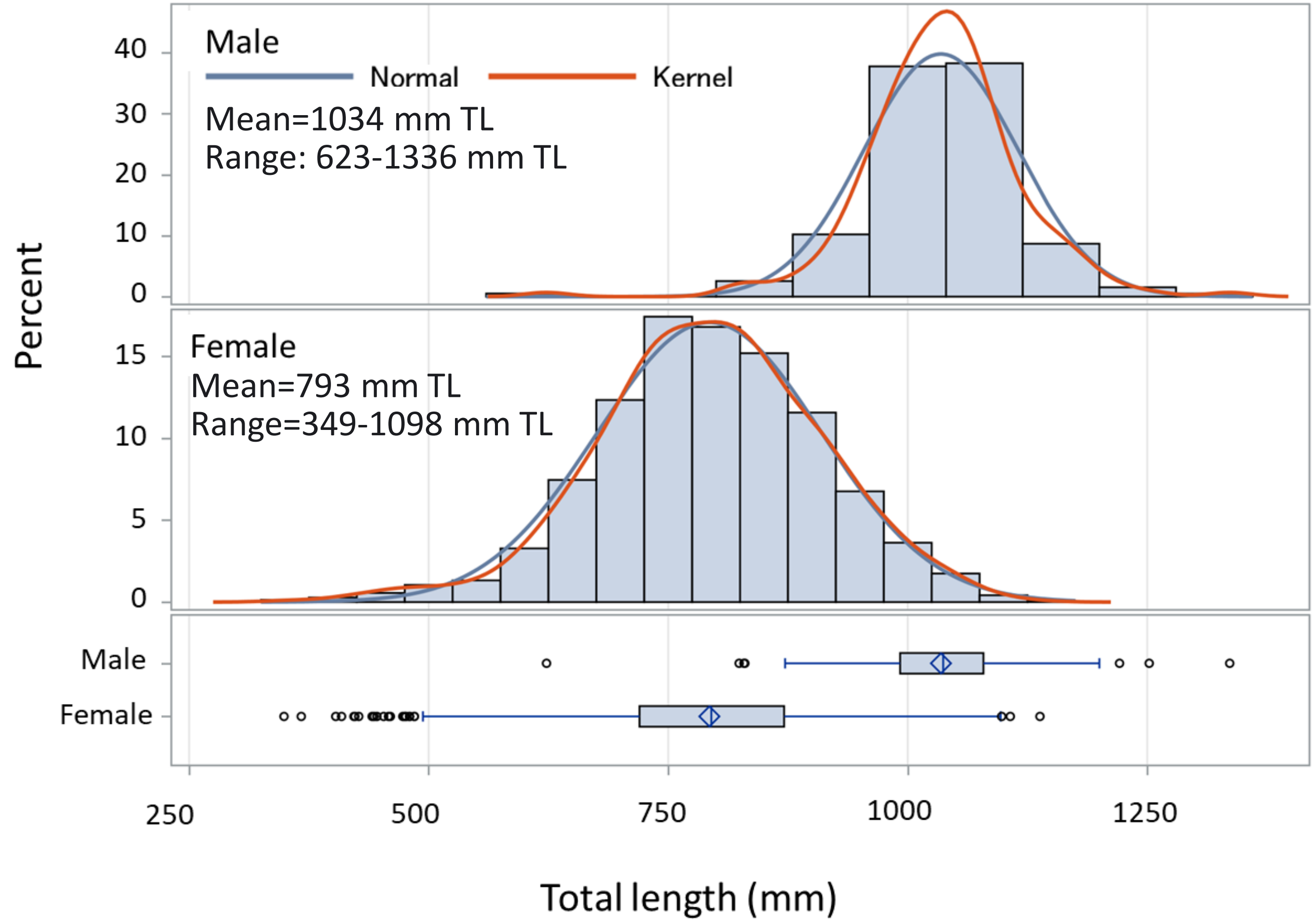


$H_0$ : **Age at 50% male (A50) has increased since the 1990s**

**Results:** Madison Swanson male A50 = 13 years and is older than previously estimated (10.9 years estimated in 1977 & 2004); males are significantly larger than females, but some small males were observed

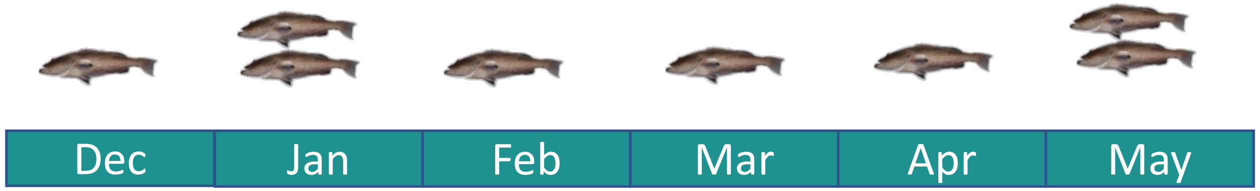


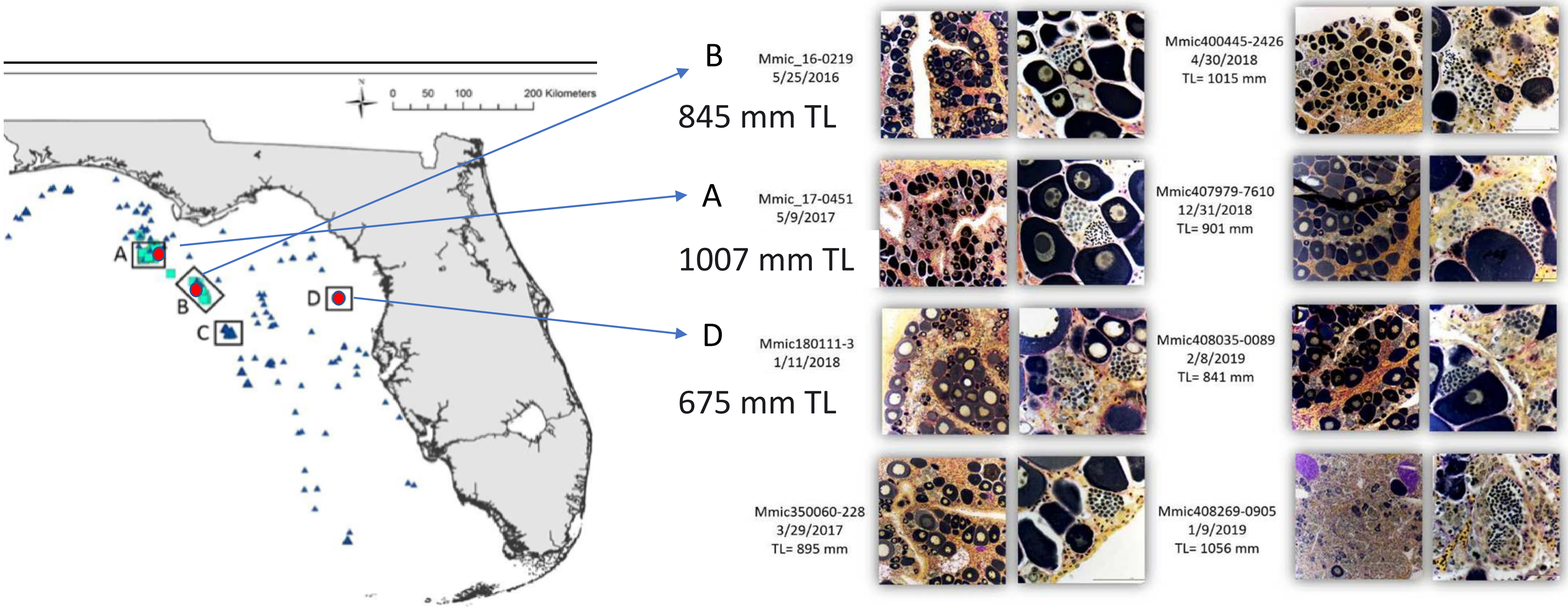

Estimated size at 50% male=1010 mm TL



HO: **Sex change only occurs on the spawning grounds and is mediated by male abundance or size (possible threshold size of 800 mm TL)**

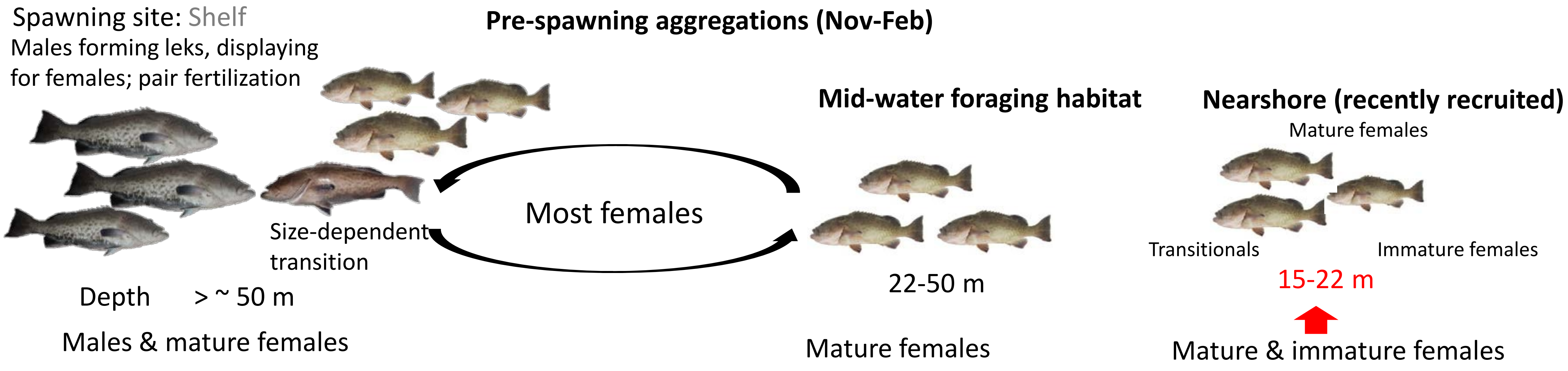
**Results**: Transitionals were rare (n=8) but not limited to the spawning grounds or by a threshold size; clearly not endogenously driven; size range: 675 mm TL to 1056 mm TL



## New sex change conceptual model

- Dogma: transition occurs only on the spawning grounds; long-term concern that gag are extremely sensitive to overfishing due to selectivity of males;
- Males not requisite for sex change; sex change duration assumed to take ~2 months
- $H_0$: female-to-female interactions play an important role, selecting for the most aggressive females to change to males prior to the spawning season. These fish will have adapted to near-shore fishing pressure with smaller, younger fish transitioning but most not making it through the gauntlet.
- $H_0$: fish still transition on the spawning grounds, but as Ellis and Powers (2012) noted sex change here will be moderated by male abundance and size dominance and thus in the MPA, only larger fish will transition



**2016 Update report**.

- Fishermen concerned rapid increase in SSB was unrealistic; continuity model less of an increase.
- Trade-offs in the data and the retrospective pattern indicate the utility of management advice resulting from this model should be carefully evaluated.
- Recent years: commercial fishermen not meeting quota

## Gag Grouper

| Year | Fishing Year | Total Reported* | Units | ACT | ACT % | ACL | ACL % | Closure Date | Data Source |
|---|---|---|---|---|---|---|---|---|---|
| 2018 | | 492,934 | | 939,000 | 52.5 | 1,217,000 | 40.5 | | |
| 2017 | | 492,095 | | 939,000 | 52.4 | 1,217,000 | 40.4 | | |
| 2016 | | 910,996 | | 939,000 | 97.0 | 1,217,000 | 74.9 | | |
| 2015 | | 542,774 | | 939,000 | 57.8 | 1,217,000 | 44.6 | | |
| 2014 | Jan 1- Dec 31 | 586,377 | gw | 835,000 | 70.2 | 1,100,000 | 53.3 | | IFQ |
| 2013 | | 575,335 | | 708,000 | 81.3 | 956,000 | 60.2 | | |
| 2012 | | 523,138 | | 567,000 | 92.3 | 788,000 | 66.4 | | |
| 2011 | | 318,663 | | 430,000 | 74.1 | | | | |
| 2010 | | 496,826 | | 1,410,000 | 35.2 | NA | NA | | |
| 2009* | | 715,814 | | 1,320,000 | 54.2 | | | | ACL_FILES_08092019 |

*Prior to 2009, Gag grouper was part of the shallow water grouper complex.

**Our results:**

- Aggregate behavior is strong in pre-spawning aggregations, where fishing pressure is high on fish recruiting to the adult population (ages 3 to 6);
- Spawning reserves do not fully protect the male recruitment process;
- Madison Swanson, the most productive spawning grounds in the Gulf has a male sex ratio of ~5%; male sex ratios outside reserve may be as low as 1%;
- What we saw was not what we got (captured).

# Can Gag male sex ratios really be this low?

**Table 2.** Percent males and transitionals in the gag population inside MSMR. Fish collected from Dec. 2007 to Dec. 2010. Fish sizes standardized to 75 cm TL and larger. F=female, T=transitional, M=male.

| Periods | F | T | M | total | % T | % M+T |
|---|---|---|---|---|---|---|
| Agg, Dec-May | 19 | 0 | 1 | 20 | 0 | 5.0 [a] ← |
| Post agg, Apr-Jul | 70 | 4 | 9 | 83 | 4.8 | 15.6 [b] |
| Pre agg, Aug-Nov | 72 | 0 | 8 | 80 | 0 | 10 [c] |
| total | 161 | 4 | 18 | 183 | 2.2 | 12.0 [b] ← |

[a] Not significantly different between inside and outside MSMR (p>0.05)
[b] Significantly different between inside and outside MSMR (p<0.0001)
[c] Significantly different between inside and outside MSMR (p<0.003)

**Table 3.** Percent males and transitionals in the gag population outside MSMR. Fish collected from Dec. 2007 to Dec. 2010. Fish sizes standardized to 75 cm TL and larger. F=female, T=transitional, M=male.

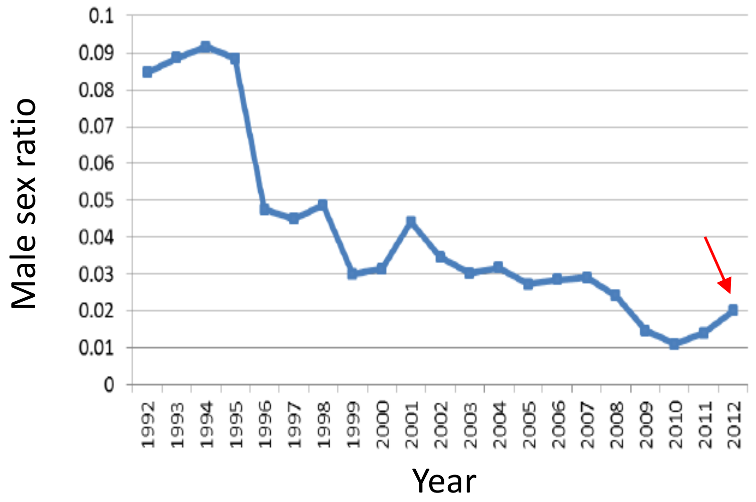
| Periods | F | T | M | total | % T | % M+T |
|---|---|---|---|---|---|---|
| Agg, Dec-May | 172 | 0 | 2 | 174 | 0 | 1.1 [a] ← |
| Post agg, Apr-Jul | 22 | 0 | 0 | 22 | 0 | 0 [b] |
| Pre agg, Aug-Nov | 9 | 0 | 0 | 9 | 0 | 0 [c] |
| total | 203 | 0 | 2 | 205 | 0 | 1.0 [b] ← |

[a] Not significantly different between inside and outside MSMR (p>0.05)
[b] Significantly different between inside and outside MSMR (p<0.0001)
[c] Significantly different between inside and outside MSMR (p<0.003)

Koenig and Coleman 2011

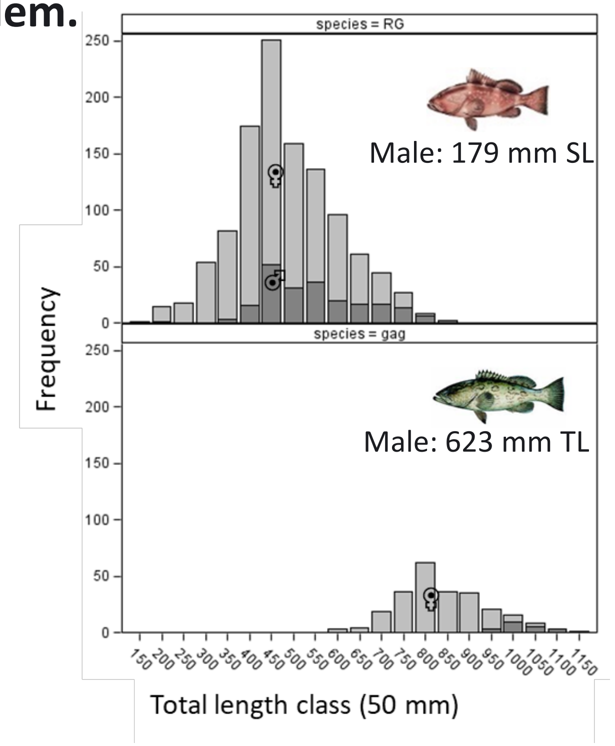
| CRP study | Total gag | M&T gag | % M&T | Years | Season | %LL | Grids |
|---|---|---|---|---|---|---|---|
| Burns and Robbins 2006 | 225 | 4 | 1.8 ← | 2004-2005 | May, June & Jan. | 100 | 99% (3,4,5) |
| Ward and Brooks 2010 | 114 | 3 | 2.6 ← | 2009 | Year round except Feb. & Mar. | 2.6 | 91% (6,7) |

- Although samples sizes were low and seasonal filters differed, results from the MARFIN study before ours (Koenig and Coleman 2011) are similar;
- As are results from 2 studies providing sex ratio estimates for the the last stock assessment
- And the stock assessment itself predicted ~2% male based on abundance at age and transition at age 10.9 y



# Productivity and sex ratios, putting Gag in perspective

**What is the relationship between productivity and sex ratio? We know zero males is a problem. Are other harvested protogynous species showing similar male sex ratio declines?**



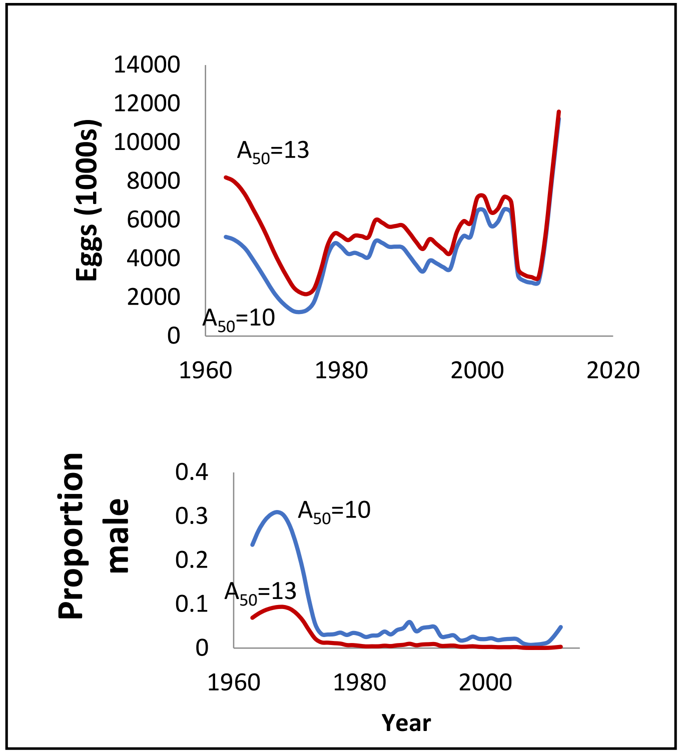

- Scamp: male sex ratios declined from ~38 to 18% from the 1970s to the 1990s; currently: 41%
  Lowerre-Barbieri et al., 2020 SEDAR68
- Red Grouper: male sex ratios increased from ~14% in the 1960s to 22% in the 1990s
  reported in Coleman et al. 1996
  - 2008-2013 19% male; 2014-2017 14% male
    Lowerre-Barbieri et al. SEDAR42 & 61
- Hogfish: male sex ratio estimated as ~12−17%
  Collins & McBride 2011

Koenig and Coleman 2011

**Table 7.** Gag sex ratio: Gulf of Mexico comparison of historical 1970s (Hood and Schleider 1992) with more recent data 1990s (Koenig et al. 1996). The numbers of females: males plus transitionals and the percentage of males plus transitionals (in parentheses) in the catch data are presented.

| | Gulf of Mexico | | |
|---|---|---|---|
| Period of Observation | 1970s | 1990s | p-value |
| Dec-Mar (Aggregation) | 301:52 (15%) | 311:6 (2%) | <0.001 |
| Apr-Jul (Post-aggregation) | 188:48 (20%) | 119:6 (5%) | <0.001 |
| Aug-Nov (Pre-aggregation) | 163:39 (19%) | 24:0 (0%) | <0.01 |

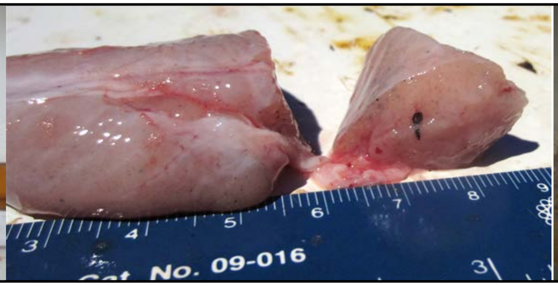
# Why we need to integrate males into the measure of reproductive potential

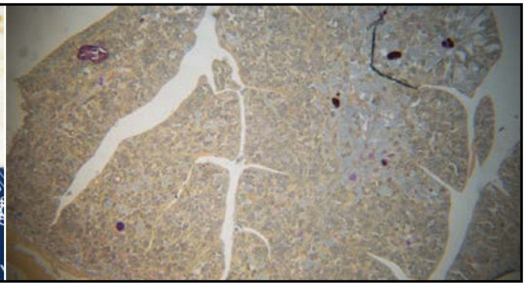



Sensitivity runs with model from SEDAR 33

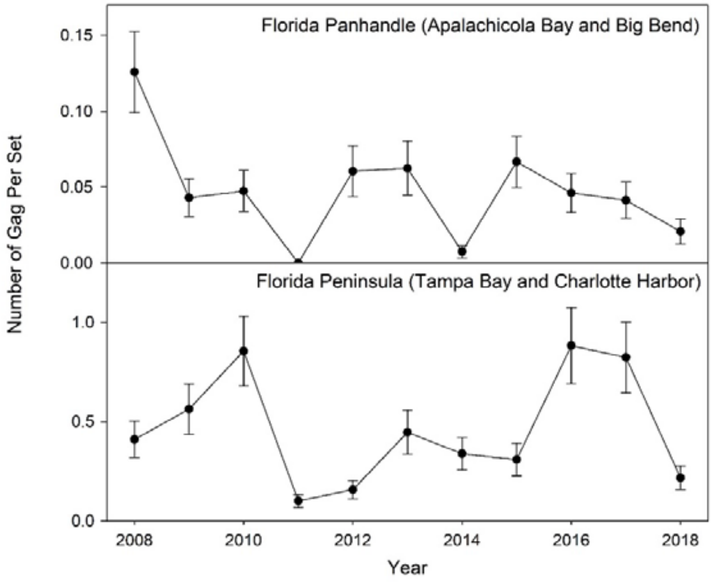
- Increased A50 with relatively low % male, may be due to decreased male recruitment & aging Madison Swanson males;
- Using female only SSB a higher A50 results in greater female reproductive potential;
- Age at 90th percentile at estimated MSY in current assessment is age 4; the youngest male we observed was age 7;
- Pre-spawning aggregations may have hyperstability;
- Important to look at long-term trends and recognize that sub-adult abundance may not significantly increase the spawning population; a strong year-class signal for years 2006 & 2007 was not seen in Madison Swanson;
- Unlike Nassau grouper, Gag believed to pair spawn (max male GSI ~0.58% compared to 16% for Nassau Grouper)

Date: 2/7/2018
Size: 1064 mm TL
Could not be strip-spawned

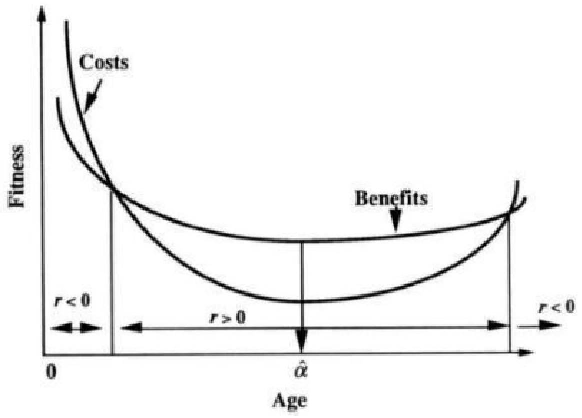
# Why we need to integrate males into the measure of reproductive potential (cont.)




- **How many males do we need?**

In captivity one male sheep can impregnate 100 females; however no natural ungulate populations have similarly skewed sex ratios, suggesting this does not lead to healthy natural populations.

  - Productivity may be severely impacted by sperm limitation, without resulting in a complete lack of strong year classes, given marine fish reproductive strategies and the impact of weather.
  - At 1-2% male sex ratios, sperm limitation is likely; estimated virgin sex ratio=37%



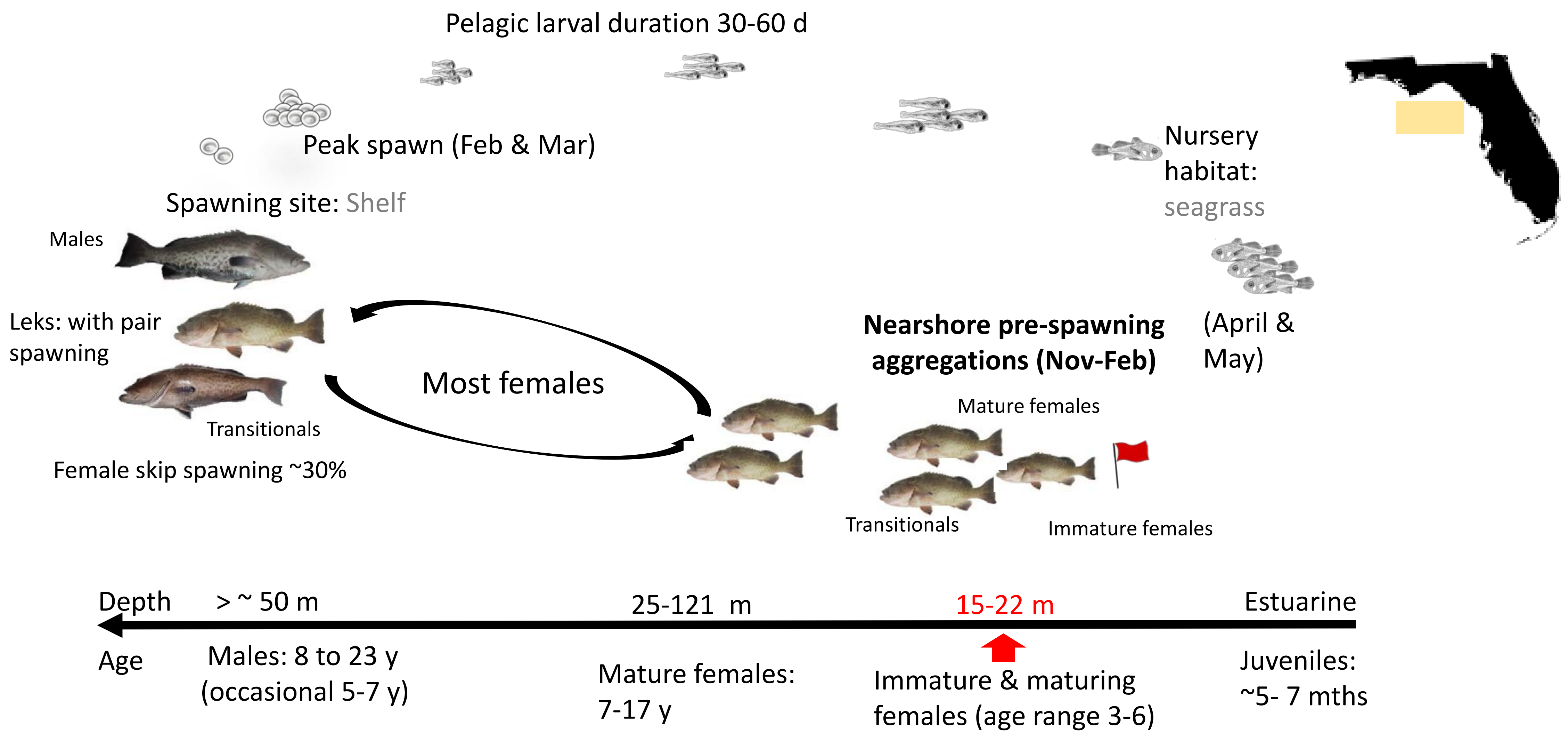

**Sex allocation:** the sex ratio expected to result in the highest reproductive success for the "community"…doubtful this is 1-2% males for Gag

Male maturation is delayed in social systems that promote competition among males for mates; which seems to be the case in Gag

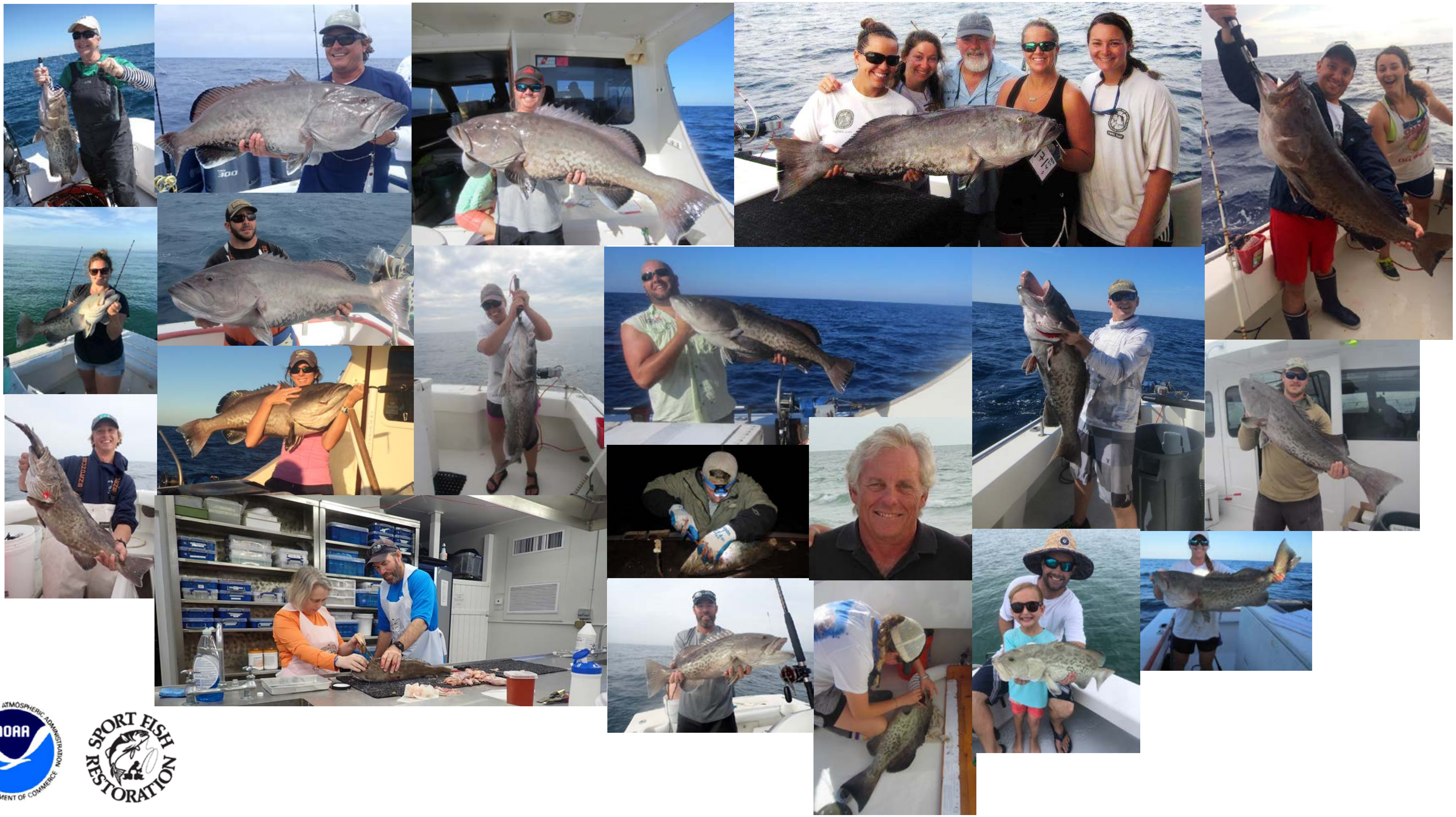
Stearns 1992

## Take home message

- The spatial distribution of the Gag life cycle, their gender system, and their mating strategy all impact sex change, male recruitment, and the spatio-temporal level of fishing mortality they can sustain.

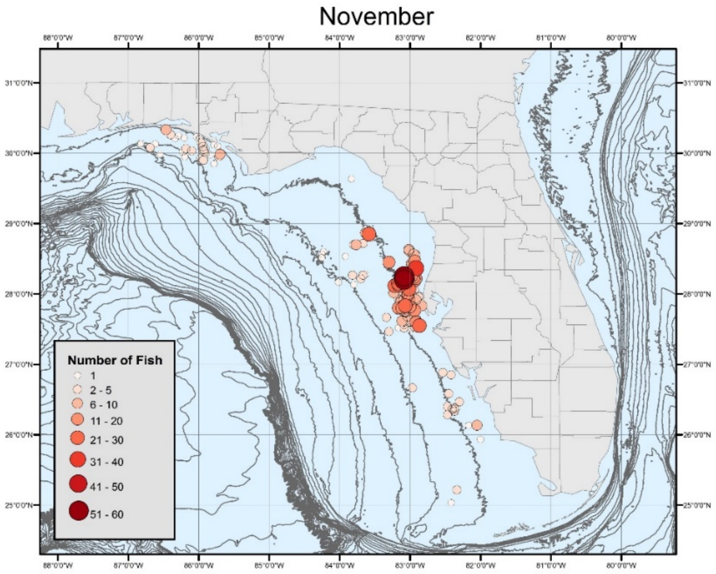


# Acknowledgements



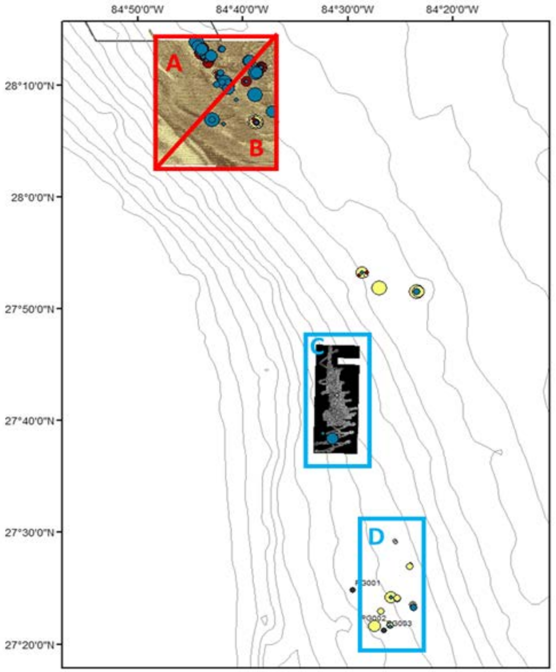
# Next steps: improving our understanding of pre-spawning aggregations & other spawning sites

- Better understanding R. Germeroth (masters student) using FDM data & results from this study to test the spatial distribution paradigm & evaluate fishing pressure on pre-spawning female aggregations in relatively shallow water in the fall




- Evaluating Gag reproductive potential in a second MPA: Steamboat Lumps and the Sticky Grounds to the south

- Proposing research to better understand pre-spawning aggregations and female movements/migrations



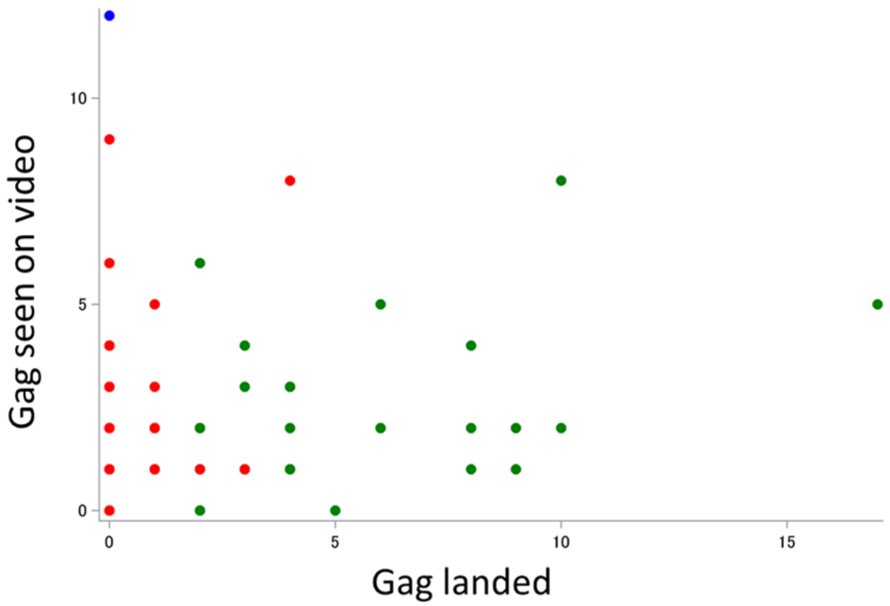


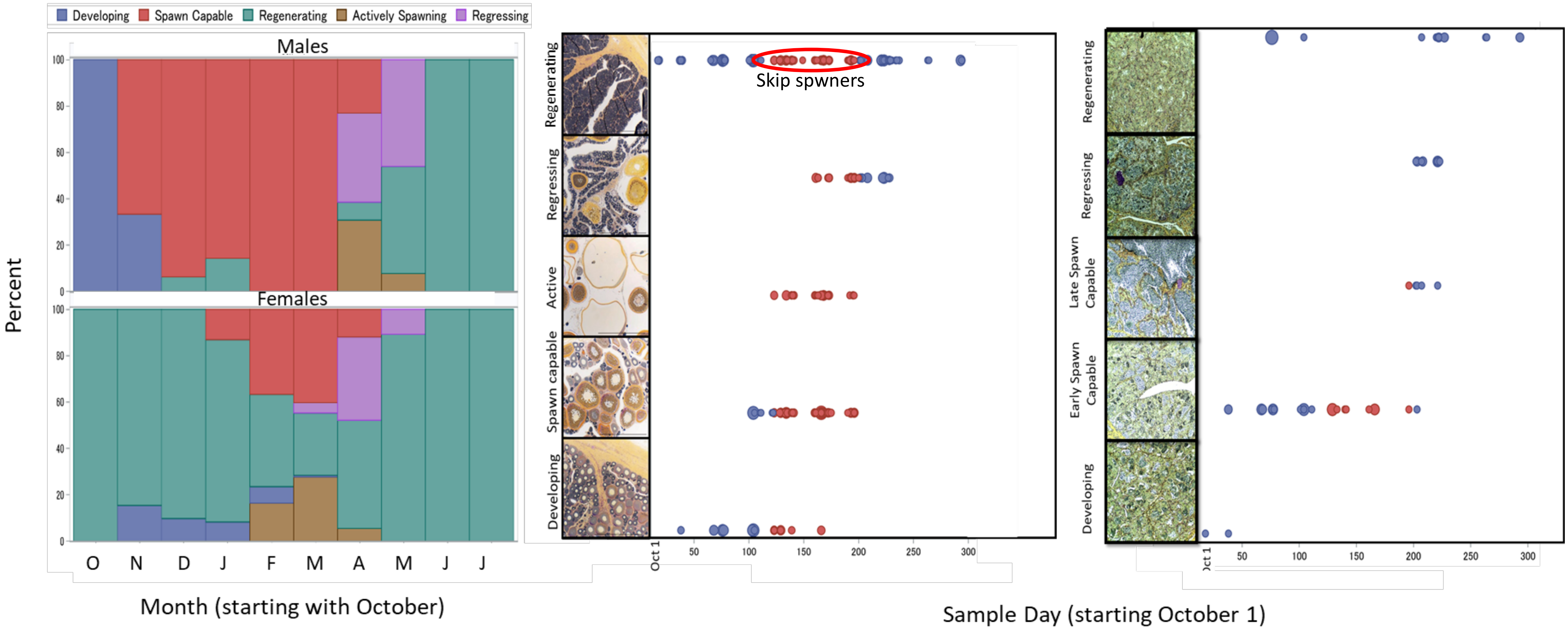

Figure 8. A comparison of the number of Gag seen with video sampling versus capture based sampling at the same site right after the video was taken. Blue=Open area; Red=The Edges; Green=Madison Swanson

# Spawning season

Spawning season based on female active spawners: 1 February through 18 April

Males spawning capable well before this

Relatively high numbers of regenerating within the spawning season (and on the spawning grounds)=skip spawners



Heppell et al. (2006) found that spawning area reserves were
the most effective management action to increase the sex ratio in a model population of gag grouper, and that to increase the adult population the most effective management action was to reduce fishing mortality on female fish, perhaps through the use of nearshore area closures.

While they may eventually result in an increased adult sex ratio, they will not alone be effective at maintaining the gag population especially should overall fishing effort increase outside reserves

Koenig et al., 1996

Only one male in the FSU-1992 colle (607 mm TL), was collected shallowe 50 m (29 m). In addition, the two sn of the three FSU-1992 transitionals collected shallower than 50 m.

The occurrence of prespawning gro in gag has been observed and videotaped (D. DeMaria and W. Parks, commercial fishers, pers. comm.). Prespawning sites were observed by Parks to occur in shallow (20-40 m) water at annually consistent sites off the south Atlantic coast of Florida typically during late December or early January. The function of the prespawning groups is unknown.

The question remains: What does a reduced proportion of males in the gag population mean in terms of reproductive capacity and ultimately recruitment? Intuitively, fewer males than is evolutionarily adaptive for a particular mating system would seem to restrict spawning opportunities for females in that system. As far as we know, there is a complete lack of information on this subject,

Transitionals were rare in all samples, historical and recent (Table 1). The size (mm TL) range of transitionals in the historical samples were: Gulf, 850 - 1 150 and Atlantic, 857 - 904. In the recent samples the size ranges of transitionals were: FSU-1992, 660 - 864; NMFS-1991, 725; NMFS-1992, 1 025 - 1 149; NMFS-1993, 525 - 1 175.

Spawning has not been directly observed in gag; however, evidence presented by Gilmore and Jones (1992) suggests that gag form hierarchical spawning groups with single-male, multiple-female spawning events. Our data support his observation. Ripe testes from gag are relatively small and contain small amounts of milt which indicates single

male spawning (i.e., no sperm competition). Red hind (*Epinephelus guttatus*), also has single male spawning and males have small testes (Sadovy et al. 1994). In contrast, Nassau grouper (*Epinephelus striatus*) males, when ripe, have large, milt-filled testes and are multiple-male spawners (Colin 1992).

The proximal causes of sex change in groupers have important implications for fisheries management (Munro 1987). Management will be quite different for species in which sex change is age- or size-mediated (endogenous control, as suggested for gag by McErlean and Smith 1964) than for those exhibiting sociodemographic control (exogenous control, e.g., Shapiro 1987). To date, the only mechanism described for sex-changing reef fish species is sociodemographic control (Shapiro et al., in press).

change occurs in gag. Our size-by-sex-frequency data (Fig. 5b) support this contention, as no small males (<800 mm) occurred in historical samples, but were present in ours. That is, if the mechanism of sex change in gag is mediated by social or demographic factors, then smaller males and transitionals would be expected in the population as exploitation eliminated the larger size classes. However, our data do not support a hypothesis of sex change in gag which is determined by size alone.

and others have shown that an protogynous species individuals ind to undergo sex change rapidly adopt s otypic male behaviors before they be functional males. The time necessa complete transition in gag is unkn however, data from artificial inducti sex change (Roberts and Schlieder 1 suggest that it may take mor

Pre-spawning aggs may play a role in transition but these ephemeral aggregations are completely unstudied