

## INCREASE IN BAY SCALLOP (*ARGOPECTEN IRRADIANS*) POPULATIONS FOLLOWING RELEASES OF COMPETENT LARVAE IN TWO WEST FLORIDA ESTUARIES

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**ABSTRACT** We propose the release of ready-to-set pediveliger larvae as a restoration strategy for bivalve shellfish. In this study, bay scallop (*Argopecten irradians*) larvae were released within two West Florida estuaries (Pine Island Sound and Boca Ciega Bay) currently closed to scallop harvest and where local scallop populations are severely depleted relative to historical abundances. Populations in both estuaries appear to have limited larval supply and show no tendency toward natural recovery after decades of decline. Larvae were either released into enclosures or free released on four separate dates in each estuary. On a given day we used 1, 2, 3, or 4 enclosures per site; multiple release sites; and multiple releases within a year. Assessments were made via several methods, including larval recruitment to collectors, juvenile quadrat surveys, adult timed surveys, and adult transect surveys. In Pine Island Sound, following the initial larval releases in 2003, an isolated recovery in adult scallops was observed at the release site in 2004 followed by a massive resurgence in the local population in 2005. This population declined dramatically in 2006, however, and had completely collapsed by 2007. In Boca Ciega Bay, the series of larval releases did not immediately produce any detectable scallop patches, but the combined releases did immediately precede a population resurgence to levels greater than had been observed in the past three decades. Scallop abundance increased 10-fold at 10 stations in Boca Ciega Bay from 2007 to 2008. In both Pine Island Sound and Boca Ciega Bay, the increases in scallop populations were probably the result of successful survival, growth, and reproduction of the released larvae, followed by successful recruitment and growth of the subsequent generation.

**KEY WORDS:** bay scallops, *Argopecten irradians*, restoration, population dynamics, larvae, recruitment, Florida

### INTRODUCTION

The restoration of coastal shellfish populations has become an increasingly common practice as native fisheries succumb to pressures of overharvesting, habitat loss or degradation, and challenges from invasive competitors and pathogens (Luckenbach et al. 1999, Rice et al. 2000, Arnold et al. 2002, Caddy & Defeo 2003, Gaffney 2006). This increase in restoration activity can also be attributed to a greater appreciation of the important role shellfish play in the ecology and economy of coastal habitats (Shumway et al. 2003). Ecological benefits from successful shellfish restoration include improved water clarity resulting from the removal of phytoplankton and suspended particles by shellfish (Newell 2004, Fulford et al. 2007); the restoration of keystone species (Coen et al. 2007); the creation of habitat for other species (Harding & Mann 1999, Breitburg et al. 2000); and, in the case of reef-building species, shoreline protection through wave dampening (Meyer et al. 1997). The economic benefits to coastal communities that depend upon the harvest, culture, and processing of shellfish seafood products are obvious (Shumway et al. 2003, Rönnbäck et al. 2007). In Florida, bay scallop (*Argopecten irradians concentricus*) commercial landings historically exceeded 50 tons of adductor muscle per year (Murdock 1955), peaking at 200 tons in 1958 at a value of \$74,601 (Rosen 1959). Currently, Florida waters are closed to commercial scallop harvest, and recreational harvest is limited.

Bay scallop populations occur discontinuously along the U.S. Atlantic coast, from Cape Cod, MA, to North Carolina and again through the eastern and northern Gulf of Mexico to Texas

(Sastry 1962). Along the west coast of Florida, the bay scallop appears to be distributed as a metapopulation (*sensu* Hanski & Simberloff 1996), consisting of a series of discrete local populations connected to each other by allochthonous larval transport (Arnold et al. 1998). During the past several decades, many of these local scallop populations have suffered drastic declines or a complete collapse to the point of endangering the stability of the metapopulation (Arnold et al. 1998, Marelli et al. 1999). In an effort to halt and possibly reverse this trend, a 2-pronged approach to rebuild these endangered local populations has been enacted: modifying the state's fisheries management plan and initiating a restoration program. The estuaries targeted for restoration (Pine Island Sound and Boca Ciega Bay) have been closed to recreational scallop fishing since 1994.

Bay scallop restoration has been attempted within many estuaries along the U.S. eastern seaboard (Morgan et al. 1980, Tettlebach & Wenzel 1993, Peterson et al. 1996, Goldberg et al. 2000, Arnold et al. 2005). Until recently, restoration strategies have essentially been limited to 1 of 2 methods. The 1st method, a harvest-based strategy, involves transporting adult scallops (usually from the nearest productive population) to the restoration site and congregating them in high-density spawner refuges, typically using on-bottom enclosures or cages (Peterson et al. 1996). The enclosures are intended to increase fertilization efficiency (assuming the scallops spawn synchronously), thereby maximizing reproductive success while reducing predatory losses. Spawning is usually inferred by histological examination of gonads, and settlement is evaluated by recruitment to artificial collectors. The 2nd method uses a culture-based strategy, in which scallop broodstock are spawned in a hatchery and the setting spat are transferred to a nursery system and grown to the

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desired size before release. These juveniles are then transported to the restoration site and released (either loosely or in cages) into seagrass beds (Morgan et al. 1980, Tettlebach & Wenczel 1993, Blake 1996, Goldberg et al. 2000, Arnold et al. 2005).

There are strengths and weaknesses to each of these approaches. Harvest-based restoration, although easy to initiate, involves removing substantial numbers of adult scallops from the donor population, subjecting them to potential stressors during transport, and acclimating them to their new surroundings. This approach also requires substantial field maintenance to monitor the health of the individuals and to counteract fouling by encrusting organisms. Culture-based restoration can produce far more scallops for planting without significantly depleting resident scallop populations. However, hatchery operations are costly and labor intensive, particularly with respect to the extended nursery grow-out phase and, more important, the resultant offspring may not be suitably adapted to conditions at the release site, particularly if the site is far removed from the nursery facility. Neither approach has resulted in unequivocal success; however, a decade-long culture-based effort in Crystal River, FL, led to a population recovery sufficient to sustain recreational harvest (Arnold et al. 2005), and harvest-based efforts in North Carolina resulted in substantial increases in localized population abundance (Peterson et al. 1996).

Harvest-based and culture-based strategies for restoring bay scallop populations have each had only partial success. Development of an approach that exploits the advantages of each of these strategies while minimizing their respective disadvantages may increase the chances for successful restoration. One such method uses a hatchery to rear larvae through most of the pelagic phase of life, which are then released into appropriate habitats (Arnold 2008). In this article, we present a novel bay scallop restoration strategy in which hatchery-spawned scallops produce large numbers of competent pediveliger larvae. We describe the timing of and methods for releasing these larvae into their natural habitat, the methods we use to follow the fate of the released larvae, and the apparent success of using this method in two coastal Florida estuaries. Finally, we discuss how this method might be successfully used on a larger scale to rebuild additional coastal scallop populations that, collectively, comprise Florida's bay scallop metapopulation.

## MATERIALS AND METHODS

### Site Selection

Pine Island Sound and Boca Ciega Bay are two estuaries along the southwest coast of peninsular Florida that have supported commercially harvestable bay scallop stocks until the 1950s (Murdock 1955), but have been closed to all scallop fishing since 1994. Scallops have essentially disappeared from both estuaries (Arnold & Marelli 1991), even though seagrass acreage has remained relatively consistent throughout this same time period (Dawes et al. 2004, Holland et al. 2006). Release sites were selected based on the following criteria: presence of current or historical scallop populations, appropriate water depth (1–2 m), continuous seagrass cover, and stable salinity regimes.

### Broodstock Collection and Spawning

Bay scallop broodstock ( $n \cong 200$ ) were collected from each respective estuary (if possible) or the nearest viable population

and transported to the Bay Shellfish Company hatchery in Terra Ceia, FL. At the hatchery, scallops were maintained in a continuous-flow seawater system and fed a constant drip suspension of live, mixed algae cultures. Reproductive development and maturation were monitored visually until the majority of scallops had developed ripe gonads.

To initiate spawning, several dozen scallops were submerged in shallow water on a table and subjected to gradual temperature fluctuations ( $\cong 5^\circ\text{C}$ ) until spawning occurred. The eggs and sperm remained on the table until fertilization was ensured ( $\sim 30$  min) and then were immediately drained off the table and rinsed onto a 25- $\mu\text{m}$  mesh screen, which retained the fertilized eggs and flushed away excess sperm. Some of the eggs were observed microscopically to evaluate quality, fertilization success, and the initiation of cell division. Fertilized eggs were transferred to temperature-controlled 5,000-L larval tanks for subsequent rearing, and the developing larvae were continuously fed a mixed diet of live algae. The larval tanks were drained every other day, the larvae briefly inspected for proper development, and the tanks replenished with fresh seawater. The larvae reached the pediveliger stage after they developed a visible and active foot (typically between days 8 and 10). At this time, the larvae were deemed "competent" (ready to initiate metamorphosis in advance of setting) and were quickly prepared for transport to the restoration site.

### Larval Release

Enclosures, if used, were set up at each restoration site prior to each release. The enclosures were used to limit larval dispersal, which would have prevented our ability to assess adequately larval settlement or juvenile recruitment associated with the releases. Enclosures were modified, high-density plastic sediment curtains (ABBCO, Cape Canaveral, FL). Each enclosure consisted of nine identical panels, and each panel consisted of a flotation collar, an impermeable curtain, and a chain anchor (Fig. 1). Each panel was secured to the substrate by tying the bottom center of the panel to the eye of a hurricane anchor screwed into the sediment. The 2 end panels were secured to one another along their adjoining edges, and the



Figure 1. Completed sediment curtain deployment forming a larval release enclosure.

completed enclosure formed a corral. Finally, a float was anchored in the center of each enclosure that remained in place after the enclosures were recovered, generally three days after the larvae were released. The float aided in relocating the release sites during subsequent monitoring and assessment efforts. In the few instances when enclosures were not used, larvae were released directly into the water and GPS coordinates were recorded for future assessments.

#### Pine Island Sound

Larvae were released four times in Pine Island Sound (Table 1): the 1st two (October 2003 and October 2005) using enclosures and the last two (June 2006 and October 2007) by free release. The 1st larval release took place at Pineland in northern Pine Island Sound in October 2003. Four enclosures were deployed 25 m apart (Fig. 2). Three enclosures were each stocked with approximately 0.5 million scallop larvae, whereas a 4th enclosure served as a control (no larvae). During October 2005, a single treatment enclosure was deployed at each of four separate locations within Pine Island Sound, two in the northern end of the Sound (Pineland and Demere Key) and two in the southern end (Powerline and FWS Refuge). During this event, each enclosure received roughly 1.2 million larvae. In June 2006, a single free release of 4 million larvae took place in the waters surrounding the Powerline location. Finally, in October 2007, a single free release of about 1.3 million larvae was made in the southern end of the estuary in Rabbit Key Basin.

#### Boca Ciega Bay

Scallop larvae were released on four occasions in Boca Ciega Bay, near the mouth of Tampa Bay (Table 1). Larvae were released simultaneously at St. Antoine Key and Tarpon Key in April 2006 (Fig. 3). Two treatment enclosures were deployed at each location; no control enclosures were used. Each enclosure received about 1 million larvae. In December 2006, larvae were released into two treatment enclosures at St. Antoine Key. Each enclosure received about 1 million larvae. In May 2007, a 3rd release (3 treatment enclosures) took place at St. Antoine Key. Each enclosure received roughly 580,000 larvae. The 4th and final larval release within Boca Ciega Bay occurred in October 2007. About 1.1 million larvae were released at each of three sites: West Mullet Key, Cunningham Key, and Bonne Fortune Key.

#### Larval Release Assessment

##### Settlement Pads

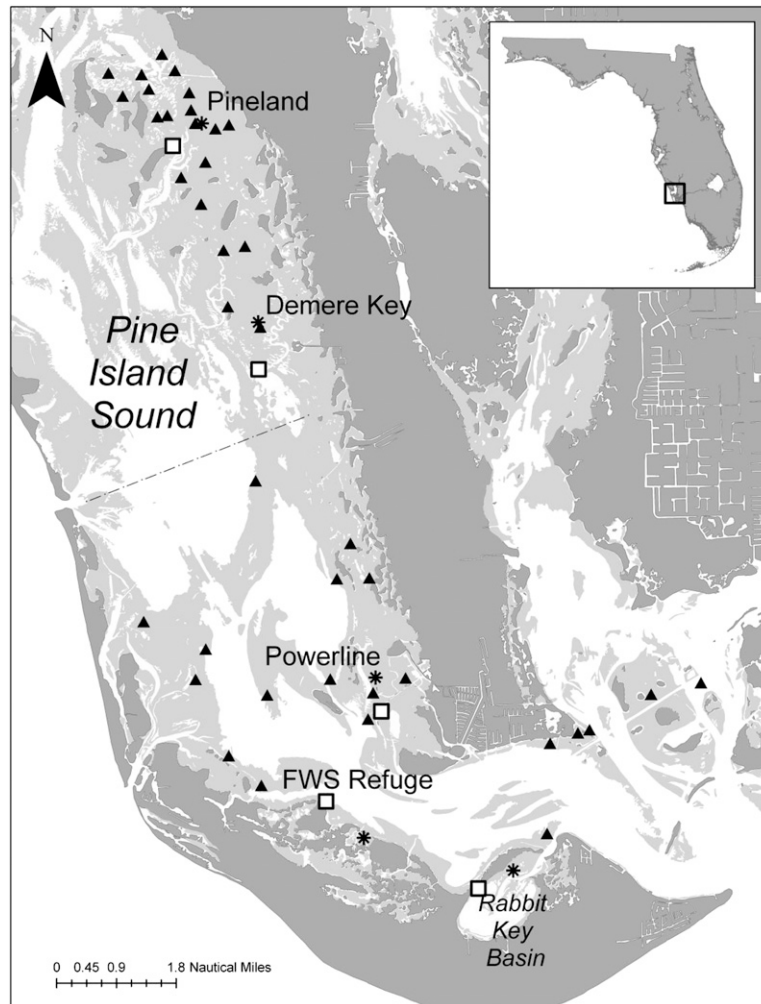
Settlement of released larvae within each enclosure was monitored using 10 × 15-cm scrub pads, which provided abundant interstitial spaces for larval attachment. Each pad was attached to a line threaded through a donut float and cement ring, so that the pad was positioned approximately 0.5 m off the bottom. Five settlement pads were placed haphazardly inside each enclosure prior to releasing the larvae and five additional pads were placed just outside each enclosure within the adjacent seagrass bed. Settlement pads were not used during

TABLE 1.

Estuary, location, larval release date, event count, release treatment and quantity, larvae released per enclosure, and the average number of spat per settlement pad for bay scallop larval releases within Pine Island Sound and Boca Ciega Bay.

Estuary	Location	Release Date	Event	Treatment (1–2 m water depth)	n	Larvae per Enclosure	Spat per Settlement Pad	
							Inside	Outside
Northern Pine Island Sound	Pineland	10/28/2003	1	Enclosure	3	$5.0 \times 10^5$	2.4	0.0
							1.8	0.0
							1.0	0.0
							0.0	0.0
Southern Pine Island Sound	Pineland	10/28/2003	1	Control	1	0	0.0	0.0
	Pineland	10/03/2005	2	Enclosure	1	$1.2 \times 10^6$	15.4	0.2
	Demere Key	10/03/2005	2	Enclosure	1	$1.2 \times 10^6$	33.3	0.8
	Powerline	10/03/2005	2	Enclosure	1	$1.2 \times 10^6$	27.2	0.8
	FWS Refuge	10/03/2005	2	Enclosure	1	$1.2 \times 10^6$	2.8	2.6
	Powerline	06/02/2006	3	Free release	0	$4.0 \times 10^6$	—	—
Boca Ciega Bay	Rabbit Key Basin	10/26/2007	4	Free release	0	$1.3 \times 10^6$	—	—
	St. Antoine Key	04/07/2006	1	Enclosure	2	$1.0 \times 10^6$	15.0	0.0
	Tarpon Key	04/07/2006	1	Enclosure	2	$1.0 \times 10^6$	13.4	0.0
							3.2	0.0
							1.6	0.2
	St. Antoine Key	12/21/2006	2	Enclosure	2	$1.0 \times 10^6$	6.4	0.2
							2.6	0.4
	St. Antoine Key	05/18/2007	3	Enclosure	3	$5.8 \times 10^5$	116.0	0.0
							77.2	1.4
							63.0	0.6
West Mullet Key	10/25/2007	4	Enclosure	1	$1.1 \times 10^6$	0.0	0.0	
Cunningham Key	10/25/2007	4	Enclosure	1	$1.1 \times 10^6$	0.0	0.0	
Bonne Fortune Key	10/25/2007	4	Enclosure	1	$1.1 \times 10^6$	0.0	0.0	

Note that the number and arrangement of enclosures differed for each release.



**Figure 2.** Pine Island Sound study area with adult abundance survey stations (triangles), recruitment collector stations (squares), and larval release stations (asterisks). The dashed line designates an imaginary line dividing the northern and southern ends of the sound.

free releases. After soaking for 3 days, the pads were retrieved (along with the enclosures), fixed in 5% formalin for 3 days, then dried at 60°C for 3 days. The dried pads were then gently shaken and brushed over a dish, thereby dislodging the spat for easier detection and enumeration.

#### Recruitment Collectors

Recruitment collectors (Brand et al. (1980) as modified from a design described in Motada (1977) and Arnold et al. (1998)) were in place year-round at select locations within each estuary to monitor natural scallop recruitment. These stations were similar to the larval release sites in that they were located in 1–2-m depths, were within *Thalassia*-dominated seagrass beds, and experienced good water quality. Each collector consisted of either a Vexar (Conwed Plastics, LLC. Minneapolis, MN) mesh panel or Netron netting (Fukui North America, Eganville, IL) inside a 35-L mesh citrus bag. Collectors were suspended 0.3 m off the bottom, and each collector was deployed for sequential 6-wk periods. A 2nd set of collectors were deployed at each site, but with a 3-wk offset to ensure that any scallops settling near the end of one deployment period would grow sufficiently large by the next retrieval date to be visually detected on the subsequent set of collectors. The collectors were deployed in

varying formations and time periods, and these modifications from the original configuration are described next for each estuary. Data were normalized to the number of spat per days deployed for each collector, and were expressed as a daily recruitment rate.

#### Pine Island Sound

In Pine Island Sound, triplicate collectors were initially placed at Pineland, Demere Key, Powerline, and FWS Refuge locations in May 2003; a 5th set was added in July 2005 in Rabbit Key Basin (Fig. 2). The deployment period changed from 6 wk to 8 wk beginning in October 2006. An additional set of 12 collectors surrounded the Powerline free-release site in June 2006 and soaked for 6 wk. Four collectors were deployed around the Rabbit Key Basin free-release site in October 2007 and soaked for 6 wk.

#### Boca Ciega Bay

Although we have been monitoring scallop recruitment in Tampa Bay since 1996, the locations and configuration of traps have changed numerous times. For this article we present only data retrieved from Boca Ciega Bay since 2000. Replicate collectors were deployed near Indian Key and Tarpon Key

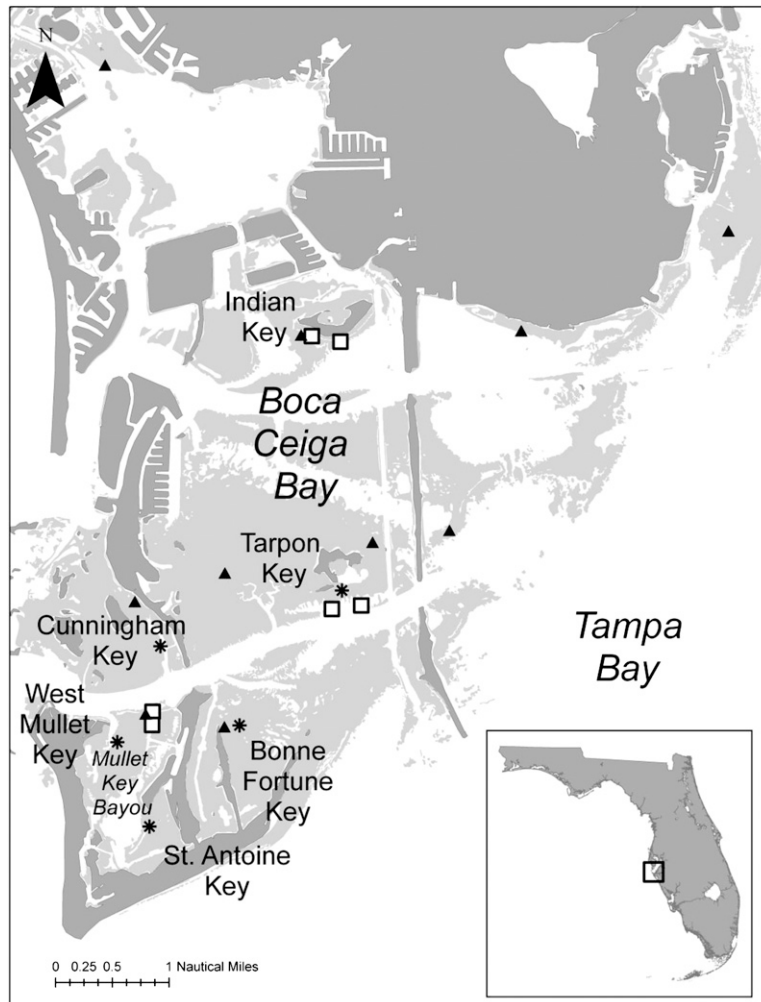


Figure 3. Boca Ciega Bay study area, located in lower Tampa Bay, with adult abundance survey stations (triangles), recruitment collector stations (squares), and larval release stations (asterisks).

(Fig. 3) in October 2000; a 3rd location near Mullet Key Bayou was added in April 2007 to detect natural recruitment in the vicinity of the larval release sites. The deployment period changed from 6 wk to 8 wk beginning in August 2006. During the October 2007 larval release, an additional set of 4 collectors were placed around each release site and 1 collector was placed inside each enclosure. These additional collectors soaked for 6 wk.

#### Juvenile Assessment

To assess the success of the larval release method, we surveyed the enclosure footprints for juvenile scallops (>10 mm shell height) roughly 3 mo after the initial release event. We used various methods to conduct these surveys, including 0.25-m<sup>2</sup> quadrats, 50-m<sup>2</sup> transects, 100-m<sup>2</sup> transects, timed surveys, and seagrass evaluation. The methods depended upon conditions at the release site on the day of assessment and are described in detail next.

#### Pine Island Sound

Juvenile scallops were surveyed using 0.25-m<sup>2</sup> quadrats in February 2004, 4 mo after the initial release. We thoroughly inspected 15 quadrats per enclosure for juvenile scallops,

including the seagrass blades and roots. A 2nd survey was made in July 2004 by establishing a 200-m concentric circle around the release footprints and making 3 randomly located and oriented 100-m<sup>2</sup> (600-m<sup>2</sup> total area) transect surveys. At the same time, the footprint of each enclosure was explored by touch because of low visibility. Scallops found during the assessments were counted and shell height (in millimeters) measured. These surveys continued for approximately 1 h, or until the surveyor was certain the area of each footprint had been thoroughly searched.

In January 2006, 3 mo after the October 2005 scallop larval release, a survey was made to locate and count juvenile scallops. At each release site, the buoy marking the center point of the footprint was located. Divers recorded the number and size of scallops encountered in 10 replicate 0.25-m<sup>2</sup> quadrats, which were haphazardly tossed within the footprint. An additional survey took place in the vicinity of broodstock collection. We did not assess the abundance of juveniles after the free releases that occurred in 2006 and 2007.

#### Boca Ciega Bay

In August 2006, 4 mo after the initial larval release in Boca Ciega Bay, we surveyed juvenile scallops by haphazardly

deploying ten 0.25-m<sup>2</sup> quadrats inside and outside each enclosure footprint. After the December 2006 release, seagrass blades were collected from inside and outside each footprint 3 days, 2 mo, and 3 mo after the release. Additional blades were also collected near the scallop recruitment stations at Indian Key and Tarpon Key 2 mo after release, and blades were collected near Bonne Fortune Key 3 mo after release. We planned to use quadrat surveys to assess juveniles from the 3rd release during May 2007, 5 mo after the release date. However, water conditions were not conducive to quantitative visual surveys, so grass blades were collected from the footprints instead, and a qualitative search of the surrounding seagrass bed was made. No juvenile assessment was made after the October 2007 release.

#### *Adult Abundance Assessment*

Assessments of adult bay scallop abundance are made annually each summer (Arnold et al. 2009). Stations are located within seagrass beds between 1 m and 2 m deep. Surveying bay scallops requires underwater observation, either by snorkeling in shallow depths with good visibility, or by scuba in deeper water, water with poor visibility, or at stations with thick seagrass or macroalgae. At each station, paired divers swim alongside a weighted transect line, ranging from 50–300 m, and count all scallops within 1 m of either side of the line. The shell height (measured in millimeters) of the 1st 30 scallops is measured and the density is reported as the number of scallops per total area surveyed.

#### **Pine Island Sound**

Since 1994, Fish and Wildlife Research Institute (FWRI) scientists have been conducting annual bay scallop surveys at 20 stations in northern Pine Island Sound (Fig. 2) (Arnold et al. 2009). In 2004, the year immediately after the 1st larval release, surveys were initiated at 20 additional stations in southern Pine Island Sound. The number of stations in southern Pine Island Sound was reduced to 10 in 2007 and 4 in 2008.

#### **Boca Ciega Bay**

Since 1995, Tampa Bay Watch, a local nongovernmental organization, has conducted an annual adult scallop search (“The Great Bay Scallop Search”). These volunteer-based surveys take place in Boca Ciega Bay and lower Tampa Bay, an area that encompasses all of our larval release and recruitment sites. The total number of stations surveyed in any given year depends on the number of participants. Survey methods are similar in design to FWRI’s, but differ in the length of the survey line (50 m), observation method (snorkel gear only), and data collected (count only). Recently, FWRI staff has conducted additional baywide scallop surveys (Arnold et al. 2009). In July 2007 and July 2008, 10 stations in Boca Ciega Bay (Fig. 3) were surveyed using the same methods used in the Pine Island Sound surveys.

## RESULTS

#### *Larval Settlement*

#### **Pine Island Sound**

Bay scallops settled on all pads within the treatment enclosures during the 1st larval release in 2003 (Table 1). No

recruits were detected in the control enclosure or on pads located outside the enclosures. In 2005, settlement on pads within the enclosures was high at 3 of the 4 release sites, with the highest settlement rates observed at Demere Key and Powerline. Settlement pads at Pineland had approximately half as many scallops as those at Demere Key and Powerline. The average settlement at Pineland was much higher in 2005 (15.4 scallops/pad) than in 2003 (<3 scallops/pad). The lowest settlement in 2005 occurred at FWS Refuge, with 2.8 spat/settlement pad. In 2005, all pads placed outside the enclosures at all sites had attached spat. This was especially noticeable at FWS Refuge, where settlement outside the enclosure was almost equal to settlement inside the enclosure.

#### **Boca Ciega Bay**

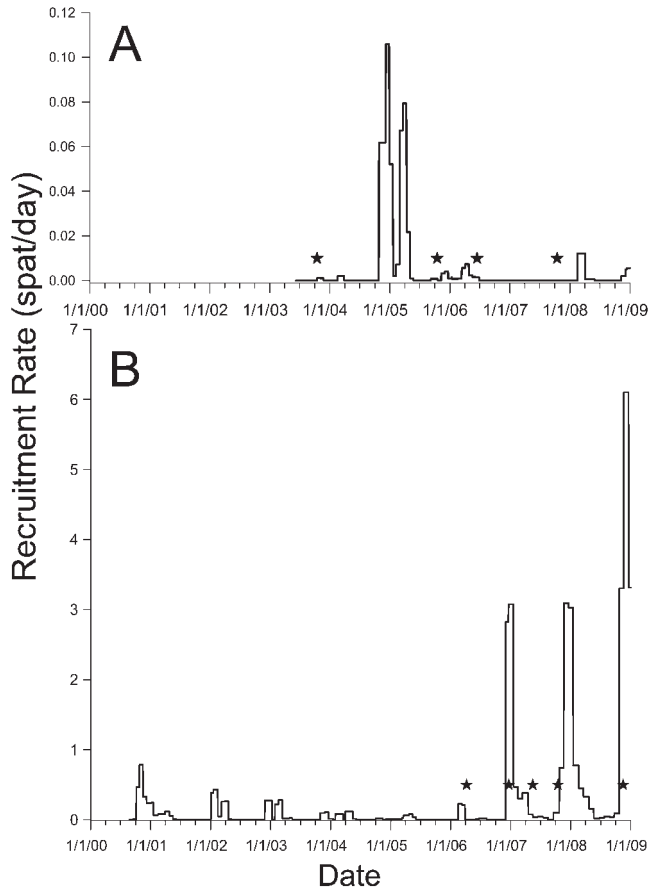
Scallops were observed on settlement pads inside enclosures at both sites during the 1st release in April 2006, although settlement was much higher at St. Antoine Key than at Tarpon Key (Table 1). No scallops were detected on pads outside enclosures at St. Antoine, but a small number were detected at Tarpon Key. Moderate settlement was observed at St. Antoine Key during the 2nd release (December 2006), with spat observed on the exterior pads as well. The highest settlement from Boca Ciega Bay larval releases occurred inside the enclosures at St. Antoine Key during the May 2007 release, when the average number of settling scallops ranged from 63–116 spat/pad. The highest settlement of scallops outside the enclosures also occurred during the May 2007 release (1.4 spat/pad). No scallops were observed on pads inside or outside the enclosures during October 2007.

#### *Recruitment Collectors*

#### **Pine Island Sound**

Natural scallop recruitment in Pine Island Sound was episodic—long periods of no recruitment followed by bursts of recruitment of varying intensity. There was essentially no recruitment to collectors within Pine Island Sound from their initial deployment in May 2003 through March 2004 (Fig. 4). A single scallop was collected at Pineland, near the site of the October 2003 larval release, in November 2003. Two spat were collected in March 2004, one at Pineland and one at Demere Key. This was followed by 7 mo of no recruitment. The only appreciable recruitment within Pine Island Sound occurred from December 2004 through May 2005 (197 spat on 105 collectors), when spat were observed at all four locations. During this period, the most spat on a single collector occurred at Pineland, and the most spat overall settled at Demere Key. After May 2005, no scallops recruited to collectors within Pine Island Sound for 4 mo. From September 2005 through June 2006, recruitment remained extremely low at all locations, with a total of 19 spat on 219 collectors. This was followed by 1.5 y of no recruitment, and then a small peak occurring over the next 3 mo starting in February 2008. This was followed by another 5 mo of no recruitment, ending with a small recruitment event in November through December 2008. Overall recruitment was low, with less than one spat/day, and scallops settling on fewer than 5% of the collectors.

After the 2006 larval free release, 10 of the 12 additional collectors deployed at the release site were retrieved. Eight spat were observed on 4 collectors; the remaining 6 collectors had no



**Figure 4.** (A, B) Daily recruitment of bay scallops in Pine Island Sound (A) and Tampa Bay (B). Recruitment rate equals the number of spat per collector per day averaged for all collectors deployed on a given date. The stars signify the timing of larval releases. Note the different scales for the y-axes between the 2 estuaries.

spat. After the October 2007 free release, no spat were observed on the 4 collectors retrieved from the release site 6 wk later.

#### Boca Ciega Bay

Since FWRI started monitoring natural recruitment in August 2000, scallop recruitment in Boca Ciega Bay has generally been greatest from December through February (Fig. 4). From August 2000 through December 2008, 36% of the collectors had scallop recruits. There was at least 1 scallop present during 60% of the collection periods. The percentage of collectors containing spat has increased annually (18.8% in 2006, 71.7% in 2007, and 81.2% in 2008). Moreover, the average number of spat per collector has increased (1.5 in 2006, 40.1 in 2007, and 67.6 in 2008), and the maximum recruitment rate during the peak recruitment period (number of scallop recruits divided by the number of deployment days) has increased more than 10-fold (0.8 spat/day in 2006, 8.5 in 2007, and 12.3 in 2008).

Additional recruitment collectors were deployed for 2 mo at West Mullet Key, Cunningham Key, and Bonne Fortune Key after larval releases in October 2007. These collectors yielded 39 scallops from within the enclosures (0.3 spat/collector/day) and 99 from outside the enclosures (0.2 spat/collector/day). Most recruits were observed at Bonne Fortune Key and were 1–2 mm in shell height.

#### Juvenile Assessment

##### Pine Island Sound

Quadrats were used to survey juveniles from within the footprint of the 4 enclosures during the 1st larval release. Eight juvenile scallops were recovered from quadrats within the 3 treatment enclosures, with shell heights ranging from 15–25 mm. No scallops were found in the control enclosure. During the 2nd assessment of the 1st release, 3 scallops were observed on the 3 transects within 200 m of the release site. The survey within each footprint yielded 3 scallops in the control footprint and 4, 20, and 33 scallops in the treatment footprints. The juvenile survey from the 2nd larval release uncovered no juvenile scallops within the treatment enclosure footprints at any of the 4 sites. No juvenile surveys took place after the 3rd and 4th larval releases in Pine Island Sound.

##### Boca Ciega Bay

Juvenile quadrat surveys after the 1st Boca Ciega Bay larval release found no scallops either inside or outside the enclosure footprints at either site. Juvenile abundance after the 2nd release was made in December 2006. The *Thalassia testudinum* seagrass blades collected inside the St. Antoine Key footprints yielded 5.21 spat/mm<sup>2</sup>, and blades collected outside the enclosure footprint yielded 0.58 spat/mm<sup>2</sup>. Seagrass blades collected in February 2007 inside the St. Antoine Key footprint yielded 1.31 spat/mm<sup>2</sup>, and outside the footprint yielded 0.35/mm<sup>2</sup>. Blades collected at the same time from 2 grass flats near Tarpon Key and Indian Key, yielded 0.32 spat/mm<sup>2</sup> and 0 spat/mm<sup>2</sup>, respectively. In March 2007, 1 scallop was found inside the footprint on a seagrass blade (0.05/mm<sup>2</sup>), and none were found outside the footprint. No assessments were performed after the 3rd or 4th releases.

#### Adult Abundance Assessment

##### Pine Island Sound

From 1994 to 2003, prior to the initiation of restoration, mean annual adult scallop density in northern Pine Island Sound ranged from 0–5.5 scallops/600 m<sup>2</sup> (Table 2). During this period, an average of 6.8 of 20 stations had at least 1 scallop present. In 2003, there were very few scallops in northern Pine Island Sound. In 2004, a localized increase in abundance was observed at the Pineland larval release site from the previous year, but with the exception of the larval release sites mentioned earlier, the mean density throughout the survey area remained lower than the 1994 to 2003 average. In 2004, only one scallop was recorded at the 20 stations in the southern end of the estuary. A dramatic increase in scallop abundance occurred throughout northern Pine Island Sound in 2005. In fact, this area had the highest scallop density of any location surveyed statewide that year! The mean adult density increased to 93.4 scallops/600 m<sup>2</sup>, and 95% of the stations had at least one scallop. During this time, both abundance and distribution of scallops also increased in southern Pine Island Sound (Fig. 5). There, scallops increased from 0.05 scallop/600 m<sup>2</sup> (a scallop at 1 of the 20 stations in 2004) to 2.4 scallops/600 m<sup>2</sup> (48 scallops among 7 of the 20 stations). The following year (2006), mean density in northern Pine Island Sound decreased to 8.2 scallops/600 m<sup>2</sup>; however, scallops were still evenly distributed throughout the area, being present at 19 of 20 stations. In southern Pine

TABLE 2.  
Annual bay scallop density in north and south Pine Island Sound (PIS) and Boca Ciega Bay (BCB), FL.

Site		1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
North PIS	Total	0	49	15	46	47	52	56	110	13	12	21	1,868	163	0	2
North PIS	Average	0.0	2.5	0.8	2.3	2.4	2.6	2.8	5.5	0.7	0.6	1.1	93.4	8.2	0.0	0.1
South PIS	Total	—	—	—	—	—	—	—	—	—	—	1	48	26	0	1
South PIS	Average	—	—	—	—	—	—	—	—	—	—	0.1	2.4	1.3	0.0	0.3
BCB – FWRI	Total	—	—	—	—	—	—	—	—	—	—	—	—	—	52	660
BCB – FWRI	Average	—	—	—	—	—	—	—	—	—	—	—	—	—	5.2	66.0
BCB – TBW	Total	—	77	74	79	27	21	18	1	—	—	12	1	18	555	641
BCB – TBW	Average	—	—	1.1	—	—	—	—	—	—	—	0.2	0.02	0.3	7.8	10.2

Data from Fish and Wildlife Research Institute (FWRI) and Tampa Bay Watch (TBW). Data are shown as both total number of scallops and the average number per area during survey years. Stations surveyed in Pine Island Sound all years and Boca Ciega Bay by FWRI during 2007 and 2008 represent 600 m<sup>2</sup> of seagrass habitat. Stations surveyed by TBW represent 100 m<sup>2</sup> of seagrass habitat. All surveys were conducted during summer months. Dashed lines indicate no survey took place that year. Average densities could not be calculated every year for the TBW data because the number of participants varied and this number was not always recorded.

Island Sound, mean density declined to 1.8 scallops/600 m<sup>2</sup>, but scallops were found at half of the stations. In 2007, no scallops were found throughout the entirety of Pine Island Sound. In 2008, only two scallops were detected in northern Pine Island Sound. Because of the low number of scallops found in the northern end of the sound, we reduced the number of stations surveyed in the southern end from 20 to 4 in 2008. A single scallop was found in the southern portion of Pine Island Sound.

#### Boca Ciega Bay

Annual adult scallop densities from Boca Ciega Bay before larval releases were initiated (1995 to 2006; Tampa Bay Watch data) showed variably low numbers, ranging from 1–79 total scallops/y (Table 2). A dramatic upshot in abundance was observed the following 2 y, with a total of 555 scallops in 2007 and 641 scallops in 2008. Again, this surge in scallop abundance occurred after local restoration began. FWRI surveys within Boca Ciega Bay have been less regular but show similar trends. In July 2007, average adult density reached 5.2 scallops/600 m<sup>2</sup>. Scallops were observed at 6 of 10 stations. In July 2008, average adult density increased to 66.0 scallops/600 m<sup>2</sup>. Scallops were observed at 9 of 10 stations; 2 stations had densities greater than 200 scallops/600 m<sup>2</sup>.

#### DISCUSSION

We have now had four opportunities to enhance bay scallop populations in both Pine Island Sound and Boca Ciega Bay through the controlled release of hatchery-reared larvae. In each estuary, we saw a dramatic increase in scallop densities after restoration activities began. In 2005, Pine Island Sound had the highest density of scallops of all the Florida estuaries we surveyed, including Steinhatchee and St. Joseph Bay, two regions that have had consistently stable scallop populations and remain open to recreational harvest (Arnold et al. 2009). Similarly, in 2007, the abundance and distribution of scallops in lower Tampa Bay was markedly increased. The most likely explanation is that, in each case, a portion of the released larvae successfully grew to reproductive age at densities sufficient for high fertilization rates. These scallops then successfully spawned and produced abundant fertilized larvae, which then dispersed to the local area at high densities, and throughout the

estuary at some lower density. This 1st generation of wild-spawned larvae then successfully recruited to our survey area and grew to a size detectable by visual survey methods. In Pine Island Sound, a smaller, but well dispersed, 2nd wild generation followed but was later decimated. In Boca Ciega Bay, the 2nd wild generation appears to have been larger and more widely dispersed, and has produced an even larger 3rd generation of recruits to our monitoring sites.

During application of this restoration technique we used 3 major assessment components to monitor progress and to evaluate success: larval recruitment monitoring using settlement pads or recruitment collectors, juvenile monitoring, and adult abundance surveys. Of these, larval recruitment monitoring provides the most direct and immediate measure of restoration impacts. Scallop larvae have to survive and grow in the hatchery, withstand transport from the hatchery to the field, and then acclimate to field conditions in a relatively short time frame. Metamorphosis from a larva to a juvenile is also very stressful, and unless all of the larvae are very healthy and properly acclimated to changes in water quality from the hatchery to the field, the possibility exists for most, if not all, to perish during the process. Despite these potential pitfalls, spat attached to settlement pads during 5 of the 6 enclosure release events, a positive indication that these obstacles were overcome. One possible reason for observing no settlement during the 6<sup>th</sup> and final enclosure larval releases was the daily spring low tides that took place after the releases that effectively drained all the water from all enclosures within Boca Ciega Bay. If similarly low tides occurred before the larvae had time to attach to settlement pads, all the larvae may have been advected away from the release site. Young scallops were able to recruit to the seagrasses at these locations during most of our larval release experiments.

Based on the combined results from both estuaries, it does not appear that the number of juveniles is a reliable indicator of restoration success. The reason for this disconnect is not clear. One explanation may lie with our methodology, whereby we are not adequately searching a large enough area to arrive at a reasonable estimate of population abundance. If we wish to maintain replication in assessing population abundance, we will probably need to increase the size of our quadrat. However, this



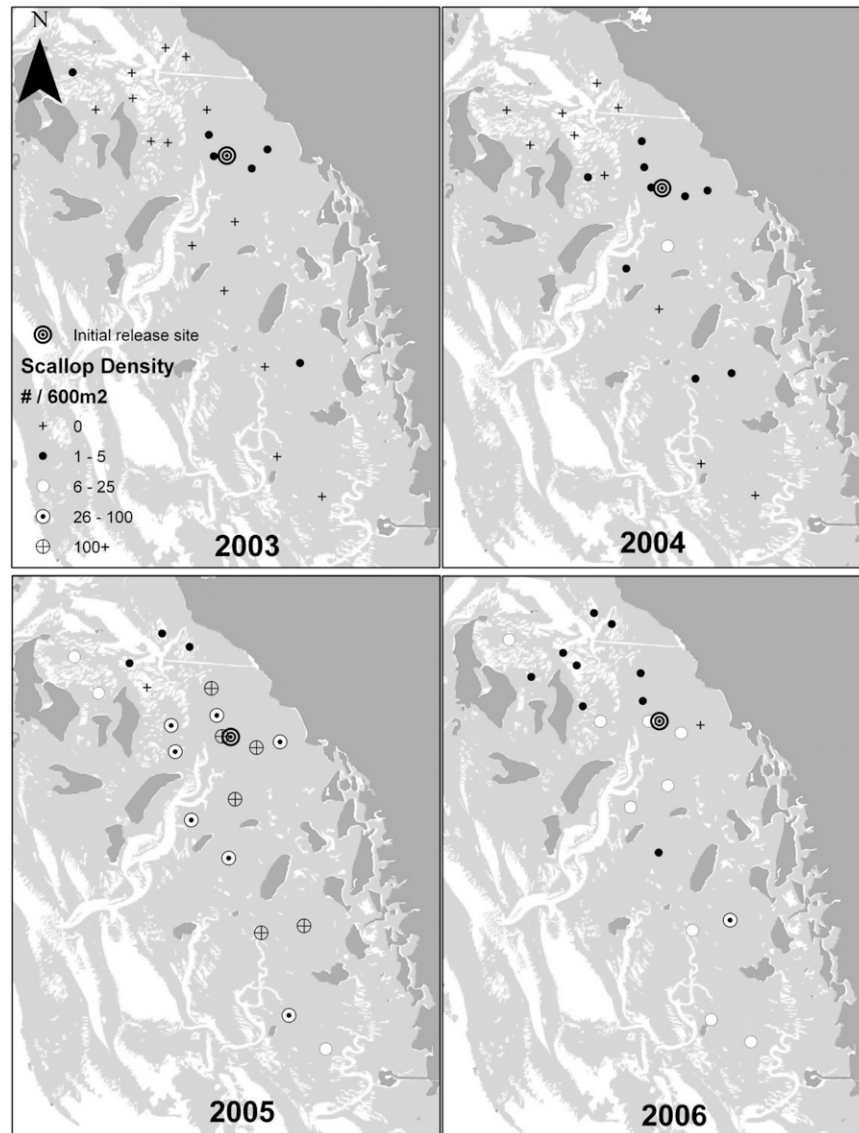


Figure 5. Density of adult bay scallops surveyed each summer in northern Pine Island Sound before and after the October 2003 larval release.

may make it more difficult to survey properly for small individuals underwater. A 2nd possibility is that young juvenile scallops are too small and cryptic, and thus are below the reasonable detection limit of a human observer. These methodological questions will be addressed in future restoration projects.

A major benefit in undertaking this restoration effort in an area like Pine Island Sound is the presence of a historical database on scallop abundance. We have been conducting annual surveys in this area since 1994, and have revisited the same locations and used the same methodology each year. Furthermore, we have conducted identical scallop surveys in 8 other Florida Gulf Coast estuaries every year over the same time span (Arnold et al. 2009). This database has become invaluable in assessing the effects of our restoration against natural fluctuations in scallop population dynamics in Pine Island Sound and throughout the state. Against this historical backdrop, it is evident that scallop abundance rebounded in Pine

Island Sound for 2 y and then declined. It took 2 y, or annual cycles, for a successful larval release to manifest itself in higher adult abundance throughout the area. After the 1st year, we had apparently established a natural spawning stock at the center of the restoration site (Fig. 5). This spawning stock was the surviving cohort from the larvae that were initially released the previous year and prevented from dispersing because of the containment enclosures. This highly concentrated assemblage of scallops in 2004 performed as a spawning stock. When spawning occurred, fertilization success was increased because the broodstock was in such close proximity to one another. The larvae from this *in situ* spawn were then free to disperse and settle naturally. There were 2 concentrated areas of adult density in 2005 (Fig. 5), one at the original restoration site and a 2nd roughly 2 km to the south. We speculate that this 2nd area of scallop abundance developed as a result of the prevailing tidal currents and local circulation patterns. Similarly, in Boca Ciega Bay it appears that in 2007, when the 1st survey after

a larval release was conducted, there was a small region of increased scallop abundance in the vicinity of our restoration efforts in lower Tampa Bay (Fig. 6). In 2008, that core spawning stock translated into a very broad distribution of scallops throughout the bay, with a huge increase in scallops centered in the vicinity of our restoration efforts. This 2nd generation produced a very large 3rd generation of recruits, as seen by the number of scallops on the recruitment collectors.

Our original hypothesis was that successful restoration in Pine Island Sound would be quantifiable as a 1 order of magnitude increase in scallop abundance. In Florida, we categorize scallop populations as collapsed ( $<5$  scallops/600 m<sup>2</sup>), transitional ( $>5$  and  $< 25$  scallops/600 m<sup>2</sup>), and healthy ( $>25$  scallops/600 m<sup>2</sup>). The average density in north Pine Island Sound reached a transitional status once in the 9 y prior to restoration efforts. After restoration, this site achieved healthy status for a single year, but then fell to transitional status the following year, before dropping back to a collapsed status. In 2005, scallop abundance increased by two orders of magnitude and, in 2006, the average abundance was still close to an order of magnitude higher than recent annual abundance values. Of equal importance in assessing the effect of our efforts was the finding that scallops were present at 95% of our survey stations. We began to find scallops at locations that had been void of scallops during the past decade. An almost identical scenario occurred in Boca Ciega Bay from initiation of larval releases in 2005 through the high levels of abundance and distribution observed in 2007 and 2008. This observed spread in the spatial distribution of scallops is imperative in rebuilding local populations to historical levels. We feel this is valuable information and therefore intend to include spatial distribution as well as abundance measures as evaluation criteria in evaluating the success of future scallop restoration projects.

Although these results are encouraging, there are reasons for caution and restraint. The 1st reason, which may also explain, in part, why we saw such an immediate response from our efforts, has to do with the natural history of the bay scallop itself. Rebuilding local populations can occur only through 1 of 3

ways: successful spawning and recruitment within surviving populations, larval transport from distant populations, or human intervention. Florida bay scallops have an annual life cycle. Individual scallops may vary in longevity, but the majority of the population dies each year. Therefore, if there are any significant adverse conditions that the population encounters in a given year, there is a good chance that the entire population may suffer a recruitment failure. Several stressors that can negatively impact bay scallops from peninsular Florida include periodic inundation of freshwater during above-normal rainy seasons that reduce salinity to less than 20 ppt for extended periods of time, prolonged hypoxia events, harmful algal blooms, and even extremely high summer temperatures. Both Pine Island Sound and Boca Ciega Bay periodically experience one or many of these potential stressors.

Freshwater inflow, especially in southern Pine Island Sound, and periodic red tides throughout both estuaries are serious impediments to establishing self-sustaining bay scallop populations over the long term. Red tides are frequent in this area (Landsberg et al. 2009) and occurred in both 2005 and 2006 (FWC-FWRI Harmful Algal Bloom database accessed on 1/27/10: <http://research.myfwc.com>) and may have played a role in the reduced scallop abundance. Numerous dead fish were observed in July 2006 during the retrieval of recruitment collectors from the Pine Island Sound Powerline larval release site. This information is critical in evaluating the potential for successful scallop restoration in this part of the estuary against a background of environmental conditions. Although it appears that the salinity stayed above the critical value of 20 ppt at our restoration sites, the area experienced a significant red tide episode, and we suspect that this will have a detrimental effect on our restoration efforts, particularly in the southern portion of the sound.

Bay scallops appear to be distributed as a metapopulation within the coastal waters of West Florida. If the number of local populations is relatively large, then even during adverse conditions there should be some local populations available to contribute offspring, leading to the overall stability of the

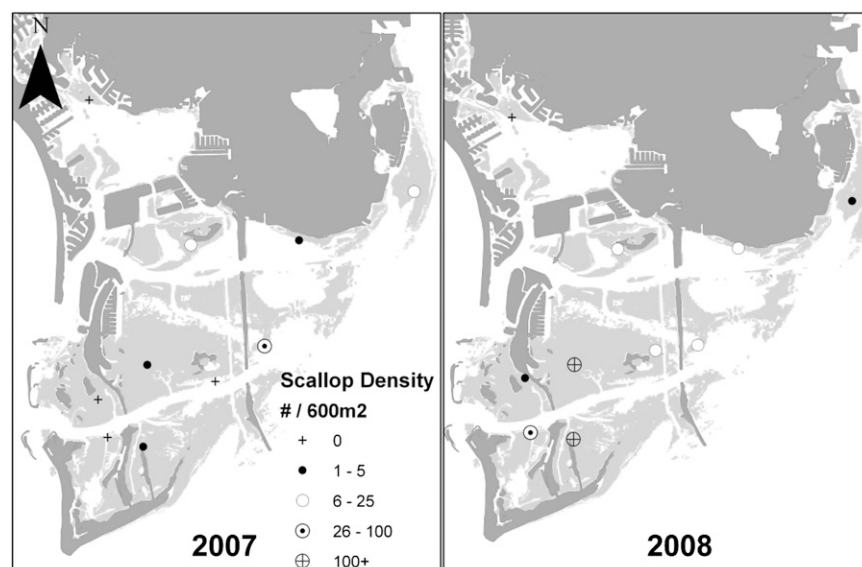


Figure 6. Density of adult bay scallops surveyed each summer in Boca Ciega Bay after larval releases were initiated.

metapopulation. Conversely, if the number of local populations is relatively small, then even under optimal conditions far fewer are available to contribute offspring to the metapopulation. Based on our statewide survey data, Florida bay scallop populations with consistently high densities are found in Steinhatchee, St. Joseph Bay, and Homosassa. These are reasonably stable populations that are capable of sustaining scallop stocks at levels sufficient to support at least recreational harvest in most years (Greenawalt-Boswell et al. 2007). Moving outward from the core of the population, local populations in Anclote and St. Andrew Bay have in the near past had lower densities and were less resilient, taking longer to recover from periods of low abundance. Anclote and 1 of the 2 estuaries targeted in this study, Boca Ciega Bay, appear to be rebounding. The long-term stability of these populations is uncertain, and no data are available to estimate the effect of opening these local populations to recreational harvest, although the dense surrounding human populations would be expected to have a strong effect. The least resilient populations occur near the geographical limits of scallops in Florida: Pensacola Bay, Pine Island Sound, and Florida Bay (Arnold et al. 2009). These populations are much more ephemeral and have lower average annual densities than the major populations in the core. These populations may be temporarily self-sustaining, but may receive only enough allochthonous larvae for the scallops to remain present at detectable levels, but are insufficient to produce consistently autochthonous larvae. These fringe populations are probably incapable of surviving any increased mortality caused by natural or harvest pressure. The historically populated estuaries of Biscayne Bay and Lake Worth Lagoon on the Atlantic coast of Florida may be completely isolated from any detectable larval supply, and no scallops have been observed there in decades. The decades-long decline in the abundance of bay scallops statewide has resulted in a destabilization of the Florida metapopulation simply as a result of a reduction in the viability of these local populations, and also may have eliminated any interaction with other bay scallop populations.

Larval release offers a restoration option for overcoming temporary population crashes once the stressor has been removed. Every time such a restoration project is undertaken, those involved gain knowledge and experience that can be useful in refining techniques and goals. One improvement to this method might include developing techniques to spawn scallops out of season so that larvae can be released on an optimized schedule. We have witnessed in our study that larvae do recruit to collectors throughout the year. Although we cannot yet assess the value of these scallops that recruit outside of peak spawning periods, we can at least postulate that diversifying the timing of life history events might add resiliency to the population as a whole in a species that has a 1-y life span. Such methods have at least been attempted with finfish restoration (Tringali 2006). Another evaluation tool would be

refinement of unique genetic markers (Chikarmane et al. 2001, Wilbur et al. 2005) to differentiate between hatchery-produced and wild scallops.

Even though the larval release method appears to generate an increase in population size, it is not an absolute or a complete method for restoration, as evidenced by the collapse in Pine Island Sound. The benefits of larval release as a restoration strategy include limited removal of individuals from already existing populations, enhanced gamete fertilization from those individuals, reduced labor and expenses associated with grow-out of shellfish, maximized hatchery and field survival, and the ability to select carefully the proper habitat for restoration. We have shown in Pine Island Sound that releasing larvae in a confined space can produce identifiable and discrete patches of scallops. We have also shown in Boca Ciega Bay that although those patches may not always be identifiable, very large spatially and temporally coincident increases in scallops occurred in the vicinity of our restoration sites. Long-term databases greatly added to both the identification of the need for this project and its evaluation. Surveys of adult scallops initially indicated that both local populations were critically depleted. Recruit monitoring showed that areas like Pine Island Sound have extremely limited larval supply, and adult surveys later showed that measurable increases in both density and distribution had occurred. Finally, recruit monitoring showed definitively that increases in spawning stock preceded increases in recruitment to the local population.

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#### LITERATURE CITED

- Arnold, W. S. 2008. Application of larval release for restocking and stock enhancement of coastal marine bivalve populations. *Rev. Fish. Sci.* 16:65-71.
- Arnold, W. S., N. J. Blake, M. M. Harrison, D. C. Marelli, M. L. Parker, S. C. Peters & D. E. Sweat. 2005. Restoration of bay scallop (*Argopecten irradians* (Lamarck)) populations in Florida coastal waters: Planting techniques and the growth, mortality and reproductive development of planted scallops. *J. Shellfish Res.* 24:883-904.
- Arnold, W. S., S. P. Geiger, M. L. Parker, S. P. Stephenson, J. C. Cobb, M. Gambordella, A. Vasilis & M. Drexler. 2009. Bay Scallop Project 2008 annual report. St. Petersburg, FL: Florida Fish and Wildlife Conservation Commission.

- Arnold, W. S. & D. C. Marelli. 1991. Assessment of bay scallop populations on the west coast of Florida. Internal report. Florida Department of Environmental Protection, Florida Marine Research Institute, St. Petersburg, FL. 19 pp.
- Arnold, W. S., D. C. Marelli, C. P. Bray & M. M. Harrison. 1998. Recruitment of bay scallops *Argopecten irradians* in Floridian Gulf of Mexico waters: scales of coherence. *Mar. Ecol. Prog. Ser.* 170:143–157.
- Arnold, W. S., D. C. Marelli, M. Parker, P. Hoffman, M. Frischer & J. Scarpa. 2002. Enhancing hard clam (*Mercenaria* spp.) population density in the Indian River Lagoon, Florida: a comparison of strategies to maintain the commercial fishery. *J. Shellfish Res.* 21:659–672.
- Blake, N. J. 1996. Demonstration of large-scale reintroduction of the southern bay scallop to Tampa Bay, Florida. Final report. Tampa Bay National Estuary Program, St. Petersburg, FL. 28 pp.
- Brand, A. R., J. D. Paul & J. N. Hoogesteger. 1980. Spat settlement of the scallops *Chlamys opercularis* (L.) and *Pecten maximus* (L.) on artificial collectors. *J. Mar. Biol. Assoc. U. K.* 60:379–390.
- Breitburg, D. L., L. D. Coen, M. W. Luckenbach, R. Mann, M. Posey & J. A. Wesson. 2000. Oyster reef restoration: convergence of harvest and conservation strategies. *J. Shellfish Res.* 19:371–377.
- Caddy, J. F. & O. Defeo. 2003. Enhancing or restoring the productivity of natural populations of shellfish and other marine invertebrate resources. FAO Fisheries technical paper 448, FAO, Rome. 159 pp.
- Chikarmane, H. M., A. M. Kuzirian, I. Carroll & R. Dengler. 2001. Development of genetically tagged bay scallops for evaluation of seeding programs. *Biol. Bull.* 201:285–286.
- Coen, L. D., R.E. Grizzle, J.L. Lowery & K.T. Paynter. 2007. The importance of habitat created by molluscan shellfish to managed species along the Atlantic Coast of the United States. Atlantic States Marine Fisheries Commission. ASMFC Habitat Management Series 8. Atlantic States Marine Fisheries Commission, Washington, D.C. 108 pp.
- Dawes, C. J., R. C. Phillips & G. Morrison. 2004. Seagrass communities of the Gulf Coast of Florida: status and ecology. St. Petersburg, FL: Tampa Bay Estuary Program. 74 pp.
- Fulford, R. S., D. L. Breitburg, R. I. Newell, W. M. Kemp & M. Luckenbach. 2007. Effects of oyster population restoration strategies on phytoplankton biomass in Chesapeake Bay: a flexible modeling approach. *Mar. Ecol. Prog. Ser.* 336:43–61.
- Gaffney, P. M. 2006. The role of genetics in shellfish restoration. *Aquat. Living Resour.* 19:277–282.
- Goldberg, R., J. Pereira & P. Clark. 2000. Strategies for enhancement of natural bay scallop, *Argopecten irradians*, populations: a case study in the Niantic River estuary, Connecticut, USA. *Aquat. Int.* 8:139–158.
- Greenawalt-Boswell, J., T. K. Frazer, C. A. Jacoby & W. S. Arnold. 2007. Mortality and exploitation rate estimates for the recreational bay scallop fishery off the Gulf Coast of Florida, USA. *North Am. J. Fish. Manage.* 27:1230–1242.
- Hanski, I. A. & D. Simberloff. 1996. The metapopulation approach, its history, conceptual domain, and application to conservation. In: I. A. Hanski & M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. San Diego: Academic Press. pp 5–26.
- Harding, J. M. & R. Mann. 1999. Fish species richness in relation to restored oyster reefs, Piankatank River, Virginia. *Bull. Mar. Sci.* 65:289–299.
- Holland, N., M. K. Hoppe & L. Cross. 2006. Charting the course: the comprehensive conservation and management plan for Tampa Bay. Prepared by the Tampa Bay Estuary Program, St. Petersburg, FL. 151 pp.
- Landsberg, J. H., L. J. Flewelling & J. Naar. 2009. *Karenia brevis* red tides, brevetoxins in the food web, and impacts on natural resources: decadal advancements. *Harmful Algae* 8:598–607.
- Luckenbach, M. W., R. Mann & J. A. Wesson, editors. 1999. Oyster reef habitat restoration: a synopsis and synthesis of approaches. Proceedings from the Symposium, Williamsburg, Virginia, April 1995. Williamsburg, VA: VIMS Press, College of William and Mary. 365 pp.
- Marelli, D. C., W. S. Arnold & C. Bray. 1999. Levels of recruitment and adult abundance in a collapsed population of bay scallops (*Argopecten irradians*) in Florida. *J. Shellfish Res.* 18:393–399.
- Meyer, D. L., E. C. Townsend & G. W. Thayer. 1997. Stabilization and erosion control value of oyster cultch for intertidal marsh. *Restor. Ecol.* 5:93–99.
- Morgan, D. E., J. Goodsell, G. C. Matthiessen, J. Garey & P. Jacobson. 1980. Release of hatchery-reared bay scallops (*Argopecten irradians*) onto a shallow coastal bottom in Waterford, Connecticut. *Proc. World Maric. Soc.* 11:247–261.
- Motada, S. 1977. Biology and artificial propagation of Japanese scallop (general review). In: S. Motada, editor. *Proceedings of the Second Soviet-Japan Joint Symposium on Aquaculture, Moscow, 1973*. Tokyo: Tokai University. pp. 75–120.
- Murdock, J. F. 1955. Investigation of the Lee County bay scallop fishery. The Marine Laboratory, University of Miami, report 55–13. Florida State Board of Conservation, Coral Gables. 11 pp.
- Newell, R. I. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve mollusks: a review. *J. Shellfish Res.* 23:51–61.
- Peterson, C. H., H. C. Summerson & R. A. Luettich, Jr. 1996. Response of bay scallops to spawner transplants: a test of recruitment limitation. *Mar. Ecol. Prog. Ser.* 132:93–107.
- Rice, M. A., A. Valliere & A. Caporelli. 2000. A review of shellfish restoration and management projects in Rhode Island. *J. Shellfish Res.* 19:401–408.
- Rönnbäck, P., N. Kautsky, L. Pihl, M. Troell, T. Söderqvist & H. Wennhage. 2007. Ecosystem goods and services from Swedish coastal habitats: identification, valuation, and implications of ecosystem shifts. *Ambio* 36:534–544.
- Rosen, A. 1959. Summary of Florida marine landings and an analysis of the catch and effort of certain species, 1958. Report to the Florida State Board of Conservation. University of Miami. Coral Gables. 55 pp.
- Sastry, A. N. 1962. Some morphological and ecological differences in two closely related species of scallops, *Aequipecten irradians* Lamarck and *Aequipecten gibbus* Dall, from the Gulf of Mexico. *Q. J. Fla. Acad. Sci.* 25:89–95.
- Shumway, S. E., C. Davis, R. Downey, R. Karney, J. Kraeuter, J. Parsons, R. Rheault & G. Wikfors. 2003. Shellfish aquaculture: in praise of sustainable economies and environments. *World Aquacult.* 34:15–18.
- Tettlebach, S. T. & P. Wenzel. 1993. Reseeding efforts and the status of bay scallop *Argopecten irradians* (Lamarck 1819) populations in New York following the occurrence of “brown tide” algal blooms. *J. Shellfish Res.* 12:423–431.
- Tringali, M. D. 2006. A Bayesian approach for the genetic tracking of cultures and released individuals. *Fish. Res.* 77:159–172.
- Wilbur, A. E., S. Seyoum, T. M. Bert & W. S. Arnold. 2005. A genetic assessment of bay scallop (*Argopecten irradians*) restoration efforts in Florida’s Gulf of Mexico coastal waters (USA). *Cons. Gen.* 6:111–122.