

Mortality and Exploitation Rate Estimates for the Recreational Bay Scallop Fishery off the Gulf Coast of Florida, USA

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Abstract.—Historically, the bay scallop *Argopecten irradians* supported recreational and commercial fisheries along Florida's Gulf Coast. Declines in density led to a ban on commercial fishing and tighter regulation of recreational fishing. In support of sustainable management, we derived estimates of mortality and exploitation from a multiyear series of preharvest and postharvest surveys of bay scallop density at five locations; catch curves from two locations during 3 years; and an aerial survey of recreational effort. Surveys at locations not subject to harvest yielded natural mortality estimates from which we derived estimates of fishing mortality and exploitation. Based solely on preharvest and postharvest surveys, we estimated the seasonal exploitation rate (u) as 0.0684. Based on all relevant surveys of bay scallop density, we calculated means and 95% confidence intervals for actual seasonal mortality ($A = 0.6365 \pm 0.06833$), daily instantaneous total mortality ($Z = 0.0153 \pm 0.00293$), daily instantaneous natural mortality ($M = 0.0145 \pm 0.00314$), and daily instantaneous fishing mortality ($F = 0.0013 \pm 0.0055$; 0.0000 replaced the negative lower confidence limit in further calculations). We used the means and confidence limits for M and F to calculate a mean and range for u (mean = 0.0575, range = 0.0000–0.2335). Effort on weekends and holidays was significantly greater than effort on weekdays. Data on effort and harvest generated u -values of 0.1244 at Homosassa and 0.1667 at Steinhatchee. Overall, our results confirm that natural mortality is substantially higher than fishing mortality for bay scallops. Simulations indicated that current levels of harvest, current bag limits, and potential variations in catches are unlikely to extirpate bay scallops if initial densities are at least 25 scallops/600 m² and if u stays within the calculated range. Our data did not indicate significant compensatory or depensatory mortality.

The bay scallop *Argopecten irradians* has long supported commercial and recreational fisheries along the eastern coast of the USA and in the Gulf of Mexico. Over the past several decades, densities of bay scallops in some areas along the west coast of Florida declined to the point where managers became concerned about extirpation at some locations (Arnold et al. 1998). The causes of these declines remain uncertain, but one or more processes and their synergistic interactions are likely contributors (e.g., overfishing, habitat degradation, and recruitment limitation; Blake 1995; Arnold et al. 1998; Marelli et al. 1999).

Managers first regulated Florida's bay scallop fishery in 1985; in 1994, all commercial harvest was banned and recreational harvest was restricted to areas north and west of the Suwannee River (Figure 1). Along with these restrictions, managers reduced bag limits from 5 to 2 gal·person⁻¹·d⁻¹ (from 18.9 to 7.6 L·person⁻¹·d⁻¹) and shortened the season from 9 months to 72 d (Florida Department of State 1998). Recently, bay scallop densities in some locations south of the Suwannee River increased to levels believed sufficient to sustain recreational harvests. Therefore, managers have allowed recreational harvests in near-shore areas between the Weeki Wachee and Suwannee rivers since 2002.

Effective management of bay scallops will benefit from quantitative estimates of natural mortality, fishing mortality, and exploitation. By combining such estimates, managers can predict sustainable levels of harvesting. However, very few estimates of mortality

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and exploitation rates are available for bay scallops along the west coast of Florida, and most estimates apply to small spatial scales or were derived from experiments that may have had artifacts (Leverone 1995; Bologna 1998).

Life history characteristics and behavior affect estimates of mortality and exploitation. Along the Gulf Coast of Florida, bay scallops occur in local populations separated by areas with low salinities (<20‰) and an absence of substantial seagrass beds (Arnold et al. 1998). Bay scallop densities along Florida's Gulf Coast do not reach the levels recorded along the Atlantic coast north of Florida. Local populations with densities greater than 25 scallops/600 m² are considered healthy because they recruit well (Arnold et al. 1998). In contrast, local populations with less than 5 scallops/600 m² appear to recruit poorly (Arnold et al. 1998).

Individual bay scallops in Florida generally spawn only once (Barber and Blake 1986). Spawning may occur in almost any month, and a peak occurs from early August to late February, perhaps in response to a drop in temperature (Barber and Blake 1986; Arnold et al. 1998; Bologna 1998). After approximately 14–20 d in the plankton, spat settle onto seagrass blades (Gutsell 1930). Spat gradually move further up the blades, where they may avoid benthic predators (Pohle et al. 1991; Ambrose and Irlandi 1992). At about 2–4 months of age, juvenile bay scallops drop to the bottom; at about 6–12 months, they become reproductive adults (Kirby-Smith 1970; Eckman 1989). Harvest generally occurs before spawning, and bay scallops exhibit high natural mortality after spawning (Barber and Blake 1986). Thus, harvestable populations primarily comprise a single year-class, which simplifies mortality estimates by removing the need to consider multiple year-classes. Although the movement of adult bay scallops is unlikely to connect local populations, bay scallops do move unknown distances, which introduces variability into the counts that form the basis for large-scale estimates of mortality and exploitation (Winter and Hamilton 1985; Hamilton and Koch 1996; Bologna 1998).

We examined three data sets to estimate mortality and exploitation rates. We compared preharvest and postharvest densities at five locations along the Florida Gulf Coast over 3, 9, or 10 years. We also estimated rates of total, natural, and fishing mortality from densities recorded in transect surveys made during the harvest season at two locations with similar habitats, comparable environmental conditions, and disjunct populations. In addition, aerial surveys of vessels and their occupants provided estimates of fishing effort for calculations of exploitation rate.

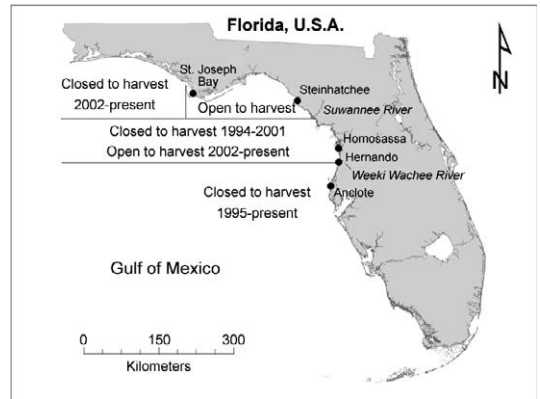


FIGURE 1.—Map showing regions open and closed for bay scallop harvest off Florida's Gulf Coast. Filled circles indicate locations of surveys.

Study Sites

Over varying numbers of years, adult bay scallops were counted at five geographically separate locations along the west coast of Florida in June (prior to the opening of the recreational harvest season) and September–October (after the recreational harvest season; Figure 1). Two of these locations, Steinhatchee and St. Joseph Bay, have consistently supported a recreational fishery. The other three locations—Homosassa, Hernando, and Anclote (all located south of the Suwannee River)—were closed to fishing in 1994. Homosassa and the northern three-quarters of Hernando were reopened in 2002.

During 2000–2002, we surveyed bay scallops more frequently at Homosassa (28°52.725'N to 28°40.845'N) and Steinhatchee (29°40.050'N to 29°32.004'N). These two locations support bay scallops because of their environmental conditions and extensive seagrass beds. The beds primarily contain turtle grass *Thalassia testudinum* and manatee grass *Syringodium filiforme* that are sometimes mixed with shoal grass *Halodule wrightii*, star grass *Halophila engelmannii*, and widgeon grass *Ruppia maritima* (Mattson 2000; Greenawalt et al. 2004; Hale et al. 2004). Environmental conditions were generally similar at both locations, although total phosphorus concentrations, chlorophyll-*a* concentrations, and color (platinum–cobalt units) tended to be higher at Steinhatchee (Table 1; Frazer et al. 1998). Both estuaries supported recreational harvest of bay scallops until low densities at Homosassa during the 1980s and early 1990s led to the closure of that recreational fishery from 1994 to 2001.

Methods

Preharvest and postharvest surveys.—We used data from preharvest and postharvest surveys of adult bay

TABLE 1.—Physical, chemical, and biological conditions at two locations along Florida’s Gulf Coast that were sampled intensively for bay scallops (DO = dissolved oxygen; TN = total nitrogen; TP = total phosphorus; chl = chlorophyll *a*; color [Pt–Co units] = color in platinum–cobalt units).

Parameter	2000						2001					
	Homosassa			Steinhatchee			Homosassa			Steinhatchee		
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD
Depth (m)	28	1.73	0.43	48	1.54	0.59	28	1.39	0.37	48	1.37	0.56
Temperature (°C)	28	27.11	3.85	48	29.51	2.25	26	28.91	1.85	45	28.83	1.73
Salinity (‰)	28	32.31	3.02	48	29.40	5.88	26	28.52	4.61	45	30.13	4.15
DO (mg/L)	28	6.34	1.20	48	6.78	1.37	26	6.00	1.94	45	7.29	1.54
TN (µg/L)	28	418.9	125.1	48	484.8	97.3	28	371.4	81.9	48	435.6	162.3
TP (µg/L)	28	10.4	3.6	48	16.5	5.7	28	8.8	2.5	48	15.5	8.5
Chl (µg/L)	28	1.15	0.66	48	2.96	2.99	28	1.05	1.10	48	2.50	2.09
Color (Pt–Co units)	28	8.9	2.8	48	19.6	13.4	28	8.7	2.2	41	28.2	37.9

scallop densities beginning in 1994 at Anclote, Steinhatchee, and St. Joseph Bay; in 1995 at Homosassa; and in 2001 at Hernando. At each of the five locations, scuba divers counted bay scallops at 20 stations located between the 0.61-m and 1.83-m depth contours. We chose random coordinates for the stations and repeated surveys at the same stations each year.

At each of the 20 stations per location, three 100-m transect lines were deployed in a large triangle to yield a total transect length of 300 m. The transect lines remained between the 0.61-m and 1.83-m depth contours. Two divers counted all bay scallops out to 1 m on either side of the transect line, producing 600-m² surveys for each station (Arnold et al. 1998).

Surveys during harvest seasons.—During the 2000 and 2001 recreational bay scallop seasons, we counted bay scallops four times at Homosassa and Steinhatchee. We conducted surveys during June, July, August, and either September or October (inclement weather delayed the September 2000 surveys until early October). At Homosassa, we established 20 stations between the 0.61-m and 1.83-m depth contours. Preharvest and postharvest surveys also took place at all of these stations. At Steinhatchee, we established 22 sampling stations between the same depth contours, and preharvest and postharvest surveys took place at 10 of these stations.

From June to September 2002, we used a different sampling design to survey bay scallops at Homosassa and Steinhatchee. We established five blocks in each location and counted bay scallops at five randomly chosen stations within each block. We chose new stations for each of seven sampling periods. Surveys took place once before the harvest season (June), five times during the recreational fishing season (late June, twice in July, mid-August, and early September), and once after the season ended (late September). This

survey design explicitly recognized the randomizing effects of bay scallop movements.

Each survey took place along four, approximately perpendicular, 50-m transects that originated at the anchor. Snorkelers or scuba divers (if depth > 1.5 m) counted all bay scallops found up to 0.5 m on either side of the 50-m transect line, yielding 200-m² surveys.

Surveys of effort.—During the 2002 harvest season (June–September), we estimated fishing effort via aerial surveys along the coast from the Weeki Wachee River to just north of Steinhatchee (Figure 1). We counted all boats in proximity to known scalloping grounds, boats with dive flags, and boats with snorkelers in the water.

We conducted 10 aerial surveys during the season. Six surveys took place on weekends or holidays, and four surveys took place on weekdays.

Analysis of preharvest and postharvest surveys.—Data from preharvest and postharvest surveys were log_e(count + 1) transformed for use in an analysis of variance (ANOVA) with locations (Lo) as a fixed factor, years (Yr) nested within locations, and preharvest and postharvest sampling periods (SP) nested within combinations of location and year:

$$\text{Count}_{ijkl} = \mu + \text{Lo}_i + \text{Yr}(\text{Lo})_{j(i)} + \text{SP}(\text{Lo} \times \text{Yr})_{k(ij)} + \varepsilon_{l(ijk)}. \tag{1}$$

Data were tested for homoscedasticity with Cochran’s tests and normality of error terms with Kolmogorov–Smirnov tests. As appropriate, we identified significant mortality between preharvest and postharvest surveys with Student–Newman–Keuls multiple comparison tests.

We classed pairs of surveys according to the initial density of bay scallops (low: ≤100 scallops/600 m²; medium: 101–200 scallops/600 m²; high: >200 scallops/600 m²) and according to harvest status (harvested if harvesting took place in at least 75% of

the location and not harvested). We calculated total seasonal mortality rates (A) for pairs of surveys demonstrating significant mortality using back-transformed means to reduce the effects of skewed data:

$$A = 1 - \frac{\text{Back-transformed mean final density}}{\text{Back-transformed mean initial density}} \quad (2)$$

These A -values were converted to daily instantaneous total mortality rates (Z) by

$$Z = \frac{-\log_e(1 - A)}{\text{Duration of survey (d)}}, \quad (3)$$

and the Z -values were used to calculate standardized A -values for a 72-d season:

$$A = 1 - e^{-Z(72)}. \quad (4)$$

The significant standardized A -values were used in two one-way ANOVAs with three classes of initial density (ID) and two classes of harvesting (H ; harvested or unharvested) as fixed factors:

$$A_{ij} = \mu + \text{ID}_i + \varepsilon_{j(i)} \quad (5)$$

and

$$A_{ij} = \mu + H_i + \varepsilon_{j(i)}. \quad (6)$$

The ANOVA based on initial density classes explored the possibility of density-dependent mortality, and the ANOVA based on harvest status explored the possibility that differences between estimates at locations with and without harvest would estimate mortality due to fishing. This latter approach assumes that a transferable estimate of natural mortality was obtained at locations where harvesting was prohibited. Before ANOVAs, data were tested for homoscedasticity with Cochran's tests and for normality of error terms with Kolmogorov-Smirnov tests.

Analysis of surveys during harvest seasons.—Counts of bay scallops from 200-m² surveys at Homosassa and Steinhatchee in 2000 and 2001 were $\log_e(\text{count} + 1)$ transformed for use in an ANOVA that contained location (Lo) and year (Yr) as fixed factors and month of sampling (Mo) nested within year:

$$\text{Count}_{ijkl} = \mu + \text{Lo}_i + \text{Yr}_j + \text{Mo}(\text{Yr})_{k(j)} + \varepsilon_{l(ijk)}. \quad (7)$$

Data were tested for homoscedasticity with Cochran's test and for normality of error terms with a Kolmogorov-Smirnov test.

If the ANOVA indicated significant variation in density through time, we generated catch curves by regressing transformed counts of bay scallops/200 m² against the week in which sampling was completed.

Where possible, we added density estimates from preharvest and postharvest surveys or averaged them with estimates from surveys during the harvest season. A significant negative slope represented an estimate of Z with a 1-week time step (Ricker 1975). We tested for differences between the slopes of significant regression lines with an analysis of covariance (ANCOVA).

Data from surveys at Homosassa and Steinhatchee in 2002 were $\log_e(\text{count} + 1)$ transformed for use in an ANOVA with sampling time (ST) as a random factor, Lo as a fixed factor, and blocks (Bl) nested within locations:

$$\text{Count}_{ijkl} = \mu + \text{ST}_i + \text{Lo}_j + \text{Bl}(\text{Lo})_{k(j)} + \varepsilon_{l(ijk)}. \quad (8)$$

Satterthwaite's formulae were used to estimate the F -statistic for location because there was no exact test (Zar 1974). Data were tested for homoscedasticity with Cochran's test and for normality of error terms with a Kolmogorov-Smirnov test.

If the ANOVA indicated significant variation in density through time, we generated catch curves by regressing \log_e -transformed counts of bay scallops/200 m² against sampling week. Where possible, we included estimates from preharvest and postharvest surveys. A significant negative slope provided an estimate of Z with a 1-week time step.

Analysis of effort surveys.—The total numbers of boats observed within the bounds of each location were $\log_{10}(\text{count} + 1)$ transformed for use in an ANOVA with location (Lo) and day (Da; either weekday or weekend day/holiday) as fixed factors:

$$\text{Boats}_{ijk} = \mu + \text{Lo}_i + \text{Da}_j + \varepsilon_{k(ij)}. \quad (9)$$

Data were tested for homoscedasticity with Cochran's test and for normality of error terms with a Kolmogorov-Smirnov test.

We used back-transformed mean numbers of boats from significant terms in the ANOVA to calculate total numbers of bay scallops removed. We based calculations on our estimate of four people per boat (the mean from aerial surveys) and the assumptions that (1) each person collected the bag limit of 2 gal of bay scallops/d (7.6 L/d) and (2) each gallon (3.8 L) held 50 bay scallops (Geiger et al. 2006). We estimated the total abundances of bay scallops by scaling back-transformed mean densities/200 m² to the total area of each location (Homosassa = 250 km²; Steinhatchee = 57 km²). We divided the estimated numbers of bay scallops removed by estimates of total bay scallop abundance to calculate the proportion removed (seasonal exploitation rate [u]; Ricker 1975).

Simulations addressing management questions.—Exploited bay scallop populations experience natural

and fishing mortality simultaneously, so they are considered type II fisheries (Ricker 1975). At locations without harvesting, we assumed that all mortality was natural mortality. We estimated mean daily instantaneous fishing mortality (F) as the difference between the mean of daily instantaneous total mortality at locations with harvesting ($Z = F + M$) and the mean of daily instantaneous total mortality at locations without harvesting ($Z = M$). We calculated the 95% confidence limits for this difference.

We combined means and confidence limits to predict changes in populations of bay scallops with an initial density of 25 scallops/600 m². Managers consider this level to represent the minimum preharvest density for healthy populations. We calculated the number of days (t) of combined fishing and natural mortality required to drive the population to near-extirpation using

$$N_t = N_0(e^{-Zt}). \tag{10}$$

Based on our estimates of M and F , we calculated u for a 72-d season and compared it with our other estimates. We used the relationships

$$u = FA/Z, \tag{11}$$

$$A = 1 - e^{-Z}, \tag{12}$$

and

$$Z = F + M. \tag{13}$$

Effort data yield estimates of potential u for a 72-d season (t). We can derive a potential Z by calculating a potential F and adding it to an assumed M . We used our estimates of the mean and 95% confidence limits for M . We assumed 100% harvesting efficiency (i.e., each harvester always collects the bag limit) and calculated potential F by iterating

$$u = tF[1 - e^{-t(F+M)}]/[t(F + M)]. \tag{14}$$

In contrast, surveys of bay scallop densities at Homosassa and Steinhatchee in 2002 yielded estimates of realized Z . The quotient of realized Z and potential Z can be considered an estimate of efficiency. If M is constant at a location in a given year, then this quotient estimates the ratio of realized F to potential F . Given that our estimates based on surveys of effort assumed 100% efficiency for all harvesters, this ratio provides an estimate of catchability (q).

Bay scallops grow rapidly up to the beginning of the harvest season in early July (Geiger et al. 2006). If the season opens earlier or recruitment is delayed, the predominance of smaller bay scallops will result in a 2-gal bag limit that contains more animals. We simulated the effect of earlier seasons or delayed recruitment

using our effort data and the associated assumptions, along with estimates of the number of bay scallops comprising 1 gal (3.8 L) in a given month at Homosassa and Steinhatchee (Geiger et al. 2006).

Simulations involved estimating values of Z for different seasons and applying equation (4) to an initial density of 25 scallops/600 m². Mean numbers of bay scallops per gallon for a given month and location were calculated by weighting mean numbers per gallon by the number of days in the appropriate months for three different 72-d seasons: 1 May–11 July, 1 June–11 August, and 1 July–10 September (essentially the current harvest season). Using our effort data, the associated assumptions, and the same equations, we calculated u -values for the six combinations of location and season. These u -values were combined with our estimates of M to iteratively solve equation (8) for F -values. The appropriate F -values and M -values were summed to yield Z -values for use in equation (4).

Results

Preharvest and Postharvest Surveys

The transformed density data were homoscedastic ($P > 0.05$), but residuals from fitting the ANOVA model were not normally distributed ($P < 0.01$). We proceeded with parametric analysis because the data were homoscedastic and balanced, so the ANOVA should have been robust to departures from normality. The ANOVA indicated significant differences between preharvest and postharvest periods within combinations of location and year (ANOVA: $F = 5.60$; $df = 4, 33$; $P < 0.001$). Student–Newman–Keuls multiple comparisons identified 15 surveys (of 38) that showed a significant decrease in bay scallop numbers or significant A -values (Table 2). The 23 surveys that did not exhibit significant mortality primarily involved low initial densities (87%; Table 3) and locations subject to harvest (61%; Table 3).

The 15 significant A -values used in the ANOVA testing for differences in mortality among classes of initial density were homoscedastic ($P > 0.05$), and the residuals were normally distributed ($P > 0.05$). Mortality rates calculated from surveys with different initial densities were not significantly different (ANOVA: $F = 0.45$; $df = 2, 12$; $P = 0.649$). Mean A -values were 0.7087 for low initial densities, 0.6622 for medium initial densities, and 0.6371 for high initial densities. The lack of significance and the similarity of mean A -values suggest an absence of compensatory and depensatory mortality; therefore, initial density was not considered in analyses of catch curves.

The 15 significant A -values used in the ANOVA testing for differences in mortality where harvests did and did not occur were homoscedastic ($P > 0.05$), and

TABLE 2.—Mortality rates for bay scallops calculated from significantly different preharvest and postharvest surveys conducted off Florida’s Gulf Coast (A = total mortality for a 72-d season; N_0 = preharvest mean; N_t = postharvest mean).

Location	Survey dates	Mean $\log_e[(\text{count}/600 \text{ m}^2) + 1]$		Back-transformed mean (count/600 m^2)		$A = (N_0 - N_t)/N_0$
		N_0	N_t	N_0	N_t	
Anclote	20 Jul–12 Oct 2000	1.8203	0.8003	5.2	1.2	0.7630
	9 Jun–11 Sep 2003	2.5458	1.4178	11.8	3.1	0.7338
Hernando	28 Jun–30 Oct 2001	2.3463	1.3608	9.4	2.9	0.6931
Homosassa	19 Jun–20 Oct 1995	1.3051	0.2394	2.7	0.3	0.8994
	7 Jun–3 Oct 2000	4.5171	3.3255	90.6	26.8	0.7039
	22 Jun–21 Oct 2001	4.9198	2.6550	136.0	13.2	0.9027
St. Joseph Bay	16 Jun–8 Oct 2003	3.6945	2.1790	39.2	7.8	0.8002
	13 Jun–26 Oct 1994	2.2267	0.4218	8.3	0.5	0.9366
	3 Jun–15 Sep 1995	3.7377	1.7486	41.0	4.7	0.8842
	1 Jun–27 Sep 1999	2.9375	0.2740	17.9	0.3	0.9824
Steinhatchee	6 Jun–3 Nov 1994	4.0841	1.7916	58.4	5.0	0.9144
	18 Jun–24 Sep 1998	2.1612	1.0761	7.7	1.9	0.7483
	11 Jun–22 Sep 2001	3.9562	2.8128	51.3	15.7	0.6945
	19 Jun–29 Oct 2002	4.3657	2.5540	77.7	11.9	0.8474
	24 Jun–25 Sep 2003	3.1156	1.4593	21.5	3.3	0.8467

the residuals were normally distributed ($P > 0.05$). Mortality rates did not differ significantly (ANOVA: $F = 1.45$; $df = 1, 13$; $P = 0.250$). Mean A -values were 0.7110 for locations and years where harvesting occurred and 0.6426 for locations and years that had no harvest, resulting in a difference of 0.0684. Power analyses indicated that this difference was approximately one-third of the minimum difference that an ANOVA would detect with $\alpha = 0.05$ and $1 - \beta = 0.80$ (the minimum detectable differences for $n = 6$ and 9 were 0.1932 and 0.1514, respectively). We can use 0.0684 as an estimate of u over a 72-d season, although we are uncertain about its reliability.

Surveys during Harvest Seasons

Transformed density data from 2000 and 2001 were homoscedastic ($P > 0.05$), but residuals were not normally distributed ($P < 0.01$). We proceeded with parametric analysis because the data were homoscedastic, so the ANOVA should be robust to departures from normality. Significant differences were only found among months nested within years (ANOVA: $F = 2.80$; $df = 6, 320$; $P = 0.024$).

Regressions based on means of \log_e transformed data indicated significant declines during the weeks of the harvest season at both locations in both years (Table 4; Figure 2). The slopes of the regression lines provided estimates of Z (with a 1-week time step) of 0.029 at Steinhatchee in 2000, 0.061 at Steinhatchee in 2001, 0.068 at Homosassa in 2000, and 0.119 at Homosassa in 2001. As expected from ANOVA results and confirmed by a nonsignificant ANCOVA ($F = 0.05$; $df = 3, 14$; $P > 0.05$), these slopes did not differ significantly. Thus, we cannot obtain a useful estimate of F by looking at the difference in Z between Steinhatchee, the location subject to harvesting, and Homosassa, the location not subject to harvesting. In fact, Z was higher at Homosassa in both years.

Transformed density data from 2002 were homoscedastic ($P > 0.05$), and residuals were normally distributed ($P > 0.05$). Significant differences were found among blocks within locations (ANOVA: $F = 7.88$; $df = 8, 48$; $P < 0.001$), combinations of sampling periods and locations ($F = 2.69$; $df = 6, 48$; $P = 0.025$), and combinations of sampling periods and blocks nested within locations ($F = 1.46$; $df = 48, 280$; $P =$

TABLE 3.—Statistically equal preharvest and postharvest surveys of bay scallops off Florida’s Gulf Coast, grouped by initial density and harvest condition.

Initial density (count/600 m^2)	Harvest condition	Location (years)	Total number of surveys
≤ 100 (low)	Harvested	Hernando (2002, 2003)	11
		Homosassa (2002)	
		St. Joseph Bay (1997, 1998, 2000–2003)	
> 200 (high)	Unharvested	Steinhatchee (1995, 1997)	9
		Anclote (1994, 1997, 1998, 2001, 2002)	
> 200 (high)	Harvested	Homosassa (1996–1999)	3
		St. Joseph Bay (1996)	
		Steinhatchee (1996, 2000)	

TABLE 4.—Regressions of bay scallop densities (scallops/200 m²) surveyed at two sites off Florida’s Gulf Coast during 2000–2002 versus the week in which surveys ended.

Location	Year	log _e (density + 1) ^a	r ²	Source	df	SS ^b	MS ^c	F	P ^d
Homosassa (6 points)	2000	3.665 – (0.068 × week)	0.752	Regression	1	1.2648	1.2648	12.10	0.025
				Error	4	0.4180	0.1045		
				Total	5	1.6828			
Steinhatchee (5 points)	2000	3.117 – (0.029 × week)	0.853	Regression	1	0.1645	0.1645	17.38	0.025
				Error	3	0.0284	0.0095		
				Total	4	0.1929			
Homosassa (5 points)	2001	4.401 – (0.119 × week)	0.922	Regression	1	2.1904	2.1904	35.54	0.009
				Error	3	0.1849	0.0616		
				Total	4	2.3753			
Steinhatchee (6 points)	2001	3.210 – (0.061 × week)	0.737	Regression	1	0.7704	0.7704	11.21	0.029
				Error	4	0.2748	0.0687		
				Total	5	1.0452			
Homosassa (8 points)	2002	2.179 – (0.013 × week)	0.024	Regression	1	0.0376	0.0376	0.15	0.715
				Error	6	1.5404	0.2567		
				Total	7	1.5780			
Steinhatchee (9 points)	2002	3.497 – (0.076 × week)	0.838	Regression	1	1.8202	1.8202	36.29	0.001
				Error	7	0.3511	0.0502		
				Total	8	2.1712			

^a Log_e(density + 1) = projected initial density – (weekly mortality rate × week of survey).

^b Sum of squares.

^c Mean square.

^d P-values < 0.05 are significant.

0.034). We can focus on combinations of sampling periods and locations, the target of primary interest, because this term was significant when tested against combinations of sampling periods and blocks within locations.

Regressions based on means of log_e transformed data from 2002 indicated significant declines during the weeks of the harvest season only at Steinhatchee (Table 4; Figure 2). The slope of the significant regression line estimated Z with a 1-week time step as 0.076. Thus, we cannot obtain a useful estimate of F from these data alone.

Effort Surveys

Transformed counts of boats were homoscedastic (P > 0.05), and the residuals were normally distributed (P > 0.05). Numbers of boats differed significantly only between weekdays and weekend days or holidays (ANOVA: F = 21.76; df = 1, 16; P < 0.001). When we combined data from both locations, back-transformed mean numbers of boats were 23.9 for weekdays and 194.3 for weekend days or holidays. At Homosassa, the back-transformed mean number of boats was 29.0 for weekdays and 201.0 for weekend days or holidays. At Steinhatchee, the back-transformed mean was 19.7 for weekdays and 187.9 for weekend days or holidays.

Given these estimates of boats and assuming that each boat holds four people who each take 100 bay scallops (2 gal at 50 scallops/gal), we predicted catches of 2,348,239 bay scallops at Homosassa and 2,048,181 bay scallops at Steinhatchee over the 50 weekdays and 22 weekend days and holidays that made up the 2002

season. Scaling back-transformed mean numbers of bay scallops/200 m² to the total area at both locations (Homosassa = 250 km²; Steinhatchee = 57 km²) yielded estimates of total bay scallop abundance at Homosassa (18,875,000 scallops) and Steinhatchee (12,283,500 scallops). The ratios of catch to total abundance generated seasonal u-values of 0.1244 for Homosassa and 0.1667 for Steinhatchee.

Simulations Addressing Management Questions

We combined the 15 significant estimates of mortality from preharvest and postharvest surveys with the 5 significant estimates of mortality from surveys conducted during the harvest season. By assuming that all mortality at locations without harvesting was natural mortality, these data allowed us to calculate means and 95% confidence limits for A, Z, M, F, and u (Table 5). The mean for M was an order of magnitude larger than the mean for F (Table 5). Using data from bay scallop surveys and a 72-d season, we estimated u-values of 0.0000 (the lower 95% confidence limit that results from replacing a negative lower 95% confidence limit for F with 0.0000), 0.0575 (mean), and 0.2335 (upper 95% confidence limit). These values bracketed our estimate based on preharvest and postharvest surveys alone (u = 0.0776) and those based on effort data (u = 0.1244 for Homosassa and 0.1667 for Steinhatchee).

Varying combinations of M and F (related to u) indicated that a 72-d harvest season resulted in final densities greater than 5 bay scallops/600 m² in eight of nine scenarios (Figure 3). Mortality based on the combination of the upper confidence limits of M and F

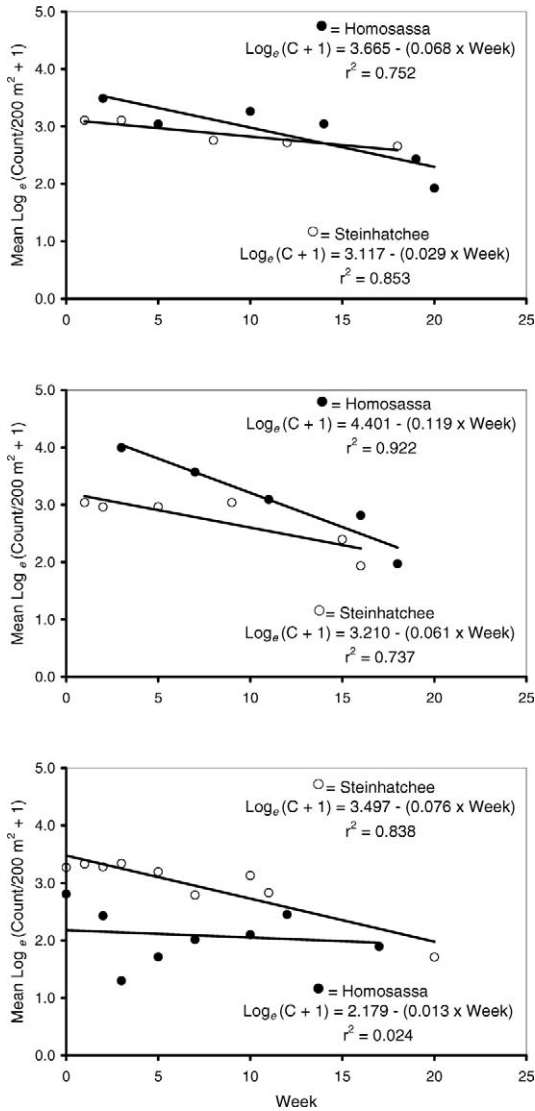


FIGURE 2.—Rates of decline in bay scallop densities (scallops/200 m², log_e[count + 1] transformed) off Florida’s Gulf Coast during three harvest seasons: (upper) 2000, (middle) 2001, and (lower) 2002. Filled circles represent data from Homosassa (closed to harvest in 2000 and 2001), and open circles represent data from Steinhatchee (open to harvest in all years).

reduced an initial density of 25 scallops/600 m² to 4 scallops/600 m² in 72 d.

Iterations based on effort data yielded potential *F*-values that varied with the choice of *M*. The upper 95% confidence limit, mean, and lower 95% confidence limit for *M* yielded potential *F*-values ranging from 0.0023 to 0.0027 for Homosassa and from 0.0030 to 0.0035 for Steinhatchee in 2002. In combination with

the appropriate *M*-values, these results yielded potential *Z*-values of 0.0141–0.0198 for Homosassa and 0.0149–0.0205 for Steinhatchee.

In 2002, only surveys at Steinhatchee yielded a useful estimate of realized *Z*, which was 0.0109 (regression slope divided by 7 d). The quotients of realized and potential *Z*-values generated estimates of efficiency that ranged from 53% to 73% (mean = 62%). If we assume that *M* did not vary, this ratio can be interpreted as an estimate of *q*, or the ratio of realized *F* to potential *F* at 100% catchability. This estimate of *q* is likely to be high because the *Z*-value derived from surveys at Steinhatchee in 2002 (0.0109) was less than the lower 95% confidence limit calculated from all surveys (0.0114).

Weighted mean numbers of bay scallops per gallon for the three simulated seasons were 77.0 (1 May–11 July), 62.8 (1 June–11 August), and 50.7 (1 July–10 September) for Homosassa and 88.1 (1 May–11 July), 75.2 (1 June–11 August), and 56.0 (1 July–10 September) for Steinhatchee. Thus, bag limits for the earliest simulated season contained 34% and 36% more bay scallops than bag limits for the latest season at Homosassa and Steinhatchee, respectively. These values were used to calculate *u* assuming an initial density of 25 scallops/600 m².

Calculations of *u* rely heavily on scaling an initial density from the transect level to the location level. Less area was considered suitable habitat for bay scallops at Steinhatchee, which meant that fewer scallops were available for harvest. In fact, calculations yielded *u*-values greater than 1.0000 for the two earliest seasons; therefore, further simulations were not performed for this location. At Homosassa, simulated *u*-values were 0.3472, 0.2833, and 0.2288.

When used in iterations based on our mean and 95% confidence limits for *M*, the *u*-values from Homosassa yielded *F*-values that ranged from 0.0066 to 0.0040 for the three simulated seasons. By summing these *F*-values with the appropriate *M*-values, we calculated nine *Z*-values ranging from 0.0161 to 0.0234.

The nine *Z*-values were used to simulate decreases in density through time (Figure 4). Only the combination of the earliest season (1 May–11 July) and the upper 95% confidence limit for *M* (0.0175) yielded less than 5 bay scallops/600 m² at 72 d. In this scenario, harvesters were assumed to collect 77.0 scallops/gal. Based on an initial density of 25 scallops/600 m², the scenario involved a *u* of 0.3472, an *F* of 0.0059, and a *Z* of 0.0234. The densities at 72 d for two of the three simulated seasons were approximately 25% lower than simulated densities derived from means and 95% confidence limits for *M*, *F*, and *u* (Table 6). The exceptions were simulations based on the earliest

TABLE 5.—Estimates of mortality and exploitation (*u*) for bay scallops derived from surveys conducted off Florida’s Gulf Coast that indicated significant mortality (* = 95% confidence limits [CLs]; § = lower CL was negative, so value was set at 0.0000; # = calculated using means and upper and lower daily instantaneous fishing mortality *F* and daily instantaneous natural mortality *M* in $u = (tF)\{[1 - e^{-t(F+M)}]/[t(F + M)]\}$.

Variable ^a	Combined surveys			Pre- and postharvest surveys	Effort surveys
	Mean	Lower value	Upper value		
Seasonal <i>A</i>	0.6365	*0.5682	*0.7048		
<i>Z</i>	0.0153	*0.0123	*0.0182		
<i>M</i>	0.0145	*0.0114	*0.0175		
<i>F</i>	0.0013	*§0.0000	*0.0069		
Seasonal <i>u</i>	#0.0575	#0.0000	#0.2335		
Seasonal <i>A</i> with harvest				0.7110	
Seasonal <i>A</i> without harvest				0.6426	
Seasonal <i>u</i>				0.0684	
Seasonal <i>u</i> at Homosassa (2002)					0.1244
Seasonal <i>u</i> at Steinhatchee (2002)					0.1667

^a *A* is total mortality; seasonal values apply to a 72-d season.

season, which yielded values nearly equal to those derived in scenarios based on the upper 95% confidence limit for *F* (Table 6).

Discussion

Our analyses and the resulting estimates of mortality and *u* provide key information for fisheries managers, especially those tasked with the responsibility of ensuring the future health of the bay scallop fishery along Florida’s Gulf Coast. Similar to other methods used to estimate mortality and *u* in an open system, our methods are based on assumptions. We assume that the locations are large enough and sufficiently independent to eliminate significant effects from emigration and immigration as suggested by a previous study of stock–recruitment relationships (Arnold et al. 1998). Secondly, based on reports from law enforcement, we assume that illegal harvest in locations closed to harvest is negligible, so declines in density at these locations result solely from natural mortality. Thirdly, we assume that bay scallops at each location within each year comprise primarily one year-class. This assumption is supported by the life history of the bay scallop and the minor variations in sizes of bay scallops from Steinhatchee and Homosassa (Greenawalt et al. 2004; Geiger et al. 2006).

Although the movement of bay scallops between locations is unlikely, bay scallops do move within locations. We addressed the effects of bay scallop movement with surveys based on randomly chosen stations during 2002. Overall, the data indicate that movement contributes to variation in counts that can lead to a lack of statistically significant mortality, especially when densities of bay scallops are low. A better understanding of movement by bay scallops

should lead to improved surveys and greater precision in estimates of mortality and *u*.

Although surveys have associated challenges, our methods provide estimates of mortality and *u* across large spatial scales without the potential artifacts from caging or tethering found in other studies. For example, Marshall (1966) studied natural mortality of bay scallops in the laboratory and with a caging experiment in the Niantic River, Connecticut. Although specific values were not published, Marshall (1966) attributed high mortality to environmental stress. Another study based on caging of bay scallops in Tampa Bay, Florida, also yielded high rates of natural mortality; cumulative mortality was as high as 85% over a 2-month period (Leverone 1995). In part, mortality was attributed to hinge disease, caging artifacts, and the postspawning mortality typically exhibited by Florida bay scallops (Leverone 1995).

The range of *M* found in our study (mean ± 95% CI = 0.0145 ± 0.00314) is at the low end of the 0.0057–0.0418 range reported by Bologna (1998). Bologna (1998) estimated mortality in a Florida estuary using a mark–recapture method that focused on a relatively small spatial scale and may have been biased by emigration (Dredge 1985; Naidu 1988; Allison and Brand 1995; Bologna 1998). Over a 72-d season, Bologna’s (1998) estimates translate into *A*-values of 0.3366–0.9507. When significant seasonal mortality was detected, our estimates ranged from 0.4964 to 0.9149 (mean ± 95% CI = 0.6365 ± 0.06833). Approximately 60% of our surveys did not detect significant mortality, but initial densities were low for 87% of those surveys (>50% had densities less than 25 bay scallops/600 m²). Therefore, our estimates of mortality should be robust for populations with initial densities of 25 scallops/600 m² or higher; such

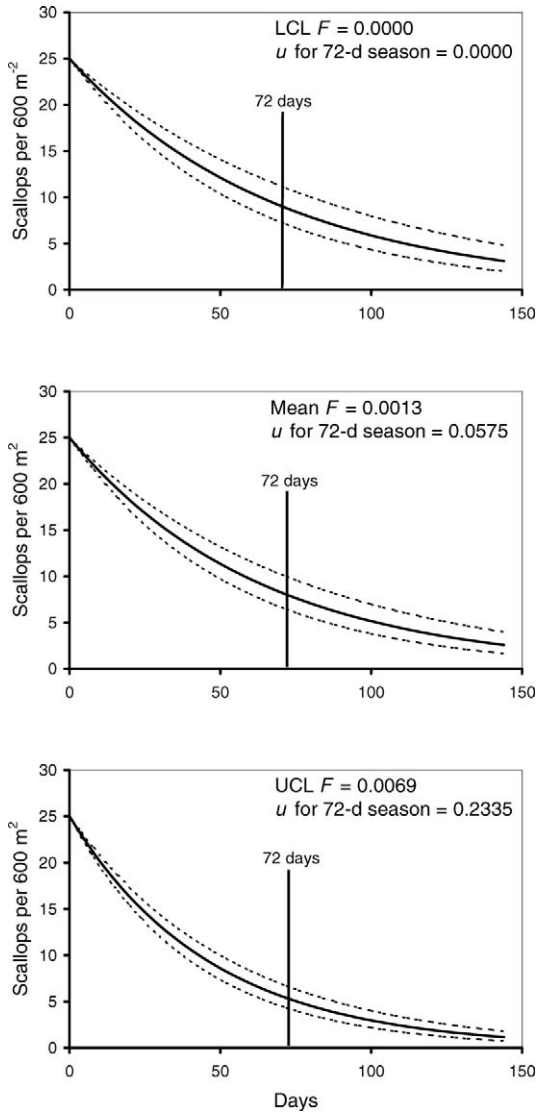


FIGURE 3.—Declines in bay scallop densities from an initial density (N_0) of 25 scallops/600 m² for nine scenarios based on values of daily instantaneous natural mortality (M), daily instantaneous fishing mortality (F), and seasonal exploitation (u) derived from surveys conducted off Florida's Gulf Coast. In each figure, the solid line is based on the mean for M (0.0145), the upper dotted line is based on the lower 95% confidence limit (LCL) for M (0.0114), and the lower dotted line is based on the upper 95% confidence limit (UCL) for M (0.0175); **(upper)** LCLs for F (0.0000) and u (0.0000); **(middle)** means for F (0.0013) and u (0.0575); **(lower)** UCLs for F (0.0069) and u (0.2335).

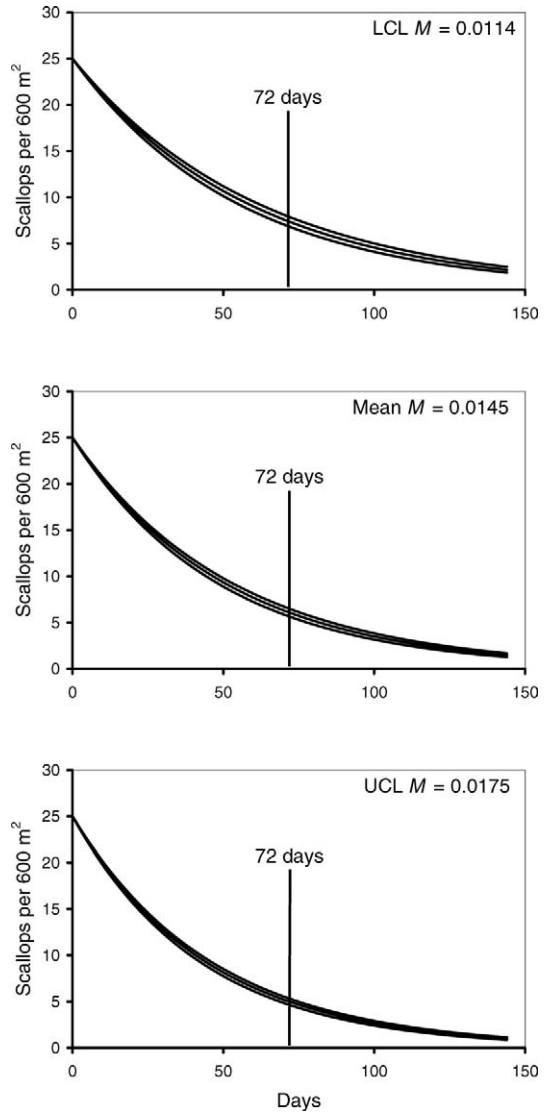


FIGURE 4.—Declines in bay scallop densities from an initial density (N_0) of 25 scallops/600 m² for nine scenarios based on values of daily instantaneous natural mortality (M) derived from surveys conducted off Florida's Gulf Coast and daily instantaneous fishing mortality (F) and seasonal exploitation (u) calculated for 72-d harvesting seasons with different opening dates (i.e., F and u vary according to the number of scallops estimated to comprise the 2-gal bag limit). In each figure, the upper line is based on a 1 May–11 Jun season with 77.0 scallops/gal, the middle line is based on a 1 Jun–11 Aug season with 62.8 scallops/gal, and the lower line is based on a 1 Jul–10 Sep season with 50.7 scallops/gal; **(upper)** lower 95% confidence limit (LCL) for M (0.0114); **(middle)** mean for M (0.0145); and **(lower)** upper 95% confidence limit (UCL) for M (0.0175).

TABLE 6.—Number of bay scallops remaining out of an initial density (N_0) of 25 scallops/600 m² for scenarios based on different rates of instantaneous natural mortality (M) combined with 72-d harvest seasons that began on three different dates, which led to different numbers of scallops in bag limits, and scenarios based on different M -values and instantaneous rates of fishing mortality (F) derived from surveys of scallops off Florida’s Gulf Coast (LCL and UCL = lower and upper 95% confidence limits; mean $M \pm 95\%$ CI = 0.0145 \pm 0.00314; mean $F \pm 95\%$ CI = 0.0013 \pm 0.00555, with LCL set at 0.0000 since calculation yielded a negative value).

Scenario based on harvest season ^a	Density (scallops/600 m ²) at 72 d		Scenario based on surveys
	Season scenario	Survey scenario	
1 Jul–10 Sep + LCL M	7.9	11.0	LCL M + LCL F
1 Jul–10 Sep + Mean M	6.5	8.8	Mean M + LCL F
1 Jul–10 Sep + UCL M	5.3	7.1	UCL M + LCL F
1 Jun–11 Aug + LCL M	7.4	10.0	LCL M + Mean F
1 Jun–11 Aug + Mean M	6.1	8.0	Mean M + Mean F
1 Jun–11 Aug + UCL M	5.0	6.4	UCL M + Mean F
1 May–11 Jul + LCL M	6.8	6.7	LCL M + UCL F
1 May–11 Jul + Mean M	5.6	5.4	Mean M + UCL F
1 May–11 Jul + UCL M	4.6	4.3	UCL M + UCL F

^a Each harvest season involves a different harvest level: 50.7 scallops/gal for 1 Jul–10 Sep; 62.8 scallops/gal for 1 Jun–11 Aug; and 77.0 scallops/gal for 1 May–11 Jul.

populations appear capable of replenishing themselves (Arnold et al. 1998).

Our estimates of M and F for bay scallops differ from those calculated for other scallop species. Calculations for mud scallops *Amusium pleuronectes* from the Indo-Pacific based on growth coefficients derived from frequency distributions of shell heights yielded annual and daily M -values of 1.9 and 0.0052, respectively, and annual and daily F -values of 5.3 and 0.0145, respectively (Del Norte 1988). We expected that our mean daily M (0.0145) would be larger because mud scallops live for approximately 2 years and bay scallops typically do not survive past 1 year in Florida. We also expected that our mean F (0.0013) would be smaller because bay scallops in Florida are not exploited commercially like mud scallops. Our mean daily M was larger than the range of values (annual rates = 0.15–1.30; daily rates = 0.0036–0.0004) reported for saucer scallops *Amusium japonicum balloti* from the Indo-Pacific, tehuelche scallops *Aequipecten tehuelchus* from South America, and Iceland scallops *Chlamys islandica* from the North Atlantic, which live longer and exhibit variation in natural mortality among co-occurring year-classes (Dredge 1985; Naidu 1988; Ciocco 1996).

Simulations based on our estimates of M and F (also expressed as u) suggested that current levels of bay scallop harvest are unlikely to extirpate local populations considered healthy (i.e., initial density \geq 25 scallops/600 m²). At the highest levels of M and F , the harvest season would have to be approximately twice as long as the current 72-d season before final densities would reach approximately 1 scallop/600 m². A full interpretation of these results awaits reliable estimates of the postharvest or pre-spawning density of adult bay

scallops required to ensure recruitment that sustains local populations.

Assuming a 72-d harvest season, we examined effects related to u . For example, we calculated the effort needed to achieve our upper estimate of u (0.2335). At Steinhatchee and Homosassa, this u -value would translate into approximately 1.5–2.0 times as many boats as the 5,000–6,000 we estimated to be operating in 2002. In addition, u depends on the number of bay scallops comprising a daily bag limit, which managers have set at 2 gal/person. Bay scallops grow rapidly between May and the July opening of the harvest season, so the number per gallon decreases. However, the season could be opened earlier or, for ecological reasons, recruitment could be delayed, leading to an increase in the number of scallops per gallon for some part of the season. Varying the start of a 72-d season from 1 May to 1 July and applying the appropriate number of bay scallops per gallon from Geiger et al. (2006) resulted in weighted mean catches that varied from 50.7 to 77.0 scallops/gal. At Homosassa, simulations based on three different seasons indicated that densities after 72 d would remain above 5 scallops/600 m², except when the season ran from 1 May to 11 July and the upper 95% confidence limit for M was assumed to apply. Again, these simulations indicated that it would take a harvest season that was twice as long to drive densities to approximately 1 scallop/600 m². At Steinhatchee, simulations indicated that there were too few bay scallops available to support the increased u . This result highlights the influence of scaling densities from transects to locations. A better understanding of the relationships between habitat and bay scallop density and abundance would improve simulations.

At Homosassa in 2002, results from our surveys of effort provide an estimate of potential Z , and results from our surveys of bay scallop density provide an estimate of realized Z . Realized Z was approximately 60% of potential Z . If M was constant, this result translates into a q of no more than 60%. Further efforts to define q will lead to an improved understanding of F and u .

Our results do not support the hypothesis that higher or lower initial densities leads to increases in mortality rates and u . In contrast, Peterson et al. (2001) identified compensatory mortality of bay scallops over a 7-year period and related it to the foraging habits of cownose rays *Rhinoptera bonasus*. Surveys based on multiple samples during harvest seasons across a wider range of initial densities may reveal density-dependent changes in mortality rates and u . Knowledge of this influence would help managers set and adjust sustainable levels of harvest.

The quantitative estimates of mortality and exploitation provided in this study are the first derived from long-term and large-scale surveys of bay scallops in Florida, which reduces the biases seen in other studies. Nevertheless, our estimates of mortality and u should be used conservatively. Many invertebrate fisheries are managed on the premise that high natural mortality rates allow for high u (Ricker 1975; Caddy 1989). However, bay scallops have demonstrated a threshold for recruitment limitation below which spawning and recruitment do not support annual renewal of local populations (Dredge 1988; Peterson and Summerson 1992; Peterson et al. 1996; Marelli et al. 1999). Experiments conducted in the same region as our study indicate a positive stock–recruitment relationship and recruitment limitation if adult densities are too low at the end of the harvest season or in the period just before spawning (Arnold et al. 1998; Marelli et al. 1999). At this time, we do not have reliable estimates of the prespawning density of adult bay scallops needed to replenish a local population. Used properly, our estimates will help managers assess recovery and prevent future declines of bay scallops and other scallop species in Florida and elsewhere.

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