A comparison of the size and age of red snapper, Lutjanus campechanus, to the age of artificial reefs in the northern Gulf of Mexico

Syc and Szedlmayer

# SEDAR31-DW12

6 August 2012





## A comparison of the size and age of red snapper, Lutjanus campechanus, to the age of artificial reefs in the northern Gulf of Mexico

Journal:	Fishery Bulletin
Manuscript ID:	Draft
Manuscript Type:	Full Article- Fishery Bulletin
Keywords:	artificial reefs, red snapper, age, production
Abstract:	Size and age of red snapper, Lutjanus campechanus, were sampled from April through November 2010 and compared with the age of the artificial reef at the site of capture. Red snapper were sampled using hook-and-line, fish trap, and SCUBA diver visual surveys. In the laboratory, all captured red snapper were weighed (0.1 g), measured (mm), and otoliths removed for aging. Mean $\pm$ SD age of red snapper showed significant differences compared across reef age, with older reefs showing older fish: 2006 reefs = $3.6 \pm 1.2$ years, 2009 reefs = $2.0 \pm 1.7$ years, 2010 reefs = $1.7 \pm 1.0$ years (ANOVA, F <sub>2, 1025</sub> = 194.23, P < 0.0001). A significant positive correlation between fish age and reef age was detected ( $r^2 = 0.37$ , P < 0.0001). Depth, distance to other reefs, and potential habitat differences based on growth rate comparisons did not significantly affect the age of red snapper on artificial reefs. This scenario of young fish – new reef and old fish – old reef supports the contention that artificial reefs in the northern Gulf of Mexico are helping in the production and not simply attracting of red snapper.

## SCHOLARONE<sup>™</sup> Manuscripts

Abstract—Size and age ofred snapper, Lutjanus campechanus, were sampled from April through 1 November 2010 and compared with the age of the artificial reef at the site of capture. Red 2 snapper were sampled using hook-and-line, fish trap, and SCUBA diver visual surveys. In the 3 4 laboratory, all captured red snapper were weighed (0.1 g), measured (mm), and otoliths removed for aging.Mean  $\pm$  SD age of red snapper showed significant differences compared across reef 5 age, with older reefs showing older fish: 2006 reefs =  $3.6 \pm 1.2$  years, 2009 reefs =  $2.0 \pm 1.7$ 6 years, 2010 reefs =  $1.7 \pm 1.0$  years (ANOVA,  $F_{2,1025} = 194.23$ , P < 0.0001). A significant 7 positive correlation between fish age and reef age was detected ( $r^2 = 0.37$ , P< 0.0001). Depth, 8 distance to other reefs, and potential habitat differences based on growth rate comparisons did 9 not significantly affect the age of red snapper on artificial reefs. This scenario of young fish – 10 new reef and old fish - old reef supports the contention that artificial reefs in the northern Gulf of 11 Mexico are helping in the production and not simply attracting of red snapper. 12

13

14	Introduction
15	Red snapper(Lutjanus campechanus, Poey, 1860) hashistorically been a species targeted by both
16	sport and commercial fishers in the Gulf of Mexico (Camber, 1955). Due to intense fishing
17	pressure, the estimated population abundance has decreased and the stock was considered
18	overfished (Schirripa and Legault, 1999; SEDAR7, 2005; SEDAR, 2009). Regulations
19	decreasing the total allowable catch and shortening the recreational season have been enacted
20	over the last several decades to reduce the harvest of this species, for the purpose of increasing
21	the stock.
22	Red snapper are a reef associated fish, using reef habitat for both shelter and prey
23	resources (Outz and Szedlmayer, 2003; Szedlmayer and Lee, 2004; Piko and Szedlmayer, 2007;
24	Gallaway et al., 2009). However, the substrate in the northern Gulf of Mexicois predominately
25	mud and sand, with comparatively few natural reef areas(Parker et al., 1983;Kennicutt et
26	al.,1995;Dufrene, 2005). The lack of naturally occurring reefs has stimulated the deployment of
27	artificial reefsby the state of Alabama, private fishers, and scientists to increase the availability of
28	reef habitat(e.g. decommissioned military tanks and concrete pyramids). Several permit areas
29	have been established off the coast of Alabama, where an estimated 15,000 artificial reefs have
30	been deployed (Minton and Heath, 1998). The deployment of new reefs each year continues to
31	add or replace reefs lost to major tropical storms.
32	Several studies have examined red snapper age and growth in the northern Gulf of
33	Mexico (Nelson and Manooch, 1982; Szedlmayer and Shipp, 1994; Patterson et al., 2001a;
34	Wilson and Nieland, 2001; Mitchell et al., 2004; Gazey et al., 2008). The results were most
35	often used for annual growth comparisons and population assessments, while a few have

2

http://mc.manuscriptcentral.com/fisherybulletin

36	examined ontogenetic shifts in habitat and diet with fish age (Szedlmayer and Conti, 1999;
37	Rookeret al., 2004; Szedlmayer and Lee, 2004). Red snapper are most often aged by
38	countingopaque bands on otoliths, with annual depositional rates validated in several studies
39	(Baker and Wilson 2001; Patterson et al., 2001a; Wilson and Neiland 2001; Allman et al., 2005;
40	Szedlmayer and Beyer,2011). Red snapper can be aged by reading whole otoliths if <7 years,
41	butolder fish require otolith sectioning (Szedlmayer and Beyer, 2011). Red snapperare a long-
42	lived species and can reach maximum ages near 50 years (Szedlmayer and Shipp, 1994; Render,
43	1995; Patterson et al., 2001a; Wilson and Nieland, 2001).
44	Age-0 red snapper begin to use reefs shortly after settling out of the plankton, and seek
45	out available low relief structured habitat(Workman and Foster, 1994; Szedlmayer and Howe,
46	1997; Szedlmayer and Conti, 1999; Szedlmayer and Lee, 2004). These new recruits quickly
47	outgrowtheir initial benthic habitats and search for larger structured habitats by the fall following
48	the spawning season (Szedlmayer and Conti, 1999; Szedlmayer and Lee, 2004;
49	Szedlmayer,2011). After this initial recruitment, the presence of age-1 and older snapper may
50	limit the immigration of new recruits to reef structure (Bailey et al., 2001; Piko and Szedlmayer,
51	2007; Gallaway et al., 2009; Mudrak and Szedlmayer, In press).
52	In the northern Gulf of Mexico, numerous artificial reefs have been placed in offshore
53	waters, with some studies suggesting increased red snapper production (Szedlmayer, 2007;
54	Gallaway et al., 2009; Shipp and Bortone, 2009), while others have suggested only attraction
55	(Cowan et al. 1999; Patterson and Cowan, 2003; Cowan et al., 2010). Results from diet studies
56	have also differed, with some only supporting attraction (McCawley et al., 2006; Wells et al.,
57	2008b), while others supported increased production (Ouzts and Szedlmayer, 2003; Szedlmayer
58	and Lee, 2004; Redman and SzedImayer, 2009). Residency and movement studies again differed

59	for red snapper, with some showing little site fidelity (Patterson et al., 2001b; Peabody, 2004),
60	whileothers reported long-termresidency on artificial reefs (Szedlmayer and Shipp, 1994;
61	Szedlmayer, 1997; Szedlmayer and Schroepfer, 2005; Schroepfer and Szedlmayer, 2006;
62	Topping and Szedlmayer, In press).
63	Thus, it is still not clear if artificial reefs produce new red snapper biomass or simply
64	attract fish and make them more vulnerable to fishing mortality. A new approach to this long
65	standing question would be a comparison of resident fish age to artificial reef age. If
66	enhancement is occurring, the reefs will initially attract new recruits, and these recruits will stay
67	and grow as the reef ages, becoming the dominate age class which will then effectively exclude
68	new recruits from immigrating to "their" habitat. In contrast, if the artificial reefs simply attract
69	red snapper, reef age will not be correlated with fish age, with little evidence of competitive
70	exclusion or habitat limitation. In the present study reefs were deployed in 2006, 2009, and 2010
71	and positions were not released to the public to reduce potential fishing mortality effects on red
72	snapper age distribution. The size and age of red snapper were compared among the three reef
73	ages.
74	
75	
76	Materials and Methods
77	
78	Sample sites
79	
80	The study area was located 20 to 30 km south of Mobile Bay, Alabama (Fig. 1). This area has
81	over 15,000 artificial and a few natural rocky reefs(Minton and Heath, 1998). Artificial reefs

82	(4.4  x  1.3  x  1.2  m metal cages)were deployed in April 2006 ( $n = 20, 4$ year old reefs), April
83	2009(n = 10, 1  year old reefs), and January 2010 ( $n = 10, 0.5  year old reefs$ ). Reef locations
84	were not published which limitedpotential fishing mortality. Depth ranges for 2006 reefs were
85	27 – 32m, 2009 reefs 18 – 24m, and 2010 reefs 23 – 31m.
86	All reefs were sampled from April through November 2010. The 2010 reefs were
87	sampled at least five months after deployment to allow adequate time for red snapper
88	immigration.Red snapper were collected with hook-and-lineand fish trap from each reef. Hook-
89	and-line sampling was standardized to 30 min, with two fishers. Fishingtime was suspended when
90	problems occurred (e.g.internally hooked fish)and continued once bothfishers could resume
91	fishing. Hook-and-line fishing used double 6/0 J hooks, 27.2 kg test monofilament line, 45.3 kg
92	test monofilament leader, and whole Gulf menhaden (Brevoortiapatronus) as bait. After
93	completion of hook-and-line, additional fish were collected with a baited fish trap (1.2 x 1.5 x
94	0.6 m; Collins, 1990). In the fish trap both Gulf menhaden and whole squid (Loligospp.) were
95	used as bait. All fish traps were set for 15 min. After collections reached approximately 50 red
96	snapper per reef, additional fish were released with one exception (73 red snapper were kept on 5
97	May 2010 due to the possibility of area closures as a result of the Deepwater Horizon oil spill).
98	When the minimum target of 30 red snapper per reef was not reached after the first fish trap set,
99	the trap was fished at least one additional time. All red snapper collected from the reef were
100	immediately packed on ice and returned to the laboratory for further processing.
101	After fish collections were completed, two SCUBA divers completed visual,
102	photographic (Nikon D200) and video (Sony Hi-8) surveys to estimate the remaining red snapper
103	at the sample site. A clear plastic jar containing cut menhaden was used to attract surrounding
104	red snapper into aggregations during the visual survey for increased accuracy of total counts.

Divers completed at least three visual counts, with the highest count used for total
abundanceestimates. Poor visibility at some sites limited total abundance estimates. In addition,
diver operations were suspended when sharks were present and visual estimates were completed
at a later date.

109

110

111 Laboratory analyses

112

Red snapper size (standard lengthSL; fork length FL; total length TL mm) and total body weight 113 (0.01 g)were measured in the laboratory within 24 h of capture. For red snapper  $\geq$  250mm TL, 114 otoliths were removed using a Bosch fine cutelectric saw. For red snapper <250mm TL, otoliths 115 were removed using a small knife. Both left and rightotoliths were removed from each fish, 116 cleaned, and stored in dry plastic vials for later analysis.Opaque bands were counted on all 117 otoliths for age estimates. For fish < 7 years, bands were counted on whole otoliths that were 118 119 immersed in water under a dissecting scope with transmitted light. If ages were  $\geq 7$  years, thin otolith sections were prepared and bands were counted at 40x with a compound microscope 120 121 (Szedlmayer and Beyer, 2011). Opaque bands of sectioned otoliths were counted along the dorsal edge of the sulcus acousticus. Bands on each otolith were counted independently four 122 times. After four readings, two readers examined remaining otoliths where counts still differed 123 124 and attempted to reach a consensus on age. If an agreement on age could not be reached the otolith was rejected. A reference collection of hatchery red snapper that were released in the 125 wild as age-0 and recaptured as age-1 (n = 22) along with a group that was reared in captivityto 126 127 age-1 (n = 13) were used to validate counting methods of wild caught age-1 fish. Some of the

128 otoliths of these known age-1 fish showed a "false" annulus(i.e. had 2 opaque bands), but 129 showed age-1 otolith shape patterns (Beyer and Szedlmayer, 2010). Thus, some wild fish < 200 mm caught in this study with two opaque bands were defined as age-1, based on age-1 shape 130 patterns similar to hatchery reared as well as hatchery born but wild reared fish. 131 Video recordings and digital photographs of the reefs were examined in the laboratory for 132 comparisons and validation of diver visual counts. In the laboratory, photographs that showed 133 the highest number of red snapper for a particular reef were selected for computer counting. All 134 red snapper in photographs were identified and counted using Image-pro software (Image-pro 135 plus vers. 4.5, MediaCybernetics, Silver Spring, MD). Two screens were used to count video 136 recordings. A single frame of the video was displayed on one screen while the video played on 137 the second screen. When a single frame of the video is captured, the quality of the image 138 139 decreases, but the live video screenallowed identification of all fish in the captured screen. The captured screen could then be marked and counted using Image-pro software. 140 141 142 **Data analyses** 143 144 Catch per unit effort was calculated for both hook-and-line (CPUE = number caught by 2 fishers 145  $30 \text{ min}^{-1}$ ) and trap (CPUE = number caught 15 min<sup>-1</sup>) for each reef. The precision of age 146 estimates between readerswas compared using a linear regression and average percent error 147 (Beamish and Fournier, 1981).Red snapper densities (number per m<sup>3</sup> of reef) were compared with 148 the number of months the reefs were deployed prior to sampling using Pearson's correlation 149 150 coefficient. An analysis of variance (ANOVA) was used to compare the SL, weights, and ages

of red snapper among the different reef ages. If significant differences were detected a Tukeytestwas used to show specific differences.

153	Growth rates were examined by linear regressions for red snapper <10 years and
154	compared among old (2006) and new (2009 and 2010) reefsusing an analysis of covariance
155	(ANCOVA). For additional comparisons, Pearson's correlation coefficients were calculated
156	between reef age and red snapper SL, weight, and age; and between proximity to other artificial
157	reefs and red snapper abundance and age. To eliminate possible depth effects, the ages of red
158	snapper collected from the same depth (30 m) were compared among 2006 reefs and 2010 reefs
159	with a t-test. Differences were considered significant at $P \le 0.05$ and all data were analyzed with
160	Statistical Analysis System software (SAS vers. 9.1, SAS Inst., Inc., Cary, NC)
161	
162	
163	Results
164	
165	Red snapper were sampled from April through November 2010 from 37 artificial reefs (2006
166	reefs <i>n</i> =18, 2009 reefs <i>n</i> =10, 2010 reefs <i>n</i> =9).Diver surveys were completed at later dateson two
167	sites due to shark presence on the original sample date, and not completed on seven reefs due to
168	poor visibility.
169	Atotal of 1028 red snapper were collected, 439 by hook-and-line, and 589 by trap. Mean±
170	SD CPUE for hook-and-linewas significantly greater on the 2006 reefs $(20.4 \pm 8.5 \ 30 \ min^{-1})$ than
171	on the 2009 (6.3 ± 8.1 30 min <sup>-1</sup> ) and 2010 reefs (2.6 ± 4.6 30 min <sup>-1</sup> ; ANOVA: $F_{2, 34}$ = 20.38, P<
172	0.0001). No significant CPUE (number 15 min <sup>-1</sup> ) differences were detected among reef years for
173	trap collections (2006 = 10.6 ± 10.9, 2009 = 16.6 ± 19.9, and 2010 = 14.3 ± 12.7; ANOVA: $F_2$ .

174	$_{34}$ = 0.61, <i>P</i> = 0.55). The SL and weight of red snapper caught by hook-and-line (429.4 ± 79.8
175	mm, $2531 \pm 1409$ g) were significantly greater than those caught by trap ( $232.6 \pm 77.6$ mm, $538$
176	$\pm$ 726 g; SL <i>t</i> -test, $t_{1018}$ = 39.56,weight $t_{1018}$ = 29.41, <i>P</i> < 0.0001). Red snapper ages were also
177	significantly different between the two sampling methods (hook-and-line = $4.1 \pm 1.3$ years, trap
178	=1.9 ± 1.1 years; <i>t</i> -test, $t_{1024}$ = 29.68, <i>P</i> < 0.0001).
179	Diver survey methods significantly affected red snapper counts. Visual survey estimates
180	(mean $\pm$ SD = 78.3 $\pm$ 54.8)were significantly higher than other methods (photograph counts
181	=30.7± 20.2, video counts =16.5± 10.3; ANOVA, $F_{2,42}$ = 13.37, P<0.0001). Due to these
182	differences, total red snapper densities were estimated by adding captured fish (hook-and-line
183	and trap samples) to visual counts.
184	Age-1 red snapper first recruited to the 2010 reefs in the early summer, and numbers
185	increased through the fall. Mean $\pm$ SD numbers of red snapper m <sup>-3</sup> of reef structure increased as
186	reef age increased (Pearson's $r = 0.48$ , $P = 0.008$ ), and were significantly greater on 2006 reefs
187	$(22 \pm 13)$ than on 2009 reefs $(12 \pm 6)$ and 2010 reefs $(8 \pm 7; ANOVA, F_{2, 27} = 4.25, P < 0.025)$ .
188	All red snapper caught ( $n=1028$ ) were used in the final age comparisons. Initial
189	agreement between the $1^{st}$ and $2^{nd}$ independent readings was 62.2% (639/1028). A $3^{rd}$ and $4^{th}$
190	reading increased the accepted otoliths to 92.3% (949/1028). Average percent error was
191	calculated for both sets of independent readings (Table 1). An age consensus was reached on all
192	remaining otoliths ( $n = 79$ ) by simultaneous examination by two readers. The reference
193	collection of age-1 hatchery ( $n = 35$ , laboratory and wild reared) red snapper showed 25.7 % with
194	two opaque bands, suggesting that counting opaque bands for age-1 fish may not be reliable.
195	Among fish that were < 200 mm SL and showed two opaque bands ( $n=72$ ), allwere identified as

age-1 based on shape, thickness, and location of the opaque bands (Szedlmayer and Beyer, 2010;Szedlmayer, personal observ.).

198	Mean ± SD red snapper SL, weight, and age were significantly different among 2006
199	reefs $(373.29 \pm 107.83 \text{ mm SL}, 1883.1 \pm 1388.1 \text{ g}, 3.6 \pm 1.2 \text{ years}), 2009 \text{ reefs} (250.20 \pm 114.71 \text{ mm SL})$
200	mm SL,852.0 $\pm$ 1464.4 g, 2.0 $\pm$ 1.7 years) and2010 reefs (222.25 $\pm$ 78.04 mm SL, 480.1 $\pm$ 710.6
201	g, $1.7 \pm 1.0$ years; ANOVA, $F_{2, 1025} = 194.23$ , $P < 0.0001$ ; Table 2;Fig.2 and 3).Reef age was
202	positively correlated with red snapper age (Pearson's $r = 0.61$ , $P < 0.0001$ ), standard length ( $r =$
203	0.71, $P < 0.0001$ ), and weight ( $r = 0.47$ , $P = 0.0035$ ). Comparisons of linear growth rates for fish
204	<10 years showed no significant differences between old (2006) and new (2009 and 2010) reefs
205	(ANCOVA, $F_{3, 1018}$ = 2.98, $P$ = 0.085, power > 0.99).
206	The depths of the 2006 reefs were significantly greater than the depths of the 2009 reefs
207	( <i>t</i> -test, $t_{26} = 16.32$ , <i>P</i> < 0.0001). Due to this depth difference, red snapper were also compared
208	among the 2006 and 2010 reefs $(n = 8)$ from the same depth (30 m). These comparisons still
209	detected significantly larger and older red snapper on 2006 reefs (mean $\pm$ SD = 368.73 $\pm$ 105.02
210	mm SL, $1820.8 \pm 1326.3$ g, $3.60 \pm 1.20$ years) compared to 2010 reefs ( $236.19 \pm 85.24$ mm SL,
211	$578.0 \pm 814.1$ g, $1.91 \pm 1.10$ years, <i>t</i> -test, <i>P</i> < 0.0001).
212	Comparisons of red snapper abundance and age on artificial reefs from this study, to
213	theproximity of other known reefs failed to detect a significant effect. Also, no significant
214	correlations were detected between abundance (Pearson's $r = -0.061$ , $P = 0.721$ ), or mean age of
215	red snapperand distance to other reefs(Pearson's $r = 0.160$ , $P = 0.345$ ).
216	
217	

## 218 **Discussion**

219	
220	
221	Evidence for production
222	
223	This study showed significantly older red snapper were associated with older artificial reefs.
224	Previous studies have compared artificial reef age with density and size estimates of resident reef
225	fishes but have not examined reef fish age. For example, there were significantly higher
226	densities of reef fishes and larger Sparids (Diplodussargus, Diplodusbellottii, and Diplodus
227	vulgaris) at older habitats(Lindberg et al., 2006; Santos et al., 2011). Since length varies directly
228	with age with these species up to age 3 (Gordoa and Molí, 1997), it is likely that the age also
229	increased with reef age similar to the present study.
230	This relation between reef age and fish age supports previous studies that indicated red
231	snapper production from artificial reefs (Szedlmayer and Shipp, 1994; Szedlmayer, 2007;
232	Gallaway et al., 2009). The increased production is likely due to an increase in available reef
233	habitat, which has been shown as a controlling factor affecting the density and growth of red
234	snapper (Szedlmayer and Shipp, 1994; Szedlmayer and Conti, 1999; Gazey et al., 2008). Red
235	snapper recruited to the newly deployed reefs rapidly as juveniles (approximately age-1) and then
236	resided on these reefs for several years based on red snapper ages in the present study and long
237	term residency shown in previous studies (Schroepfer and Szedlmayer 2006; Topping and
238	Szedlmayer, In press). If these reefs were only attracting red snapper, fish age and reef age
239	would not be correlated. Red snapper would freely move back and forth among reefs and show
240	random age distributions at each reef site. If artificial reefs are enhancing the population and
241	experiencing no fishing pressure, Powers et al. (2003) estimated that these reefs could increase

production by 6.45 kg wet wt 10 m<sup>-2</sup> in the first year. Since the reefs used in the present study
were unpublished, fishing mortality was limited and following Powers et al. (2003) had the
potential to increase production.

Several studies suggest that red snapper populations were overfished and that habitat 245 limitation was not the most important controlling factor (Schrippa and Legault, 1999; Patterson 246 et al., 2001b; Cowan et al., 2010). Clearly there was significant fishing mortality of red snapper 247 in the northern Gulf of Mexico (Gillig et al., 2000). However, if fishing mortality was the 248 limiting factor for red snapper and habitat was not important, we would not expect significant 249 250 reef age effects on fish age (i.e. all reefs whether fished or not would show similar age distributions). Red snapper enter the fishery around age 2, (recreational size minimum = 406251 mm, commercial = 330 mm), with the catch predominately consisting of 2 to 4 year old fish. If 252 253 fishing mortality was limiting red snapper, these ages would have been harvested and not show significant increases on older reefs. However, these ages represented 59 % (n = 602) of the total 254 catch, indicating that fishing mortality was not limiting red snapperabundance on the reefs in the 255 present study. 256

Onesubstantial difference between the present study that suggests habitat limitation and previous studies that suggested fishing mortality limitation was the use of fishery independent data compared to fishery dependent data. While other studies mainly used fishery dependent data of red snapper caught by sport and commercial fishers (Szedlmayer and Shipp, 1994; Baker and Wilson, 2001; Patterson et al., 2001a; Wilson et al., 2001), this study used fishery independent methods from unpublished artificial reef sites. These fishery independent methods could also sample smaller red snapper that were unavailable from fishery dependent methods. In addition,

fishing mortalityat reef sites in the present study was probably greatly reduced, because reeflocations were unpublished which limited fisher access.

Several alternate factors, aside from reef age, could have affected the size and age of red 266 snapper caught. First, larger fish on the older reefs may have resulted from differential habitat 267 value among reef ages, but growth rate differences among different reef ages were not detected. 268 269 Thus reefs in this study were providing similar resources. Second, the mean depth of the 2006 reefs was 30 m while the mean depth of the 2009 reefs was 20 m, and previous studies have 270 indicated that larger, older red snapper were more common in deeper offshore waters compared 271 272 to shallower nearshore waters (Render, 1995; Mitchell et al., 2004). However, in this study reefs from the same depth (30 m) still showed significantly larger and older red snapper on the 2006 273 reefs compared to the 2010 reefs. Third, distance from natural or artificial reefs has been shown 274 275 to be an important factor affecting the density of reef fishes (Jessee et al., 1985; Sogard, 1989;Strelcheck et al., 2005; Shipley and Cowan, 2010). In this study, no significant relations 276 were detected between reef proximity and red snapper ages and abundance. Forth, older reefs 277 may provide better habitat and older red snapper are transient and migrate to these higher quality 278 habitats. However, recent telemetry studies have showed long term residence of red snapper to 279 the present or similar study sites up to 1099 d (Schroepfer and Szedlmayer 2006; Topping and 280 Szedlmayer, In press) 281

282

283

284 **Comparison of collection methods** 

285

286 This study supports previous studies on the importance of using several collection methods to adequately estimate size and age distribution of red snapper on artificial reefs (Myers and 287 Hoenig, 1997; McClanahan and Mangi, 2004; Szedlmayer, 2007; Wells et al., 2008a; Gallaway et 288 al., 2009). Hook-and-line and fish traps were size selective, with hook-and-line consistently 289 290 catching larger red snapper than the fish trap. Visual diver counts were used to estimate the remaining red snapper still present on the 291 reef after hook-and-line and trap sampling. The video and photograph methods had significantly 292 lower counts than diver visual surveys. These differences were mostly due to fish swimming 293 294 throughout the water column that were not within the field of view of the cameras. The use of a bait jar was intended to attract fish closer to reduce these differences, but only had limited 295 success. Comparisons of remote underwater baited cameras have reported similar results, with 296 297 visual SCUBA surveys showing the greatest abundance and diversity (Tessier et al., 2005; Langlois et al., 2006). Due to lower counts from photographs and video recordings, the diver 298 visual counts were used in the red snapper density estimates for each reef. However, the 299 300 photographs and video recordings were important in verifying species identification. 301 302 Artificial reef succession and red snapper densities 303 304 305 Many studies have shown that artificial habitats are rapidly settled by reef fishes (Solonsky, 1985; Walsh, 1985; Leitão et al., 2008; Redman and Szedlmayer, 2009; Szedlmayer, 2011; 306 Mudrak and Szedlmayer, in press). In a four year study of an artificial reef system in the U.S. 307 Virgin Islands, most reef fishes that immigrated to reefs were juveniles which then stayed on the

14

309	reefs through adulthood(Ogden and Ebersole, 1981). Also, fish will re-colonize reefs back to
310	pre-event densities following a catastrophic event in which the abundance of fish was decreased
311	(Bohnsack, 1983). Two years after a red tide event off the coast of Florida, the invertebrate and
312	demersal fish communities were similar to those before the red tide (Dupont et al., 2010). The
313	artificial reefs used in this study showed similar patterns where new reefs fill up quickly over the
314	first year then reach a carrying capacity with little change in density over the next few years.
315	The reefs in the present study supported higher densities of red snapper compared to
316	previous studies. In a demolition study of nine offshore oil platforms, mean density was 0.24 red
317	snapper m <sup>-3</sup> (Gitschlag et al., 2000). In another study of platforms that used stationary
318	hydroacoustics and visual diver counts, the mean density was 0.16 red snapper m <sup>-3</sup> (Stanley and
319	Wilson, 1997). The total red snapper density estimates in the present study were substantially
320	higher than these platform estimates and ranged from $1.6 - 47.9$ , with a mean of 15.7red snapper
321	$m^{-3}$ . One difference between the present study and these previous studies on platforms, were
322	substantial differences in the size of the structures, since the platforms encompass the entire
323	water column. The volume of the platforms ranged from $1037 - 29,860 \text{ m}^3$ (Gitschlag et al.,
324	2000) and 19,800 m <sup>3</sup> (Stanley and Wilson, 1997), whereas all reefs in the current study had a
325	volume of 6.9 m <sup>3</sup> . However, even if the volume estimates of the platforms were reduced by two-
326	thirds (upper water column habitat not typically used by red snapper), mean platform red snapper
327	densities of 0.73 $\text{m}^{-3}$ (Gitschlag et al., 2000) and 0.47 $\text{m}^{-3}$ (Stanley and Wilson, 1997) would still
328	be considerably less than present metal cage estimates.

These differences in the density of red snapper among artificial habitats may be due to increased habitat complexity of cage reefs, providing better protection from predation for younger red snapper, additional prey resources, and fewer resident larger predators compared to

332	platforms. The densities of lemon damselfish (Pomacentrusmoluccensis) found on highly
333	complex coral reefs with predators were similar to reefs where predators were excluded,
334	indicating that these corals provided protection for the species (Beukers and Jones, 1997).
335	Similarly, higher densities of young (age-0 and age-1) red snapper were shown with increasing
336	complexity of reef structure (Lingo and Szedlmayer, 2006; Piko and Szedlmayer, 2007) and
337	absence of predators (Mudrak and Szedlmayer, in press). With large structures, such as
338	platforms, complexity probably decreases and the abundance of potential predators probably
339	increases compared to the smaller artificial reefs used in the present study. Therefore, these larger
340	reefs do not support as many red snapper per unit volume as the more complex smaller
341	structures. For example, an inverse relation was shown between red snapper abundance and the
342	density of offshore platforms, possibly due to an increased exposure of young red snapper to
343	predator aggregations around the platform (Gallaway et al., 1999). The higher densities of red
344	snapper on the reefs used in the present study indicate that these reefs are providing red snapper
345	protection from predation, and increasing the overall carrying capacity.
346	
347	

348 Conclusions

Significant differences in red snapper ages among the different reef ages provides support for increased red snapper production from artificial reefs.However, at some point the number of artificial habitats placed off the coast of Alabamawill surpass the habitat limitation and the addition of more artificial structures will no longer increase the population. Future research examining the carrying capacities of artificial habitats is needed and would provide information on when an overall environmental carrying capacity for red snapper has been reached.

355	Additional fishery independent studies using similar methods as in the present study throughout
356	the northern Gulf of Mexico would be useful for making better management decisions regarding
357	catch limits for red snapper.
358	
359	Literature cited
360	
361	Allman, R. J., G. R. Fitzhugh, K. J. Starzinger, and R. A. Farsky. 2005. Precision of age
362	estimation in red snapper (Lutjanus campechanus). Fish. Res. 73:123–133.
363	Bailey IV, H. K., J. H. Cowan Jr., and R. L Shipp. 2001. Experimental evaluation of potential
364	effects of habitat size and presence of conspecifics on habitat association by young-of-
365	the-year red snapper. Gulf Mex. Sci. 2:119–131.
366	Baker Jr., M. S., and C. A. Wilson.2001. Use of bomb radiocarbon to validate otolith section
367	ages of red snapper Lutjanus campechanus from the northern Gulf of Mexico.
368	Limnol.Oceanog. Bull. 46:1819–1824.
369	Beamish, R. J., and D. A. Fournier. 1981. A method for comparing the precision of a set of age
370	determinations. Can. J. Fish.Aquat. Sci. 38:982–983.
371	Beukers, J. S., and G. P.Jones. 1997. Habitat complexity modifies the impact of piscivores on a
372	coral reef fish population. Oecologia 114:50–59.
373	Beyer, S. G., and S. T. Szedlmayer. 2010. The use of otolith shape analysis for ageing juvenile
374	red snapper, Lutjanus campechanus. Environ. Biol. Fishes 89:333-340.
375	Bohnsack, J. A. 1983. Resiliency of reef fish communities in the Florida Keys following a
376	January 1997 hypothermal fish kill. Environ. Biol. Fishes 9:41–53.

377	Camber, C. I.1955. A survey of the red snapper fishery of the Gulf of Mexico, withspecial
378	reference to the Campeche Banks. Fla. Board Conserv. Tech. Ser. No. 12:1-64.
379	Collins, M. R. 1990. A comparison of three fish trap designs. Fish. Res. 9:325–332.
380	Cowan Jr., J. H., W. Ingram, J.McCawley, B. Sauls, A. Strelcheck, and M. Woods. 1999. The
381	attraction vs. production debate: Does it really matterfrom the management perspective?
382	A response to the commentaryby R. L. Shipp. Gulf Mex. Sci., 17: 137-138 (1999).
383	Cowan Jr., J. H., C. B. Grimes, W. F. Patterson III, C. J. Walters, A. C. Jones, W. J. Lindberg, D.
384	J. Sheehy, W. E. Pine III, J. E. Powers, M. D. Campbell, K. C. Lindeman, S. L. Diamond,
385	R. Hilborn, H. T. Gibson, and K. A. Rose. 2010. Red snapper management in the Gulf of
386	Mexico:science- or faith-based? Rev. Fish Biol. Fish. published online April 3, 2010, 18
387	p.
388	Dufrene, T. A. 2005. Geological variability and Holocene sedimentary record on the northern
389	Gulf of Mexico inner to mid-continental shelf. M.S.thesis, Louisiana State Univ., Baton
390	Rouge, LA, 100 p.
391	Dupont, J. M., P. Hallock, and W. C. Jaap. 2010. Ecological impacts of the 2005 red tide on
392	artificial reef epibenthicmacroinvertebrate and fish communities in the eastern Gulf of
393	Mexico. Mar. Ecol. Prog. Ser. 415:189–200.
394	Gallaway, B. J., J. G. Cole, R. Meyer, and P.Roscigno. 1999. Delineation of essential habitat for
395	juvenile red snapper in the northwestern Gulf of Mexico. Trans. Am. Fish. Soc. 128:713-
396	726.
397	Gallaway, B. J., S. T. Szedlmayer, and W. J. Gazey.2009. A life history review for redsnapper in
398	the Gulf of Mexico with an evaluation of the importance of offshorepetroleum platforms
399	and other artificial reefs. Rev. Fish. Sci. 17:48-67.
	18

400	Gazey, W. J., B. J. Gallaway, J. G. Cole, and D. A. Fournier.2008. Age composition, growth, and
401	density-dependent mortality in juvenile red snapper estimated fromobserver data from
402	the Gulf of Mexico penaeid shrimp fishery. N. Am. J. Fish. Manage. 28:1828–1842.
403	Gillig, D., T. Ozuna Jr., and W. L. Griffin. 2000. The value of the Gulf of Mexico recreational
404	red snapper fishery. Mar. Resour.Econ. 15: 127–139.
405	Gitschlag, G. R., M. J. Schirripa, and J. E. Powers.2000. Estimation of fisheries impacts due to
406	underwater explosives used to sever and salvage oil and gas platforms in the U.S. Gulf of
407	Mexico: Final Report. OCS Study MMS 2000–087. Prepared by the National Marine
408	Fisheries Service. U.S. Dept. of the Interior, Minerals Mgmt. Service, Gulf of Mexico
409	OCS Region, New Orleans, LA, 80 p.
410	Gordoa, A., and B. Molí. 1997. Age and growth of the sparids <i>Diplodus vulgaris</i> , <i>D. sargus</i> , and
411	D. annularis in adult populations and the differences in their juvenile growth patterns in
412	the north-western Mediterranean Sea. Fish. Res. 33:123–129.
413	Jessee, W. N., A. L. Carpenter, and J. W. Carter. 1985. Distribution patterns and density
414	estimates of fishes on a southern California artificial reef with comparisons to natural
415	kelp-reef habitats. Bull. Mar. Sci. 37:214–226.
416	Kennicutt, M. C., W. W. Schroeder, and J. M. Brooks. 1995. Temporal and spatialvariations in
417	sediment characteristics on the Mississippi-Alabama continental shelf.Cont. Shelf Res.
418	15:1–18.
419	Langlois, T., P.Chabanet, D. Pelletier, and E. Harvey. 2006. Baited underwater video for
420	assessing reef fish populations in marine reserves. SPC Fisheries Newsletter 118:53–57.

421	Leitão, F., M. N. Santos, K. Erzini, and C. C. Monteiro. 2008. Fish assemblages and rapid
422	colonization after enlargement of an artificial reef off Algarve coast (Southern Portugal).
423	Mar. Ecol. 29:435–448.
424	Lindberg, W. J., T. K. Frazer, K. M. Portier, F. Vose, J. Loftin, D. J. Murie, D. M. Mason, B.
425	Nagy, M. K. Hart. 2006. Density-dependent habitat selection and performance by a
426	large mobile reef fish. Ecol. Appl. 16:731–746.
427	Lingo, M. E., and S. T. Szedlmayer. 2006. The influence of habitat complexity on reef fish
428	communities in the northeastern Gulf of Mexico. Environ. Biol. Fishes 76:71–80.
429	McCawley, J. R., J. H. Cowan Jr., and R. L. Shipp. 2006. Feeding periodicity and prey habitat
430	preference of red snapper Lutjanus campechanus (Poey, 1860), on Alabama artificial
431	reefs. Gulf Mex. Sci. 1:14–27.
432	McClanahan, T. R., and S. C. Mangi. 2004. Gear-based management of a tropical artisanal
433	fishery based on species selectivity and capture size. Fish. Manage. Ecol. 11:51–60.
434	Minton, R. V., and S. R. Heath. 1998. Alabama's artificial reef program: building oases in the
435	desert. Gulf Mex. Sci. 16:105–106.
436	Mitchell, K. M., T. Henwood, G. R. Fitzhugh, and R. J. Allman. 2004. Distribution, abundance
437	and age structure of red snapper (Lutjanus campechanus) caught on research longlines in
438	U. S. Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Science
439	Center, SEDAR7-DW9, Pascagoula, 18 p.

- 440 Myers, R. A., and J. M. Hoenig. 1997. Direct estimates of gear selectivity from multiple
- 441 tagging experiments. Can. J. Fish.Aquat. Sci. 54:1–9.
- 442 Mudrak, P. A., and S. T. Szedlmayer.In press.Proximity effects of larger resident fishes on
- 443 recruitment of age-0 red snapper in the northern Gulf of Mexico.Trans. Am. Fish.Soc.

444	Nelson, R. S., and C. S. Manooch III.1982. Growth and mortality of the red snapper, Lutjanus
445	campechanus, in the west-central Atlantic and northern Gulf of Mexico. Trans. Am. Fish.
446	Soc. 111:465–475.
447	Ogden, J. C., and J. P. Ebersole. 1981. Scale and community structure of coral reef fishes: A
448	long-term study of a large artificial reef. Mar. Ecol. Prog. Ser. 4:97–103.
449	Ouzts, A. C., and S. T. Szedlmayer. 2003. Diel feeding patterns of red snapper on artificial reefs
450	in the north-central Gulf of Mexico. Trans. Am. Fish. Soc. 132:1186–1193.
451	ParkerJr., R. O., D. R. Colby, and T. D. Willis. 1983. Estimated amount of reef habitaton a
452	portion of the U.S. South Atlantic and Gulf of Mexico continental shelf.Bull. Mar. Sci.
453	33:935–940.
454	Patterson III, W. F., J. H. Cowan Jr. 2003. Site fidelity and dispersion ofred snapper associated
455	with artificial reefs in the northern Gulf of Mexico. Am. Fish. Soc. Symp., 36: 181–193
456	Patterson III, W. F., J. H. Cowan Jr, C. A. Wilson, and R. L. Shipp. 2001a. Age and growth of
457	red snapper Lutjanus campechanus from an artificial reef area off Alabama in the
458	northern Gulf of Mexico. Fish. Bull. 99:617–627.
459	Patterson III, W. F., J. C. Watterson, R. L. Shipp, and J. H.Cowan Jr. 2001b.Movement of tagged
460	red snapper in the Northern Gulf of Mexico.Trans. Am. Fish. Soc. 130:533–545.
461	Peabody, M. B. 2004. The fidelity of red snapper (Lutjanus campechanus) to petroleumplatforms
462	and artificial reefs in the northern Gulf of Mexico. M.S. Thesis, Louisiana State Univ.,
463	Baton Rouge, LA, 81 p.
464	Piko, A. A., and S. T. Szedlmayer. 2007. Effects of habitat complexity and predator exclusion
465	on the abundance of juvenile red snapper. J. Fish Biol. 70:758–769.

466	Powers, S. P., J. H. Grabowski, C. H. Peterson, W. J. Lindberg. 2003. Estimating enhancement
467	of fish production by offshore artificial reefs: uncertainty exhibited by divergent
468	scenarios. Mar. Ecol. Prog. Ser. 264:265-277.
469	Redman, R. A., and S. T. Szedlmayer. 2009. The effects of epibenthic communities on reef
470	fishes in the northern Gulf of Mexico. Fish. Manage. Ecol. 16:360–367.
471	Render, J. H. 1995. The life history (age, growth, and reproduction) of red snapper (Lutjanus
472	campechanus) and its affinity for oil and gas platforms. Ph.D. diss., Louisiana State
473	Univ., Baton Rouge, LA, 76 p.
474	Rooker, J. R., A. M. Landry Jr., B. W. Geary, and J. A. Harper. 2004. Assessment of a shell
475	bank and associated substrates as nursery habitat of postsettlement red snapper.
476	Estuar.Coast. Shelf Sci. 59:653-661.
477	Santos, M. N., F. Leitão, A. Moura, M. Cerqueira, and C. C. Monteriro. 2011. Diplodus spp. on
478	artificial reefs of different ages: influence of the associated macrobenthic community. J.
479	Mar. Sci. 68:87–97.
480	SEDAR7. 2005. Stock assessment report of SEDAR 7, Gulf of Mexico Red Snapper. NMFS,
481	SEFSC, NOAA, Charleston, South Carolina. Available:
482	http://www.sefsc.noaa.gov.(January 2009).
483	SEDAR. 2009. Stock Assessment of Red Snapper in the Gulf of Mexico: SEDAR Update
484	Assessment. NMFS, SEFSC, NOAA, Miami, Florida. Available:
485	http://www.sefsc.noaa.gov.(January 2009).

- 486 Schirripa, M. J., and C. M. Legault. 1999. Status of the red snapper in U.S. waters of the Gulf of
- 487 Mexico: updated through 1998. Southeast Fisheries Science Center, MiamiLaboratory,
- 488 NMFS, SFD-99/00-75, 44 p.

489	Schroepfer, R. L., and S. T. Szedlmayer.2006. Estimates of residence and site fidelityfor red
490	snapper Lutjanus campechanus on artificial reefs in the northeastern Gulf of Mexico.
491	Bull. Mar. Sci. 78:93–101.
492	Shipley, J. B., and J. H.Cowan Jr. 2010. Artificial reef placement: a red snapper, Lutjanus
493	campechanus, ecosystem and fuzzy rule-based model. Fish. Manage.
494	Ecol.doi: 10.1111/j.1365-2400.2010.00765.x, 14 p.
495	Shipp, R. L., and S. A.Bortone.2009. A prospective of the importance of artificial habitat on the
496	management of red snapper inthe Gulf of Mexico. Rev. Fish. Sci. 17:41–47.
497	Sogard, S. M. 1989. Colonization of artificial seagrass by fishes and decapods crustaceans:
498	importance of proximity to natural eelgrass. J. Exp. Mar. Biol. Ecol. 133:15–37.
499	Solonsky, A. C. 1985. Fish colonization and the effect of fishing activities on two artificial
500	reefs in Monterey Bay, California. Bull. Mar. Sci. 37:336–347.
501	Stanley, D. R., and C. A. Wilson. 1997. Seasonal and spatial variation in the abundance and size
502	distribution of fishes associated with a petroleum platform in the northern Gulf of
503	Mexico. Can. J. Fish.Aquat. Sci. 54:1166–1176.
504	Strelcheck, A. J., J. H. Cowan Jr., and A. Shah. 2005. Influence of reef location on artificial-
505	reef fish assemblages in the northcentral Gulf of Mexico. Bull. Mar. Sci. 77:425–440.
506	Szedlmayer, S. T. 1997. Ultrasonic telemetry of red snapper, Lutjanus campechanus, at
507	artificial reef sites in the northeast Gulf of Mexico. Copeia 4:846-850.
508	Szedlmayer, S. T. 2007. An evaluation of the benefits of artificial habitats for redsnapper,
509	Lutjanus campechanus, in the northeast Gulf of Mexico. Proc. Gulf Caribb.Fish. Inst.
510	59:223–229.

511	Szedlmayer, S.T. 2011. The artificial habitat as an accessory for improving estimates of juvenile
512	reef fish abundance in fishery management. In The use of artificial reefs in fishery
513	management (S. A. Bortone, F. P. Brandini, G. Fabi, and S. Otake, eds.), p. 31-44. CRC
514	Press, Boca Raton, FL.
515	Szedlmayer, S. T., and S. G. Beyer. 2011. Validation of annual periodicity in otoliths of red
516	snapper, Lutjanus campechanus. Environ. Biol. Fishes.doi: 10.1007/s10641-011-9774-6,
517	12 p.
518	Szedlmayer, S. T., and J. Conti. 1999. Nursery habitats, growth rates, and seasonality of age-0
519	red snapper, Lutjanus campechanus, in the northeast Gulf of Mexico.Fish. Bull. 97:626–
520	635.
521	Szedlmayer S. T., and J. C. Howe. 1997. Substrate preference studies in age-0 red snapper,
522	Lutjanus campechanus. Environ. Biol. Fishes 50:203–207.
523	Szedlmayer S. T., and J. D.Lee. 2004. Diet shifts of juvenile red snapper(Lutjanus campechanus)
524	with changes in habitat and fish size. Fish. Bull. 102:366–375.
525	Szedlmayer, S. T., and R. L. Schroepfer. 2005. Long-term residence of red snapper onartificial
526	reefs in the northeastern Gulf of Mexico. Trans. Am. Fish. Soc. 134:315–325.
527	Szedlmayer, S. T., and R. L. Shipp. 1994. Movement and growth of red snapper, Lutjanus
528	campechanus, from an artificial reef area in the Northeastern Gulf of Mexico. Bull. Mar.
529	Sci.55:887–896.
530	Tessier, E., P.Chabaneta, K.Pothin, M.Soria, and G.Lasserre. 2005. Visual censuses of tropical
531	fish aggregations on artificial reefs:slate versus video recording techniques. J. Exp. Mar.
532	Biol. Ecol. 315:17–30.

533	Topping, D. T. and S. T. Szedlmayer. In press.Use of ultrasonic telemetry to estimate site
534	fidelity, residence time and movement patterns of red snapper Lutjanus campechanus
535	(Lutjanidae). Mar. Ecol. Prog. Ser.
536	Walsh, W. J.1985. Reef fish community dynamics on small artificial reefs: the influence of
537	isolation, habitat structure, and biogeography. Bull. Mar. Sci. 36:357-376.
538	Wells, R. J. D., K. M Boswell, J. H. Cowan Jr., and W. F. Patterson III. 2008a. Size selectivity
539	of sampling gears targeting red snapper in the northern Gulf of Mexico. Fish. Res.
540	89:294–299.
541	Wells, R. J. D., J. H. Cowan Jr., and B. Fry. 2008b. Feeding ecology of red snapper Lutjanus
542	campechanus in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 361:213–225.
543	Wilson, C. A., A. L. Stanley, and D. L. Nieland. 2001. Age estimates from annuli in otoliths of
544	red snapper, Lutjanus campechanus, from the northern Gulf of Mexico. Proc. Gulf
545	Caribb.Fish.Inst. 52:48–62.
546	Wilson, C. A., and D. L.Nieland.2001. Age and growth of red snapper, Lutjanus campechanus,
547	from the northern Gulf of Mexico off Louisiana. Fish. Bull. 99:653–664.
548	Workman, I. K., and D. G. Foster. 1994. Occurrence and behavior of juvenile red snapper,
549	Lutjanus campechanus, on commercial shrimp fishing grounds in the northeastern Gulf
550	of Mexico. Mar. Fish Rev. 56:9–11.

551

- Table 1Average percent error for both sets of independent readings. Included are the
- percentages of agreement for each difference ( $1^{st}$  and  $2^{nd}$  reading  $r^2 = 0.83$ , P < 0.0001;  $3^{rd}$  and  $4^{th}$
- 554 reading  $r^2 = 0.96$ , P < 0.0001).

	First and Second Reading	Third and Fourth Readings
Average percent error	7.85	1.41
Standard deviation	0.12	0.05
0	62.16 %	92.32 %
± 1	35.89 %	7.39 %
± 2	1.95 %	0.29 %
≥ 3	0 %	0 %



Table 2Comparison of red snappermean  $\pm$  SD standard length, weight, and age for each reef year using ANOVA and a Tukeytest. Different letters are used to indicate significant differences (*P* $\leq$  0.05).

Reef Year	SL (mm)	Weight (kg)	Mean Age
2006	373.29 ± 107.83 (a)	1.883 ± 1.388 (a)	3.54 ± 1.24 (a)
	( <i>n</i> = 581)	( <i>n</i> = 581)	(n = 587)
2009	250.20 ± 114.71 (b)	$0.852 \pm 1.464$ (b)	1.98 ± 1.70 (b)
	(n = 280)	(n = 280)	(n = 280)
2010	222.25 ± 78.04 (c)	0.480 ±0.711 (c)	$1.72 \pm 1.00$ (c)
	( <i>n</i> = 161)	( <i>n</i> = 161)	( <i>n</i> = 161)



Figure 1 Locations of artificial reefs. Reef years are indicated by different shading. 322x348mm (72 x 72 DPI)



Figure 2 Red snapper SL (mm) percent frequency by reef year, separated into 100 mm categories (e.g. 100 = 100 - 199 mm). 189x202mm (300 x 300 DPI)



Figure 3 Percent frequency of red snapper age (years) by reef year. Total number of fish caught for each age class indicated by numbers above bars. 193x212mm (300 x 300 DPI)