Fish assemblages on sunken vessels and natural reefs in southeast Florida, USA

P. T. Arena · L. K. B. Jordan · R. E. Spieler

Abstract Derelict ships are commonly deployed as artificial reefs in the United States, mainly for recreational fishers and divers. Despite their popularity, few studies have rigorously examined fish assemblages on these structures and compared them to natural reefs. Six vessel-reefs off the coast of southeast Florida were censused quarterly (two ships per month) to characterize their associated fish assemblages. SCUBA divers used a non-destructive point-count method to visually assess the fish assemblages over 13- and 12-month intervals (March 2000 to March 2001 and March 2002 to February 2003). During the same intervals, fish assemblages at neighboring natural reefs were also censused. A total of 114,252 fishes of 177 species was counted on natural and vessel-reefs combined. Mean fish abundance and biomass were significantly greater on vessel-reefs in comparison to surrounding natural reef areas. Haemulidae was the most abundant family on vessel-reefs, where it represented 46% of total fish abundance. The most abundant family on natural reefs was Labridae, where it accounted for 24% of total fish abundance. Mean species richness was significantly greater on vessel-reefs than neighboring natural reefs and also differed among vessel-reefs. Both mean fish abundance and mean species richness were not significantly different between natural reefs neighboring vessel-reefs and natural reefs with no artificial structures nearby. This suggests the vessel-reefs are not, in general, attracting fish away from neighboring natural reefs in our area. Additionally, economically important fish species seem to prefer vessel-reefs, as there was a greater abundance of these species on vessel-reefs than surrounding natural reef areas. Fish assemblage structure on natural versus artificial reefs exhibited a low similarity (25.8%). Although no one species was responsible for more than 6% of the total dissimilarity, fish assemblage trophic structure differed strikingly

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between the two reef types. Planktivores dominated on vessel-reefs, accounting for 54% of the total abundance. Conversely, planktivores only made up 27% of total abundance on natural reefs. The results of this study indicate vessel-reef fish assemblages are unique and that these fishes may be utilizing food resources and habitat characteristics not accessible from or found at natural reefs in our area. Production may also be occurring at vessel-reefs as the attraction of fish species from nearby natural reefs seems to be minimal.

Keywords Artificial reef · Vessel · Coral reef · Habitat

Introduction

The popularity of recreational fishing has risen dramatically in the past 50 years and with this increase in fishers has come additional pressure on global fish stocks, the majority of which, have been classified as either fully- or over-exploited (Murray & Betz, 1994; FAO, 1997a, b). For example, the state of Florida, USA has 13 560 km of coastline, more than 800,000 registered boats, and over one million registered recreational fishing licenses (FWRI, 2004; White, 2004). Given these numbers it is clear there is mounting pressure on state resource managers to protect and sustain coastal fisheries. A popular management option currently in use is the deployment of artificial reefs, as these structures are known to harbor high abundances of fishes.

Derelict vessels have been intentionally deployed to increase fishing success since 1935 (Stone, 1985) and support for their use has come from the fishing industry (recreational and commercial), tourist industry, diving community and environmental managers (Murray & Betz, 1994; Jones & Welsford, 1997; MacDonald et al., 1999). Murray & Betz (1994) reported all groups of respondents (commercial fishermen, recreational fishermen, sport divers, and environmentalists) from a mail survey preferred artificial reefs constructed from ships and barges. In particular, sport divers have shown a preference for vessel-reefs due to high densities of fishes at these sites and the aesthetic qualities offered by the struc-

ture itself (Brock, 1994; Murray & Betz, 1994; Jones & Welsford, 1997). The demand for vessel-reefs will undoubtedly escalate as a result of the growing sport diving industry, which reported 50,000 new worldwide diving certifications each year since the early 1980s (Gilmore, 2004).

The popularity of vessel-reefs has led to legitimate questions about their effectiveness as fisheries enhancement tools (Seamen & Jensen, 2000). An understanding of fish assemblage structure on vessel-reefs is required to determine if they are achieving the goals set forth by resource managers. Yet, there have been surprisingly few studies comparing vessel-reef fish assemblages to those on adjacent natural reefs (Jones & Thompson, 1978; Markevich, 1994) and few of these have been statistically rigorous.

Broward County, Florida has a wide diversity and abundance of vessel-reefs, as well as a substantial natural reef system, which afforded us an excellent opportunity to conduct comparative surveys of fish assemblages. Our objectives were to: (1) compare the fish assemblages on six vessel-reefs to adjacent natural reefs, and (2) compare the fish assemblages among the various vessel-reefs.

Materials and methods

Study site

Broward County's reef complex is approximately 1.5 km wide and is composed of three relic coral reef terraces, each separated by sand substrate, which run parallel to the coastline in sequentially deeper water (Goldberg, 1973; Lighty, 1977; Moyer et al., 2003). The three reef terraces have been locally named the inner, middle and outer reefs (Fig. 1). These high-latitude coral communities consist of typical Caribbean fauna, however benthic community structure is highly variable and cannot be characterized by existing reef classification or zonal schemes (Goreau, 1959). Moyer et al. (2003) suggested water quality, sedimentation, and/or hurricane recurrence might determine benthic community structure in this area.

During this study, the prevailing winds were typically 10–15 knots from the southeast. Wave
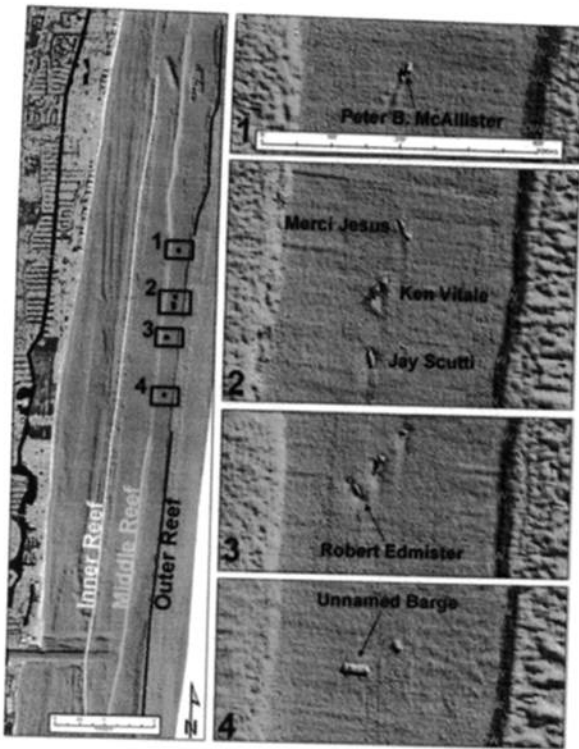
Fig. 1 Natural and vessel-reef study sites in southeast Florida, USA

North due to the influence of the Florida Current, but the authors (unpublished), as well as Soloviev et al. (2003) have observed a reversal of this trend during late summer. Water visibility was never below a measured 7.5 m and estimated to be 10–15 m on average (maximum estimated at 33 m).

The six vessel-reefs used in this study were intentionally deployed in the sand flat that separates the middle and outer reefs at approximately 20–25 m water depth (Fig. 1). The width of this sandy substrate and subsequent distance between middle and outer reef varies from 325 m to 350 m. The six vessel-reefs varied in size, vertical relief, horizontal orientation, vessel type, deployment date, and proximity to middle and outer reef terraces (Table 1). All vessel-reefs were approximately 1.80 km from shore.

During a 13-month (March 2000 to March 2001) and 12-month period (March 2002 to February 2003) SCUBA divers used a non-destructive visual census method, commonly called a point-count, to determine species richness and abundance at vessel-reefs and nearby natural reefs (Bohnsack & Bannerot, 1986). Each vessel-reef was censused at least four times during the year, two vessel-reefs per month. The census of the adjacent natural reef occurred at irregular time intervals throughout the first 13 months but concurrent with vessel-reef censuses during the second year of the study.

action varied by season with the heaviest seas occurring during winter months (January–March). Fish surveys were conducted in currents that ranged from calm to a maximum speed estimated at 2.0 knots. Current direction usually flowed

Table 1 Location and physical characterization of vessel-reefs

	Unnamed Barge	Edmister	Scutti	Tracy/Vitale	Merci Jesus	McAllister
Latitude	26 08.520 N	26 09.193 N	26 09.520 N	26 09.573 N	26 09.635 N	26 10.185 N
Longitude	80 04.886 W	80 04.837 W	80 04.777 W	80 04.754 W	80 04.747 W	80 04.707 W
Vessel type	Barge	USCG Cutter	Tugboat	Freighter	Freighter	Tugboat
Deployment date (month/year)	c1970	12/89	09/86	03/99	08/98	06/98
Depth (m)	21.3	21.3	19.5	19.5	19.5	21.0
Distance to outer reef terrace (m)	208	223	212	185	160	193
Distance to middle reef terrace (m)	135	102	142	162	180	180
Length (m)	24	28.5[a]	29	40	27	25.5
Maximum vertical relief (m)	3.0	3.0	9.0	8.1	5.4	6.9
Estimated volume (m^3)	706	588	1208	861	556	623
Orientation	E/W[b]	N/S[b]	N/S[b]	NE/SW[b]	NW/SE[b]	NW/SE[b]

[a] Length at time of deployment

[b] Direction of bow

The census methodology used was a point-count of fishes in an imaginary 15 m diameter cylinder, extending from the substrate to the surface, providing a 176.63 m^2 footprint. The published methodology has the diver remaining in the center of the cylinder during the census (Bohnsack & Bannerot, 1986). Due to the extensive topographical relief associated with vessel-reefs, we modified this aspect of the methodology to allow the diver to swim freely within the cylinder during the census.

The diver recorded all species seen during a five-minute period. After the five-minute species count was completed, the abundance of each fish species and the minimum, maximum and mean total length were recorded to the nearest cm. A 7.5 m radius line was laid out prior to the count as an aid in estimating the cylinder boundary and the diver used a 1-m rod with a ruler attached at one end in a T-configuration to aid in length estimation.

The bow, stern, port and starboard sides were censused on five of the six vessel-reefs to obtain a mean estimate of the ship's fish assemblage per count. Two additional mid-ship counts were performed at the sixth vessel-reef (*Edmister*) due to its high complexity and extensive footprint. A total of 218 point-counts were made on vessel-reefs over the study period.

A concurrent study, also using the point-count method, counted fishes on the natural reefs of Broward County. This concurrent study inventoried the fishes on East–West running transects every 463 m along the coastline of Broward County. On each transect a point-count was made at the eastern and western edges, as well as the crest of each reef terrace (for details on methodology see Ferro et al., 2005). Ten transects were made in the vicinity of the vessel-reefs censused in this study from 2000 to 2001 (Table 1). Therefore, we have also included data from the edges of the reef terraces that border the vessel-reefs. Specifically, 10 point-counts on the eastern edge of the middle reef and 10 counts from the western edge of the outer reef are included, for a total of 32 natural reef counts during the first year (Fig. 1). During the second year of this study we performed an additional 29 counts at neighboring natural reefs. Only edge data nearest the vessel-reefs were included because of their close prox-

imity and the fact that the edges have the most complex habitat and hold the most species and total fish of reef tract sites (Ferro et al., 2005). The assumption is, if adult fishes are moving between natural and artificial reefs, or being aggregated from natural to artificial reefs, they will most likely come from neighboring sites. Also, comparing neighboring reef areas of high topographical relief and large numbers of fishes to vessel-reefs also showing these characteristics is probably a more realistic comparison than those incorporating low relief hardbottom.

Data analysis

Prior to analysis, the estimated biomass and trophic preference of each species was determined (Froese & Pauly, 2004). Total length (TL) estimates allowed for post-census calculation of biomass using length-weight equations (Bohnsack & Harper, 1988). Fishes were classified according to their predominant trophic ecology as follows: planktivores, herbivores, piscivores, benthic carnivores, and omnivores (see Electronic Supplementary Material). The tomtate, *Haemulon aurolineatum* (Cuvier), is generally a nocturnal benthic carnivore as an adult, but both juveniles and adults commonly feed diurnally on vessel-reef planktonic prey items (personal observation). We have characterized the trophic ecology of this species as a benthic carnivore for analysis.

Fish abundance, biomass, species richness and trophic preference were examined using a mixed model analysis of variance (ANOVA) technique and a post-hoc Tukey–Kramer (TK) comparison of means per count using SAS V9.1 software (SAS Institute Inc., Cary, NC, USA). A probability value of less than 0.05 in both ANOVA and TK was accepted as a significant difference. The data that were not normally distributed and had high heteroscedasticity (i.e. abundance and biomass) were log-transformed [$\log_{10} (x + 1)$] prior to analysis (Zar, 1996)

An MDS using Bray–Curtis dissimilarity indices, an examination of similarity percentages of particular species (SIMPER) and analysis of similarity (ANOSIM) were used to examine potential differences in fish assemblage structure among sites (Field et al., 1982) using the Plymouth

Routines in Multivariate Ecological Research statistical package (PRIMER v5).

Results

Abundance

A total of 114,252 fishes was counted on natural and vessel-reefs combined (59,467 during the first sample period, 54,785 during the second). There was no statistical difference in abundance between the two sample periods, so they were pooled for subsequent analyses. With all vessel-reefs combined there were no statistical differences among months. Likewise, no differences were detected among months for natural reefs when the two edges were combined ($P > 0.05$, ANOVA). There was significantly greater mean fish abundance per count on vessel-reefs than natural reefs combined (Table 2) and the east edge of the middle terrace (Mean ± SE, 154.55 ± 22.46) was significantly greater than the west edge of the outer terrace (82.40 ± 6.30) ($P < 0.05$, ANOVA). No differences were found when comparing the abundance of individual vessel-reefs.

The abundance of individual species observed on natural and vessel-reefs is presented in Electronic Supplementary Material. The 10 most abundant species represented 79% of the total fish abundance on vessel-reefs and 64% on natural reefs. The most abundant species on all vessel-reefs combined was *H. aurolineatum*, which made up 53% of the total haemulid abundance. This species was the most abundant

species on the *Edmister*, *Tracy/Vitale*, and *Scutti* (excluding *Haemulon* juveniles). The most abundant species on the *McAllister*, *Merci Jesus* and the *Unnamed Barge* were the round scad, *Decapterus punctatus* (Cuvier), bluehead wrasse, *Thalassoma bifasciatum* (Bloch), and masked goby, *Coryphopterus personatus* (Gill), respectively. The most abundant species on all natural reefs combined was the bicolor damselfish, *Stegastes partitus* (Poey).

The most abundant family on all vessel-reefs combined was the grunts (Haemulidae), which comprised 46% of total vessel-reef fish abundance. Haemulidae was the most abundant family on all vessel-reefs except the *McAllister* (where carangids were most abundant) and the *Merci Jesus* (where labrids were most abundant). There were significantly more *H. aurolineatum* on vessel-reefs than natural reefs ($P < 0.05$, ANOVA) (see Electronic Supplementary Material). In addition, there were significant differences in *H. aurolineatum* abundance among individual vessel-reefs with the *Unnamed Barge* (34.17 ± 27.80) having the lowest abundance compared to all other vessel-reefs, and the *Edmister* (170.44 ± 30.27) having a higher abundance than the *Merci Jesus* (51.25 ± 10.86) ($P < 0.05$, ANOVA, TK).

The most abundant family on natural reefs was the wrasses (Labridae), which accounted for 25% of the total fish abundance. The dominant labrid species was *T. bifasciatum*, which represented 52% of the total wrasse abundance. *T. bifasciatum* was significantly more abundant on vessel-reefs than natural reefs ($P < 0.05$, ANOVA) (see Electronic Supplementary Material). There was also a significant difference among vessel-

Table 2 Mean ± SEM per count of fish abundance, biomass and species richness between vessel- and natural reefs and among individual vessel-reefs (within a column, sites with differing subscript numbers or letters are significantly different (P 0.05, ANOVA, TK))

Site	n	Abundance	Biomass (kg)	Richness
Vessel-reefs	218	$490.80 \pm 38.70_1$	$31.71 \pm 3.04_1$	$21.51 \pm 0.28_1$
Natural reefs	61	$119.07 \pm 12.62_2$	$6.37 \pm 0.60_2$	$20.13 \pm 0.58_2$
Edmister	54	518.72 ± 98.50	39.49 ± 6.60	$22.15 \pm 0.60_A$
McAllister	32	805.53 ± 149.00	56.79 ± 10.77	$21.50 \pm 0.76_{AB}$
Merci Jesus	32	317.16 ± 28.43	27.75 ± 6.24	$20.88 \pm 0.58_{AB}$
Scutti	32	426.16 ± 48.92	15.27 ± 2.53	$22.25 \pm 0.58_{AB}$
Tracy/Vitale	32	383.09 ± 76.90	35.72 ± 9.64	$18.53 \pm 0.74_B$
Unnamed Barge	36	500.25 ± 77.35	14.60 ± 2.26	$23.14 \pm 0.58_A$

reefs. The *Edmister* (17.44 ± 1.88) had a lower *T. bifasciatum* abundance than all other vessel-reefs ($P < 0.05$, ANOVA, TK).

Twenty-six percent of the total vessel-reef abundance was classified as juveniles (mean size ≤ 5 cm TL) and 58% of the total juveniles belonged to the family Haemulidae. The mean abundance of juvenile haemulids was found to be significantly greater on vessel-reefs when compared to previous results of fish counts performed on all three local reef terraces (inshore, middle and outer) ($P < 0.05$, ANOVA, TK) (Fig. 2) (Ferro et al., 2005). Eighty percent of all juvenile haemulids were observed on two vessel-reefs, the *Edmister* (34%) and *Unnamed Barge* (46%). Natural reef fish assemblages were composed of 25% juveniles, of which 58% were bicolor damselfish.

Planktivores were most abundant on vessel-reefs, accounting for 53% of the total fish abundance and were statistically greater on vessel-reefs (60.11 ± 7.43) than natural reefs (15.01 ± 1.77) ($P < 0.05$, ANOVA), where they accounted for 27% of total abundance (Fig. 3). Planktivore abundance statistically differed among vessel-reefs with the *McAllister* (111.82 ± 28.43) ($P < 0.05$, ANOVA, TK) having a greater abundance than all vessel-reefs, except the *Unnamed Barge* (77.66 ± 17.12) ($P > 0.05$, ANOVA, TK).

Benthic carnivores accounted for 38% of the total fish abundance on both natural and vessel-reefs, but were significantly greater on vessel-reefs (23.10 ± 2.25) than on natural reef (4.46 ± 0.53) ($P < 0.05$, ANOVA) (Fig. 3). There were significantly more benthic carnivores on the *Edmister* (27.75 ± 3.64) than all other vessel-reefs and the lowest abundance was found on the *Unnamed Barge* (8.41 ± 4.48) ($P < 0.05$, ANOVA, TK).

Herbivores represented 13% of the total natural reef fish abundance and 2% of the total vessel-reef fish abundance. Natural reef herbivore abundance (4.68 ± 0.35) was significantly greater than vessel-reefs (3.29 ± 0.19) ($P < 0.05$, ANOVA) (Fig. 3). Significant differences occurred with regard to time of vessel-reef deployment with the oldest vessel-reef, the *Unnamed Barge*, harboring more herbivores than all other vessel-reefs ($P < 0.05$, ANOVA, TK). Omnivores represented 21% of total fish abundance on natural reefs and 4% on vessel-reefs; however, there was no significant difference between the two ($P > 0.05$, ANOVA) (Fig. 3).

Piscivores represented 4% of the total vessel-reef fish abundance and 1% of the total natural reef fish abundance. Vessel-reef piscivore abundance (5.94 ± 0.53) was significantly greater than natural reefs (1.45 ± 0.11) ($P < 0.05$, ANOVA) (Fig. 3). There were also significant differences among vessel-reefs with the *McAllister* (7.59 ± 1.14) having more piscivores than the *Scutti* (3.57 ± 0.41) and the *Unnamed Barge* (6.40 ± 1.56) ($P < 0.05$, ANOVA, TK).

Fig. 2 Mean abundance ± SEM per count of juvenile *Haemulon* spp. Means with differing letters are statistically different ($P < 0.05$, ANOVA, TK) (n = number of counts performed at each reef, (f = number of times *Haemulon* sp. were observed)
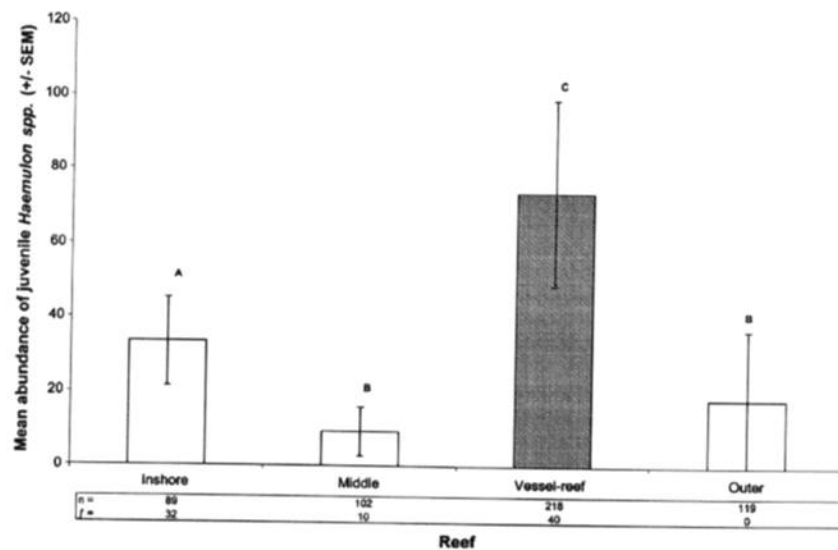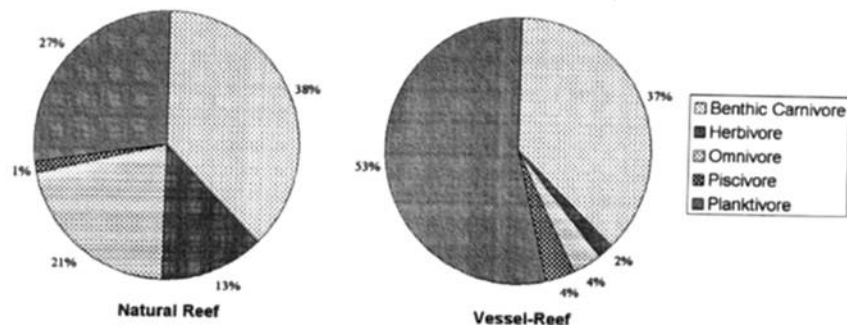
Fig. 3 Trophic composition as a percent of total fish abundance on vessel- and natural reefs

The importance of each species to fisheries (recreational and commercial) was determined by utilizing Florida's recreational and commercial regulations, as well as criteria from Bohnsack et al. (1994). The abundance of fisheries-important species was compared between natural and vessel-reefs. Vessel-reefs had a significantly greater abundance (38.90 ± 4.40) than natural reefs (6.40 ± 1.81), with both reefs having *H. aurolineatum* as the most abundant fisheries-important species ($P < 0.05$, ANOVA). Forty-eight percent of the total fish abundance on vessel-reefs was categorized as fisheries-important species. The majority of these fisheries-important species were comprised of the families Haemulidae (64%), Carangidae (25%), and Lutjanidae (9%). Sixteen percent of the total fish abundance on natural reefs was categorized as fisheries-important species. The majority of these fisheries important species were comprised of the families Haemulidae (66%), Serranidae (6%) and Labridae (5%).

The surrounding natural reefs censused in this study were compared to the results of previous research (Ferro et al., 2005), which assessed natural reefs with no artificial structures nearby. There was no significant difference in mean species richness between natural reefs surrounding vessel-reefs (20.13 ± 0.58) and natural reefs with no artificial structures nearby (20.00 ± 0.71). Additionally, mean fish abundance at natural reef sites surrounding vessel-reefs (119.07 ± 12.62), was not significantly different from natural reef areas with no artificial structures nearby (118.57 ± 8.38) (Ferro et al., 2005). Furthermore, there was no statistical difference in the abun-

dance of fisheries-important species between these two areas.

Biomass

The mean vessel-reef biomass per count was significantly greater than natural reefs ($P < 0.05$, ANOVA) (Table 2). There were also significant differences in biomass among vessel-reefs with the *McAllister* having greater biomass than the *Scutti*, *Tracy/Vitale*, or *Unnamed Barge* ($P < 0.05$, ANOVA, TK) (Table 2). Excluding the natural reefs but with all vessel-reefs combined there was a difference among months, with February (68.76 ± 19.49) having a higher mean biomass per count than July (28.35 ± 16.48) ($P < 0.05$, ANOVA, TK). No difference in biomass was noted among months for natural reef sites.

Species richness

A total of 106,989 fishes of 159 species from 43 families was recorded from the 218 point-counts on all vessel-reefs combined. The most speciose families were groupers (Serranidae: 18 species), parrotfishes (Scaridae: 12 species) and damselfishes (Pomacentridae: 12 species). Together these three families comprised 26% of the vessel-reef species pool. There were 58 species, which were found exclusively on vessel-reefs.

On natural reefs, 7,263 fishes of 118 species were recorded in 61 point-counts. A total of 35 families was recorded on natural reefs. The most speciose families were groupers (Serranidae: 15 species), parrotfishes (Scaridae: 11 species) and damselfishes (Pomacentridae: 11 species).

Together these three families comprised 31% of the natural reef species pool. Fifty-eight species were found exclusively on natural reefs.

Although the east edge of the middle reef had significantly greater mean species richness per count (22.16 ± 0.79) than the west edge of the outer reef (18.03 ± 0.68), there were significantly more species on vessel-reefs than both natural reef areas combined ($P < 0.05$, ANOVA) (Table 2). There were also differences in species richness among vessel-reefs with the *Tracy/Vitale* having significantly lower species richness than the *Edmister* and *Unnamed Barge* (Table 2). Furthermore, there was a linear relationship between mean species richness and vessel-reef age ($R^2 = 0.06$, $P < 0.05$) (Fig. 4). No difference was noted in species richness between months on all vessel-reefs combined.

Of the 159 species recorded on vessel-reefs, 58 were not found on natural reefs and were exclusive to artificial reefs. In this study, 16 (28%) of the exclusive species on vessel-reefs were only recorded once and can be considered rare. On natural reefs 18 of the 118 species recorded were not observed on vessel-reefs. Ten (56%) of these

exclusive species were observed only once (see Electronic Supplementary Material).

Assemblage structure

The results of the multidimensional scaling (MDS) showed distinct differences in fish assemblage structure between natural and vessel-reefs with little overlap (Fig. 5). The ANOSIM comparing natural and vessel-reefs produced an R-statistic of 0.718, supporting the MDS showing distinct fish assemblages between the reef types (Field et al., 1982). Further separation clearly reveals individual differences among vessel-reefs, with the *Unnamed Barge* and *Edmister* fish assemblages clearly distinct from the remaining cluster of vessel-reefs (Fig. 6). Here again, the ANOSIM R-statistic supported our findings with the highest R-values associated with comparisons between both the *Unnamed Barge* and *Edmister* with all other vessel-reefs combined. Also an R-statistic of 0.748 was produced when comparing the *Unnamed Barge* to the *Edmister*, indicating that, even though the fish assemblages at these
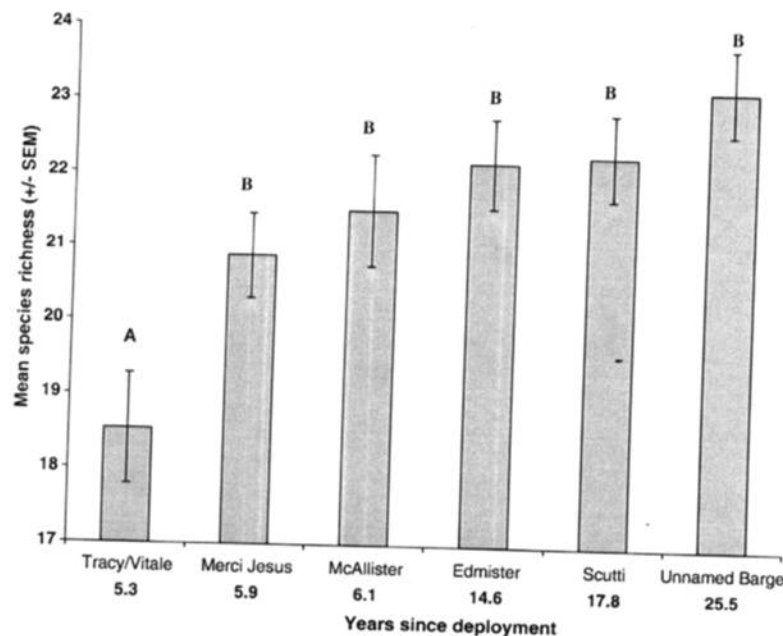

Fig. 4 Mean species richness ± SEM per count for vessel-reefs of various ages. Means with differing letters are statistically different ($P < 0.05$, ANOVA, TK)
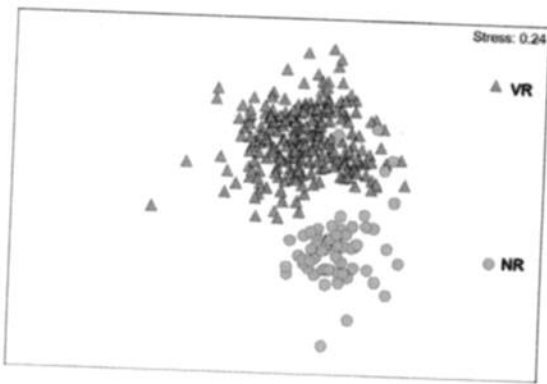
Fig. 5 MDS plot of Bray–Curtis dissimilarity indices of vessel- and natural reefs. VR = vessel-reef; NR = natural reef
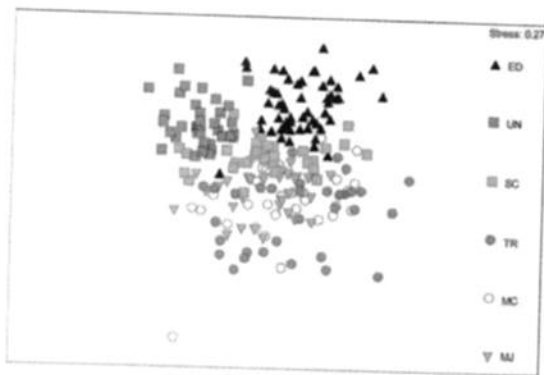

Fig. 6 MDS plot of Bray–Curtis dissimilarity indices of individual vessel-reefs. ED = *Edmister*, UN = *Unnamed Barge*, SC = *Scutti*, TR = *Tracy/Vitale*, MC = *McAllister*, and MJ = *Merci Jesus*

two vessel-reefs were quite distinct from all other vessel-reefs, they were also very different from each other.

The SIMPER analysis revealed the species contributing most to the differences indicated by the MDS plots. There was a 74% dissimilarity found between natural and vessel-reefs with *H. aurolineatum* contributing more to the dissimilarity (6.05%) than any other species (Table 3). The SIMPER analysis comparing individual vessel-reef fish assemblages to all natural reefs combined revealed the *McAllister* had the highest dissimilarity (77%) and the *Unnamed Barge* (71%) had the lowest. When individual vessel-reefs were compared to each other, the highest dissimilarity (69%) was found when comparing the oldest vessel-reef (*Unnamed Barge*) to the youngest (*Tracy/Vitale*).

Discussion

Most artificial reef research has shown artificial reefs have greater fish abundance and biomass than natural reefs with similar community structures (see Bohnsack et al., 1991). In this study there was a mean of 154.55 ± 22.46 individuals on the eastern edge of the middle terrace, 82.40 ± 6.30 on the western edge of the outer terrace and 490.80 ± 38.70 on vessel-reefs. The lower numbers on natural reefs were apparently not a function of a lower sampling frequency, which missed a period of increased abundance. A previous study in Broward County, also using point-counts, reported mean abundances of 108.00 ± 49.00 and 75.00 ± 16.00 on the eastern middle terrace and western outer terrace edges, respectively (Ferro et al., 2005). Additionally, the comparison between natural and vessel-reefs

Table 3 SIMPER percentages of the top 10 species contributing most to the differences between vessel- and natural reefs

Common name	Scientific name	Dissimilarity (%)	Cumulative dissimilarity (%)
Tomtate	*Haemulon aurolineatum*	6.05	6.05
Mask Goby	*Coryphopterus personatus*	4.18	10.23
Purple Reeffish	*Chromis scotti*	3.70	13.93
Yellowhead Wrasse	*Halichoeres garnoti*	3.13	17.06
Bicolor Damselfish	*Pomacentrus partitus*	3.05	20.11
Creole Wrasse	*Clepticus parri*	3.00	23.12
Bluehead Wrasse	*Thalassoma bifasciatum*	2.90	26.02
Grey Snapper	*Lutjanus griseus*	2.73	28.75
Tobacco Fish	*Serranus tabacarius*	2.41	31.16
Sharpnose Puffer	*Canthigaster rostrata*	2.23	33.38

provides insight into the aggregation hypothesis, which proposes that fishes on artificial reefs have been aggregated from nearby natural reefs. Because no differences in species richness or abundance were found between natural reef areas surrounding vessel-reefs and natural reefs with no artificial structures nearby (Ferro et al., 2005), it appears that vessel-reefs are not, in general, attracting fishes away from nearby natural reef areas. This conclusion is also supported by preliminary results from research studying fish colonization on a newly deployed vessel-reef in Broward County, which revealed that production, rather than strictly attraction, may be an important component contributing to vessel-reef fish assemblages (authors unpublished).

The differences in biomass, noted in this study, parallel the differences in abundance among vessel-reefs and between natural and vessel-reefs. This indicates the greater fish abundance on vessel-reefs is not due simply to large number of juveniles, as they typically weigh dramatically less than adults. This study supports the common finding of greater abundance of fishes on artificial reefs and the results of the MDS, SIMPER, and ANOSIM clearly indicate fish assemblage structure on vessel-reefs differ from nearby natural reefs.

While approximately 57% of the species recorded in this study were common to both natural and vessel-reefs, 58 species were unique to vessel-reefs. Some of these species were relatively rare (e.g., *Epinephelus itajara* (Lichtenstein), *Mycteroperca bonaci* (Poey)) noted only once or twice, and it is unclear if their presence represented a preference or simply chance occurrence (see Electronic Supplementary Material). However, some of the species unique to vessel-reefs in this study have never been recorded in natural reef surveys in Broward County (i.e. margates, *Haemulon album* (Cuvier); greater amberjack, *Seriola dumerili* (Risso); little tunny, *Euthynnus alletteratus* (Rafinesque); blackfin snapper, *Lutjanus buccanella* (Cuvier); snowy grouper, *Epinephelus niveatus* (Valenciennes); and a single 35 cm cubera snapper, *Lutjanus cyanopterus* (Cuvier)). The unique presence of the snapper and grouper fishes is particularly interesting, as they are typically deepwater species

of recreational and commercial value, which appear to prefer vessel-reefs to nearby natural habitats. Arena et al. (2004) reported that juveniles of both blackfin snapper (10–26 cm) and snowy grouper (10–15 cm) were recorded only on vessel-reefs throughout Broward County and noted that previous research had also observed juveniles of these species on smaller artificial reef modules at depths both comparable to and shallower than this study. The authors suggested vessel-reefs are supplying blackfin snapper and snowy grouper with ancillary nursery/juvenile habitat that may be in short supply in deeper areas, which has been described as low-relief hardbottom.

The red grouper, *Epinephelus morio* (Valenciennes), is one species important to fisheries that was unique to natural reefs in this study. This species has been observed on vessel-reefs in the Gulf of Mexico, an area with limited natural hardbottom habitat (J. Franks, personal communication, November 2003). This suggests that *E. morio* may utilize artificial reef structures in habitat limited areas, but prefer natural reefs when they are available. Past research has shown that some reef fishes at artificial reef sites have narrower diets than those found in natural areas due to the limited availability of food resources (Sierra et al., 2001). *E. morio* may prefer natural reef areas when they are present, due to greater, species-specific food availability in those habitats.

Polovina (1991) suggested in order for artificial reefs to increase production, they need to provide habitat that can improve larval settlement, growth, and survival. The high vertical relief of vessel-reefs may increase settlement of juveniles by extending habitat into areas higher in the water column, possibly attracting larval fishes located closer to surface waters (Rilov & Benayahu, 2002). Our results indicate there were significantly more juveniles on vessel-reefs, the majority of which were *Haemulon* spp., than any natural reef terrace in our area (Ferro et al., 2005) (Fig. 2). This is an interesting result as previous research has indicated that Broward County's shallow, inshore reef was important habitat for juvenile grunts, yet our results reveal a greater mean abundance of these juveniles on vessel-reefs (Jordan et al., 2004). Another study utilizing small

1 m relief artificial reefs deployed at similar depths (21 m) and in the same sand flat between the middle and outer reefs also recorded high densities of juvenile *Haemulon* spp. and may be an indication that high vertical relief is not a requirement for all fish species (Sherman, 2000). The majority of *Haemulon* juveniles (80%) were recorded on two particular vessel-reefs, 34% on the *Edmister* and 46% on the *Unnamed Barge*. These two vessel-reefs have the lowest vertical relief (3 m) and a high amount of complexity near the seafloor, which may have increased the survival of juvenile grunts. These results suggest a possible settlement preference by *Haemulon* larvae for complex structures near the seafloor, which may enhance juvenile grunt survival and growth. This suggestion is supported by the fact that larval grunts have rarely been collected near the surface (Richards, 1981), indicating they may be epibenthic.

Although there were some species completely absent from the vessel-reefs and others absent from natural reefs, the dissimilarity in assemblage structure between natural and vessel-reefs was primarily due to differences in abundance of species common to both. *H. aurolineatum*, contributed the most to the dissimilarity between natural and vessel-reefs and was also a top contributor to differences seen among vessel-reefs. *H. aurolineatum* is one of the most abundant fish on reefs, live bottom areas and inshore habitats in the Greater Caribbean, Gulf of Mexico, and along the southeast Atlantic coast of the United States (Darcy, 1983). Juveniles are primarily diurnal planktivores; as they grow and mature they shift their feeding, in large measure, to open sand and seagrass beds, where they forage for benthic invertebrates (Darcy, 1983; Sedberry, 1985).

Due to their ubiquity and high abundance, *H. aurolineatum* may be important in transferring energy, from the sandy substrate adjacent to reef areas, to hardbottom habitat and artificial reef communities (Darcy, 1983; Meyer et al., 1983; Sedberry, 1985). Lindquist et al. (1994) speculated sandbottom benthic productivity might be more important than previously thought in supporting the nekton on the continental shelf. Additionally, *H. aurolineatum* are known to be

prey for many recreationally and commercially important species, such as groupers, snappers and jacks (Darcy, 1983; Froese & Pauly, 2004). The mean size of *H. aurolineatum* on all vessel-reefs combined was 16.0 cm TL, with the maximum and minimum size recorded as 26.0 and 3.0 cm, respectively. At a mean size of 16.0 cm these fish should primarily be nocturnal feeders searching for sand dwelling invertebrates (Manooch & Barans, 1982; Sedberry, 1985), although due to the range of sizes recorded and observations of feeding behavior on vessel-reefs, these fish were also utilizing planktonic resources.

The optimal foraging theory predicts that *H. aurolineatum*, as well as most haemulids, will utilize habitats in close proximity to soft bottom feeding areas to reduce the amount of energy spent on travel between resting and foraging sites (Stephens & Krebs, 1986). *H. aurolineatum* are typically found in shelf-edge habitats, near areas of bottom relief and at the edge of rock ledges protruding into the sand (Manooch & Barans, 1982; Darcy, 1983; Sedberry, 1985). Vessel-reefs seem to be providing this species with similar habitat characteristics. The vessel-reef habitat provides shelter and resting sites within their natural foraging areas decreasing energy expenditures and risk of predation associated with travel to these sites. In addition, the ability of *H. aurolineatum* to feed diurnally in the plankton, presumably makes vessel-reefs even more advantageous to this species, which may, in turn, increase its growth rate and ultimately its fitness. *H. aurolineatum* has been shown to grow faster than many previously studied reef fishes from the South Atlantic Bight (Darcy, 1983). This exhibition of increased growth may be due to its ability to take advantage of both planktonic and benthic food resources.

Another major difference between fish assemblages on natural and vessel-reefs is the abundance of planktivores, the dominant trophic group on vessel-reefs. Of the top 10 species by mean abundance on vessel-reefs, seven were planktivores and accounted for 50.80% of the total vessel-reef fish abundance (see Electronic Supplementary Material). In contrast, only three of the top 10 species by mean abundance on natural reefs were planktivores, accounting for

22% of the total natural reef fish abundance. In addition, the SIMPER analysis showed that four of the top seven species (*C. personatus*, *Chromis scotti* (Emery), *Clepticus parrae* (Bloch & Snyder), *T. bifasciatum*] contributed most to the dissimilarity (13.48%) between natural and vessel-reefs were planktivores, with a fifth (*H. aurolineatum*) that feeds secondarily in the plankton (Table 3).

These results are comparable to previous studies utilizing artificial reefs with high vertical relief. Rilov & Benayahu (2000) reported the two most numerous species found on oil jetty platforms were planktivores. Linquist & Pietrafesa (1989) conducted a study that assessed fish assemblages on a tugboat with 8.3 m of vertical relief. They reported the two most abundant species on these structures were planktivores. Additionally, Stephan & Lindquist (1989) reported that planktivores dominated the fish assemblage on a dredge and FADS, with 6 and 14.7 m of vertical relief, respectively. Plankton productivity has been shown to be greatest within the top 30 m of the water column and it has been suggested that artificial reefs with high vertical relief allow the upper portion of the structure to interact with these planktonic resources closer to the surface (Rilov & Benayahu, 2000). However, artificial reefs with low vertical relief have also been shown to have a high abundance of planktivores in comparison to natural reefs (Bohnsack et al., 1994). This suggests that vertical relief may not be the only factor influencing planktivores.

Location of the artificial reef may also be an important influence on planktivore production. Diurnal planktivores depend on currents to supply food. Larger diurnal planktivores are known to move from nocturnal resting sites to diurnal feeding sites with strong currents near the shelf edge (Hobson, 1991). The vessel-reefs in this study were located between two continuous reef terraces that run in a N–S direction. The sand flat separating these reefs offers an uninterrupted current flow. Conversely, at natural reef sites, the passing currents and associated plankton are exposed to a 'wall of mouths' upstream, which can dramatically deplete plankton downstream (Hamner et al., 1988) (Fig. 1). Vessel-reefs in this study provide habitat relatively unexposed to

upstream planktivores, and this may, in turn, allow resident planktivores access to more planktonic resources. Thus, planktivores, may be using the upper works of vessel-reefs to access an abundant and unexploited food resource.

Donaldson & Clavijo (1994) have suggested holozooplankton are currently underutilized as a food resource by many planktivorous fishes due to the lack of shelter from predation on open sand bottoms. Although planktonic resources or diets of planktivores were not censused here, the vessel-reefs may provide these fishes with shelter they need to access these resources that would be otherwise unavailable. Vessel-reefs not only provide planktivores with shelter from predation, but also from strong currents and passing internal waves (Grove & Sonu, 1985; Grove et al., 1991).

In addition to shelter, vessel-reef habitat may entrain planktonic resources, further increasing planktivore feeding efficiency. Lindquist & Pietrafesa (1989) suggested an upcurrent vortex reversal at vessel-reefs concentrates planktonic resources, and also reduces the amount of energy required to swim against the incoming current flow. Our experience supports this suggestion. For example, during one census at the *Unnamed Barge*, a school of brown chromis, *Chromis multilineata* (Guichenot), was observed feeding on plankton on the upcurrent side of the vessel-reef during a strong current flow. The first author swam over to their location and instantly noticed a reduction in current flow and maintained his position with little effort.

The abundance of planktivores on vessel-reefs can provide direct trophic links from open-water to coral reef communities through two main avenues. First, energy can be transferred to both demersal and pelagic piscivores, which utilize planktivores as prey. Although no studies on diet were performed, the statistically higher abundance of piscivores on vessel-reefs and repeated observations of predatory behavior by these fishes, as well as documentation of their prey items, indicate they are likely feeding on planktivores (Froese & Pauly, 2004). Additionally, demersal piscivores, such as lutjanids, at vessel-reefs may also be preying upon planktivores.

A second energy transfer is through planktivore feces, not only to detritivores, but also to

other planktivorous fishes. Robertson (1982) reported that many fecal strings from planktivores are devoured by other species of fishes before they reach the bottom. The feces of some planktivores can be a valuable resource, especially when zooplankton is abundant. Hobson (1991) observed zooplankton passing through the guts of planktivores so rapidly that very little signs of digestion were observed in the feces. The majority of energy derived from planktonic resources may have not been utilized and would possibly be swept away with the current if vessel-reef habitats were unavailable (Hamner et al., 1988). Also, when planktivores return to their vessel-reef resting sites they continue to defecate and these added nutrients may enhance the production of vessel-reef benthic communities. Past research has shown corals that harbor large schools of fishes grow faster, presumably due to the constant influx of nutrients from fish feces (Meyer et al., 1983).

While distinct fish assemblages on vessel-reefs exist, the results suggest that as vessel-reef age increases they become more similar to surrounding natural reef assemblages. The SIMPER analysis comparing individual vessel-reefs to natural reefs showed the oldest vessel-reef, *Unnamed Barge*, was most similar (29%) to nearby natural reef fish assemblages. The *Unnamed Barge* had low vertical relief (3 m), possibly reducing the abundance of planktivores on that vessel-reef, thereby making it more similar to the natural reef assemblage. However, comparisons of planktivore abundance among vessel-reefs revealed the *Unnamed Barge* planktivore abundance was not significantly different from the *McAllister*, which had the greatest planktivore abundance of all vessel-reefs. Additional results revealed a strong positive linear relationship ($R^2 = 0.86$) between mean species richness and vessel-reef age (Fig. 4). These findings may be due to increased food resources and substrate complexity, provided by a richer fouling community on older vessel-reefs, and/or additional recruits that colonized vessel-reefs over time (Chandler et al., 1985; Potts & Hulbert, 1994; Tupper & Hunte, 1998).

Lastly, an important distinction between natural and vessel-reefs can be clearly seen when comparing fish species of recreational or commercial value. Vessel-reefs were found to have significantly more fisheries-important species than nearby natural reefs. The majority of vessel-reef fisheries-important species were comprised of the families Haemulidae (64%), Carangidae (25%), and Lutjanidae (9%). While the most abundant species overall was the tomtate, there were many more fisheries-important species, such as gray snapper, blackfin snapper, lane snapper, and amberjacks; all more abundant on vessel-reefs than natural reefs. These results indicate that vessel-reef habitats provide important contributions to local fishery resources.

Conclusions

This study supports the results of previous research indicating artificial reefs harbor a greater fish abundance, including fisheries-important species, and biomass than natural reef areas. Greater species richness, as well as the many exclusive species on vessel-reefs, suggests these artificial reef types are providing unique habitat characteristics, which may not be found on surrounding natural reefs. Additionally, the comparisons between natural and vessel-reef fish assemblages do not support the aggregation hypothesis and may be an indication that fish production is occurring on vessel-reefs in Broward County. However, we cannot discount the possibility that large demersal fishes, such as serranids, which have been overexploited in our study area, may be attracted to vessel-reefs in other areas. In such a situation vessel-reefs would contribute to overexploitation of some species. Acoustic telemetry, diet and growth studies, as well as estimates of fishing pressure of specific vessel-reef species, would help determine the effects vessel-reefs are having on natural reef fish assemblages.

References

Arena, P. T., T. P. Quinn, L. K. B. Jordan, R. L. Sherman, F. M. Harttung & R. E. Spieler, 2004. Presence of juvenile blackfin snapper, Lutjanus buccanella, and snowy grouper, Epinephelus niveatus, on shallow-water artificial reefs. Proceedings of the Fifty-fifth Gulf and Caribbean Fisheries Institute 55: 700–712.

Bohnsack, J. A. & S. P. Bannerot, 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. U.S. Dept. of Commerce, NOAA Technical Report NMFS 41: 1–15.

Bohnsack, J. A. & D. E. Harper, 1988. Length–weight relationship of selected marine reef fishes from southeastern United States. NOAA Technical Memorandum NMFS-SEFC. U.S. Dept. of Commerce.

Bohnsack, J. A., D. L. Johnson & R. F. Ambrose, 1991. Ecology of artificial reef habitats and fishes. In Seamen, W. & L. M. Sprague (eds), Artificial Habitats for Marine and Freshwater Fisheries. Academic Press, San Diego, 61–108.

Bohnsack, J. A., D. E. Harper, D. B. McClellan & M. Hulsbeck, 1994. Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off Southeastern Florida, USA. Bulletin of Marine Science 55: 796–823.

Brock, R. E., 1994. Beyond fisheries enhancement: artificial reefs and ecotourism. Bulletin of Marine Science 55: 1181–1188.

Chandler, C. R., R. M. Sanders Jr. & A. M. Laundry Jr., 1985. Effects of three substrate variables on two artificial reef fish communities. Bulletin of Marine Science 37: 129–142.

Darcy, G. H., 1983. Synopsis of biological data on the grunts Haemulon aurolineatum and H. plumieri (Pisces: Haemulidae). FAO Fisheries Synopsis No. 133, NOAA Technical Report NMFS Circular 448. 37 pp.

Donaldson, P. L. & I. E. Clavijo, 1994. Diet of Round Scad (Decapterus punctatus) on a natural and artificial reef in Onslow Bay, North Carolina. Bulletin of Marine Science 55: 501–509.

Ferro, F. M., L. K. B. Jordan & R. E. Spieler, 2005. Spatial variability of the coral reef assemblages offshore Broward County, Florida. NOAA Technical Memorandum NMFS-SEFSC-532.

Field, J. G., K. R. Clarke & R. M. Warwick, 1982. A practical strategy for analyzing multispecies distribution patterns. Marine Ecology Progress Series 8: 37–52.

FAO (Food and Agriculture Organization), 1997a. Review of the state of the world fishery resources: marine fisheries. FAO Fisheries Circular 920, Rome, Italy.

FAO (Food and Agriculture Organization), 1997b. Review of the state of world fisheries and aquaculture: 1996. FAO, Rome, Italy .

Froese, R. & D. Pauly (eds), 2004. FishBase. World Wide Web electronic publication. www.fishbase.org, 06 April 2004.

FWRI (Fish and Wildlife Research Institute), 2004. Recreational Fisheries. Retrieved September 17, 2004 from Florida Fish and Wildlife Conservation Commission website: http://research.myfwc.com/support/view_faqs.asp?id = 25.

Gilmore, C., 2004. PADI Diver Statistics. Retrieved March 15, 2004: http://www.padi.com/english/common/padi/statistics/.

Goldberg, W. M., 1973. The ecology of the coral–octocoral communities off the southeast Florida coast: geomorphology, species composition, and zonation. Bulletin of Marine Science 23: 465–488.

Goreau, T. F., 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. Ecology 40: 67–90.

Grove, R. S. & C. J. Sonu, 1985. Fishing reef planning in Japan. In D'itri, F. M. (ed.), Artificial Reefs: Marine and Freshwater Applications. Lewis Publishers, Michigan, 187–252.

Grove, R. S., C. J. Sonu & M. Nakamura, 1991. Design and engineering of manufactured habitats for fisheries enhancement. In Seamen, W. & L. M. Sprague (eds), Artificial Habitats for Marine and Freshwater Fisheries. Academic Press, San Diego, 109–153.

Hamner, W. M., M. S. Jones, J. H. Carleton, I. R. Hauri & D. M. Williams, 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bulletin of Marine Science 42: 459–479.

Hobson, E. S., 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In Sale, P. F. (ed.), The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, 69–95.

Jordan, L. K. B., P. T. Gilliam, D. S., R. L. Sherman, P. T. Arena, F. M. Harttung, R. M. Baron & R. E. Spieler, 2004. Spatial and temporal patterns of juvenile grunts (Haemulon spp.) in South Florida. Proceedings of the Fifty-Fifth Gulf and Caribbean Fisheries Institute 55: 322–336.

Jones, R. S. & M. J. Thompson, 1978. Comparison of Florida reef fish assemblages using a rapid visual technique. Bulletin of Marine Science 28: 159–172.

Jones, A. T. & R. W. Welsford, 1997. Artificial reefs in British Columbia, Canada. OCEANS 97: MTS/IEEE, Artificial Reef Society of British Columbia pp. 415–418.

Lighty, R. G., 1977. Relict shelf-edge Holocene coral reef: southeast coast of Florida. Proceedings of the Third International Coral Reef Symposium, Vol. 2, 215–221.

Lindquist, D. G. & L. J. Pietrafesa, 1989. Current vortices and fish aggregations: the current field and associated fishes around a tugboat wreck in Onslow Bay, North Carolina. Bulletin of Marine Science 44: 533–544.

Lindquist, D. G., L. B. Cahoon, I. E. Clavijo, M. H. Posey, S. K. Bolden, L. A. Pike, S. W. Burk & P. A. Cardullo, 1994. Reef fish stomach contents and prey abundances on reef and sand substrata associated with adjacent artificial and natural reefs in Onslow Bay, North Carolina. Bulletin of Marine Science 55: 308–318.

MacDonald, C. D., C. A. Mitsuyasu & E. Corbin, 1999. A planned underwater dive attractions program for Hawaii. Ocean Resources Branch, State of Hawaii Department of Business, Economic Development and Tourism. Ocean Resources Branch Contribution No. 147, pp.180–187.

Manooch, C. S. & C. S. Barans, 1982. Distribution, abundance, and age and growth of the tomtate, Haemulon aurolineatum, along the southeastern United States coast. Fishery Bulletin 80: 1–19.

Markevich, A. I., 1994. Species composition and ecological characteristics of fishes of artificial shelters in Peter the Great Bay, Sea of Japan. Russian Journal of Marine Biology 20: 169–173.

Meyer, J. L, E. T. Schultz & G. S. Helfman, 1983. Fish schools: an asset to corals. Science 220: 1047–1049.

Moyer, R. P, B. Riegel, K. Banks & R. E. Dodge, 2003. Spatial patterns and ecology of benthic communities on a high latitude South Florida (Broward County, USA) reef system. Coral Reefs 22: 447–464.

Murray, J. D. & C. J. Betz, 1994. User views of artificial reef management in the Southeastern U.S. Bulletin of Marine Science 55: 970–981.

Polovina, J. J., 1991. Fisheries applications and biological impacts of artificial reefs. In Seamen, W. & L. M. Sprague (eds), Artificial Habitats for Marine and Freshwater Fisheries. Academic Press, San Diego, 154–176.

Potts, T. A. & A. W. Hulbert, 1994. Structural influences of artificial and natural habitats on fish aggregations in Onslow Bay, North Carolina. Bulletin of Marine Science 55: 609–622.

Richards, W. J., 1981. Kinds and abundance of fish larvae in the Caribbean Sea. In Lasker, R. & K. Sherman (eds), The Early Life History of Fish: Recent Studies. ICES, Woods Hole, 240–241.

Rilov, G. & Y. Benayahu, 2000. Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. Marine Biology 136: 931–942.

Rilov, G. & Y. Benayahu, 2002. Rehabilitation of coral reef-fish communities: the importance of artificial-reef relief to recruitment rates. Bulletin of Marine Science 70: 185–197.

Robertson, D. R., 1982. Fish feces as fish food on a Pacific coral reef. Marine Ecology Progress Series 7: 253–265.

Seamen, W. & A. C. Jensen, 2000. Purposes and practices of artificial reef evaluation. In Seamen, W. (ed.), Artificial Reef Evaluation: With Application to Natural Marine Habitats. CRC Press, Florida, 1–20.

Sedberry, G. R, 1985. Food and feeding of the tomtate, Haemulon aurolineatum (Pisces, Haemulidae), in the South Atlantic Bight. Fishery Bulletin 83: 461–466.

Sherman, R. L., 2000. Studies on the roles of reef design and site selection in juvenile fish recruitment to small reefs. Ph.D. Dissertation. Nova Southeastern University, 173 pp.

Sierra, L. M., R. Claro & O. A. Popova, 2001. Trophic biology of the marine fishes of Cuba. In Claro, R., K. C. Lindeman & L. R. Parenti (eds), Ecology of the Marine Fishes of Cuba. Smithsonian Institute Press, London, 115–148.

Soloviev, A. V., M. E. Luther & R. H. Weisberg, 2003. Energetic baroclinic super-tidal oscillations on the southeast Florida shelf. Geophysical Research Letters 30: np.

Stephan, C. D. & D. G. Lindquist, 1989. Comparative analysis of the fish assemblages associated with old and new shipwrecks and fish aggregating devices in Onslow Bay, North Carolina. Bulletin of Marine Science 44: 698–717.

Stephens, D. W. & J. R. Krebs, 1986. Foraging Theory. Princeton University Press, NJ, 247 pp.

Stone, R. B., 1985. History of artificial reef use in the United States. In D'itri, F. M. (ed.), Artificial Reefs: Marine and Freshwater Applications. Lewis Publishers, Michigan, 3–12.

Tupper, M. & W. Hunte, 1998. Predictability of fish assemblages on artificial and natural reefs in Barbados. Bulletin of Marine Science 62: 919–935.

White, D. J., 2004. Finding common water. Retrieved September 17, 2004 from Florida Wildlife Federation website: http://www.flawildlife.org/pubs/fwn-4-01/chair.htm.

Zar, J. H., 1996. Biostatistical Analysis. Prentice Hall, N.J. 662 pp.