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research paper

Fish assemblages on shipwrecks versus natural reefs in Colombo, Sri Lanka

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ABSTRACT.—Shipwrecks provide important habitats for reef fishes, but few studies have addressed how fish assemblages on wrecks compare to natural communities on nearby reefs in terms of species composition, diversity, richness, and density, particularly in the Indian Ocean. To fill this knowledge gap, we conducted standardized diver-operated video transect surveys on three shipwrecks and three nearby natural sandstone reefs in Colombo, Sri Lanka. The shipwrecks provided a habitat that is structurally more complex than the surrounding reefs. A total of 2918 fishes from 20 families and 30 genera were recorded, with 749 observed on reef sites and 2169 on the wrecks. A higher mean density of fishes was observed on wrecks [mean (SE) = 17.2 (5) per 125 m^2] than on natural reefs [11.9 (4) per 125 m^2]. This difference was predominantly due to the snappers (Lutjanidae), which tended to aggregate in large schools in and around wrecks and constitute a resource for local artisanal fisheries. Wrecks and natural reefs presented similar levels of diversity at the family and genus level and shared 86.7% of genera. They nonetheless showed significant differences in community composition at both the family and genus level. Higher abundances of snappers, cardinalfishes (Apogonidae), and fusiliers (Caesionidae) were recorded on wreck sites while the natural reefs presented higher abundances of damselfishes (Pomacentridae) and barracudas (Sphyraenidae). These results differ from previous similar studies, indicating that differences in fish communities between wrecks and natural reefs can be idiosyncratic. This study highlights the role of shipwrecks as artificial reef structures and their relevance for small-scale fisheries and SCUBA diving tourism.

The term *wreck* refers to the remains of a vessel that are partially or completely submerged by water as a result of accidents, acts of war or terrorism, or intentional sinking. The UNESCO Convention for Underwater Cultural Heritage estimated over three million shipwrecks exist worldwide. A key characteristic of shipwrecks is that they form a structurally complex habitat through their intricate designs, providing hard substrate for benthic organisms and diverse cave-like structures in the wreck's interior (Consoli et al. 2015, Meyer-Kaiser et al. 2022). Shipwrecks contribute to ecosystem processes, conservation, and socioeconomic activities by providing substrate for species recruitment (Consoli et al. 2015, Correia et al. 2020, Hamdan et al. 2021), limiting the use of nets for fishing (Muñoz-Pérez 2008, Kingsley 2010), or offering an attraction for recreational SCUBA diving (Shani et al. 2012).

Wrecks as artificial reef (AR) structures can be distinguished on the basis of their intentional versus unintentional deployment. The development of ARs to sustain marine communities and enhance fish productivity was motivated by the global loss of marine habitats and reef degradation (Stone et al. 1991, Seaman 2007). Regardless of whether ARs were deployed intentionally or unintentionally, they provide habitat as nursery grounds (Mercader et al. 2017) and food sources (Fabi et al. 2006, Dance et al. 2018), and support socioeconomic activities such as tourism (Stolk et al. 2007, Shani et al. 2012). Previous studies have highlighted a positive correlation between habitat complexity and biomass, abundance, and diversity of fishes (Roberts and Ormond 1987, Gratwicke and Speight 2005, Willis et al. 2005, Graham and Nash 2013). In this respect a relevant property of structurally complex habitats is that they provide refuge and shelter from predation (Hixon and Beets 1993, Almany 2004a), reduce competition for space within habitats (Almany 2004b), contribute to the upwelling of nutrients, and decrease wave energy impacts (Liu et al. 2013, Kim et al. 2014, Androulakis et al. 2020).

Studies have revealed higher fish abundance, biomass, and species richness on shipwrecks in comparison to surrounding habitats and highlighted the increased access to food resources and complex habitats on shipwrecks (Arena et al. 2007, Fowler and Booth 2012, Simon et al. 2013, Consoli et al. 2015, Sreekanth et al. 2019, Paxton et al. 2020, Şensurat-Genç et al. 2022, Paxton et al. 2024). The literature also points to the aggregation of economically valuable species on shipwrecks, as well as the presence of vulnerable or endangered species, e.g., the Atlantic cod (*Gadus morhua*; IUCN: vulnerable) in the North Sea (Lengkeek et al. 2013). Nevertheless, relatively few studies have compared fish communities on wrecks and nearby natural reefs, especially in high-diversity tropical contexts (Arena et al. 2007, Fowler and Booth 2012, Simon et al. 2013, Sreekanth et al. 2019). Furthermore, the literature on the ecological role of wrecks as ARs and their value for coastal areas is geographically restricted. In particular, the review by Ramm et al. (2021), which identifies 1074 AR sites from 71 countries, shows that AR studies are conspicuously lacking in the Indian Ocean.

This is well illustrated in Sri Lanka, which features a high concentration of shipwrecks around the island's coastline. To date, a total of 114 wrecks have been recorded by the National Shipwreck Database of Sri Lanka, with 25 shipwrecks identified off Colombo on the west coast. All the shipwrecks in Colombo are classified as accidental, i.e., not intentionally sunk to serve as ARs, and have therefore not been appropriately cleared of chemicals before sinking. The majority of the shipwrecks are accessible, and just a few are protected for their historical value. Thus, the Colombo shipwrecks are often visited by local SCUBA tour operators and recreational divers. The first initiative for protecting shipwrecks as marine cultural heritage was taken by the National Aquatic Resources Research and Development Agency (NARA) in the 1980s, which established the Inter-Ministerial Committee on Shipwrecks (IMCW; Devendra and Muthucumarana 2013, Muthucumarana 2019). However, literature on the ecological value of shipwrecks in Sri Lanka remains limited. Preliminary surveys of the HMNS SS Sagaing World War II shipwreck in Elephant Island, Trincomalee, assessed the value of the wreck for ecotourism and AR structure (Jayawardena et al. 2018, Munasinghe et al. 2018). Semiquantitative assessments of benthic and pelagic species inhabiting the wreck were performed as an ecological baseline intended for long-term monitoring, and observational data indicated a high recruitment rate on the wreck. Nevertheless, these studies did not address quantitatively how the communities on the wreck compare to the ones on natural reefs.

The main objective of our study is to compare fish communities on wreck and natural reef sites in terms of species composition, diversity, richness, and density. This study presents the first effort to quantify the ecological role of shipwrecks as ARs in Colombo and provides a baseline to determine the biological value of shipwrecks as AR structures, i.e., their potential to provide habitat for local species.

Methods

Fieldwork.—The study was conducted on three selected shipwrecks and three natural reefs by means of diver-operated video (DOV) transects. The fieldwork was carried out from 10 to 28 March, 2022 in Colombo, Sri Lanka. The work was divided into preliminary dives for the assessment of the survey sites and the fish surveys conducted with video transects. The analysis of survey video footage was completed at the Leibniz Centre for Tropical Marine Research (ZMT) in Bremen, Germany.

Six survey sites were selected for this study, including three natural reefs and three wrecks. The sites were within proximity of each other (<10 km; Fig. 1) and had a depth range of 6–30 m (average 22.3 m; Table 1, Online Fig. S1). The site selection considered the distance between the locations, which range from approximately 1 to 9 km. The maximum depth of the sites varied between 23 to 32 m (Table 1). The wreck sites Nilgiri (32 m) and Medhufaru (30 m) were deeper, while T Sierra (23 m) was closer in depth to the reef sites (23–25 m). The natural reef sites Barracuda Reef, Anchor Point, and New Reef are similar in structure and are part of a continuous, sandstone ridge located parallel to the coastline at around 3 km from the shore. The survey sites encompassed three different sections of the approximately 5 km long reef. The reef is composed of old sandstone rock with multiple cracks and small overhangs. However, vertical relief is limited with depths ranging from 20 m at the top of the reef to 24 m on sand on both the seaward and leeward sides. The width of the reef is approximately 50 m. The rock relief has been colonized by a mixture of hard and soft corals as well as small gorgonians and sea whips and contains a diverse invertebrate fauna. The reef surveys provided the baseline data for the natural species composition on hard substrate in the surrounding area.

The selected wreck sites are Nilgiri, Thermopylae (T) Sierra, and Medhufaru (Table 1). The wrecks were constructed from steel and did not endure any major damage while sinking. The shipwrecks are surrounded by areas of flat sandy substrate without close proximity to natural reefs (>1 km). The T Sierra is a 155 m bulk carrier that sank in 2012, making it the youngest of the surveyed wrecks. The wreck sits at 25 m with the decks at 8–10 m and sections of the superstructure above the waterline. The wreck has a high degree of structural complexity with cargo holds and overhangs creating spaces for fishes. It also has the highest vertical relief of all wrecks in Colombo. The decks of the wreck have been colonized by hard corals, mainly *Pocillopora damicornis*

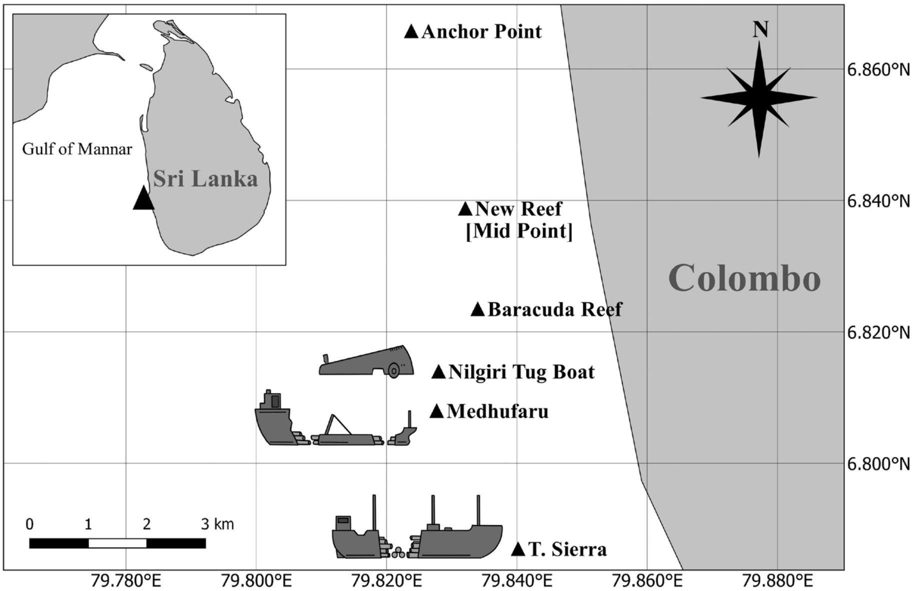

Figure 1. Map of six study sites on the coast of Colombo, Sri Lanka. The distances between shipwrecks range between 0.5 and 3 km, the distances between natural reefs range between 1.5 and 5 km, and the distances between shipwrecks and natural reefs range between 1 and 9 km.

and *Pocillopora verrucosa*. Medhufaru is a 79 m long cargo vessel that sank in 2009. It sits on a sandy bottom at 30 m with the highest point of the wreck reaching 16 m. The wreck provides significant habitat for fishes with cargo holds, open cabins, and an intact superstructure. There is very little hard or soft coral compared to other wrecks in the area. Nilgiri is a tugboat that sank in 1997 and is located on a sandy bottom at 30 m. It is positioned upside down with the hull containing significant growth of soft corals. It therefore provides less structural complexity than the other wrecks except for a large swim-through under its decks. Both natural reefs and shipwrecks are frequented by local SCUBA diving operators, particularly during the weekends; however, there is a stronger demand for dive tours on the wreck sites over natural

Table 1. Selected study sites and characteristics of wrecks and reefs. Information obtained from open access National Shipwreck Database of Sri Lanka. Width refers to the beam of the shipwrecks and to the distance between one ledge and the other side for the natural reefs.

Features	Nilgiri Wreck	T Sierra Wreck	Medhufaru Wreck	Barracuda Reef	Anchor Point Reef	New Reef (Mid Point)
Type	Utility Barge	Bulk Carrier	General Cargo Ship	Sandstone Reef	Sandstone Reef	Sandstone Reef
Year Sunk	1997	August 2012	May 2009	- - -	- - -	- - -
Year Built	1976	1985	1976	- - -	- - -	- - -
Depth (m)	23–32	6–23	14–30	20–25	20–23	20–25
Length (m)	54.9	155	77	>5000	>5000	>5000
Width (m)	11.9	27	11.8	10–20	10–20	10–20
Coordinates	06°48.842´N 79°49.677´E	06°47.220´N 79°50.410´E	06°48.481´N 79°49.664´E	06°49.407´N 79°50.040´E	06°51.945´N 79°49.430´E	06°50.329´N 79°49.923´E
Abbreviation	NW	TSW	MW	BR	AP	NR

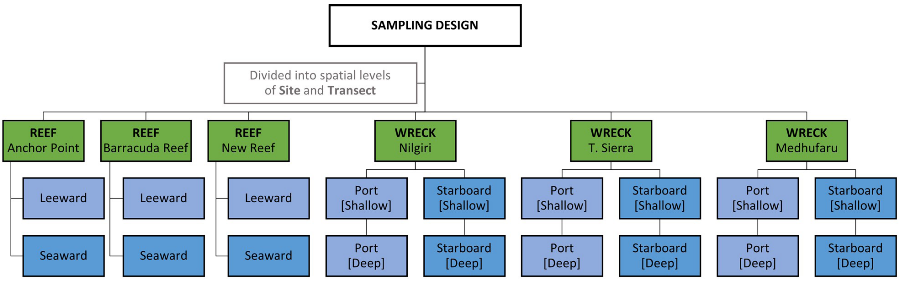

Figure 2. Sampling design flowchart. The transects along selected survey sites were distributed over two areas for the reefs and four areas for the wrecks. Color coded according to site (green) and transect (blue).

reefs. The sampling design was adapted to only conduct surveys during weekdays and when no other divers were on the sites to minimize disturbances to the fish community (Fig. 2).

The transects were conducted on sections of the survey sites, with each site divided into Starboard and Port (wreck) or Leeward and Seaward (reef; Online Fig. 2). A total of 18 transects were conducted: four for each wreck site and two for each reef site. The surveys were conducted at a depth range of 10–29 m (average 22.4 m; Online Fig. S1). The topography of the wreck sites required two additional transects to include the deep and shallow profiles of the area (the depth range varied between approximately 5 and 10 m). These additional transects allowed for a better representation of the species composition on the wreck sites. The reef sites did not require deep and shallow transects since the depth range was narrower (max 4 m). The transects were 25 m long by 5 m wide, for a total area of 125 m^2. The transects were separated by at least 20 m to minimize potential overlap of fish recordings, with the exception of the shipwreck Nilgiri; due to its capsized placement, the distance between the shallow transects was approximately 10 m. The sampling design was adapted by conducting the wreck surveys with alternating sides and depths during one dive, i.e., port (deep) and starboard (shallow) on day one and port (shallow) and starboard (deep) on day two. The laying of the transects resulted in the "first disturbance", triggering fish displacement. To account for this impact on fish behavior, the team laid the tape and retreated 5 m away from the starting point for 3 min to allow for fish resettlement and acceptance of diver presence before starting the video transect. Once the transect swim was completed, the tape was removed, and the team proceeded to the next survey point. A standardized approach was applied for all surveys to allow for the comparison of wreck and reef sites.

Fish assemblages were surveyed with a single-camera DOV system. Video surveys have been found to increase the precision and accuracy of fish estimates compared to in situ observations (Harvey et al. 2001, Cappo et al. 2003, Davis et al. 2015, Goetze et al. 2015). A mobile approach was favored over stationery counts in order to survey a larger area (Willis et al. 2000, Dorman et al. 2012, Hardinge et al. 2013). The video system setup consisted of a GoPro camera Hero Black 7 mounted on a Mares EOS 10RW support with two handles for a secure hold during the survey (Fig. 3A). The camera was set to a resolution of 1080 with 30 frames per second (fps) and auto stabilization (Goetze et al. 2019, Rigby et al. 2019). The field of view was set to record

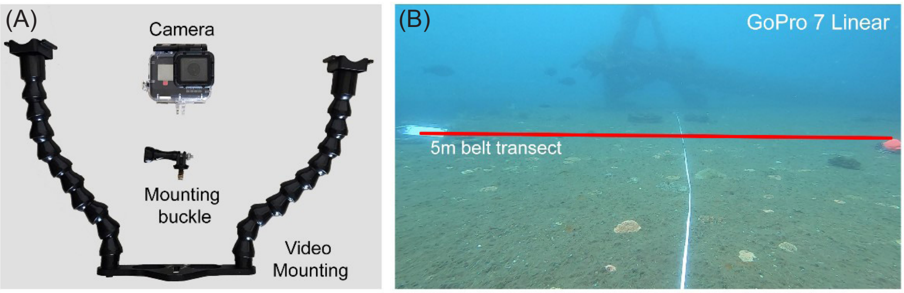

Figure 3. (A) Camera set-up with individual mounting equipment; (B) 5 m belt transect from video trial to test field of view for the distance between objects set to 5 m.

within a 5 m area, with the camera angled to capture 1/3 of the benthic and 2/3 of the pelagic area (Fig. 3B), capturing a water column height of 3 m above the substrate. Lights were not used to limit attraction and repulsion behaviors. The DOV system allowed for a nondestructive, cost-effective, and straightforward approach to record fish assemblages on the survey sites. It also provides a video record that may be reexamined in different research contexts in the future (Online Table S1).

Data Analysis.—The video transects were analyzed with SeaGIS EventMeasure, based on a species list with updated species ID and codes from the Codes for Australian Aquatic Biota (CAAB) database (Rees et al. 1999). Fish ID guides and the FishBase database were used for identification and all fishes were recorded as point measurements (count data). The video analysis was completed by the person who conducted the video surveys (A Hannak). The video data were exported from EventMeasure and compiled into a taxonomically categorized system with family, genus, and species for the point measurement data set. To account for potential observer bias in the video analysis, a subset of six transects were randomly selected and analyzed independently by two observers as part of an agreement analysis. The assessment of A Hannak was compared to the assessment of an independent observer with more experience in reef fish identification in the area (N Perera). The agreement analysis was conducted in RStudio (R Core Team 2021) with the SimplyAgree package. The agreement limit was set to 95% to produce Lin's Concordance Correlation Coefficient (CCC). The analysis indicated a strong agreement for taxa identification and fish counts between the two observers (CCC $\geq$ 0.95) and provided confirmation that the total transect evaluation could be completed by A Hannak.

The objective of the analyses was to compare the shipwrecks and natural reefs in terms of diversity, richness, density, and species composition. In order to account for the difference in sampling effort between the reefs and wrecks, the average from the deep and shallow wreck transects on Port and on Starboard were considered as a single transect. This resulted in two groups for the comparison, each with three site replicates and six transects per group. The study did not aim to address the difference between individual sites, this level was therefore excluded from the analysis. Since some fish were difficult to identify at the species level, the analyses were conducted at the genus or family level.

The diversity on wrecks and reefs was estimated with the Simpson index of diversity and the Shannon–Wiener index at the genus level. To run an overall comparison of fish assemblages on reef and wreck sites, the individual sites were grouped according to type (Reef and Wreck). A nonmetric multidimensional scaling (nMDS) analysis of individual transects was conducted to visualize the level of similarity of fish communities. The data were square root transformed for this analysis, as recommended for decreasing the skew of the data and reducing the effect of larger values. A one-way permutational multivariate analysis of variance (PERMANOVA) was performed to test for differences between natural reefs and wrecks at the family and genus levels. SIMPER analysis was conducted with nontransformed data to identify the percent contribution of individual families and genera to the difference between study sites. Independence between study sites was assumed and statistically significant levels were set to 0.05 ($\alpha = 0.05$). Statistical analysis was performed with RStudio (R Core Team 2021) and PRIMER v7 with the PERMANOVA+ add-on (Plymouth Routines In Multivariate Ecological Research; Clarke and Gorley 2015).

Results

A total of 2918 fishes were recorded in the survey transects, with 30 genera identified from 20 families (Table 2). Overall, 749 fishes were observed on reef sites and 2169 on the wrecks. The most diverse families at the genus level were damselfishes (Pomacentridae, 4 genera) and wrasses (Labridae, 4 genera). No invasive taxa were recorded in the surveys. Additional observations of megafauna include *Rhincodon typus* (whale shark) on the wreck survey site Nilgiri.

The Simpson index indicated a high biodiversity on both reef (0.835) and wreck (0.820) sites. The same was observed for the Shannon–Wiener index, which provided a value of 2.34 on reefs and 2.14 on wrecks. There were no marked differences in richness and diversity of fish assemblages between reef and wreck sites at the genus level, although slightly higher values were consistently observed on reefs. The overall reef and wreck comparison presented a strong similarity, with 32 genera occurring on the reef and 28 on the wreck sites, but it is to be noted that the sampling effort was higher on the wrecks. The shipwrecks and reefs were 80% and 87% similar in terms of presence of families and genera, respectively. Two families and genera were recorded exclusively on reefs (*Sphyraena*, Sphyraenidae and *Priacanthus*, Priacanthidae) and two on wrecks *(Pterois*, Scorpaenidae and *Parapercis*, Pinguipediae).

The results show a higher mean density on wrecks [mean (SE) = 17.2 (5) per 125 m^2] than on natural reefs [11.9 (4) per 125 m^2]. The PERMANOVA analysis showed a significant difference in fish composition between reef and wreck sites at the genus and family level (Table 3). At the family level, Lutjanidae (32%), Caesionidae (18%), and Pomacentridae (14%) were identified by the SIMPER analysis as the main contributors to the difference between habitats. They were followed by Apogonidae (10%) and Sphyraenidae (9%), and other families contributed ≤5% to the dissimilarity between the two groups (Online Table S2). The mean densities of key families on the reefs and wrecks are presented in Figure 4. The families Lutjanidae and Apogonidae were more abundant on the wrecks, while Sphyraenidae were more abundant on the reefs. At the genus level, *Lutjanus* (22%), *Pomacentrus* (16%), *Neopomacentrus* (13%), and *Pterocaesio* (12%) were identified by the SIMPER analysis as the main contributors to the difference between habitats. They were followed by *Apogon* (7%), *Chromis* (6%), and *Sphyraena* (6%), and other families contributed <3% to the dissimilarity between the two groups (Online Table S3). The genera *Lutjanus,*

Table 2. Families and species observed on natural reefs (R) and shipwrecks (W) in the Colombo area (Sri Lanka). Feeding guilds were referenced from FishBase (Froese and Pauly 2000).

Family	Species	Feeding guild	Habitat
Acanthuridae	*Acanthurus* sp. Forsskål, 1775	Omnivores	R, W
Apogonidae	*Apogon* sp. Lacépède, 1801	Omnivores	R, W
Balistidae	*Sufflamen* sp. Jordan, 1916	Omnivores	R, W
Caesionidae	*Pterocaesio chrysozona* (Cuvier in Cuvier and Valenciennes, 1830)	Planktivores	R, W
	Caesio caerulaurea Lacépède, 1801	Planktivores	R, W
Chaetodontidae	*Chaetodon decussatus* Cuvier, 1829	Corallivores, Herbivores	R, W
	Chaetodon sp. Linnaeus, 1758	Corallivores, Herbivores	R, W
	Heniochus acuminatus (Linnaeus, 1758)	Omnivores	R, W
	Heniochus sp. Linnaeus, 1758	Omnivores	R, W
Haemulidae	*Plectorhinchus schotaf* (Forsskål, 1775)	Planktivores, Carnivores	R, W
	Plectorhinchus sp. Forsskål, 1775	Planktivores, Carnivores	R, W
Labridae	*Bodianus axillaris* (Bennett, 1832)	Carnivores	R, W
	Labroides dimidiatus (Valenciennes in Cuvier and Valenciennes, 1839)	Omnivores	R, W
	Leptojulis cyanopleura (Bleeker, 1853)	Planktivores	R, W
	Thalassoma lunare (Linnaeus, 1758)	Carnivores	R, W
Lutjanidae	*Lutjanus fulvus* (Forster in Bloch and Schneider, 1801)	Carnivores	R, W
	Lutjanus lutjanus Bloch, 1790	Carnivores	R, W
	Lutjanus quinquelineatus (Bloch, 1790)	Carnivores	R, W
Nemipteridae	*Scolopsis vosmeri* (Bloch, 1792)	Carnivores	R, W
Pempheridae	*Pempheris* sp. G. Cuvier, 1829	Planktivores, Carnivores	R, W
Pinguipedidae	*Parapercis* sp. Bleeker, 1863	Planktivores	W
Pomacanthidae	*Apolemichthys xanthurus* (Bennett, 1833)	Omnivores	R, W
	Centropyge sp. Kaup, 1860	Omnivores	R, W
	Pomacanthus annularis (Bloch, 1787)	Omnivores	R, W
	Pomacanthus imperator (Bloch, 1787)	Omnivores	R, W
	Pomacanthus semicirculatus (Cuvier in Cuvier and Valenciennes, 1831)	Omnivores	R, W
Pomacentridae	*Chromis* sp. Cuvier, 1814	Planktivores	R, W
	Dascyllus trimaculatus (Rüppell, 1829)	Planktivores	R, W
	Dascyllus sp. Cuvier, 1829	Planktivores	R, W
	Neopomacentrus cyanomos (Bleeker, 1856)	Planktivores	R, W
	Pomacentrus philippinus Evermann and Seale, 1907	Planktivores	R, W
	Pomacentrus similis Allen, 1991	Planktivores	R, W
	Pomacentrus sp. Lacépède, 1802	Planktivores	R, W
Priacanthidae	*Priacanthus hamrur* (Forsskål, 1775)	Carnivores	R
Scorpaenidae	*Pterois volitans* (Linnaeus, 1758)	Carnivores	W
	Pterois sp. Oken, 1817	Carnivores	W
Scaridae	*Scarus* sp. Forsskål, 1775	Corallivores, Herbivores	R, W
Serranidae	*Cephalopholis formosa* (Shaw in Shaw and Nodder, 1812)	Carnivores	R, W
Siganidae	*Siganus javus* (Linnaeus, 1766)	Herbivores	R, W
	Siganus sp. Fabricius, 1775	Herbivores	R, W
Sphyraenidae	*Sphyraena chrysotaenia* Klunzinger, 1884	Carnivores	R
Zanclidae	*Zanclus cornutus* (Linnaeus, 1758)	Omnivores	R, W

Table 3. Results of the permutational multivariate analysis of variance for the factor site type (Reef/Wreck) on total fish assemblages at the family and genus level. Data were square root transformed based on Bray–Curtis similarities. The table provides the permutation *P*-value, with 999 permutations performed and 401 (family) and 421 (genus) classified as unique.

Source of variation	df	MS	Pseudo-*F*	*P* (perm)
Family				
Site (Type)	1	2069.4	2.3882	0.022
Res	10	866.5		
Total	11			
Genus				
Site (Type)	1	5242.5	3.4934	0.01
Res	10	1500.7		
Total	11			

Neopomacentrus, *Pterocaesio*, and *Apogon* were more abundant on wrecks, while the genera *Pomacentrus* and *Sphyraena* were more abundant on reefs. Further analysis of the Pomacentridae family indicated marked differences between habitats, with higher mean densities of the genera *Chromis*, *Dascyllus*, and *Neopomacentrus* on shipwrecks and the genus *Pomacentrus* on natural reefs (Fig. 5, Online Table S4).

The nMDS indicated that fish communities on wrecks and reefs are broadly distinct at the family and genus level, although the reef transect APS clustered with wreck transects at both the family and genus level and the reef transect BRS clustered with wreck transects at the family level (Fig. 6). The similarity between reef and wreck communities was lower at the genus level (<40%) than at the family level (<60%).

Discussion

The results from our surveys revealed similarities and differences in fish assemblages between natural reefs and shipwrecks in Colombo. The fish community differed between the two habitats at both the family and genus level, and the shipwrecks presented an overall higher fish abundance. On the other hand, richness and diversity were similar across the two habitats at both the family and genus level. Furthermore, 80% of families and 86.7% of genera were observed in both habitats.

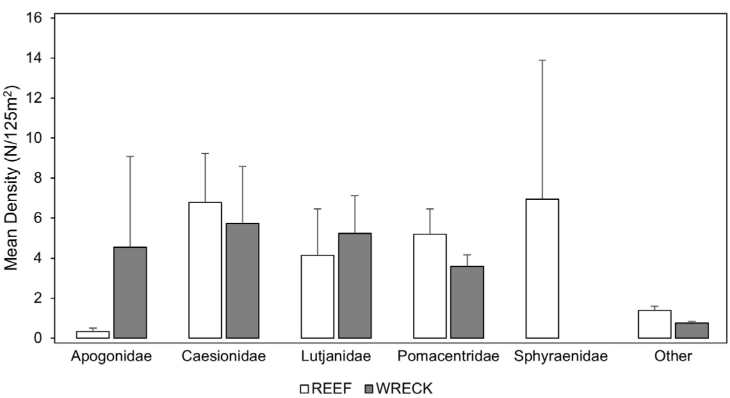

Figure 4. Mean density of key families [*n* (SE) per 125 m^2] for reef and wreck sites.

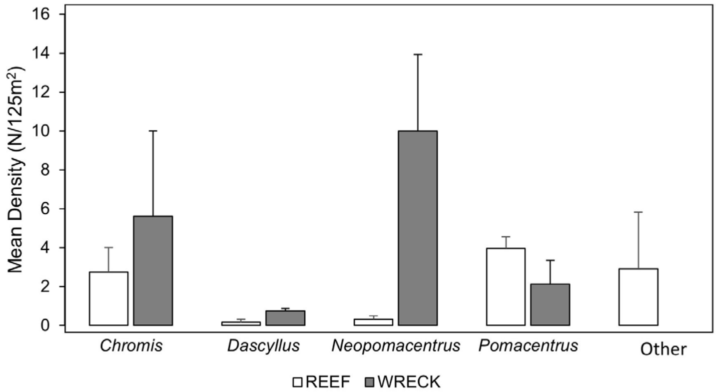

Figure 5. Mean density of Pomacentridae genera [*n* (SE) per 125 m^2] for reef and wreck sites. "Other" refers to individuals from the Pomacentridae family not identified to genus level.

This strong overlap indicates that shipwrecks provide a suitable habitat for a large majority of local reef-associated species. In this regard, they constitute adequate AR structures.

The families Lutjanidae, Caesionidae, Pomacentridae, Apogonidae, and Sphyraenidae were the main contributors to the difference between reef and wreck communities, with higher relative abundances of the genera *Lutjanus*, *Neopomacentrus*, *Pterocaesio*, and *Apogon* on shipwrecks while *Pomacentrus* and *Sphyraena* were more prevalent on reefs. The structural complexity of the shipwrecks yielded larger fish aggregations, especially for the schooling species in the families Lutjanidae and Caesionidae. Lutjanidae were represented by one genus (*Lutjanus*) that commonly preys on fishes and crustaceans at night and aggregates in schools on reefs throughout the day (Froese and Pauly 2000, Nagelkerken et al. 2000). They were observed in large schools of 70 to 100 individuals on shipwrecks. The structural complexity of the wrecks—including caves and overhangs in the ships' interior, fallen debris, and concrete pipes—provide shelter for these schools. Although similar in schooling behavior, Caesionidae are planktivores, preying on zooplankton in the water column above reefs and along slopes during the daytime (Froese and Pauly 2000). They commonly aggregate in groups on sheltered reefs and were observed in large schools of 80 to 100 individuals in and around shipwrecks, with two species (*Pterocaesio chrysozona* and *Caesio caerulaurea*) identified from the video transects. Although surveys were only conducted during the day, we assume these two families to have similar aggregation and feeding behaviors on wrecks as documented on reefs. Both families include species of commercial value that are targeted by the Sri Lankan fisheries (MFARD 2018, Reksten et al. 2020).

Pomacentridae were abundant on both reefs and wrecks, with four genera (*Chromis, Dascyllus, Neopomacentrus,* and *Pomacentrus*) identified. The members of this family are usually associated with coral reef habitats and often display territorial behavior (Froese and Pauly 2000). Members of this family are valued for the aquarium trade and may therefore be of interest for this sector in Sri Lanka. Whereas *Pomacentrus* presented a higher abundance on reefs, *Neopomacentrus cyanomos* was 45 times more abundant on wrecks, where it was recorded in large schools of 50 to

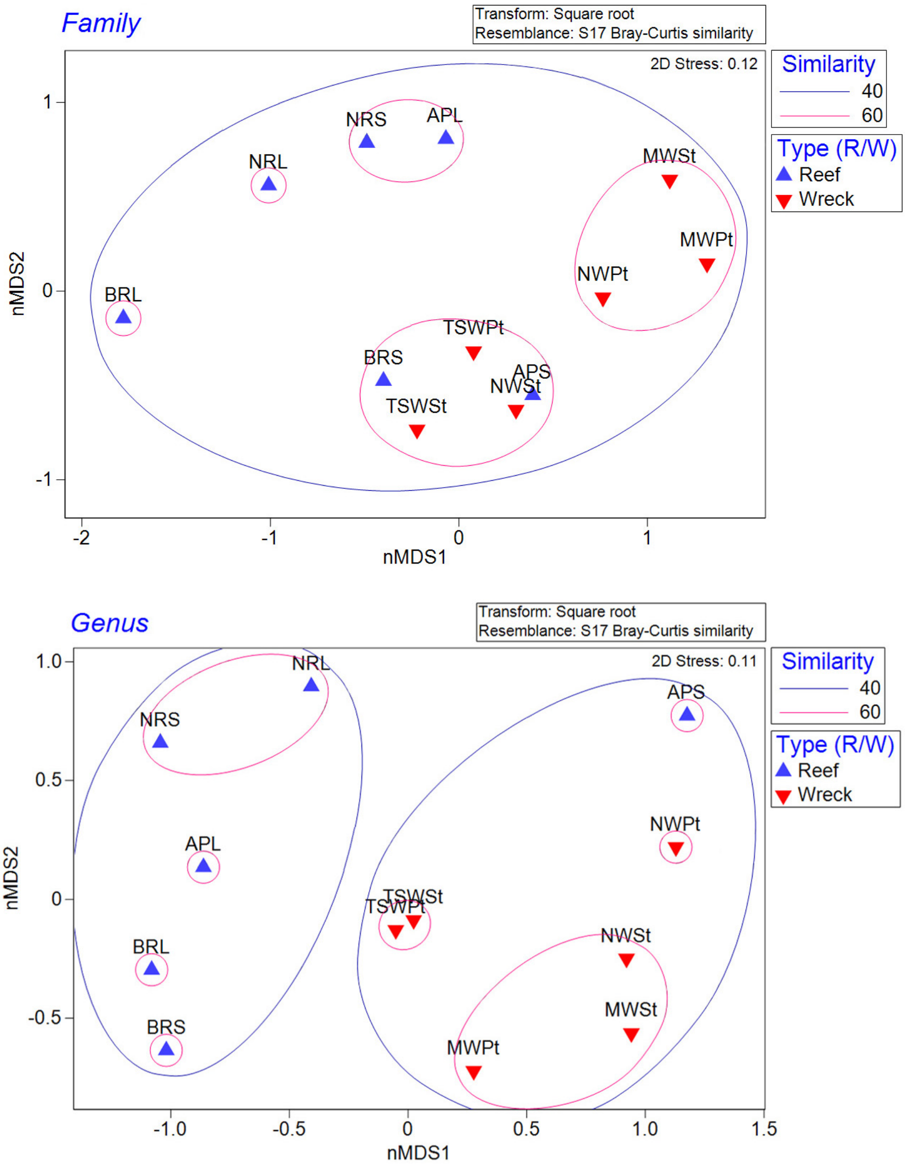

Figure 6. Results of the nMDS analysis for individual transects from reef and wreck sites at the family (top panel) and genus (bottom panel) level with Bray–Curtis similarity levels of 40% and 60% (family stress = 0.12, genus stress = 0.11). The site type is identified by the color and shape, with the abbreviation codes of the site name and the orientation (Starboard/Port and Leeward/Seaward) provided: APL = Anchor Point Leeward, APS = Anchor Point Seaward, BRL = Barracuda Reef Leeward, BRS = Barracuda Reef Seaward, NRL = New Reef Leeward, NRS = New Reef Seaward, NWSt = Nilgiri Wreck Starboard, NWPt = Nilgiri Wreck Port, TSWSt = T Sierra Wreck Starboard, TSWPt = T Sierra Wreck Port, MWSt = Medhufaru Wreck Starboard, MWPt = Medhufaru Wreck Port.

70 individuals. This result resonates with the fact that this species is associated with petroleum infrastructure in the Greater Caribbean, where it was recently introduced and established (Robertson et al. 2018, 2021). The fact that this species is naturally associated with AR structures in the Colombo area, where it is native, supports the hypothesis that it was introduced in the Greater Caribbean through the movement of offshore petroleum infrastructure (Robertson et al. 2021). Thus, while the lack of invasive species in our surveys is an indicator of good health of the marine fish communities in the Colombo area and does not point to negative effects of wrecks in this respect (as reported in other cases, e.g., Soares et al. 2022), species that are strongly associated with wrecks like *N. cyanomos* deserve nonetheless particular attention due to their invasive potential through the movement of ARs.

From the family Sphyraenidae, one species (*Sphyraena chrysotaenia*) was identified and recorded only in the natural reef transects. This pelagic species aggregates in large schools and preys on schooling fishes and crustaceans (Froese and Pauly 2000, Osman et al. 2019). Nevertheless, previous observations by A Hannak and N Perera in 2014 indicate that this species can also be found on wrecks. Its absence in 2022 may be linked to movements associated with feeding and spawning (Osman et al. 2019). This illustrates that our study is limited by its temporal scope, which is relevant since large schools often move between areas (N Perera, Blue Resources Trust, pers observ). Continuous monitoring will be required to document the transient use of wrecks, which may be significant for some species and of interest for artisanal fisheries. From the family Apogonidae, the genus *Apogon* was identified, with a higher abundance recorded on shipwrecks in comparison to the reefs. This taxon is common on coral reefs and preys on zooplankton and small benthic invertebrates as a nocturnal feeder (Froese and Pauly 2000). The higher occurrence of Apogonidae on wrecks is consistent with the fact that these fishes are generally associated with structurally complex, hard substrates that provide shelter during the day.

The occurrence of higher fish abundances on wrecks than on nearby natural reefs has been reported before (Arena et al. 2007, Sreekanth et al. 2019), but does not appear to be universal (Fowler and Booth 2012). The same applies to diversity, which has been reported to be either similar in both habitats or higher on wrecks (Arena et al. 2007, Fowler and Booth 2012, Sreekanth et al. 2019). Part of these conflicting results may be real and reflect the idiosyncrasies of fish communities on reefs and wrecks at different study sites. This includes for example the distance between wrecks and reefs, as well as wreck size and age (Perkol-Finkel et al. 2005, Fowler and Booth 2012, Hannak 2014, Spagnolo et al. 2014). On the other hand, part of these differences may be due to methodological issues. Although a particular effort was made here in this respect, it remains challenging to survey natural reefs and wrecks in the same way due to the higher structural complexity (and depth range in our case) of wrecks. Furthermore, the comparison between the two habitats may be confounded by area. The shipwrecks in our study constitute an island-like habitat by providing a hard structure within an area of flat sediment substrate. Differing to the surrounding reefs, these wreck sites are smaller and tend to represent highly concentrated areas of marine life. Reefs tend to be more extensive than wrecks, which is expected to decrease fish encounter rates compared to wrecks. Nonetheless, when higher abundances were recorded on wrecks, the observation that this difference is driven in large part by economically valuable schooling species is consistent with previous studies (Arena et al. 2007, Sreekanth et al. 2019). The other result that is consistent with previous studies is the fact that fish communities differ between reefs and wrecks. Here again, the specifics differ between studies, but the observation that Lutjanidae, Pomacentridae and Apogonidae contribute to this difference is consistent with previous studies (Arena et al. 2007, Fowler and Booth 2012, Sreekanth et al. 2019). Other families have also been identified by previous studies, notably Haemulidae (Arena et al. 2007, Sreekanth et al. 2019). In our case, this family includes one genus (*Plectorhinchus*) that contributes less than 1% to the difference between reefs and wrecks, which here again reflects the idiosyncrasies of specific study sites. Nonetheless, it is worth pointing out that Haemulidae are functionally similar to Lutjanidae and tend to aggregate in schools. Thus, fish communities on wrecks may be more similar from a functional perspective than from a taxonomic one. In this respect, our results indicate that the major functional groups that contribute to the difference between the two habitats are predators and planktivores, which is consistent with previous studies (Arena et al. 2007, Fowler and Booth 2012, Sreekanth et al. 2019).

The available literature on standardized methods for surveying natural reefs and shipwrecks is limited (Ramm et al. 2021), and the findings of this study as well as the methodology provide as a baseline for future studies. It was an opportunity for a first assessment of fish assemblages on shipwrecks in Colombo and to test the strengths and weaknesses of the video transects. The proposed methodology was appropriately evaluated at the end of the sampling period. The study design was set to apply a non-invasive approach for surveying the marine communities. This was achieved by conducting video-transect surveys to quantify the associated fish assemblages on the shipwreck and natural reef sites in Colombo and provide a comparison of species compositions. The application of video transects presented an attempt to shift away from the dependency on diver underwater visual census (UVCs) and provided an opportunity to review observations in a later setting. An additional advantage is the ability to archive the video recordings for long-term monitoring of the survey sites.

Perspectives.—The marine environment remains an important resource for the livelihood of the fisheries industry and the Sri Lankan economy (MFARD 2018). The occurrence of commercially valuable species is an indicator of the economic value of wrecks and the study was able to successfully quantify the presence of these target species, with their concentrated aggregation in a restricted habitat area providing the opportunity for targeted fishing. Additional factors would include the continued revenue of the local SCUBA tourism industry and the reduction of fishing pressure on natural reefs to support their recovery. This can be achieved through the initial action of safeguarding shipwrecks from the risks of salvaging activity. The loss of these habitats would result in the damage of biological as well as economic advantages provided by shipwrecks. The present destruction and degradation of marine environments emphasizes the need for higher protection of existing habitats, with this study presenting the opportunity for new conservation efforts and highlighting an ecological and socioeconomic motive for the protection of shipwrecks. With the ongoing deployment of ARs on a global basis, Sri Lanka has the advantage of harboring an existing community of structurally complex ARs around its coastlines. This study served as an indicator for the potential development of research programs on shipwrecks as ARs in Sri Lanka. In consideration of the long-term applications of this project, we need to discuss the lessons learned and applications to other regional and international coastal communities. One example of this would be the development of AR designs that support the enhancement and recovery of marine communities as well as the livelihood of coastal regions.

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