Temporal variation of grouper diversity and distribution on the continental shelf of Sri Lanka: a revisit after four decades

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Abstract

Groupers (family Epinephelidae, subfamily Epinephelinae) are reef fishes of high value as food resources that generate export revenue to Sri Lanka. Yet, with less attention and poor resource management, grouper population dynamics remain understudied. This paper investigates the temporal variation of grouper species on the continental shelf of Sri Lanka in relation to seasonal, regional, and seafloor depth variables using data based on quantitative sampling of demersal fish conducted in 1978, 1979, 1980, and 2018 with a bottom trawl on the R/V Dr. Fridtjof Nansen, where the authors joined the 2018 survey. A total of 277 trawl samples were included in the analysis. The analysis of variance of all the grouper species found that the average density significantly declined from 0.89 t/NM^2 (tones per square nautical mile) in 1979 to 0.28 t/NM^2 in 2018. The contribution of groupers to the total catch (by weight) was also higher in 1979 (9.06%) than in 2018 (1.28%). The distribution patterns also significantly differed among the six regions of the Sri Lankan shelf. In addition, seafloor depth was negatively correlated with grouper density. The results point to an urgent need for better management and conservation of the grouper resources.

Keywords: bottom trawl survey; density; grouper; regional variation; Sri Lanka; temporal variation

1. Introduction

Fish in the subfamily Epinephelinae are called the groupers, consisting of about 160 species (Ma and Craig, 2018). Groupers are bottom-living, sedentary, and slow-growing fishes that are economically valuable, nutritional, and important livelihoods, especially to artisanal fishers in the world's tropical and subtropical seas (Sadovy de Mitcheson et al., 2020b). Most of the groupers are protogynous hermaphrodites and mature as females while changing sex after gonadal maturity if not suppressed by a dominant male. The group consists mainly of top predators, typically feeding on fish, octopus, and crustaceans (Sluka and Sullivan, 1996). In general, demersal fish groups concentrate on specific geographical locations and habitats (Bianchi, 1991). A wide range of body size among species is a particular feature of groupers, while some species have a body size of over 100 cm. These biological attributes make groupers more susceptible to overfishing. Groupers occupy a broad range of water depth (typically from 1m to 300 m) and a variety of habitats (Chiappone et al., 2000). While a large body of literature studied on management of pelagic fishery (e.g., vessel monitoring system study (Gunasekare and Rajapaksha, 2016), trophic interaction study (Haputhantri et al., 2008), seasonality study (Gunawardena et al., 2016)), much less attention has been rendered to demersal species, especially groupers.

Apart from biogeographical factors, anthropogenic and environmental factors also influence the sustainability of grouper resources (Caddy and Sharp, 1986). Because several examples are showing the collapse of some well-managed stocks due to environmental factors, not always due to human intervention. Anthropogenic influence on the stocks themselves or their habitats causes community structure changes and even creates irreversible damage but also assists in rebuilding stocks. For instance, Richards et al. (2012) identified impacts of various habitat characteristics on demersal fish communities, such as coverage of coral reef, macroalgae, sand, rubble, oceanographical parameters, fishing intensity, and human population density. Nogueira et al. (2017) reported a collapse of some demersal stocks due to environmental factors not necessarily caused by economic activities. Therefore, Understanding the influences of anthropogenic and environmental factors and their interrelationship can be essential for effectively managing multispecies stocks (Caddy and Sharp, 1986).

As grouper harvesting is regarded as a traditional artisanal fishery in Sri Lanka, small-scale landing sites are scattered around the country. The existing fisheries data collection system does not cover all these landing sites, and thus official harvest data tend to underestimate actual landings (Gunawardena et al., 2016). Some species form spawning aggregations and migration, allowing good catches for fishers even at relatively low stock levels. Groupers are particularly vulnerable to over-fishing because of the relatively high fishing mortality, especially for larger individuals, slow growth rate, sexual inversion with few large dominant males, and relatively small spawning batch sizes (Polovina and Ralston, 1987). The removal of reproductively active fish in larger quantities will be detrimental to resource sustainability.

Further, as protogynous species, males will be older, heavier, and tend to be less abundant than females (Sadovy et al., 1994). Fishers preferring larger-sized fish are inherent in population dynamics studies and management (Bannerot et al., 1987; Mangel et al., 2017). According to the FAO statistics, total commercially targeted grouper landings increased from 237,000 mt in 1950 to 450,000 mt in 2015 worldwide, where South, Southeast, and East Asian countries together accounted for 85 % of the global grouper harvest (Sadovy de Mitcheson et al., 2020b).

There are 39 species of groupers has been recorded on the continental shelf of Sri Lanka in shallow water reef areas and some hardbottom, deep-water habitats in the past (De Bruin et al., 1994). Sri Lanka has a narrow continental shelf, with diverse coral reefs, hard rocky bottom, sponge habitats, sandy and muddy bottom habitats, river outlets, brackish water lagoons, and mangroves (Long et al., 2010). These diverse habitats have traditionally nurtured an abundance of groupers. The annual southwest (SW) and northeast (NE) monsoon events also contribute to biologically rich habitats around the country (Athukoorala et al., 2021). Groupers are harvested for local consumption and export, and the total export was valued at USD 257 million in 2017 (MFAR, 2018). Even so, literature has paid limited attention to the population dynamics and other biological aspects of grouper resources in Sri Lanka. Investigated grouper landing data are scarce in Sri Lanka because the small-scale fishery is scattered all around the coastline. The existing data collection systems do not extensively cover these small-scale landing sites, and more attention is paid to large and small pelagic landings.

Comprehensive surveys were conducted by the R/V Dr. Fridtjof Nansen (DFN) in Sri Lankan waters in 1978, 1979, and 1980 (Saetersdal et al., 1999). Since then, no survey was carried out over the four following decades. In 2018, a similar survey was completed as part of the same program. Apart from those resource surveys, no other survey has ever been conducted on the country's demersal fish species. Therefore, this study utilized the DFN survey data, even though they were not focused on grouper resources. No other analysis of the grouper population structure has covered the area investigated in our paper to the authors' knowledge. Drawing on these data, this study conducts a statistical analysis of the changes in diversity and abundance of groupers on the continental shelf in Sri Lanka.

2. Methodology

2.1 Data

The DFN surveys were part of the collaboration between Sri Lanka and the Food and Agriculture Organization of the United Nations (FAO) and part of the EAF-Nansen Program. The program in Sri Lanka is a long-term partnership of the FAO, the Norwegian Agency for Development Cooperation (Norad), and the Institute of Marine Research (IMR) in Norway for sustainable management of fisheries in partner countries. The surveys' temporal coverage is uneven. The DFN performed the first three surveys, and after 38 years, the last survey was joined by the authors (AASHA and JOK) with a new vessel of the same name. The periods, numbers of trawl samples, and the seasons of the four surveys are summarized in Table 1. Only the 1980 survey was conducted during the NE monsoon period while the three other surveys were conducted in the SW monsoon.

Table 1

Overview of R/V Dr. Fridtjof Nansen surveys conducted on the Sri Lankan continental shelf.

Survey Year	Period	Monsoon season	Total trawl samples	Grouper present samples	Per region (NW, SW, S, SE, CE, NE)		% of grouper present samples
					Total	Grouper present	
1978	16th Aug -26th Nov	Late SW	34	12	(7, 8, 3, 7, 1, 8)	(0, 2, 3, 6, 0, 1)	35.3
1979	25th Apr -16th Jun	Early SW	90	45	(13,11, 6, 15, 11, 34)	(5, 5, 4 7, 6, 18)	50.0
1980	7th Jan -10th Feb	NE	84	24	(19, 15, 11,	(2, 6, 6	28.6

					12, 4, 23)	4, 0, 6)	
2018	24th Jun -16th Jul	SW	69	27	(5, 13, 11, 18, 10, 12)	(3, 7, 5 8, 4, 0)	39.1

NW: northwest; SW: southwest; S: south; SE: southeast; CE: central east; NE: northeast.

The sampling method was standardized for all the surveys, which was mainly trawling, either bottom or pelagic (Blindheim et al., 1979; De Bruin and Saetersdal, 1978; Krakstad et al., 2018). In this paper, a total of 277 bottom trawl samples were used for the analysis. The mean values between the start seafloor depth and the final seafloor depth were taken as the seafloor depth for each sample. The same bottom trawl gear was used in 1978, 1979, and 1980, whilst a "Gisund super bottom trawl" was used in 2018. The trawls were otherwise similar and are assumed to have the same catchability, and therefore comparable (Table 2). The respective survey reports described the specifications for bottom trawls used in each survey (Krakstad et al., 2018; Saetersdal et al., 1999). Grouper density was calculated by following Athukoorala et al. (2021) as follows:

$$D = c \cdot \frac{A}{a}$$

$$a = TD \times SS \times WS \qquad \text{Eq. (1)}$$

where D is the density in tons per square nautical mile (t/NM^2), c is the conversion factor from kg/m^2 to t/NM^2, A is the total catch per haul (kg), a is the swept area (m^2), TD is the tow duration (hour), SS is the speed of the ship (m/hour), and WS is wing spread (m) which is the distance between the two wing ends.

Table 2

Specifications for bottom trawl gear used in each of the four surveys

Specification	1978/1979/1980	2018
Headline length (m)	29	31
Ground rope (m)	19	47
Width of rubber bobbins (m)	0.5	0.3
Distance between wing ends (m)	15.0	18.5
Vertical opening (m)	5.0	5.5
Cod end mesh size (mm)	20	20
Front net mesh size (mm)	40/30	40/30

The four surveys covered the same areas of the coast. The surveys were confined to the country's continental shelf and not beyond the edge of the shelf (**Fig. 1**). For analytical purposes, the survey area was divided into six regions: northwest (NW), southwest (SW), south (S), southeast (SE), central east (CE), and northeast (NE) (**Table 1** and **Fig. 1)**. The shelf is comparatively narrow, not extending more than 12 nautical miles average width except in the northern part, and the edge is sharp and steep. Following the echo recordings, possible trawling grounds were selected for the survey. The shallower areas were excluded from sampling (less than 10 m in the surveys from 1978 to 1980 and less than 20 m in 2018) because of the difficulty in navigation. In addition, sensitive habitat areas like coral reefs and sponges were excluded from the surveys. Despite the smooth and even seafloor suitable for trawling, the country's northern shallow region was banned from all the surveys as it was too shallow for the DFN to navigate.

The recorded species were classified according to the population threshold levels as per the IUCN Red List (IUCN, 2019). The species that nearly met the thresholds and conditions were listed in the Least Concern (LC) category. The Data Deficient (DD) group was used when information on quantitative thresholds was unavailable or insufficient to place the species.

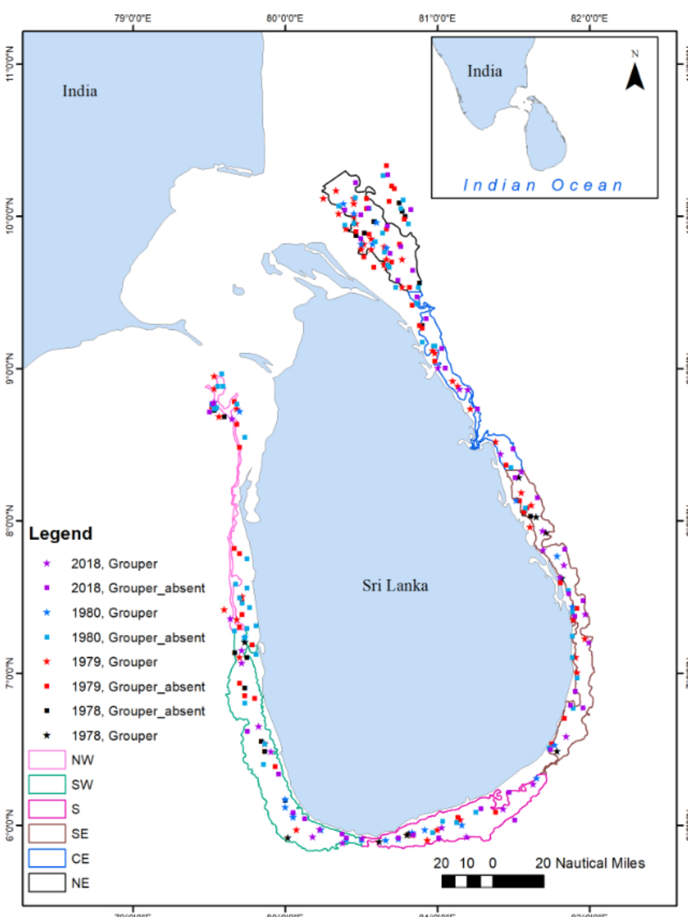

Fig. 1 Trawl sampling stations in the six regions of Sri Lanka in the 1978, 1979, 1980, and 2018 surveys. The regions are shown by 20-100 bathymetry lines. NW: northwest, SW: southwest, S: south, SE: southeast, CE: centraleast, and NE: northeast

2.2 Statistical analysis

Descriptive statistics were used to present grouper species aggregation for the different regions and depth strata and to identify the species dominating each. The grouper density was expressed in the unit of tons per square nautical mile (t/NM^2). Density differences across the surveys, regions, and species were examined using the one-way analysis of variance (ANOVA), followed by the Tukey HSD test, and analysis of similarities (ANOSIM) which is the test with a ranked dissimilarity matrix to determine the difference among subsamples (Massutí and Moranta, 2003; Schwartzkopf et al., 2020). Furthermore, the Pearson correlation coefficient was utilized to examine how grouper density changed with seafloor depth. The analysis was performed with R 4.0.2 (R core Team, 2020)and STATA 17 (StataCorp., 2021).

3. Results

It was found that grouper density changed within the four decades (F=4.92, df=276, p=0.002 and ANOSIM, $R = 0.856$, $p < 0.001$) as shown in **Fig. 2**(A). Grouper density between regions across all years was significantly differed (ANOSIM, R=0.797, p=0.001) (**Fig. 2**(B)). The larger R for year groups than the region groups indicated inter-annual changes (temporal) are more than inter-regional (spatial) changes. The average density also was found to vary significantly among species (ANOSIM, R = 0.849, $p < 0.001$) (**Fig. 2** (C)). The average grouper density decreased by two-thirds from 0.89 ± 0.20 t/NM^2 in 1979 to 0.28 ± 0.71 t/NM^2 in 2018 (**Fig. 3**). The weight contribution to the total catch followed a similar trend, being highest (9.06%) in 1979 and lowest (1.28%) in 2018.

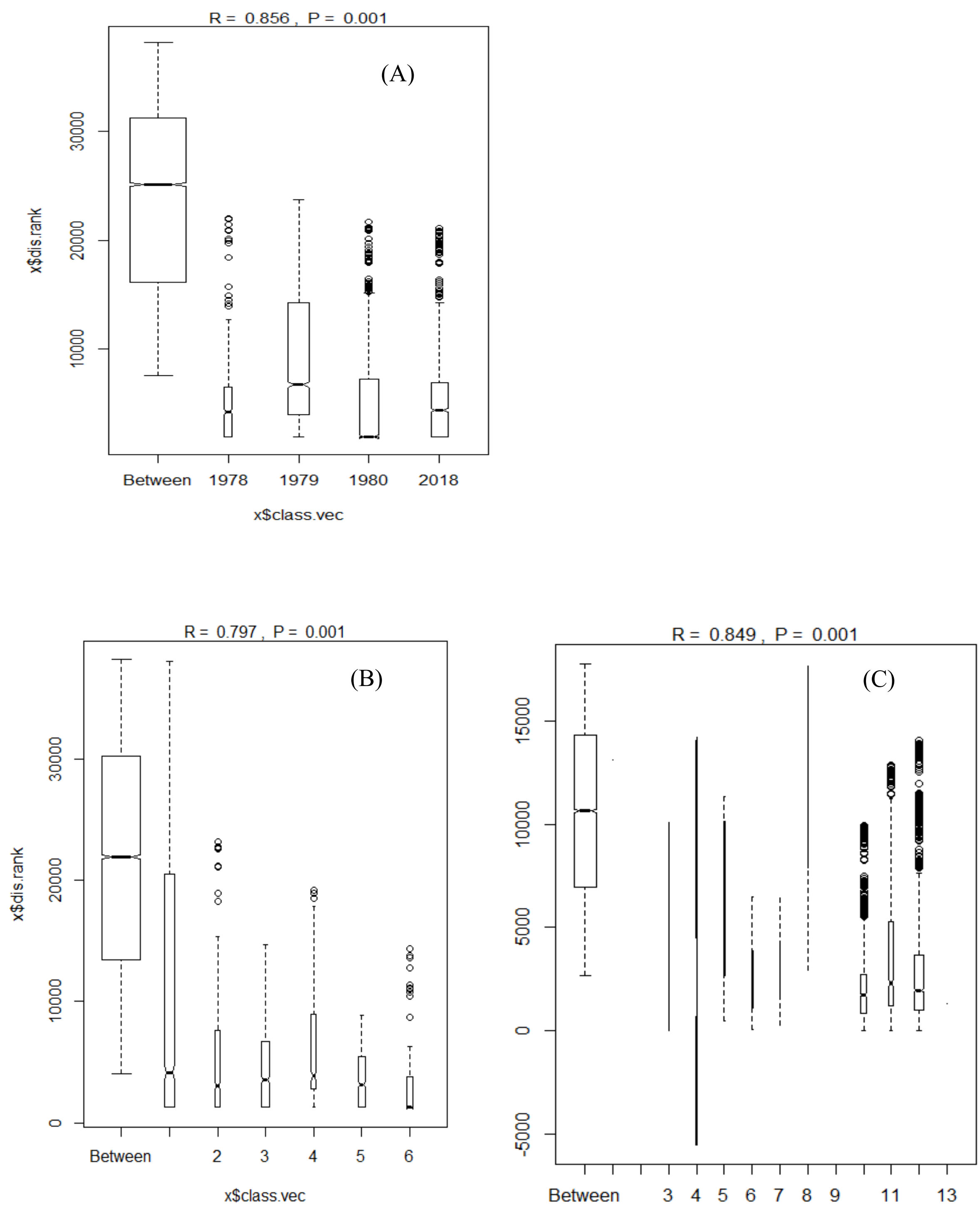

Fig. 2 Analysis of similarities (ANOSIM) showing the density differences (A) across years, (B) across regions (1 = NW, 2 = SW, 3 = S, 4 = SE, 5 = CE, 6 = NE), and (C) among species (numbers 1-13 refer to species ID in Table 3).

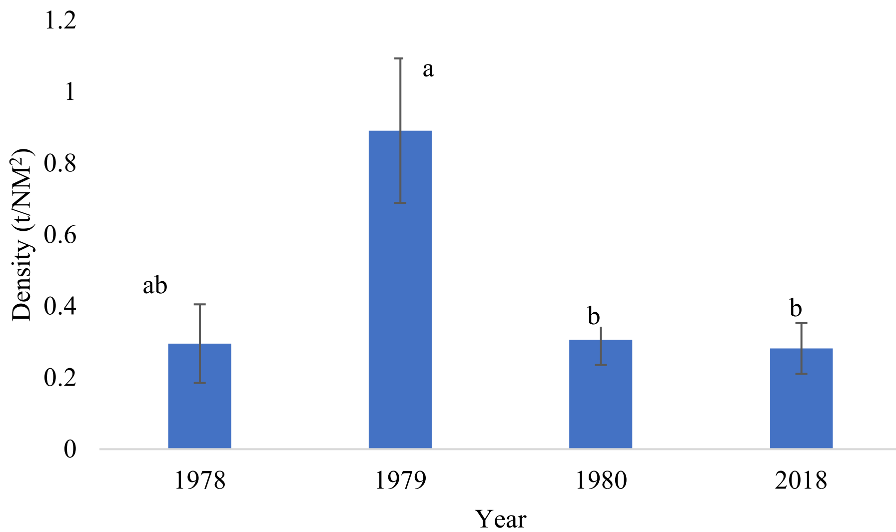

Fig. 3 Mean ± standard error of grouper density (t/NM^2) in each of the four surveys (1978, 1979, 1980, 2018) on the continental shelf of Sri Lanka. Note: Mean values with different superscripts are significantly different at the 5 % level according to the Tukey HSD test.

The highest grouper density was recorded in the south region, and the overall tendency remained similar in the four surveys (Fig. 4). There were no groupers found in the northeast region in the last survey, but there were in the first three surveys.

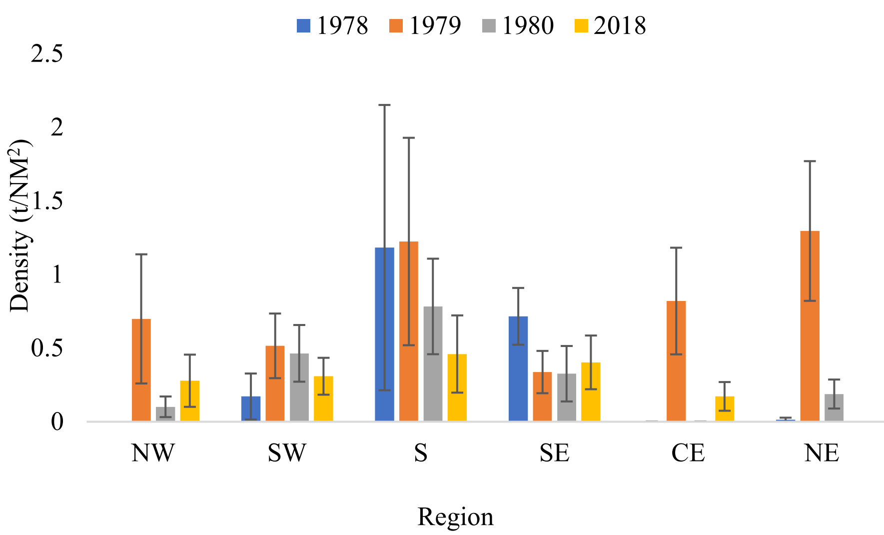

Fig. 4 Mean ± standard error of grouper density (t/NM^2) in each of the four surveys in the six regions of Sri Lanka. NW: northwest, SW: southwest, S: south, SE: southeast, CE: centraleast, and NE: northeast

During all the surveys, groupers were identified to species level (ten species), genus level (two genera), and a subfamily level (one subfamily). The recorded number of species differed between the surveys: five species in 1978, seven in 1979, six in 1980, and nine in 2018 (**Table 3**). The taxonomic identification was more complete in 2018 than in the older surveys, probably indicating the increase in species identified. All species recorded belonged to the subfamily Epinephelinae; nine species were from the genus *Epinephelus*, while two were from the genus *Cephalopholis*. The genus *Epinephelus* was more prominent in the occurrence and relative density compared to the genus *Cephalopholis* across the surveys. *E. undulosus* was the most represented species by abundance (317 individuals) and registered the highest total density (about 58 t) in all the surveys. *E. tauvina* was observed in the first three surveys but deficient in the 2018 survey. In the 2018 survey, *E. coioides* was the most prominent species. The genus *Cephalopholis* and Aethaloperca were presented only in the 2018 survey. Among the three genera, *Cephalopholis* contributed the least to the total catch.

Table 3

The mean grouper density ± standard error (t/NM^2) by species for the four surveys (the numbers of individuals are in the parentheses)

ID	Species	1978	1979	1980	2018
1	*Aethaloperca rogaa*				0.59±0.46(5)
2	*Cephalopholis sonnerati*				0.004±0.00(6)
3	*Cephalopholis* sp.	0.12(1)		0.86(1)	0.01(3)
4	*Epinephelus areolatus*	0.02(1)	0.10(2)	4.20(2)	0.04±0.03(4)
5	*Epinephelus coioides*				0.95±0.36(22)
6	*Epinephelus longispinis*		0.48±0.14(26)		0.04(2)
7	*Epinephelus malabaricus*				0.67±0.20(11)
8	*Epinephelus merra*		0.52(2)	4.85±3.55(5)	
9	*Epinephelus rivulatus*		0.19(1)		
10	*Epinephelus* sp.	0.64±0.31(53)	0.61±0.14(39)	0.34±0.13(15)	0.36±0.15(6)
11	*Epinephelus tauvina*	0.53±0.11(7)	1.78±0.54(47)	0.90±0.19(14)	
12	*Epinephelus undulosus*		1.17±0.21(205)	0.77±0.17(90)	0.43±0.07(22)
13	Epinephelinae (subfamily)	0.21±0.18(20)			

The mean density (t/NM^2) of groupers was lower in shallow depth classes in the 2018 survey than in the first three surveys (Fig. 5). As mentioned, sampling was not conducted at the 10-20 m depth in the 2018 survey. Moreover, 99% of them belonged to the genus *Epinephelus* in all depth classes. Grouper density and depth classes showed a negative linear correlation (r = -0.154, p = 0.010) according to the Pearson correlation coefficient.

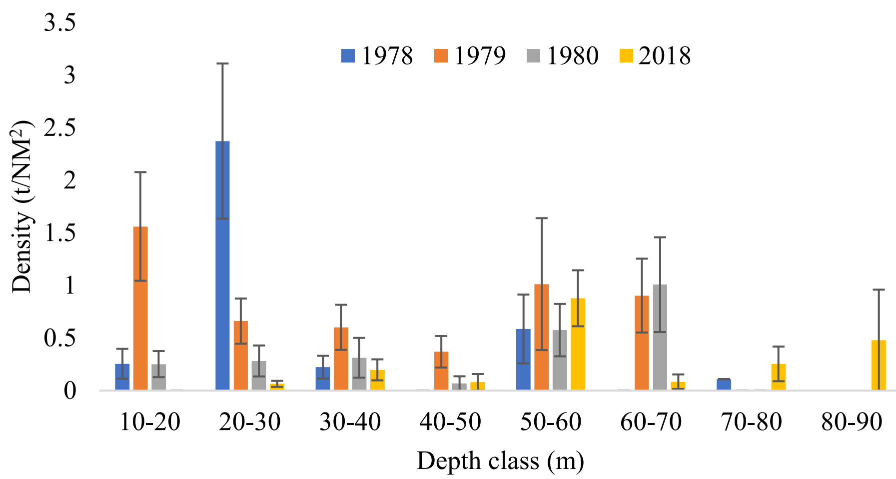

Fig. 5 The mean grouper density ± standard error (t/NM^2) by depth classes in the 1978, 1979, 1980, and 2018 surveys

4. Discussion

This analysis of temporal variation in grouper density exhibited a significant decline in grouper resources in the four decades. The grouper contribution to the total density was nearly one tenth compared to four decades before. As a clue to the declining grouper density, it is worth noting that various types of active fishing vessels operated and active fishers increased in the coastal zone of Sri Lanka from 1995 to 2018. The number of active fishing vessels doubled from 27,000 in 1995 to 51,000 in 2018, while the number of active fishers more than tripled from 56,000 in 1982 to 182,000 in 2018 (MFAR, 2020). These are some of the significant factors that can cause overexploitation. The gradual increase in total coastal production is the best evidence for this, from 165,000 t in 1980 to 249,000 t in 2018. The number of boats and active fishers can consider as an index of fishing effort. This growing number of fishing efforts (fishing vessels and fishers) is one of the critical factors causing reduced density in 2018 compared to the first three surveys.

Grouper-specific behavioral characteristics such as spawning aggregation and slow growth may also lead to overfishing. A similar study conducted in the eastern Caribbean, Belize, Mexico, and Bermuda proved that the fish stock decline in the region was due to overfishing on spawning aggregations (Chiappone et al., 2000). Other species forming spawning aggregations also disappeared over the last few decades of the 20th century (Sadovy and Domeier, 2005). However, grouper stock status is vastly unknown due to insufficient or absent reporting, especially in artisanal fisheries in developing countries in the tropical and subtropical areas (Patrícia Amorim et al., 2018). Sadovy de Mitcheson et al. (2020b) described that grouper population characteristics might be hidden due to heavy fishing intensity and improper monitoring and landings in the Asian region, even though they were categorized in the LC groups.

Several researchers emphasized the need for specific management systems for sequential hermaphrodites species such as groupers through seasonal or area closure on spawning aggregations (Hughes et al., 2020; Sadovy and Domeier, 2005), introducing minimum size limits (Kindsvater et al., 2017), gear or effort controls, establishing marine protected areas, fishing zoning, mapping of fishing spots, and studies on local knowledge (Begossi et al., 2019). The findings in this study strongly support the need for such a specific management plan to Sri Lanka.

This study found regional variations in grouper density across the decades. The highest density was recorded in the South region. During both SW and NE monsoon, the central upwelling region is located along the country's southern coast (De Vos et al., 2014). Therefore, the southern belt can be considered a highly productive zone. This area contains lots of coral reefs, reefs, and seagrass beds (Rajasuriya and White, 1995), which presumably provided a nursery area for a number of valuable demersal species. Several grouper species typically exhibit migratory behavior in sync with the season, lunar cycle (Harmelin and Harmelin-Vivien, 1999; Johannes et al., 1999), and spawning aggregation behavior (Aronov and Goren, 2008). The SW monsoon is prominent, persistent, and robust, bringing heavy currents from the Arabian Sea from the western side to the eastern side of the country from May to October (De Vos et al., 2014). During the SW monsoon, coastal upwellings with nutrient-rich cold water are significant in the Arabian Sea (Siddeek et al., 1999). Consequently, primary production and fisheries production is likely to increase (McIlwain et al., 2011). The SW monsoon (summer) period is the peak spawning season for many *Epinephelus* species, especially *E. tauvina* and *E. coioides* (Achmad et al., 2019; Ohta et al., 2017).

However, a study on India's southwest coast by Banse (1968) reported the virtual disappearance of demersal fishes due to low oxygen water transferred from the deep layer by upwellings in summer months. When mixing and upwellings reach 100 m depths, the peaked commercial catch occurs after the monsoon in the Arabian Sea (Madhupratap et al., 2001).

The grouper density in 1978 was lower than in 1979. Groupers are highly sensitive to environmental variations and changes, and they show rapid migration patterns even within the season (Dahlgren et al., 2016). The SW monsoon is the best example that showed significant changes in environmental parameters and fish behavior (Shankar et al., 2019). The 1978 survey was conducted from August to September, which belongs to the later part of the SW monsoon. During this survey period, a layer with less oxygen was prominent, which was 1 ml/l oxygen at about 50 m depth (Saetersdal et al., 1999). There is evidence that demersal fish species had temporarily disappeared at the later SW monsoon (McIlwain et al., 2011). This change in the bottom water oxygen content probably explains the low abundance of groupers observed in 1978.

As noted, the 1979 survey was implemented during the early SW monsoon period, while the 1980 survey was conducted during the NE monsoon. Assuming that the fishing pressure and other external factors are similar during the period from September 1978 to February 1980, the results might suggest that the best catches occurred during the early SW monsoon period. There are examples of the seasonal spawning migration of groupers (Beets and Friedlander, 1992). These aggregations are the targets for fishers worldwide, which may make it detrimental to the stocks. The 2018 survey also provided a snapshot of the SW monsoon after the four decades, which showed a significantly lower density than in the 1979 survey. Therefore, our results suggest that there has been a significant reduction in grouper density within the four-decade period. However, we recommend conducting further surveys to cover both monsoons equally.

The correlation analysis showed the negative relation between seafloor depth and grouper density, which is consistent with the finding by (Sadovy de Mitcheson et al., 2020a) on the Indo-Pacific grouper aggregation patterns. Further, literature suggests some additional factors affecting the demersal fish assemblages, substrate types, and reefs (Bianchi, 1992; Mcclatchie et al., 1997; Porteiro et al., 2013). Therefore, groupers may be regarded as shallow-water species, and this finding would be helpful in management plan preparation, such as for area closure, fishing ground zoning, and limited access area declaration.

Wavy-lined grouper (*E. undulosus*) was found to be the most abundant species over the period, which is consistent with the study by Heemstra and Randall (1993) in India and Sri Lanka. The recent survey did not cover the shallow depths because of the safety depth limit set for the modern DFN vessel, while the previous sampling was performed at less than 20 m (up to 10 m) bottom depths. Among all the species, only *E. tauvina* was listed in the DD (Data Deficient) group in the IUCN Red List, while all other species were listed in the LC (Least Concern) group (IUCN, 2019) (Appendix A). Species *E. coioides* and *E. malabaricus*, recorded in the last survey, had been identified as decreasing populations according to the IUCN Red List (P. Amorim et al., 2018; Samoilys et al., 2018).

Aside from the fishing pressure, climate change may be another factor causing the decline in grouper resources, as it has been identified as a crucial factor affecting fisheries production (Booth et al., 2017). The lifting of the Oxygen Minimum Zone (OMZ) as a consequence of global warming can have critical effects on the survival of demersal species on the shelf of Sri Lanka, while the warming itself may cause increased metabolism, affect growth rates and survival, and displace species from their original habitats (Pratchett et al., 2017). Further studies should be conducted to determine the climate-induced changes in the hydrographical properties of seawater. Suitable management measures are needed to regularly maintain the stock status, such as gear restrictions and the establishment of marine reserves, and control of artisanal fishing pressure (number of vessels) (Roberts and Polunin, 1991). It is also recommended to designate pre-identified aggregation sites as limited entry or permanently closed sites. Johannes et al. (1999) argue that the conservation of spawning aggregation sites by area closure, limited entry, or gear restriction is the most effective management option for grouper species and that Bermuda, the Dominican Republic, and Puerto Rico had entirely restricted fishing on spawning aggregations. Accordingly, further studies are suggested to identify spawning aggregation sites in Sri Lanka.

There are several limitations to our study. First, the seasonal coverage of the surveys was uneven. One survey was conducted during the NE monsoon, while the three other surveys were conducted in the SW monsoon. This unequal seasonal coverage may give overweight to the temporal changes in grouper stocks. Second, daily and monthly variations in grouper catch were not considered during sampling. Third, DFN did not have access to shallow waters, especially in the 2018 survey. Fourth, reefs and coral reefs were waived from sampling where groupers were supposed to be abundant. Therefore, we recommend repeating this type of survey and other fishery-dependent surveys to critically validate the findings from this study.

5. Conclusion

Fishery is one of the primary income sources in Sri Lanka, and groupers are significantly valued and increasingly influential commodities in the local and international fish trade. On the other hand, hydrographical determinants of grouper abundance and their changes over time remained unclear. This study showed the changes in grouper density after four decades by utilizing the R/V Dr. Fridtjof Nansen survey data collected on the continental shelf of Sri Lanka in 1978, 1979, 1980, and 2018. The result showed a noticeable decline in grouper density on the continental shelf of Sri Lanka. On the other hand, the density was found to be higher in the south region but similar in the five other regions, which may justify joint management of the broad fishing areas. The seafloor depth was significantly related to density, which may be considered when making management plans. Two grouper species recorded in the Sri Lankan waters are currently categorized into the Red List with decreasing population globally. This study may help initiate new research areas for conservation of the threatened species and take preventative measures in specific resource management plans in Sri Lanka.

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

List of groupers according to the IUCN Red List status and size at first maturity (L_m) as FishBase, LC = Least Concern, DD = Data Deficient

Species	Red List category	Population trend (global)	L_m
E. undulosus	LC.	unknown	41
E. tauvina	DD.	unknown	61
E. rivulatus	LC.	unknown	-
E. merra	LC.	stable	11
E. malabaricus	LC.	decreasing	64
E. longispinis	LC.	unknown	23
E. coioides	LC.	decreasing	48
E. areolatus	LC.	unknown	20
C. sonnerati	LC.	stable	-
A. rogaa	LC.	unknown	-

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